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The epiphytic habitat on a living host: reflections on the orchid–tree relationship

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In a living tree crown, the surface expands from year to year and the limbs of the tree thicken, as a consequence of primary and secondary growth. An epiphytic plant fixed on a bark surface is thus subject to constant and, at times, rapid successional change, to which the epiphyte must acclimate or die. These changes concern physical and chemical development in the bark substrate and changes in microclimatic conditions. Thus, the width of the tolerance range of an epiphytic species in principle defines its typical longevity. Epiphytes are distributed in a non-random fashion with respect to crown part occupied, the zone of habitation being delimited by the youngest crown position offering conditions for establishment and the position preventing further survival of the epiphytic species in question. The orchid life cycle is crucially dependent on other organisms, such as pollinating animals and symbiotic fungi, but the relationship between epiphytic orchid and phorophyte tree is currently receiving the least attention, despite the likely relevance for conservation of rare and threatened orchid species. Although many correlative studies have recorded occurrence of mature epiphytic orchids, the dynamics created by the growth of the phorophyte are often disregarded. We call for more experimental approaches, such as transplantation studies of seeds and seedlings, to reveal the still largely unknown mechanisms by which orchid distribution is biased towards certain phorophyte species, age stages and crown positions. We provide a compilation of noteworthy cases that could serve as starting points for studies into bias mechanisms.

ADDITIONAL KEYWORDS: bark ecology – commensalism – environmental succession – epiphytism – Orchidaceae – specificity – symbiosis – tree physiology.

INTRODUCTION

The life cycle of orchid is crucially dependent on other organisms, such as pollinating animals, symbiotic fungi and the trees that are the physical support for epiphytic orchids. Of these, the relationship between orchids and phorophyte trees is currently receiving the least attention, despite the likely relevance for the conservation of rare and threatened orchid species. The epiphytic habitat is complex, especially when the inner workings of a growing tree are taken into account. It is an often-overlooked fact that the habitat of an epiphytic plant changes from year to year due to the growth of the phorophyte. As a consequence of crown development, the successful epiphytic orchid seedling will germinate on a limb in the crown that is considerably less mature than the one on which the plant is subsequently observed flowering, years or decades later. During the lifetime of the orchid, nearly everything in its local habitat changes, including irradiation, humidity and bark features. Only its distance from the ground and from the main trunk remains relatively stable, provided that no catastrophic events occur.

It is known that epiphytic plant species diversify in habitat within tree crowns, some species being confined to the twig zone, others to larger branches or to trunks (Johansson, 1974; Zotz, 2007) and a subset of species preferentially grow in trees of small stature. With regard to phorophyte species, orchid species rarely have a one-to-one relationship, but bias for and

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against certain tree species are well documented in a number of orchid species. With this diversification of niches among tree species and within tree crowns, we still know little about the mechanisms that enable orchid species to establish themselves in a place in the canopy, which is clearly not random (Wagner, Mendieta-Leiva & Zotz, 2015).

Since orchid observation and identification is usually confined to flowering individuals, the life stage at which site selection occurs is largely unknown. Growing site could be determined by the manner in which seeds are dispersed, by attachment mechanisms of seeds on the bark or by differential success in germinating and seedling survival. Orchid seedlings are often difficult to identify floristically before they flower, and colonization attempts could easily be overlooked. Strictly speaking, colonization is only successful when the whole life cycle is completed; a tree species or crown part might enable seeds to germinate but not provide conditions for further seedling development and/or flowering. In each particular case, unless we know the life stage in which colonization by the orchid species in question fails, we are in the dark when searching for the underlying mechanism, be it microclimatic, chemical or physical traits of that particular phorophyte species and that crown position.

In this review, we would like to encourage a dynamic view on the phorophyte and the habitat it offers, combined with a focus on the orchid seedling establishment as a key to understanding the distribution of mature plants within tree crowns. In recent years, much improved tools have been developed for experimenting with orchid seedling establishment processes. Phorophyte species bias is another major question in epiphytic orchid biology and should, in our opinion, also be targeted by a focus on the earliest life stages. As possible study cases into phorophyte bias mechanisms, we have assembled a list of more or less corroborated reports of presumably narrow (mono- and oligo-) specificity based on observations mentioned in *Genera Orchidacearum* (Pridgeon *et al.*, 1999–2014) and other sources. These could also be cases of particular conservation interest.

A GROWING TREE CROWN AS A HABITAT

In the literature on epiphytes, the phorophyte tends to be implicitly regarded as static. A statement such as 'many epiphytes live at exposed sites all year long' (Zotz & Hietz, 2001) implicitly suggests a lasting condition, which it is not, unless the substrate is a non-growing object. The time–space gradient in the epiphytic habitat on account of crown development is generally an overlooked phenomenon. A position in the tree crown can be defined either by its distance from the tree base, measured along living limbs which is stable, or by its distance from the living foliage at the periphery of the crown, which is continuously growing. In terms of microclimate and bark features, the distance, or number of shoot generations, from the foliage is the most important.

Primary growth in the tree

Wind-dispersed seeds land randomly in the tree crown, and local conditions then decide whether they attach, whether they are able to germinate and how long time they can grow there. We know little about how an orchid seed attaches to tree bark, how old the shoot typically is when it happens, and how long it may be attached before germinating. An added complication is the necessary involvement of a compatible mycobiont in germination. The distribution of such fungi within the tree crown is quite unknown. We would expect that much of the initial colonization takes place on young shoots, the seeds taking advantage of a pioneer position on the substrate recently made available, with limited competition from other epiphytes such as lichens. If for simplicity we assume that an orchid seed attaches during the first season of a shoot, where primary (longitudinal) growth prevails in the shoot, the seed/seedling will begin its life in maximum exposure, covered only partly by foliage (Fig. 1A). However, already in the second growth season, the environment will have changed dramatically around the propagule, as the apical bud has added a segment to the main shoot, and new axillary branches and a new cohort of leaves have developed (Fig. 1B). Additional branching in the tree the following years continues that trend (Fig. 1C). At the site of the epiphytic propagule, elongation of the substrate is no longer possible since primary growth has stopped. Its position remains stable relative to the ground, but in relation to the expanding crown surface, the young orchid will appear to 'sink' into deeper and deeper shade. This dynamic applies, whether germination occurs on the youngest shoots (as it evidently does in twig epiphytes; Chase, 1987) or on more mature branches. Depending on the specific architecture and density of branching of the species of tree, the environmental change will be more or less dramatic and obviously more so in evergreen trees, compared to deciduous trees (Cardelús & Chazdon, 2005).

