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REGULAR PAPER

Bark peeling does not explain the distribution of epiphytes between six phorophyte species of a tropical dry forest of Mexico

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Background and aims – Contradictory evidence exists regarding the influence of bark peeling on the distribution of epiphytes among phorophyte species and vertical tree strata. However, there is little experimental evidence. The objectives of this study were to test whether bark-peeling rates differ between vertical strata and between phorophyte species, and whether the peeling rate correlates with epiphyte load among species of phorophytes.
Materials and methods – In a tropical dry forest of central Mexico, bark exfoliation rates were measured over a period of 310–322 days in six woody species previously reported with different epiphyte distribution, including *Bursera copallifera*, *B. glabrifolia* (phoropytes with high epiphyte load), *B. fagaroides*, *Conzattia multiflora*, *Ipomoea pauciflora* and *Sapium macrocarpum* (phorophytes with low epiphyte load). In three strata (trunk, inner branches and outer branches) of five individuals of each phorophyte, three areas per individual were marked with paint and with a determined number of small plastic tubes stuck to the bark, in order to easily monitor the speed and quantity of any loss of this marked bark over time. These treatments were replicated on an adjacent pinewood board in order to quantify any loss of painted area or plastic tubes that occurred as a result of deterioration of the marking materials rather than peeling of the marked bark.
Key results – The methods used for measuring bark peeling were strongly different. Plastic tubes gave an overestimation of bark peeling in the bark and in the pinewood boards; while paint remained in the pinewood boards, suggesting that paint loss on the bark was caused by peeling. Bark peeling rates differed slightly among the tree species and strata, regardless of whether or not the bark had peeling appearance. No pattern was found between bark peeling rate and the epiphyte load on each host.
Conclusions – Our results support previous research which estimated that bark peeling with paint method provides a better estimate of peeling rate. In general, the bark peeling rate was the highest reported in literature for trees in a forest, suggesting that the epiphytes of this forest are adapted to colonize trees with high bark peeling rates. However, this attribute may be less important than others for determining host quality for epiphytes.

Key words – Host-epiphyte association, plant-plant interactions, tropical dry forest, central Mexico, phorophyte.

INTRODUCTION

Interactions occur between plants via physical and chemical mechanisms through which species create the conditions for the establishment of other plants (e.g. succession), limit the existence of other plants (Mazzoleni et al. 2007) or, in groups, mutually buffer stressful effects of the environment (Callaway et al. 2002a). Some tree characteristics, such as bark peeling or exfoliation, have the potential to limit other groups of plants (e.g. lianas and epiphytes) (Zimmerman & Olmsted 1992, Talley et al. 1996).

Every woody plant species sheds bark (Callaway et al. 2002b), but only those in which the peeled layers remain as sheets attached to the plant are described as species with ex-

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foliating bark. Species with these characteristics have been reported in the families Apocynaceae, Bignoniaceae, Burseraceae, Combretaceae, Crassulaceae, Ebenaceae, Euphorbiaceae, Fabaceae, Flacourtiaceae, Fouqueriaceae, Julianiaceae, Myrtaceae, Platanaceae, Polygonaceae, Rhamnaceae, Rubiaceae, Sapindaceae, Sapotaceae, Tiliaceae and Verbenaceae (Callaway et al. 2002b, Heywood et al. 2007, López-Villalobos et al. 2008).

Bark peeling is a secondary characteristic which derives from the growth of the trees, but it has been suggested that it also acts to reduce colonization of the trees by lianas and epiphytes (Zimmerman & Olmsted 1992, Talley et al. 1996). Despite the generalizations made about bark peeling and its potential effect on epiphytes, there have only been two experimental studies of bark peeling rates (Callaway et al. 2002b, López-Villalobos et al. 2008). In a temperate forest of the Sapelo Island National Estuarine Reserve, USA, Callaway et al. (2002b) recorded after 22 months of observation that individuals of *Ilex opaca* Aiton had not lost bark, and that in another six species, the accumulated loss of bark was less than 5 %, with the highest bark peeling rates found in the species *Celtis laevigata* Willd. (6 %), *Juniperus virginiana* L. (20 %, after 22 months) and *Pinus taeda* L. (33 %, after 22 months). Bark peeling occurred in tree species with bark that appeared non-exfoliant (e.g. *Celtis laevigata* and *Quercus virginiana* Mill.) and the bark peeling behaviour did not determine phorophyte quality for epiphytes, since the coefficient of determination between the abundance of epiphytes on the phorophytes and the percentage of bark stability was found to be 0.14 (r = 0.37).

