SHORT COMMUNICATION

Do host bark traits influence trunk epiphyte communities?

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Abstract: Host bark traits are known to affect the characteristics of epiphyte communities in forests worldwide; however, few investigations of such relationships have been undertaken in New Zealand forests. By examining the trunk epiphyte communities on four co-occurring forest tree species (*Agathis australis, Dacrydium cupressinum, Knightia excelsa* and *Vitex lucens*) representing a range of bark characteristics, we sought evidence that bark traits may shape these communities. Sampling was conducted on tree trunks in the Waitakere and Hunua ranges in the Auckland Region. As expected, the rough but lightly shedding bark of *Vitex lucens* was found to support many epiphytes, whereas the coarsely flaking bark surface of *Dacrydium cupressinum* supported few epiphytes. Conversely, despite bark with a smooth texture that sheds in large flakes, and contrary to the suggestions of previous authors, *Agathis australis* trunks were found to support the greatest numbers of epiphytes and this species was one of the most frequent epiphyte hosts. The individual epiphytes found on *Agathis australis*, however, were significantly smaller and more appressed to the trunk than those on the other trees, and species composition differed from the other host species.

Keywords: *Agathis australis*, kauri; *Dacrydium cupressinum*, rimu; *Knightia excelsa*, rewarewa; *Vitex lucens*, puriri

Introduction

Tree bark is a common substrate for many epiphyte species, a number of which grow almost exclusively on this surface (Dawson 1986). Observations of the distribution of bark epiphytes on trees of different species suggest host-specific differences in composition and abundance, with the bark characteristics of the host tree affecting the ability of different epiphytes to establish, remain attached, and grow on the bark surface (Oliver 1930; Benzing 1980). Studies undertaken in several locations have demonstrated the effects of specific bark traits in shaping epiphyte communities (Billings & Drew 1938; Bates 1992; Talley et al. 1996; Callaway et al. 2002; Bergstrom & Carter 2008; López-Villalobos et al. 2008).

Bark shedding has frequently been described as an adaptation to prevent the establishment of epiphytes and lianes on the bark's surface (Todzia 1986; Stevens 1987; Zimmerman & Olmsted 1992; Talley et al. 1996; López-Villalobos et al. 2008), a hypothesis that, in a New Zealand context, has commonly been made in regard to *Agathis australis.* Previous authors suggest that epiphytes and lianes do not persist for long on *Agathis australis* trunks due to the continuous shedding of flakes of bark from these trees, so bark epiphyte communities never build up in extent or diversity, resulting in 'clean' trunks (Cockayne 1908; Laing & Blackwell 1940; Salmon 1980; Ecroyd 1982; Steward & Beveridge 2010). The shedding of bark is certainly a regular disturbance to bark epiphyte communities, removing the epiphytes present on the areas sloughed off and creating new bare areas for colonisation (Todzia 1986; Stevens 1987; Zimmerman & Olmsted 1992; Talley et al. 1996; López-Villalobos et al. 2008).

In addition to shedding patterns, bark texture is an important characteristic that influences epiphyte community composition. For example, Oliver (1930) noted that rough-barked trees support more epiphytes on their trunks than smooth-barked trees due to their better 'holding surface', which provides superior anchorage for epiphytes and can allow the build-up of a greater layer of 'canopy soil' (sensu Williams & Sillett 2007) on the trunk surface. However, surfaces that are too rough increase the likelihood of desiccation of epiphytes as the plants are held above the surface at a distance such that they can only receive moisture in the form of rain, rather than also as stemflow (Benzing 1990).

By examining the nature of trunk epiphyte communities on four co-occurring forest trees with a range of bark traits (*Agathis australis, Dacrydium cupressinum, Knightia excelsa* and *Vitex lucens*), we aimed to investigate whether epiphyte community characteristics vary in relation to host species' barks. We hypothesised that a gradient in epiphyte loading would be observed, with *Vitex lucens* (rough bark, low shedding rate) supporting the greatest epiphyte loads and *Agathis australis* (smooth bark, high shedding rate) supporting the least.