Secondary growth and bark development

Second-year and older stems and branches are subject to width increase. Thickening growth stretches the bark tangentially and proceeds as long as the tree limb in question is alive. Over the years, this process will change the bark surface profoundly. Creeping rhizomes of many orchid species thus need to be extendable

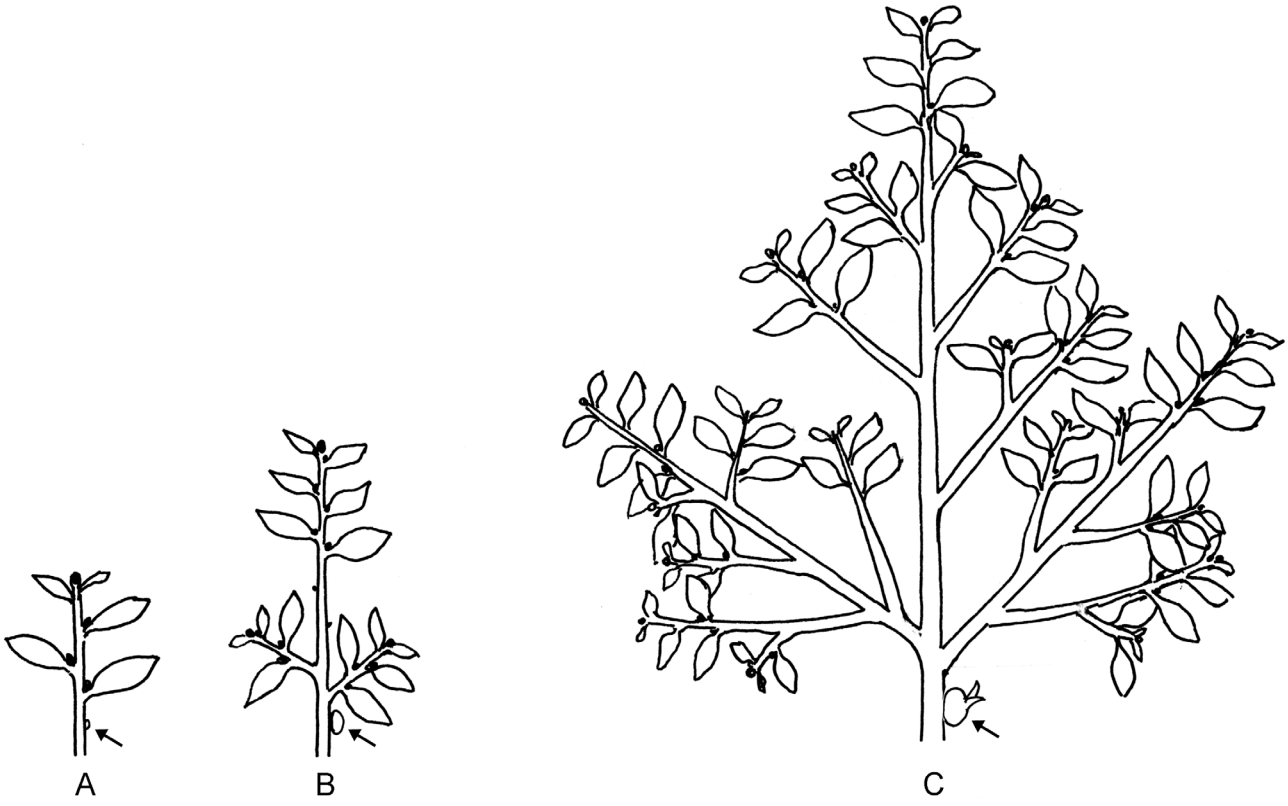

Figure 1. The transient nature of an epiphytic microhabitat. A, an imaginary propagule lands on a first-year branch (arrow). B, after one growth season, the site is covered in a new cohort of leaves and new primary shoots. C, the situation as imagined in year 5, assuming moderate branching (zero to two laterals/shoot) and deciduous habit. In case of more extensive branching and evergreen habit (i.e. the foliage remains functional for more than one growth season), the canopy closure above the epiphyte will be more dramatic. Here, we assume seed attachment on young bark and rapid seedling development, but germination stage may take place also in B, C or later, depending on the seed and germination requirements of the orchid species in question.

to accommodate for tangential bark expansion or to orient their growth along rather than across the limb. As implied in one study, the breaking up of the bark may mean that orchid species of small stature and with a creeping rhizome form new colonies by rupture of established plants (Wyse & Burns, 2011). Although rhizome orientation in terrestrial orchids is normally diageotropic, the tropisms regulating growth of rhizomes of epiphytes do not appear to have been under experimental study. In a group of epiphytic ferns, species of *Davallia* (L.) Sm., the rhizome initially grows diageotropically and then turns to positive geotropism and generally follows the substrate contact (thigmotropism; Croxdale, 1976). Since epiphytic orchids are normally observed either in the short term in nature or in the long term on non-expanding sticks in a greenhouse, we do not know how they cope with a substrate that expands.

During the first years of thickening growth, the epidermis in most tree species remains intact and maintains an even surface except for scattered stomata and developing lenticels. Subsequent thickening leads to rupture of the surface and the development of peripheral cork cambia, which eventually eliminates the epidermis and covers the whole circumference with secondary cell layers. Deeper in the bark, dilation tissues are generated from parenchyma rays and phloem parenchyma (e.g. Srivastava, 1964; Angyalossy *et al.*, 2016). If dilation tissues are evenly distributed, the bark tends to remain macroscopically smooth for many years. More heterogeneously distributed dilation tissue generates uneven and eventually deeply furrowed and flaking bark. At a certain age, however, even smooth-barked tree species develop a rugged bark and high growth rate of the individual tree tends to accelerate the process (H. N. Rasmussen, pers. observ.).

Each tree displays a gradient in bark age from the youngest branches to the basal trunk, and this is reflected in physico-chemical features such as the thickness, water-holding capacity and acidity of bark. Water-holding capacity, in terms of weight of absorbed water per unit of bark dry mass, tends to decrease from

top to base of the tree (H. E. Larsen, H. N. Rasmussen, T. Nord-Larsen, unpubl. data), probably as a result of the development of water-repellent cork in the old bark. Also, bark pH in many cases declines significantly from the top of the tree, that is as the bark ages, it becomes more acidic (Marmor, Tõrra & Randlane, 2010; Rambo, 2010; H. N. Rasmussen, unpubl. data). Thus, there are several gradients in bark quality that could influence the germination and development of the epiphyte according to the age of its substrate.

Microclimatic gradients within the crown generally mean increasing relative humidity and decreasing light intensity from the crown surface, that is the youngest branches, into the centre and towards the base of the tree. As an example, inner-crown environment measured in two tree species varied from 5.8 to 12.3% in light intensity and from 93.0 to 86.5% in relative humidity, compared to ambient conditions, the range reflecting a difference in density of crown architecture (Cardelús & Chazdon, 2005). For other records on the variation in environmental factors within tree crowns, reflecting the microclimatic conditions for epiphytes in a time-limited situation, see de la Rosa-Manzano *et al.* (2014) and Petter *et al.* (2016). Light quality also changes as increasing layers of foliage filter away the photosynthetic active radiation and preferably let long-red and green wavelengths pass.

Tree decline

If the orchid is long-lived, it may coexist with the phorophyte into the ageing stage of the tree when maximum height has been reached and when increased wind exposure and mechanical stress leads to failure of major limbs and damage to the root system during strong winds. Small relative growth rates in old trees reduce the capacity to repair such damage. Periodical drought stress due to failing root system and great height may lead to top-drying of exposed branches (e.g. Clark & Matheny, 1991). This is to emphasize that normal ageing processes may cause larger limbs of the upper canopy to become defoliated or shed, and thus allow more light and wind into the centre of the crown. If ageing trees are standing in a dense stand, neighbouring younger trees will eventually fill that canopy gap, whereas for solitary trees, the increased exposure of epiphytic habitats may be more lasting. These ageing symptoms in many cases resemble the effects of catastrophic events, such as hurricanes or lightning strikes, in which tree crowns can also become partly disrupted, although in those cases trees of any age may be affected.

It is rarely possible to directly observe the gradual loss of limbs as mature trees slowly age. By accurate sketches of a stand of deciduous Danish trees, drawn by the same artist over a 25-year interval, we can see the normal self-thinning process of ageing trees conveyed (Fig. 2). We have added imagined epiphytic propagules to the figure to illustrate how a habitat would change into higher exposure during the ageing of a mature tree. A schematic representation of the same principles was provided by Benzing (1979: Figs 1–6).