López-Villalobos et al. (2008) studied the bark peeling rate of *Bursera fagaroides* (Kunth) Engl. in a tropical dry forest of the central coastal zone of Veracruz, Mexico. These authors marked determined areas of bark with paint and monitored the survival of seedlings of the epiphyte species *Tillandsia paucifolia* Baker and *T. palmasolana* Matuda (≈ *T. concolor* L.B.Sm.). The highest bark peeling rate was presented on the trunk (0.12 % per day) and decreased towards the branches and twigs (0.04 % per day). The greatest cause of mortality of the epiphyte seedlings on the twigs was bark peeling, while on the branches and trunk, this was bark peeling and drought. *Tillandsia paucifolia* and *T. palmasolana* were abundant on *B. fagaroides*, showing that exfoliant bark does not preclude colonization by epiphytes. These authors suggest that, in order to colonize *B. fagaroides*, epiphytes must counteract the zones of high bark peeling or inhabit zones of high insolation and lower rates of bark peeling.

In a tropical dry forest of central Mexico, Vergara-Torres et al. (2010) found that epiphytes present a biased distribution; they are highly concentrated on three phorophyte species while the other phorophyte species can be almost empty and, as a consequence, these epiphytes are highly host limited. Three phorophyte species ('preferred phorophyte', 16 % of the individuals of the forest) concentrate 72 % of the individual epiphytes, while 13 % of the epiphytes are found on five species of limiting hosts (39 % of the individuals of the forest). The epiphyte distribution on another two phorophyte species suggests that these phorophytes are neither preferred nor limiting (indeterminate phorophytes); however, further research indicated that at least one of the indeterminate phorophyte species (*Sapium macrocarpum* Müll.Arg.) is also a limiting phorophyte (Cortés-Anzures 2015). Phorophyte size and three characteristics of the bark (thickness, texture and appearance of peeling) were not related to epiphyte distribution (Vergara-Torres et al. 2010, Cortés-Anzures 2015). In this same study area, it has been found that chemical extracts of the bark of three limiting phorophyte species reduced the germination of *Tillandsia recurvata* up to 60 % (Valencia-Díaz et al. 2010), due to the action of mixtures of compounds (Valencia-Díaz et al. 2013). In addition to allelopathic compounds in the bark, bark peeling could determine the epiphyte distribution patterns, but its influence may have been obscured in the study of Vergara-Torres et al. (2010) and Cortés-Anzures (2015) since peeling was determined only from the appearance of the bark and monitoring of bark loss was not considered.

This study examined the bark peeling behaviour of six phorophyte species, two species with high epiphyte loads (preferred) and four where epiphyte abundance was lower than would be expected by chance (limiting), in the tropical dry forest of San Andrés de la Cal (Vergara-Torres et al. 2010). We hypothesized (1) that the preferred phorophytes will have lower bark peeling rates than the limiting phorophytes; and (2) that the bark peeling rate will decrease towards the upper strata (branches and twigs), as reported previously (López-Villalobos et al. 2008), and we tested whether bark-peeling rates differ between vertical strata and between phorophyte species, and whether the peeling rate correlates with epiphyte load among species of phorophytes.

MATERIALS AND METHODS

Study area and species

This study was conducted in the tropical dry forest of the hill Tenextepetl, San Andrés de la Cal, Tepoztlan, Morelos, Mexico (99°06′50.2″N 18°57′22.2″W; 1 495 m a.s.l.). This site has a mean annual temperature of 20.5 °C and mean annual precipitation of 1 091.8 mm (Vergara-Torres et al. 2010). The rainy season extends from May to October. The soil is a luvic phaeozem (Ruiz-Rivera 2001) and the most abundant woody species (dbh > 3 cm) are *Sapium macrocarpum* Müll.Arg. (Euphorbiaceae) (18.4 % of the woody individuals) *Bursera fagaroides* (Kunth) Engl. (14.8 %, Burseraceae), *B. glabrifolia* (Kunth) Engl. (11 %), *Ipomoea pauciflora* M.Martens & Galeotti (9.8 %, Convolvulaceae), *Conzattia multiflora* (B.L.Rob.) Standl. (6.5 %, Fabaceae) and *Ipomoea murucoides* Roem. ex Schult. (5.7 %) (Vergara-Torres et al. 2010).