Methods

Study species and sites

The tree species investigated were selected to provide a variety of bark characteristics in terms of texture and peeling patterns. Species selected were *Agathis australis* (kauri, Araucariaceae, bark smooth and shed in large flakes), *Dacrydium cupressinum* (rimu, Podocarpaceae, bark rough and shed in large flakes), *Knightia excelsa* (rewarewa, Proteaceae, bark smooth and not shed at observable rates) and *Vitex lucens* (puriri, Lamiaceae, bark rough and shed at low rates). These species are all present in mature forest within the same geographic areas, allowing differences in epiphyte communities between the tree species to be attributable to host-specific rather than environmental factors.

Study sites were situated in areas of mature forest in the Waitakere Ranges (36°54' S, 174°31' E) and the Hunua Ranges (37°05' S, 175°12' E) in the Auckland Region. Annual rainfall in both ranges is 1200 mm at sea level, and reaches 2200 mm at 430 m in the Waitakere Ranges and 2400 mm at 640 m in the Hunua Ranges (Griffiths & McSaveney 2003).

Within each range, sites were chosen based largely on the availability of mature *Agathis australis* specimens. *Agathis australis* has a patchy distribution within northern forests naturally (Ogden & Stewart 1995), with mature stands even more sporadic in modern times due to former logging activity in many areas, including the study locations (Silvester 1964; Esler 1983). The routes of walking tracks often specifically target *Agathis australis* stands in these ranges, so we used these to access stands. In order to develop a sample set of relatively independent observations, we randomly selected a few trees from each of a range of well-separated areas containing stands; six in the Waitakere Ranges (on the Fairy Falls, Goodfellow, Upper Kauri, Filtration Plant, Pukematekeo and the Auckland City Walk tracks) and four in the Hunua Ranges (on the Massey and Puriri Grove tracks, and off the Workman and Moumoukai Hill roads). In each area accessed, sample *Agathis australis* (*n* = 3–5 trees) were selected at random. Trees immediately adjacent to tracks were avoided, with trees selected up to 50 m distant from tracks. Trees selected for sampling required a diameter at breast height (dbh) of at least 20 cm. Sample trees of other species were then chosen in the same general area as each *Agathis australis* zone to ensure all trees sampled were subject to the same potential species pool of epiphytes. Twenty trees of each species were sampled in the Hunua Ranges, and in the Waitakere Ranges 28 *Agathis australis*, 23 *Dacrydium cupressinum*, 22 *Knightia excelsa* and 20 *Vitex lucens* were sampled. Trees with trunks covered by lianes to more than approximately 25% of the bark surface and/or that were tilted more than 10° from the vertical were not assessed due to the potentially confounding effects these factors would have upon the trunk epiphyte communities.

Sampling

The dbh and GPS coordinates of each study tree were recorded, and their trunks between 0.5 and 3 m height searched for epiphytes. For each epiphyte observed, we recorded its species, height above the ground, compass orientation, and size (along axes in three dimensions), as well as whether any bryophytes were associated with it. We found it difficult to distinguish reliably among small individuals of the perching lilies *Astelia solandri*, *Collospermum hastatum* or *C. microspermum* (Asteliaceae) at a species level, so these were grouped for analysis.

Data analysis

A chi-squared test of epiphyte counts was used to determine whether the distribution of these epiphytes was random with respect to host, based on what would be expected given the trunk areas surveyed. Expected epiphyte count for a host species was calculated as:

$$E_H = \frac{E_T}{A_T} \times A_H ,$$

where E_H is the expected epiphyte count for the host species, E_T is the total epiphyte count across all of the host species, A_T is the total trunk area surveyed for all the host species, and A_H is the trunk area surveyed for the host species.

One-way mixed-effects analysis of variance (ANOVA), with host species as a fixed effect and range (Waitakere vs Hunua) as a random effect, was used to test for differences in epiphyte coverage between host species, and on the data pertaining to each individual epiphyte to determine if the trunk area covered by the individual epiphytes or the distances the epiphytes extended from their host's trunk surface differed among epiphytes on different host species. The ANOVA tests were performed on square-root-transformed data so that the assumption of homogeneity of variance could be met. Pair-wise comparisons of the investigated variables were made among host species using Tukey's HSD tests.