Epiphyte challenges in a living tree

As outlined above, the epiphytic orchid seed or seedling is subject to increasing shade from year to year, and the inferred time trend in light exposure will be accompanied by a roughly opposite trend in relative humidity (Fig. 3). Apart from the microclimatic changes, there are also changes in physical and chemical features of the bark substrate. At a certain point during this transition, we may imagine that conditions are favourable to seed attachment and germination, and at a later stage, the seedling may find conditions that stimulate flowering and pollination. Optimum sites for germination and flowering are not necessarily the same (Otero, Aragón & Ackerman, 2007). The trend of microclimatic change can, of course, be disturbed by catastrophic events such as breakage of neighbouring branches or windfall of neighbouring trees that may again expose the growing site. Such events may clearly cause orchid mortality (Rodríguez-Robles, Ackerman & Meléndez, 1990) but could in fact also rejuvenate orchid populations on remaining branches.

The orchid species must be adapted, not to a certain microenvironment, but to a range of environmental change, a broad range if the orchid species in question is long-lived or if the most suitable phorophyte is growing strongly. When a flowering specimen is recorded, it is important to remember that the conditions under which it established were probably different from the current ones.

Many studies have found a correlation between size of individual trees and epiphytic biodiversity (e.g. Köster, Nieder & Barthlott, 2011). As size is usually correlated with tree age, one reasoning is that the larger tree has been exposed to colonization for a longer time (besides offering a larger substrate area). However, by the age of a tree we normally understand the age of its basal part, the twigs being no older than they are on a young tree. Thus, major parts of the crown in an old and large tree have not been exposed for long. What makes a difference is the number of shoot generations and thus the length of the microenvironmental gradient within the tree. Thus, it is not surprising that trees may need to attain a certain age before colonization becomes apparent (Taylor & Burns, 2015) because a certain range of conditions must be available for an epiphyte to reach maturity.

CROWN ZONATION

Epiphytes are distributed in a non-random fashion within crowns. Johansson (1974) was one of the pioneers

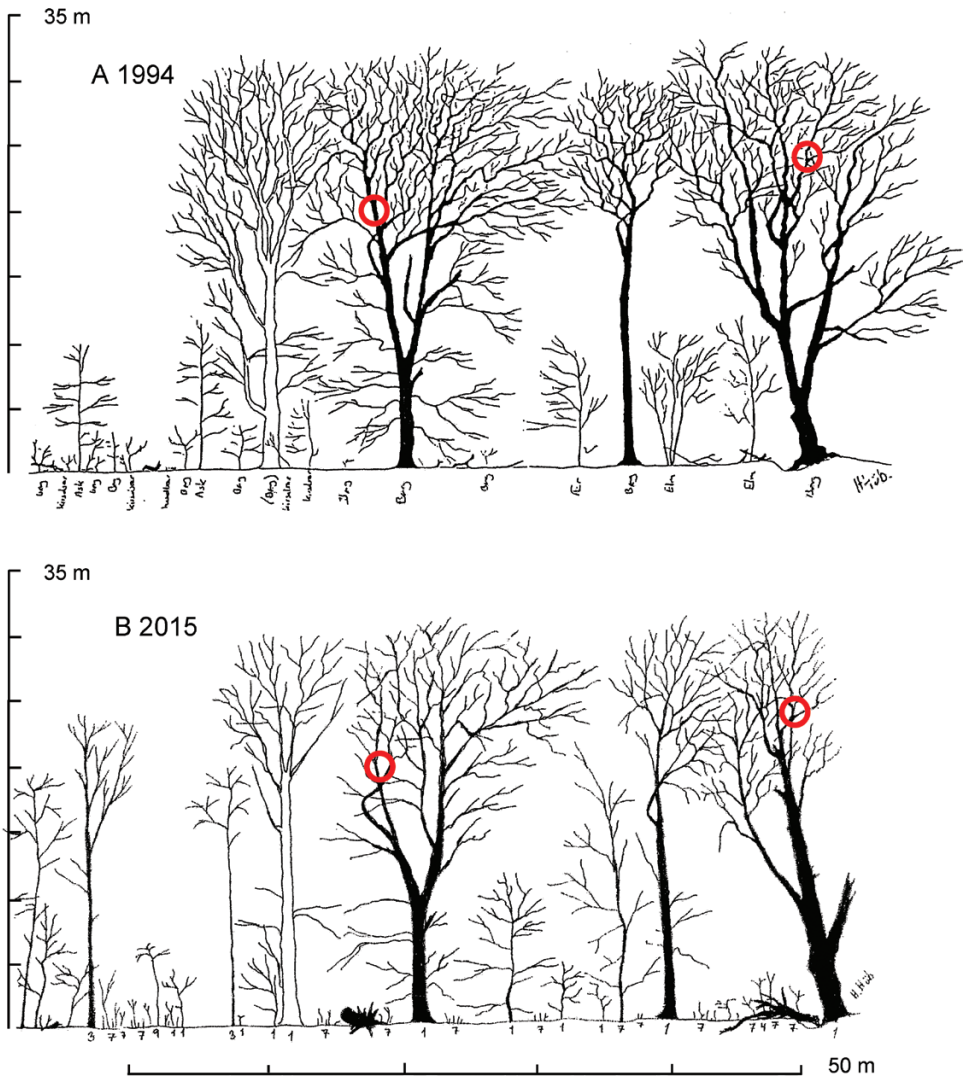

Figure 2. Sketches of a hedgerow in Denmark. A, most trees are mature, with well-developed crowns, and the understory is suppressed. B, twenty-six years later, the trees are ageing; loss of branches means that growing sites within the canopy become more exposed. The understory has increased in height. Red circles show corresponding positions in the canopy; if a long-lived epiphyte had grown in these positions, it would now experience increased irradiation and less moisture. Artist Hanne Hübertz, detail reproduced here with permission.

in epiphytic ecology. He subdivided the habitats rather intuitively into trunk base area, upper stem, larger branches, minor branches and twigs, and could refer different guilds of epiphytes to different parts of the crown (Fig. 4). Several later workers have found this zonation descriptive also to other geographical regions than West Africa, including Central America (Migenis & Ackerman, 1993; Martínez-Meéndez, Pérez-Farrera & Flores-Palacios, 2008), East Africa (Mucunguzi, 2008), South America (Ek, Ter Steege & Biesmeijer, 1997) and Japan (Hirata, Kamijo & Saito, 2009). Among 97 species of orchids, Johansson found *c*. 23% on the mid-part of large branches, and almost as many (20%) spanned the basal part to mid-part of large branches. Only 3% were exclusively found at the tip part of branches, and 5% were confined to stem and trunk (Fig. 4). A small group of species were found to specialize on trees that were short in stature. In a different part of the tropics, Henderson (1935) found that the majority of orchid species grew on the trunk and the lower part of major branches. More broadly, zones can be categorized mainly on light regime as 'shade tolerant', 'light exposed to intermediate' and 'high light exposed', with an additional group of