Field methods

In this study, we used six woody species in which epiphyte distribution differs (Vergara-Torres et al. 2010). The preferred phorophytes were *Bursera copallifera* (DC.) Bullock and *B. glabrifolia*, while *B. fagaroides*, *Conzattia multiflora*, *Ipomoea pauciflora* and *Sapium macrocarpum* were considered limiting phorophytes (Vergara-Torres et al. 2010, Cortés-Anzures 2015).

Table 1 – **Mean diameter (± standard deviation) of the sections of trunk and branches used to measure bark peeling rates in six tree species of the tropical dry forest of Tepoztlan, Central Mexico.**
N = five trees per species.

Tree species	Canopy stratum		
	Trunk (cm)	Inner branches (cm)	Outer branches (cm)
Bursera copallifera	23.0 ± 1.6	10.5 ± 1.2	4.1 ± 1.2
Bursera fagaroides	19.2 ± 4.9	10.9 ± 1.4	3.6 ± 1.4
Bursera glabrifolia	15.2 ± 2.6	8.1 ± 1.5	3.6 ± 1.1
Conzattia multiflora	27.3 ± 9.0	13.2 ± 2.9	4.9 ± 1.6
Ipomoea pauciflora	14.7 ± 5.6	9.3 ± 2.5	3.2 ± 0.6
Sapium macrocarpum	23.0 ± 10.3	12.5 ± 4.7	2.9 ± 0.7

In order to determine the bark peeling rate, three sections of bark were painted on five individual trees per species, with each chosen section located in a different stratum (trunk, inner and outer branches), for an overall sample of 90 sections of bark (6 phorophyte species × 5 individuals × 3 strata) (table 1). Tree individuals were selected at random from a sample taken as part of an earlier study (Vergara-Torres et al. 2010). Each painted area was 1 cm wide and 5 cm long and was painted with vinyl paint using a cardboard stencil (Callaway et al. 2002b, López-Villalobos et al. 2008) (fig. 1). On the structure where each section was painted (branch/trunk), the perimeter was measured and marked with tape (Forestry suppliers, Inc., Texas brand solid color vinyl flagging, United States of America). Each painted area (one per strata, three strata per tree) was reviewed monthly, over a period of eleven months (May 2009–March 2010, 310–322 days) and the percentage of painted bark area lost was measured. In order to measure the area of bark lost, a cardboard stencil was placed on the area. This stencil was identical to that used to paint the bark but held an acetate with 20 marked squares of size 0.5 × 0.5 cm. With this grid, the number of squares in which paint was no longer visible could be quickly quantified on each visit. In addition to each tree, on the area adjacent to the painted area, ten small plastic tubes were glued (fig. 1). These tubes were glued over an area equal in size to that of the painted area and were distributed equidistantly (fig. 1). The tubes measured an average of (±SD, minimum–maximum) 1.7 mm in width (±0.2, 1.4–2.1 mm), 5.9 mm in length (±0.4, 5.1–7.3 mm) and weighed 31 mg (±3.0, 29.6–31.9 mg). Each month, the number of tubes that remained stuck to the area of bark was quantified.

On each trunk and inner and outer branch with areas marked with paint and groups of plastic tubes, a control was established in order to quantify any loss of paint or tubes that occurred through deterioration of the paint or failure of the glue. This control consisted of a piece of pinewood (2.5 cm wide × 20 cm long × 0.63 cm thick) with a painted area and an area of glued plastic tubes similar to that placed on the tree (fig. 1).