Results

On a tree-by-tree basis, only 32% of the total 173 study trees had any trunk epiphytes in the sampled region, although epiphytes grew on 44% of the 48 *Agathis australis* trees investigated. This percentage was one of the highest of the tree species sampled and provides concrete evidence that epiphytes do accumulate on the trunks of some individuals of this species. Of the other host species investigated, *Vitex lucens* had epiphytes present on the greatest percentage of sampled trees (45%), whereas *Dacrydium cupressinum* had the lowest (12%). Epiphytes were recorded on 29% of *Knightia excelsa*. The total area surveyed for each host species must also be considered as, for example, the trunk area of *Knightia excelsa* surveyed was approximately half that of *Agathis australis* and *Vitex lucens* (Table 1), reducing the probability of finding epiphytes. However, the densities at which epiphytes occurred per square metre of trunk surface also differed considerably among host species (Table 1), and the total epiphyte distribution was found to be non-random with respect to host ($\chi^2_3 = 70.9$, $P < .001$). Epiphyte species composition varied substantially among host species (Table 1).

Agathis australis was the only host species on which epiphytes were recorded at a higher density than would be expected if the epiphytes were randomly distributed with respect to the host (Table 1). The most abundant epiphyte, *Ichthyostomum pygmaeum* (Orchidaceae), predominantly occurred on this host species, generally in association with moss of the genus *Macromitrium* (Orthotrichaceae); 84% of the epiphytes recorded on *Agathis australis* were *I. pygmaeum* or *Hymenophyllum* spp. (Hymenophyllaceae), which all possess a creeping growth habit and form flat mats against the surface of the trunk. *Knightia excelsa* and *Vitex lucens* supported the next highest epiphyte densities but epiphyte composition on these host species was dominated by perching lilies (Asteliaceae), *Microsorum pustulatum*, *M. scandens* and *Pyrrosia eleagnifolia* (Polypodiaceae; Table 1). *Drymoanthus adversus* was found only on *Knightia excelsa*, and *Anarthropteris lanceolata* only on *Vitex lucens*. Epiphyte density on *Dacrydium cupressinum* was the lowest of the four hosts, at less than 20% of the density expected by chance (Table 1).

The perching lily epiphytes (*Astelia solandri, Collospermum hastatum* and *C. microspermum*), which can reach large sizes and grow from one local point of attachment, were generally present on trunks as small individuals only a few centimetres across and occurred on all tree species examined.

Table 1. Epiphyte densities (per square metre) of taxa on host tree species, in descending order. Values represent densities combined across all study sites in the Waitakere and Hunua ranges. Expected densities are those that could be statistically expected to be found on each host species if epiphytes were distributed randomly with respect to host species, and were calculated based on the total trunk area surveyed for each species.

	Agathis australis	*Dacrydium cupressinum*	*Knightia excelsa*	*Vitex lucens*
Number of trees of host species	48	43	42	40
Trunk area surveyed (m^2)	227.2	173.6	110.9	218.8
Ichthyostomum pygmaeum (Orchidaceae)	0.224	0	0.009	0
Astelia or *Collospermum* spp. (Asteliaceae)	0.035	0.017	0.027	0.037
Hymenophyllum sanguinolentum (Hymenophyllaceae)	0.062	0	0.009	0
Hymenophyllum revolutum (Hymenophyllaceae)	0.053	0	0	0
Pyrrosia eleagnifolia (Polypodiaceae)	0	0.012	0.036	0.027
Microsorum pustulatum (Polypodiaceae)	0.004	0.006	0.027	0.027
Anarthropteris lanceolata (Polypodiaceae)	0	0	0	0.041
Microsorum scandens (Polypodiaceae)	0	0.006	0.018	0.014
Winika cunninghamii (Orchidaceae)	0.022	0	0	0
Drymoanthus adversus (Orchidaceae)	0	0	0.036	0
Asplenium flaccidum (Aspleniaceae)	0	0	0.018	0.005
Blechnum filiforme (Blechnaceae)	0	0	0.018	0.005
Earina mucronata (Orchidaceae)	0.004	0	0.009	0
Dicksonia squarrosa (Dicksoniaceae)	0	0	0.009	0
Hymenophyllum dilatum (Hymenophyllaceae)	0.004	0	0	0
Hymenophyllum rarum (Hymenophyllaceae)	0.004	0	0	0
Total observed density	0.414	0.040	0.216	0.155
Expected density	0.218	0.218	0.218	0.218

Species names follow Manaaki Whenua – Landcare Research Database Ngā Tipu Aotearoa – New Zealand Plants (http://nzflora.landcareresearch.co.nz/).