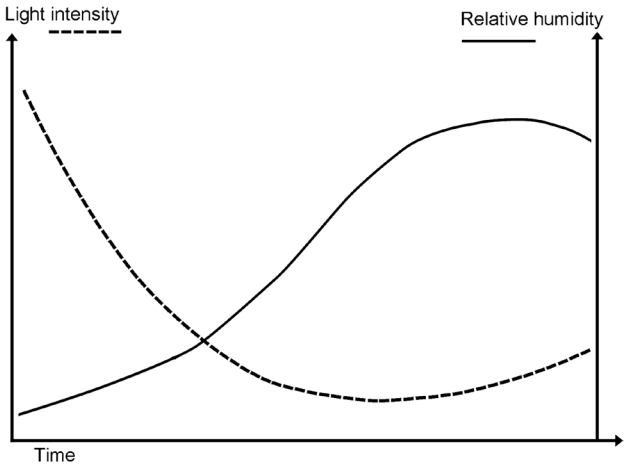

Figure 3. The changing exposure of a fixed reference point within the crown of a solitary tree. Declining light intensity and increasing relative humidity characterize the habitat of the epiphyte, as the tree crown develops above it. Eventually, as the tree reaches the ageing stage, top-drying of the tree crown may reverse these trends. At some point along this trend, the conditions are suitable for germination and at another point for the decline of the epiphyte. To our knowledge, there are no actual long-term recordings at fixed tree-crown points. The graph is thus completely conjectural and only attempts to convey year-to-year trends, not the underlying seasonal patterns.s

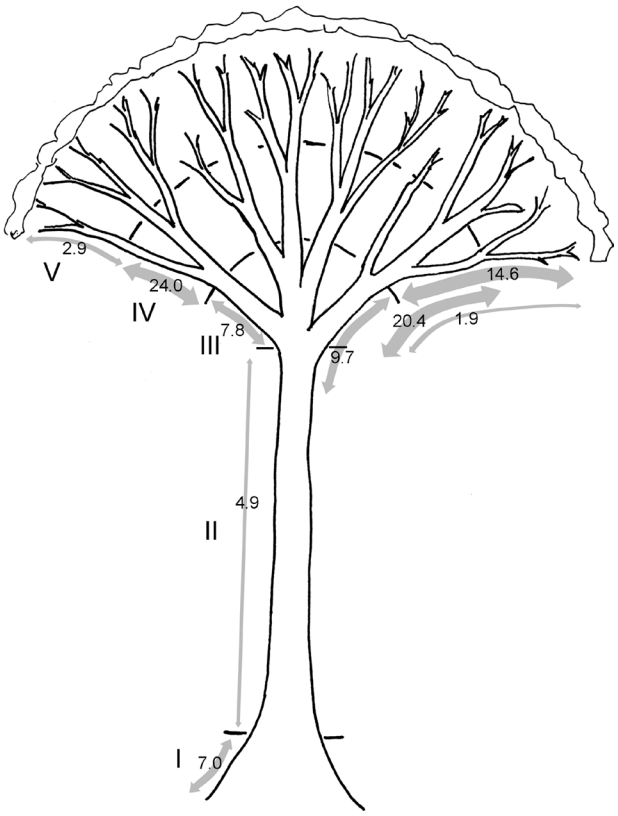

Figure 4. Zonation in epiphytic habitats, redrawn from Johansson (1974), with original Roman numbering I–V. Arrows indicate the percentage of orchid species found in that study in each zone (left side of the tree) or zone combination (right side). About 6% of the species were confined to small trees and shrubs and are not shown here.

species being 'indiscriminating', that is found in many different positions (Ek *et al.*, 1997). The zonation is clearly a convenient, if somewhat arbitrary, subdivision of environmental gradients in the tree crowns, which seem to regulate the occurrence of epiphytic orchids. Using clustering and discriminant analysis, however, Zotz (2007) also found objective evidence of zonation in epiphytic distribution and detected a group of species confined to small trees. However, the mechanisms behind zonation within the tree appear more complicated if the dynamics of tree growth, as above described, are taken into account.

Orchids living in the twig zone have received a fair amount of attention (Chase, 1987; Benzing, 1990; Ackerman, Sabat & Zimmerman, 1996). Obviously, the orchid species in question must germinate on young shoots and have a rapid progression from seedling to flowering stage to be found flowering in the twig zone (Mondragón, Maldonado & Aguilar-Santelises, 2007). Twig epiphytes must be short-lived and die when the twig is either developed into a larger branch or overshadowed and shed from the tree. Presumably, such orchids favour an exposed environment, and their seed structure suggests that they are adapted to cling to young smooth bark (Chase, 1987). Young seedlings of a twig orchid may nevertheless occur in atypical locations such as the trunk, indicating that the species can germinate, but probably not develop further in 'unsuitable' crown locations (Ackerman *et al.*, 1996).

Since other parts of the tree crown are also transient, as described above, orchids occupying these zones have similar challenges. For instance, orchid species that associate with the basal part of larger branches (Fig. 4) may have germinated on young bark on the main branches when the tree was young and taken a long time to reach flowering stage while the branch increased in size, or may have germinated on old bark followed by a brief transition to flowering.

The crown zone occupied by an orchid species is thus a function of its germination site preferences and its habitat tolerance range, and the latter defines its longevity. Orchid species must necessarily differ in these features if they differ in preference of crown position.

Among the environmental factors that could influence germination, flowering phase and death of the epiphytic orchid, obvious candidates would be the changing light and humidity regimes and changing bark quality during tree development. Slow growth

rate of the phorophyte, and thus slow change of conditions, would enable orchids to have a long life. Generally, we would expect the juvenile individuals of an epiphytic orchid to be located in younger parts of the crown than the mature individuals, as has indeed been observed in *Encyclia nematocaulon* (A.Rich.) Acuña on *Gymnopodium floribundum* Rolfe (de la Rosa-Manzano *et al.*, 2014).

Gradients in microclimate and bark features may all contribute to define the optimum germination site of an epiphytic orchid species that may be decisive for the subsequent crown zonation. At present, little has been explored about germination site preferences in trees. A positive association with moss seems to be widespread (e.g. Frei, 1973), and a possible symbiosis between orchid mycobionts and mosses was suggested by Osorio-Gil, Forero-Montana & Otero (2008). Spontaneous seedlings of *Pomatocalpa maculosum* (Lindl.) J.J.Sm. (as *P. naevata* J.J.Sm.) were found on water-retentive bark with rough surface, mainly on vertical branches and trunks with cryptogam cover and in the lower canopy of evergreen forest (Watthana, 2004). This suggests that the germination was intolerant of exposure on young bark. Similar occurrence applies to *Lepanthes caritensis* Tremblay & Ackerman (Tremblay *et al.*, 1998).

What we have outlined above suggests that the fast-growing healthy tree may be a stressful environment for the epiphytes because they need to acclimate to a rapid succession of microsite conditions in its crown. Epiphytic development could thus be relatively enhanced on individual trees that are slow growing compared to others of their kind and on branches that are slow growing compared to other parts of a tree crown. A decrease in growth rate is characteristic of old branches, even in monopodial tree models (Benzing, 1979). For an epiphytic species requiring quasi-stable conditions, the old branch or trunk will be the only option to carry through a long life history. It follows that epiphytic biodiversity in a forest should increase with increasing tree sizes and stand age, as observed by Sáyago *et al.* (2016).