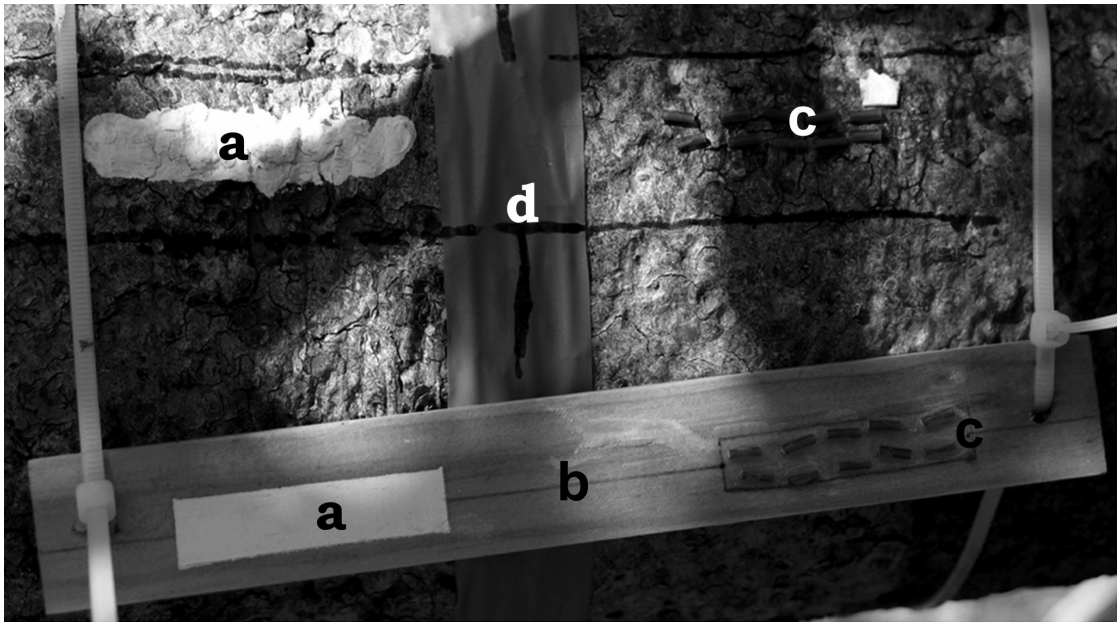

Figure 1 – Paint (a) and tube (c) plots (1 cm × 5 cm) used to measure the bark peeling behaviour of six tree species in the tropical dry forest of San Andres de la Cal, central Mexico. For each tree, plots were established on the tree and on an adjacent piece of pinewood (b) as a control. Each plot group was marked with flagging (d), which also served as a reference for each sampling point.

Data analysis

We performed general linear models to test the effect of tree species and strata on the peeling rate (% of bark loss per day), time to the first peeling event (days) and time to reach maximum peeling (days). In these models, tree species was the main fixed factor (six levels), individual tree was a random factor (five levels per species) nested inside the species, and stratum was a fixed factor (three levels) within each individual tree (Sahai & Ageel 2000). The response variable peeling rate (% of bark loss per day) was arcsine transformed in order to comply with the model assumptions (Zar 2010). All data analyses were conducted in Stata 13.1.

To test whether the bark peeling rate correlates with phorophyte quality for the epiphytes, we performed a non-parametric correlation analysis (Kendall τ, Hollander & Wolfe 1999). In this analysis, we correlated the peeling rate (% per day) with the logarithm of the mean number of epiphyte individuals per individual tree. The mean numbers of epiphytes per tree species were obtained from the data reported in Vergara-Torres et al. (2010). Mean values for each species of phorophyte were (in ascending order) 1.0 (*Ipomoea pauciflora*), 4.7 (*Sapium macrocarpum*), 5.9 (*Conzattia multiflora*) and 11.8 (*Bursera fagaroides*) for the limiting phorophytes, and 70.5 (*B. glabrifolia*) and 77.7 (*B. copallifera*) for the preferred phorophytes.

RESULTS

No paint loss was observed in the pinewood controls for the paint treatment. Tubes on the trees, and on the pinewood controls, began to fall before the paint, giving a rapid estimation of peeling (fig. 2A), and also reached its maximum value of falling (peeling) before that of the paint (fig. 2B). During the first three months of observation, 87 % of the tube-plots on the trees and 59 % on the controls presented their first peeling losses; while only 21 % of the paint plots on the trees presented paint loss. After more than 260 days of observation, only 31 % of the paint plots had reached their estimated maximum peeling (fig. 2B), while 50 % of the tree and control tube plots reached their estimated maximum peeling in less than 171 days (fig. 2B).