The larger individuals of this group encountered, though still only up to 10 cm along each axis, were often found growing in clumps of the moss *Leucobryum candidum* (Dicranaceae).

The highest average epiphyte coverage was found on *Agathis australis* trees, although there was considerable variation around this value, whereas the lowest epiphyte coverage was recorded on *Dacrydium cupressinum* trunks (Fig. 1a). No significant differences, however, were detected in the coverage of host trunks by epiphytes among the four host species ($F_{3,\,165} = 1.3718$, $P = 0.2532$).

Of the individual epiphytes recorded on the study trees, there were highly significant differences among host species in regard to the mean surface areas they covered and the distances the epiphytes extended from the trunk surfaces ($F_{3,155} = 7.9124$ and 15.9006 respectively, $P < 0.0001$ in both cases) (Fig. 1b, 1c). The epiphytes found on *Agathis australis* covered significantly less trunk area (Tukey's HSD, $P < 0.05$; Fig. 1b) and were significantly more appressed to the trunk surface than those on all other hosts (Tukey's HSD $P < 0.05$; Fig. 1c).

Discussion

New Zealand forests, particularly moist podocarp–broadleaved forests, have a richer epiphyte flora than can be found in many temperate rainforests such as in Tasmania and southern Australia (Zotz 2005), and the epiphytic biomass in some New Zealand forests has been shown to be comparable with that of tropical systems (Hofstede et al. 2001). While the trees surveyed here do not represent objective samples of the forests, our study suggests that lower trunk epiphytes are not common on the studied host species in the forests investigated, with only 32% of all the sampled trees hosting any epiphytes on the trunk section examined. On average, 8% of the sampled areas of the trunks of the study trees were covered by epiphytes, a result that is not unexpected when compared with previous research in other forest ecosystems. For example, in South American forests ter Steege and Cornelissen (1989) found the low trunk region supported the lowest epiphyte abundances and diversities. The contribution of trunk epiphytes to total epiphyte diversity was also found to be generally low in other areas of lowland tropical rainforest (Gentry & Dodson 1987; Nieder et al. 2000; Mehltreter et al. 2005).

The patterns of epiphyte occurrence on three of the host species was broadly as expected with *Vitex lucens* supporting a higher density of epiphytes and *Dacrydium cupressinum* a lower density. In contrast, however, to our hypothesised gradient in relative epiphyte load, and the suggestions of previous authors that the shedding of *Agathis australis* bark prevents epiphyte persistence and build-up (Cockayne 1908; Laing & Blackwell 1940; Salmon 1980; Ecroyd 1982; Steward & Beveridge 2010), we found that epiphytes are well able to establish on the trunks of *Agathis australis*, and that the