PHOROPHYTE BIASES BY EPIPHYTIC ORCHIDS

Some orchid species appear to be indiscriminating with respect to phorophyte species (Ackerman, Montalvo & Vera, 1989), whereas others have either a positive 'preference' for certain tree species and 'avoidance' of other (e.g. Adhikari, Fischer & Fischer, 2012). Phorophyte bias differs in strength. Some examples are striking and cannot be explained by dispersal limitation or chance: in forests where *Cestrum aurantiacum* Lindl. and a species of *Saurauia* Willd. (as '*S. penduliflora*') grew in dense mixture, Went observed *Oberonia oxystophyllum* J.J.Sm. exclusively on *Saurauia*, and *Liparis bilobulata* J.J.Sm. only on *Cestrum*, even when branches of the two tree species were right next to each other (Went, 1970). Although orchids are rarely monospecific in their relationship with a phorophyte species, the range of phorophytes inhabitable for a particular orchid species often appears to be narrow. In a study of 105 epiphytic orchid species, *c.* 40% associated with fewer than five kinds of phorophytes (among 132 tree species available) and their bias differed (Silva *et al.*, 2010). In cases where strong phorophyte preferences are not found, there may still be a considerable number of the local tree species that are not colonized and appear to be unsuitable hosts (Migenis & Ackerman, 1993). Tree species and age composition in forests could thus be a relevant concern for epiphytic orchid conservation, particularly when land use and climates are changing (Köster *et al.*, 2011).

In Table 1 we provide a compilation of cases from the literature in which association with one or a few phorophyte species is reported, and where research into bias mechanisms might be of interest. Records are often geographically limited, or the range of local tree species is limited, thus weakening the evidence for specific species interaction. Far from being an exhaustive list, and corroborated only in some cases, the table is intended as an inspiration for future studies. Hopefully, these and other cases may be scrutinized along the principles of Wagner *et al.* (2015). Some of these close relationships may find fairly obvious physical explanations, such as large debris-collecting leaf sheaths providing a microhabitat for orchids (Velloziaceae and certain palms; see Zona & Christenhusz, 2015, for a review of litter-trapping plants). Transplantation experiments by Callaway *et al.* (2002) suggest that phorophyte preference reactions continue beyond the germination stage of the epiphyte, and more mature epiphytes may potentially perform better on trees that are not prioritized for establishment (Gowland *et al.*, 2011).

Phorophyte bias during germination could be related to the availability of compatible mycobionts, but the search for such a connection was so far unsuccessful (Gowland *et al.*, 2013). However, phorophytes might be distinguished by the performance of mycobionts on their bark, rather than mere presence, and physico-chemical factors related to bark and crown microclimate could thus be involved in the outcome of the symbiosis. The preference of some orchid species for evergreen trees (Table 1) could mean that the seeds in question require continuous shade for germination or seedling development. Tree species favoured by orchids in the Philippines were noted for usually finely canalled bark surface with numerous scales persisting

Table 1. Examples of orchids that have been observed to show some degree of preference for or avoidance of certain phorophytes

Orchid genus, species or group	Orchid–phorophyte observations	References
Aeranthes crassifolia Schltr., *A. parvula* Schltr.	On *Tamarindus* L. (Fabaceae) in semi-deciduous woodland, Madagascar.	Cribb (2014), GO 6
Aerides multiflora Roxb.	On *Dillenia* L. (Dilleniaceae) and *Fraxinus* L. (Oleaceae) on river banks in Bhutan. On *Mangifera indica* Wall. (Anacardiaceae) in India.	Wood (2014), GO 6
Aerides odorata Lour.	On *Terminalia catappa* L. (Combretaceae), high branches in littoral vegetation on Borneo, Kalimantan.	Wood (2014), GO 6
Agrostophyllum cyathiforme J.J.Sm.	On *Castanopsis argentea* (Blume) A.DC. (Fagaceae) [as *Castanea* Mill.], other species of *Castanopsis* (D.Don) Spach and species of *Quercus* L. Avoids species of *Saurauia* Willd. (Actinidiaceae) *Eugenia* L. (Myrtaceae), and *Glochidion cyrtostylum* Miq. (Phyllanthaceae). Java.	Went (1940)
Alamania punicea Lex	Species of *Quercus* L. (Fagaceae), on mossy branches in seasonally dry forest, Mexico.	Soto Arenas (2005), GO 4
Ambrella longituba H.Perrier	On *Viguieranthus alternans* (Benth.) Villiers (Fabaceae) [as *Calliandra* Benth.], northern Madagascar.	Cribb (2014), GO 6
Angraecum palmicolum Bosser	On *Dypsis decipiens* (Becc.) Beentje & Dransf. (Arecaceae), Madagascar.	Cribb (2014), GO 6
Angraecum rubellum Bosser	On species of *Pandanus* L.f. (Pandanaceae), Madagascar.	Cribb (2014), GO 6
Caespitose species of *Barkeria* Knowl. & Westc.	Some degree of phorophyte specificity, perhaps due to particular physical bark properties. Short life cycle. Seasonally dry coastal habitats, Mexico and Central America.	Soto Arenas (2005), GO 6
Barkeria scandens (Lex.) Dressler & Halbinger	Species of *Randia* L. (Rubiaceae). Twig epiphyte. Mexico.	Soto Arenas (2005), GO 4
Bulbophyllum pygmaeum (Sm.) Lindl. [as *Ichthyostomum pygmaeum* (Sm.) D.L.Jones, M.A.Clem. & Molloy]	Almost exclusively on *Agathis australis* (D.Don) Lindl. (Araucaceae), New Zealand.	Wyse & Burns (2011)
Cardiochilus williamsonii P.J.Cribb	On species of *Protea* L. (Proteaceae). In mist forest in Malawi and Tanzania.	Cribb (2014), GO 6
Species of *Chilopogon* Schltr.	On species of *Alangium* Lam. (Cornaceae), *Eugenia* L. (Myrtaceae), and *Ficus* L. (Moraceae), New Guinea-Melanesia.	Wood (2005), GO 4
Chiloschista parishii Seidenf.	*Panax pseudoginseng* Wall. (Araliaceae), on branches. Bhutan.	Pearce & Cribb (2002); Wood (2014), GO 6
Coelogyne pianmaensis R.Li & Z.L.Dao	Only on species of *Tsuga* Carrière (Pinaceae) China, Yunnan.	Li & Dao (2014)
Conchidium pusillum Griff.	Species of *Viburnum* L. (Adoxaceae) and *Symplocos* Jacq. (Symplocaceae). On mossy trunks. Sikkim.	Cribb (2005), GO 4
Constantia cipoensis Porto & Brade	Only on *Vellozia piresiana* L.B.Smith and *V. compacta* Mart. ex Schult.f. (Velloziaceae). The pollinator, *Xylopus* cf. *artifex* builds its nest inside branches of the phorophytes. Brazil, Minas Gerais.	Matias, Braga & Freire (1996)