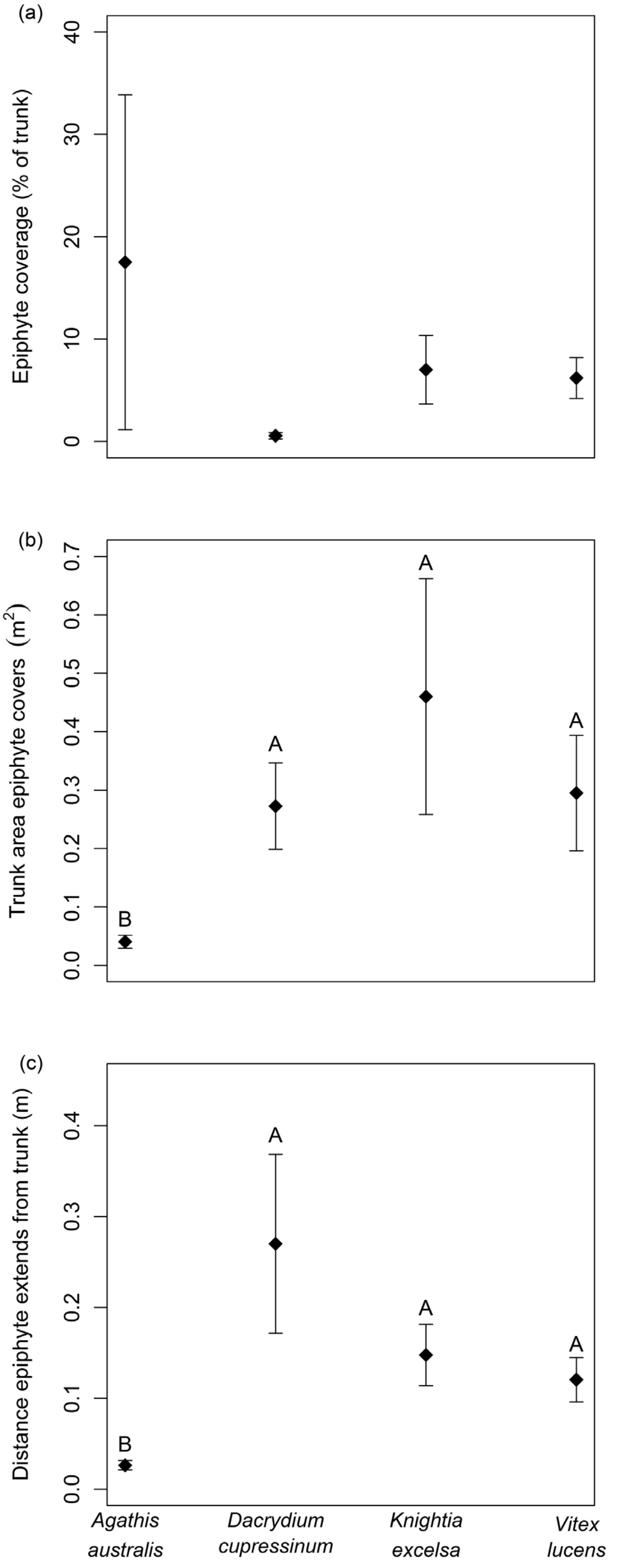

Figure 1. (a) Percentages of *Agathis australis*, *Dacrydium cupressinum*, *Knightia excelsa* and *Vitex lucens* trunk surfaces covered by epiphytes, (b) trunk areas covered by individual epiphytes on the four host species, and (c) the distance the individual epiphytes extended from the host trunk surface. Error bars represent the standard error of the mean; different letters signify significant differences (Tukey HSD, $P < 0.05$).

area covered by epiphytes on these trunks is not significantly different from that of three other common New Zealand trees. Unexpectedly, this species was one of the hosts that most often supported epiphytes and had the greatest density of individual epiphytes recorded on it.

Epiphyte species composition was found to differ amongst host species, most notably between *Agathis australis* and the other three tree species. For example, the epiphytes found abundantly on *Agathis australis*, *Ichthyostomum pygmaeum* and *Hymenophyllum* spp., were uncommon or absent on the other hosts investigated, whereas epiphytes like *Pyrrosia eleagnifolia, Microsorum scandens* and *Blechnum filiforme* (Blechnaceae) found on many other trees were not recorded on *Agathis australis.* As the host species were co-occurring in all of the study sites, and therefore would have experienced the same environmental conditions and been exposed to the same epiphyte species pools, the observed epiphyte differences among species are likely to have resulted from differences in host traits. Bark characteristics, both physical and chemical, are some of the most predominant host traits that would have a bearing on the composition of trunk epiphyte communities and are well known for doing so in forests elsewhere (Billings & Drew 1938; Bates 1992; Talley et al. 1996; Callaway et al. 2002; Bergstrom & Carter 2008; López-Villalobos et al. 2008). We suggest, therefore, that characteristics of *Agathis australis* bark may play a large role in selecting for particular types of epiphytes in comparison with other tree species, allowing only certain species to successfully establish and survive on the trunk surface. However, the substrate upon which epiphytes are growing is not the only habitat factor of importance; variables such as differences in vertical gradients of light and other microclimatic variables under different host trees are also likely to be contributing factors (Parra et al. 2009) and should be further investigated.