Table 1. *Continued*

Orchid genus, species or group	Orchid–phorophyte observations	References
Cymbidiella pardalina (Rchb.f.) Garay	Only on *Platycerium madagascariense* Baker (Polypodiaceae), an epiphytic fern specific to *Albizia gummifera* (J.F.Gmel.) C.A.Sm. Madagascar.	Herndon (1996); Kennedy (1972); Rauh (1973) [as *C. rhodochila* Rolfe]
Cymbidium canaliculatum R.Br.	On species of *Eucalyptus* L'Her. (Myrtaceae), roots penetrating into the centre of living trees at scars from fallen branches. NE Australia.	Cribb (2009), GO 5
Dendrobium falcorostrum Fitzg.	100% associated with *Nothofagus moorei* (F.Muell.) Krasser. NE Australia.	Wallace (1981); *fide* Benzing (1990)
Dendrobium mutabile (Blume) Lindl.	Primarily on *Glochidion* J.R.Forst. & G.Forst. (Phyllanthaceae), but also on *Ficus variegata* Blume. Java.	Went (1940)
Dendrobium taurinum Lindl.	Only seen on species of *Pterocarpus* Jacq. (Fabaceae). Philippines, Sierra Madre Mts.	Sulit (1950)
Dendrobium treacherianum Hook.f. [as *D. lyonii* Ames]	Always on *Shorea polysperma* Merr. and *S. palosapis* Merr. (Dipterocarpaceae). Philippines.	Sulit (1950)
Encyclia nematocaulon (A.Rich.) Acuña	Strong preference for *Gymnopodium floribundum* Rolfe (Polygonaceae) among ten potential phorophyte species. Preferred phorophyte the most abundant, presenting largest colonizable area (large branches) and rugose bark. Mexico.	de la Rosa-Manzano *et al*. (2014)
Epidendrum magnoliae Muhl.	Strong preference for *Magnolia grandifolia* L. (Magnoliaceae), less so for *Quercus virginiana* Mill. (Fagaceae), among eight available tree species. Prefers evergreen foliage and large individual trees. South-eastern North America.	Bergstrom & Carter (2008)
Erycina pusilla (L.) N.H.Williams & M.W.Chase [as *Psygmorchis pusilis* (*sic* = *pusilla*) (L.) Dodson & Dressler]	Avoids species of *Psidium* L. (Myrtaceae). Tropical America.	Benzing (1990)
Erycina glossomystax (Rchb.f.) N.H.Williams & M.W.Chase [as *Psygmorchis glossomystax* (Rchb.f.) Dodson & Dressler]	Almost consistently on species of *Psidium* L. (Myrtaceae). Tropical America.	Benzing (1990)
Eulophiella elisabethae Linden & Rolfe	On *Dypsis utilis* (Jum.) Beentje & Dransf. (Arecaceae) [as *Vohinitra* (sic) *utilis* Jum.]. Madagascar.	Rauh (1973)
Grammatophyllum stapeliiflorum (Teijsm. & Binn) J.J.Smith	Species of *Arenga* DC. and *Metroxylon* Rottb. (Arecaceae). On trunks. Sumatra.	Wood (2009), GO 5
Graphorchis concolor (Thouars) Kuntze var. *alphabetica* F.Rasm.	On species of *Raphia* P.Beauv. (Arecaceae) and *Mangifera* L. (Anacardiaceae). In humid lowland and littoral forest. Madagascar	Cribb (2009), GO 5
Grobya cipoensis F.Barros & Lourenço	Exclusively on *Vellozia gigantea* N.L. Menezes & Mello-Silva (Velloziaceae). In open rocky vegetation. Brazil.	de Barros (2009), GO 5
Hagsatera brachycolumna (L.O.Williams) R. Gonzáles	Obligate on *Quercus elliptica* Née (Fagaceae). In open humid pine-oak forest. Mexico.	Soto Arenas (2005), GO 4
Species of *Hintonella* Ames	Only on species of *Quercus* L. (Fagaceae). In broad-leaved forest. Mexico.	Chase (2009), GO 5

Table 1. *Continued*

Orchid genus, species or group	Orchid–phorophyte observations	References
Laelia rubescens Lindl.	Strong preference for *Gymnopodium floribundum* Rolfe (Polygonaceae) among ten phorophyte species. Associated with large branches and rugose bark. Mexico. Avoids *Albizia saman* (Jacq.) Merr. (Fabaceae). Mexico, Central America.	de la Rosa-Manzano *et al.* (2014); Trapnell & Hamrick (2006)
Laelia speciosa (Kunth) Schltr.	Obligate on *Quercus deserticola* Trel. (Fagaceae), the only tree species in the forest. Mexico.	Soto Arenas (1994)
	Seedlings germinate mostly on lichens (*Parmelia* spp.) that cover the host oak stem. 16–19 years from seed to flowering.	Soto Arenas (2005), GO 4
Lepanthes caritensis Tremblay & Ackerman	On *Micropholis guyanensis* (A.DC.) Pierre (Sapotaceae). Only on large trees and associated with corticolous moss. Puerto Rico.	Tremblay *et al.* (1998)
Lepanthopsis vellozicola R.C.Mota, F.Barros & Stehmann	Only on *Vellozia compacta* Mart. (Velloziaceae). Brazil.	da Mota, de Barros & Stehmann (2009)
Leptotes vellozicola van den Berg, E.C.Smidt & Marçal	Only on members of Velloziaceae.	Van den Berg, Smidt & Marcal (2006)
Species of *Listrostachys* Rchb.f.	On *Lophira alata* C.F.Gaertn. (Ochnaceae) and *Coula edulis* Baill. (Olacaceae). On large branches. Lowland humid forest. Tropical Africa.	Cribb (2014), GO 6
Meiracyllium trinasutum Rchb.f.	Often on *Licania arborea* Seem. (Chrysobalanaceae). Mexico and Central America.	Soto Arenas (2005), GO 4
Microcoelia microglossa Summerh.	On *Strombosiopsis tetranda* Engl. (Olacaceae). Dense lowland rain forest. East Africa.	Jonsson (1981)
Microcoelia perrieri (Finet) Summerh.	Typically on *Alluaudia procera* Drake (Didiereaceae), but also on various species of *Euphorbia* L. (Euphorbiaceae). Madagascar.	Jonsson (1981)
Mystacidium tanganyikense Summerh.	On species of *Cupressus* L. and *Juniperus* L. (Cupressaceae), growing on their cones. East Africa.	Cribb (2014), GO 6
Nephrangis filiformis (Kraenzl.) Summerh.	In *Piptadeniastrum africanum* (Hook.f.) Brenan (Fabaceae), *Cryptosepalum pseudotaxus* Baker.f. (Fabaceae), and species of *Uapaca* Baill. (Euphorbiaceae). In the canopy, moist semi-deciduous forest, savanna, and woodland. Tropical Africa.	Cribb (2014), GO 6
Octarrhena bilabrata (P.Royen) W.Kittr.	On *Cordyline terminalis* (L.) Kunth (Asparagaceae). New Guinea.	Wood (2005), GO 4
Paralophia epiphytica (P.J.Cribb Du Puy & Bosser) P.J.Cribb	*Elaeis guineensis* Jacq., *Raphia farinifera* (Gaertn.) Hyl. and possibly species of *Dypsis* Noronha ex Mart. (Arecaceae). Growing in the leaf bases. Madagascar.	Cribb, Du Puy & Bosser (2002); Cribb (2009), GO 5
Phalaenopsis amabilis (L.) Blume	Prefers *Antidesma ghaesembilia* Gaertn. (Phyllanthaceae) and *Vitex pinnata* L. [as *V. pubescens* Vahl] (Lamiaceae). Philippines, Palawan.	Sulit (1953)