Once epiphytes have survived the vulnerable juvenile stage, the chief reason for their loss is from being unable to remain fixed to the trunk surface. This occurs either as the bark they are attached to is shed off, or, particularly when the surface is smooth, when their weight becomes such that they fall off the bark (Oliver 1930; Benzing 1980; Zotz 1998). Vascular epiphytes that display a creeping growth form, such as *Ichthyostomum pygmaeum* and *Hymenophyllum* spp., were the predominant type of epiphyte found on the smooth, flaking, *Agathis australis* bark. *Macromitrium* spp., the predominant bryophytes found on *Agathis australis*, also display a creeping growth form. In contrast, epiphyte species that grow from a single point of attachment, such as the perching lilies, were represented only by a few small individuals despite their high abundance in the surrounding forest, suggesting they may become dislodged from trunks when they reach too large a size. This pattern was also evident on the rough, flaking, *Dacrydium cupressinum* bark. However, while the creeping growth form was common to many of the epiphyte species on *Knightia excelsa* trunks, it was not obviously dominant, suggesting that this growth form is particularly advantageous in regard to an epiphyte retaining a hold on a more unstable substrate.

Those plants with a creeping growth form develop into flat mats pressed against the surface of the trunk, which results in the distribution of their weight over a large area and allows the retention of organic matter and moisture. Because these epiphyte species are attached to the trunk at multiple points, the shedding of a flake of bark under a large epiphytic mat is unlikely to completely remove the whole plant from the trunk.

Rather we hypothesise that as the bark is shed off, part of the plant is removed with it while the remainder remains attached to the tree, able to continue growth. The shedding of the bark would therefore act to fragment the clumps of these epiphytes, explaining the small areas covered by the individual epiphytes on *Agathis australis*, and the high numbers of individual epiphytic mats found on this host species.

While the data on the four tree species investigated in this study suggest that the epiphytes *Ichthyostomum pygmaeum* and *Hymenophyllum* spp. are primarily restricted to *Agathis australis*, the Auckland Museum Herbarium records show that these species frequently occur on other host trees, as well as on rocks and logs (for a range of examples see AK208953, AK264792, AK248052, AK231905, AK268086, AK114641 and AK207652). Holloway (1923) also records *Hymenophyllum* spp. on a range of substrates. These epiphyte species, therefore, are not restricted to the habitat provided by *Agathis australis*, yet are some of the few species able to survive upon it.

We found that epiphytes were generally only able to occur on the smooth-barked species when they were in association with a moss clump. The relatively smooth surfaces of these trunks would prevent many seeds from lodging directly on the bark, and prevent much humus or water being able to collect or be retained. The presence of moss, however, provides both a rough surface and a moist environment, allowing seeds to adhere and germinate, and reducing the likelihood of seedling mortality through desiccation – the main cause of epiphyte seedling loss (Zotz 1998). Oliver (1930) observed that there is a succession in the colonisation of bark by epiphytes in New Zealand forests, with mosses and lichens generally arriving first, followed by ferns and then the higher vascular plants; although he noted that orchids can also occur on reasonably clear bark surfaces. Blick and Burns (2009) also discuss potential facilitation interactions among epiphyte species.

This investigation has demonstrated that host bark traits affect the characteristics of the epiphyte communities that develop on trunk surfaces. As hypothesised, the rough, stable surface of *Vitex lucens* was correlated with a high abundance of trunk epiphytes, while the highly unstable surface of *Dacrydium cupressinum* was correlated with a low abundance. In contrast to our hypothesis and the suggestions of previous authors, the results show that the shedding of *Agathis australis* bark does not prevent the accumulation of epiphytes on the trunk surface, and that this tree species is a frequent epiphyte host. The species composition of the epiphytes on the trunks of *Agathis australis* differed from that of the other hosts, being predominantly epiphyte species that possess a creeping growth form and are able to form flat mats against the trunk. The *Agathis australis* epiphytes also tend to be more numerous and of a smaller size than those on the other hosts investigated.

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