Table 1. *Continued*

Orchid genus, species or group	Orchid–phorophyte observations	References
Phalaenopsis aphrodite Rchb.f. and *P. schilleriana* Rchb.f.	80% of individuals grow on *Diplodiscus paniculatus* Turcz. (Malvaceae).	Sulit (1950)
	The remaining 20% occur on *Cordia dichotoma* G.Forst. (Boraginaceae), *Planchonia spectabilis* Merr. (Lecythidaceae), *Terminalia edulis* Blanco (Combretaceae) and *Pentacme contorta* Merr. & Rolfe (Dipterocarpaceae). Philippines.	
Phalaenopsis sanderiana Rchb.f.	About 50% grow on *Castanopsis philipensis* (Blanco) Vidal and *C. javanica* (Blume) A.DC. (Fagaceae). Philippines.	Sulit (1950)
Phreatia densiflora (Blume) Lindl.	On species of *Castanopsis* (D.Don) Spach [as *Castanea* Mill.] and *Quercus* L. (Fagaceae). Java.	Went (1940)
Pinalia alba Buch.-Ham.	On *Quercus griffithii* Miq. (Fagaceae) and *Pinus wallichiana* A.B.Jackson (Pinaceae). On branches and stems. Mountain dipterocarp forest. Bhutan.	Cribb (2005), GO 4
Pinalia multiflora (Blume) Kuntze [as *Eria multiflora* Lindl.]	On every individual of *Castanopsis argentea* (Blume) A.DC. (Fagaceae) [as *Castanea argentea* Blume]. Avoids *C. tunggurut* (Blume) A.DC., *Glochidion cyrtostylum* Miq. (Phyllanthaceae) and species of *Saurauia* Willd. (Actinidiaceae). Java.	Went (1940)
Species of *Poaephyllum* Ridl.	On *Gymnostoma sumatranum* (de Vriese) L.A.S.Johnson (Casuarinaceae). Indomalesia and New Guinea.	Wood (2005), GO 4
Polystachya dendrobiiflora Rchb.f.	Only on species of *Vellozia* Vand. (Velloziaceae). Kenya.	Rauh (1973) [as *P. tayloriana* Rendle]
	Specific to *Xerophyta* spp. Juss. (Velloziaceae), on stems and branches. Tropical Africa.	Cribb (2014), GO 6
Polystachya johnstonii Rolfe	Exclusively on *Xerophyta splendens* L.B.Smith & Ayensu (Velloziaceae) – among eight potential phorophyte species. South Malawi.	Porembski (1996, 2003)
	Specific to species of *Xerophyta* Juss. (Velloziaceae), on stems and branches. Tropical Africa.	Cribb (2014), GO 6
Polystachya microbambusa Kraenzl.	Exclusively on *Afrolepis pilosa* (Boeckeler) J.Raynal (Cyperaceae, a mat-forming sedge). West Africa.	Porembski (2003)
Polystachya neobenthamia Schltr.	On species of *Xerophyta* Juss. (Velloziaceae). May also be lithophytic. Tanzania.	Cribb (2014), GO 6
Pomatocalpa maculosum (Lindl.) J.J.Sm. [as *P. naevatum* (sic = *naevata* J.J.Sm.)]	Preference for *Scleropyrum pentandrum* (Dennst.) Mabb. (Santalaceae). Avoids species of *Mangifera* L. (Anacardiaceae). South-eastern Thailand.	Watthana (2004)
Pomatocalpa spicatum Breda, Kuhl & Hasselt	Strong preference for *Myristica succadaena* Blume (Myristicaceae) and species of *Syzygium* Gaertn. (Myrtaceae). Indonesia, Seram.	Mursidawati, Norton & Astuti (1999)

Table 1. *Continued*

Orchid genus, species or group	Orchid–phorophyte observations	References
Porphyroglottis maxwelliae Ridl.	Particularly on species of *Tristaniopsis* Brogn. & Griseb. (Myrtaceae). Often in forks of tree stems. Open low-grown heath forest. Malaysia and Indonesia.	Wood (2009), GO 5
Pygmaeorchis seidelii Toscano & Moutinho	On members of Velloziaceae. Brazil.	van den Berg (2005), GO 4
Rhynchostylis gigantea (Lindl.) Ridl.	On species of *Acacia* Mill. (Fabaceae) at 600 m in Burma, On *Mangifera indica* L. (Anacardiaceae) in India and Philippines.	Wood (2009), GO 5
Sarcochilus australis (Lindl.) Rchb.f.	On species of *Nothofagus* Blume (Nothofagaceae). Twig epiphytes on small trees and shrubs. Tasmania.	Adams, Cribb & Schuiteman (2014), GO 6
Schoenorchis juncifolia Blume	On species of *Castanopsis* (D.Don) Spach, especially *C. javanica* (Blume) A.DC. [as *Castanea* Mill.], and species of *Quercus* L. (Fagaceae). Java.	Went (1940)
Schoenorchis sarcophylla Schltr.	On *Tristania exiliflora* F.Muell. (Myrtaceae). On the outermost branches, overhanging rapidly flowing creeks. Queensland, Australia.	Wood (2014), GO 6
Sophronitis brevipedunculata (Cogn.) Fowlie	On species of *Vellozia* Vand. (Velloziaceae). Brazil, Minas Gerais.	van den Berg (2005), GO 4
Tetramicra malpighiarum J.A.Hern. & M.A.Diaz	Only on species of *Malpighia* L. (Malpighiaceae). Cuba.	Hernández & Diaz (2000)
Thelasis carinata Blume	On *Lumnitzera littorea* (Jack) Voigt (Combretaceae). Coastal forest, Borneo.	Wood (2005), GO 4
Thelasis micrantha (Brogn.) J.J.Sm.	On members of Theaceae. Dipterocarp forest, Borneo.	Wood (2005), GO 4
Thelasis pygmaea (Griff.) Lindl.	On species of *Calophyllum* L. (Clusiaceae). Solomon Islands.	Wood (2005), GO 4
Thrixspermum odoratum X.Q.Song, Q.W.Meng & Y.B.Luo	Only on *Quercus bawanglingensis* C.C.Huang, Z.X.Li & F.W.Xing (Fagaceae). China, Hainan Island.	Song *et al.* (2009)
Thrixspermum subulatum (Blume) Rchb.f.	Almost exclusively on *Schima noronhae* Reinw. (Theaceae). Java.	Went (1940)
Triceratorhyncus viridiflorus Summerh.	On *Olea welwitschii* Gilg & G.Schellenb. (Oleaceae) and species of *Podocarpus* L'Her. ex Pers. (Podocarpaceae). Dense, primary evergreen forest. Central Africa.	Cribb (2014), GO 6
Trichocentrum oerstedii (Rchb.f.) R.Jiménez & Carnevali [as *Lophiaris oerstedii* (Rchb.f.) R.Jiménez, Carnevali & Dressler]	Strong preference for *Gymnopodium floribundum* Rolfe (Polygonaceae) among ten potential phorophyte species. Mexico, Yucutan.	de la Rosa-Manzano *et al.* (2014)
Trichocentrum yucatanense (Centzal & Carnevali) R.Jiménez & Solano [as *Cohniella yucatanensis* Centzal & Carnevali]	Strong preference for *Gymnopodium floribundum* Rolfe (Polypodiaceae) among ten other potential phorophytes. On large branches with rugose bark. Mexico.	de la Rosa-Manzano *et al.* (2014)
Vanda sanderiana (Rchb.f.) Rchb.f.	On members of Dipterocarpaceae. On the highest branches. Philippines.	Sulit (1950)
Zygopetalum maxillare Lodd.	Almost exclusively restricted to tree-ferns. Wet and shady conditions. Brazil and Paraguay.	Pupulin (2009), GO 5

Table 1. *Continued*

Orchid genus, species or group	Orchid–phorophyte observations	References
Large epiphytes, such as species of *Grammatophyllum* Blume, *Coelogyne* Lindl. and *Cymbidium* Sw.	Common on *Dipterocarpus oblongifolius* Bl. (Dipterocarpaceae). Seems to avoid *Saraca indica* L. (Fabaceae) [as *S.bijuga* Prain]. Malaysia.	Henderson (1935)

GO *n* refers to volumes of *Genera Orchidacearum* (Pridgeon *et al.*, 1999–2014). Nomenclature of orchids as in *Genera Orchidacearum* or *World checklist of Orchidaceae* (Govaerts, 2016) and phorophytes as in *The Plant List* v. 1.1 (2013).

for a long time on the stems (Sulit, 1950). It was suggested that the rainwater and debris contained in such shallow bark crevices would enhance orchid seed attachment and seedling nourishment.

Tree species differing in water-holding capacity of their living bark could differentiate their suitability as orchid phorophytes, offering growing sites for either drought-tolerant or moisture-requiring species. As mentioned above, tree species and individual trees may differ in the time span that the bark remains smooth. There are few studies of the importance of bark profile in establishment of epiphytic orchids, and the evidence is equivocal, at least for *Psychilis monensis* Sauleda (Ackerman *et al.*, 1989; Otero *et al.*, 2007). In a collective study involving many epiphytic species, there was no bark profile favoured by all (Boelter *et al.*, 2014). The same conclusion was drawn by Went (1940) with respect to bark profile.

Harshani, Senanayake & Sandamali (2014) made aqueous extracts from barks and found that the tree species recorded as phorophytes chemically enhanced seed germination and growth of a mycobiont, whereas the extracts from non-phorophytes were inhibitory. The compounds involved are so far unidentified. Frei & Dodson (1972) suggested hydrolysable tannins as the agent in discrimination between phorophyte species of *Quercus* L.

EFFECTS OF EPIPHYTISM ON TREES

The epiphyte–phorophyte relationship is often described as commensalistic (e.g. Sáyago *et al.*, 2016). From the perspective of the phorophyte, there are no obvious benefits from epiphytism, but epiphytes have from time to time been blamed for inhibiting the growth of colonized branches (Johansson, 1977; Benzing & Seemann, 1978), either directly or indirectly, for example, as structural parasitism (Montaña, Dirzo & Flores, 1997).

In connection with fern and orchid epiphytes, Ruinen (1953) reported fungal infections in stem cortex of the supporting tree branch beneath rhizomes and roots of epiphytes. Hyphae also entered conducting tissues in the branches, blocking vessel function, and inhibited cambial growth and normal growth ring patterns in the colonized parts. The structure of hyphae within the phorophyte suggested that some of these fungi were stages of *Rhizoctonia* DC., forming features such as intracellular coils and monilioid cells, otherwise attributed to orchid mycorrhizal colonization (for a list of such attributes, see Rasmussen & Rasmussen, 2014). No nutrient transfer was demonstrated from the phorophyte through such hyphae, as pointed out by Benzing (1979). However, several indications of malfunction in the colonized branches were noted, such as delayed bud break, reduced bud size, inhibited lateral buds, smaller leaves and early leaf fall, compared to unaffected branches.

Ruinen's (1953) study materials mostly included large ornamental shrubs in cultivation in Bogor (Indonesia), and some examples involved species combinations that would naturally be geographically separated. Certain groups (Rubiaceae, Myrtaceae, Verbenaceae) were reported as particularly susceptible to colonization and rapidly showed considerable signs of damage, whereas others (Myristicaceae) were considered 'axenic', that is not housing any epiphytes, or only affected by colonization to a minor extent.

Ruinen (1953) referred to plantations of coffee, tea and *Citrus* L. from which epiphytes are removed routinely for obtaining better crops. Experimental removal, also in Ruinen's study, resulted in a measurable recovery in features such as leaf size. The observation that weeding epiphytes away may benefit tree crops would seem to contradict the notion that mycobionts are the cause of phorophyte decline, first, because the fungi would largely remain on and in the bark when the epiphytes are removed and, second, because the orchid mycobionts presumably have been present on the phorophyte before entering into symbiosis with the germinating epiphyte seeds. Ruinen's interpretations thus seem to imply that association with the orchid may change the fungal behaviour in direction of virulence, for which there is presently no evidence. Ruinen announced forthcoming results of experimental

inoculations with epiphytes and of studies *in vitro* with the mycobionts isolated. Unfortunately, such publications seem not to have been published. Nevertheless, the information presented in Ruinen (1953) appears to be thorough and deserves to be re-examined critically.

Epiphytes could present another problem for the phorophyte, namely light competition. Chlorophyll occurs naturally in bark of any tree at almost any age (H. N. Rasmussen, pers. observ.). Bark photosynthesis is a shade-adapted process that is driven by the dim light passing through the outer bark. Respiratory CO_2 within the stem tissues is thought to be the main carbon source (Pfanz, 2008). The possible importance of bark photosynthesis, besides local energy production, could be amelioration of low oxygen and high carbon dioxide pressures that tend to develop in dense stem tissues (Wittmann & Pfanz, 2014). Stem photosynthesis would suffer from a dense epiphyte cover, and thus, it does not appear unlikely that a selective pressure could exist on trees favouring mechanisms that repel colonization on the bark (Montaña *et al.*, 1997).

Patterns of colonization on a single tree species may show that it can have a repellent effect on some epiphytes, a positive association with other species, but no effect on most epiphytes (Laube & Zotz, 2006). In the same study in the same area, different tree species showed roughly similar association patterns, but involving different groups of epiphytes. The assumed repellence mechanisms should thus be species specific to the phorophyte and target a limited group of epiphytic species. This suggests much more refined interaction mechanisms than might be accounted for by physical bark features.

PERSPECTIVES

In the first sections, we assumed that the phorophytes define the epiphytic habitat and that orchids and other epiphytes adjust to the changing conditions, but the table is turned if we accept that epiphytes may affect the trees profoundly. Provided that epiphytes are able to restrict growth in the branches they colonize, the microclimatic succession as outlined in Figure 3 could be slowed or reversed.

It has been emphasized in several studies that epiphytic orchids can be found in profusion on dead trunks or processed wooden objects such as telephone poles and fences (Johansson, 1974; Zimmerman & Olmstead, 1992) and that dead trees may in fact be among the prevailing substrates of a species even at the seedling stage (Otero *et al.*, 2007). The main point about the epiphytic life strategy would thus appear to be the escape from competition and light limitation on the ground, rather than a requirement for living trees *per se*. As discussed above, the growth of the phorophyte must, in fact, present a challenge to the epiphytes sitting in its crown.

More research is needed on the chemical or physical features of epiphytic habitats to explain why the same tree species may enable some orchid species to establish and others to fail on their bark. A tree species may be generally uninhabitable to an orchid species due to toxicity and other characteristics, but it could also avoid colonization by a particular epiphytic species by simply not providing that 'window of opportunity' between a position amenable to germination and one suited for reproduction.

Currently, most data and inferences about the epiphytic habitat and distinguishing phorophyte features are based on correlative studies, but with many co-varying factors, which is not a very informative approach. Experimental sowing of epiphytic orchids is possible using the mounting technique with Rasmussen–Whigham type seed packets on bark (Zettler *et al.*, 2011) or heat-sealed soft seed bags, tied to bark surfaces, and a method of seed spraying on bark for observation of germination *in situ*, in addition to a system for testing the effect of bark on seeds *in vitro*, have been developed by Yang *et al.* (2017). Similar approaches could be used to explore the effects of microenvironmental changes along the bark age gradient, in relation to mycobiont growth and seed germination (e.g. Harshani *et al.*, 2014). Field sowings could furthermore be used for continuous observation (e.g. Zotz, 1998, but extending to bark areas not holding mother plants), combined with environmental manipulation, to establish timing and influential factors for germination in the bark microenvironment. Transplantation experiments might be used to understand conditions for the survival of seedlings and more mature plants.

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