The peeling rate estimated with the painted areas on the tree sections was lower than that estimated with the tube-plots (fig. 3). In fact, the proportion of peeled bark estimated with paint followed the opposite pattern presented by the tubes glued to the bark (fig. 3). The peeling estimated in the control tube-plots followed a pattern that was more similar to that of the paint plots; however, control tube-plots showed a lower number of plots with an estimated peeling of below 20 % than was the case with the paint plots (fig. 3) and a higher number of plots with peeled bark above 20 % than was the case in the paint plots (fig. 3). For the rest of the analysis, we only present data based on the paint plots, since these gave a more cautious measure of the peeling rate.

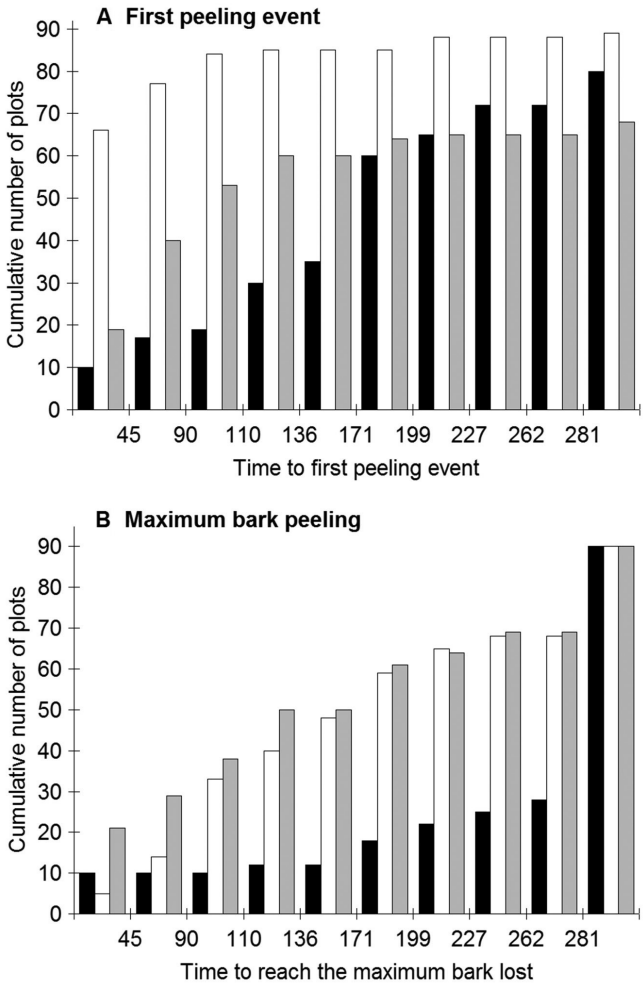

Figure 2 – Cumulative distribution of experimental plots where bark peeling behaviour was estimated with paint on the trees (solid bars), plastic tubes on trees (empty bars) and plastic tubes on the pinewood control (grey bars). The cumulative distribution is shown with time to the first peeling event (A) and time to reach maximum peeling (B). For time intervals, only the upper limit is shown.

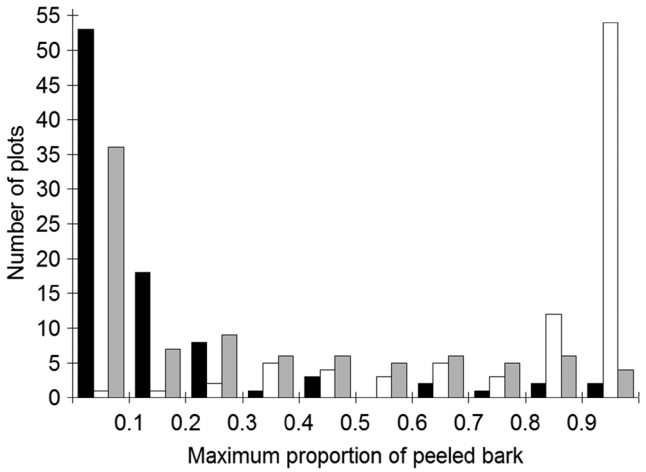

Figure 3 – Frequency distribution of bark sections and pinewood boards (control) according to their estimated bark peeling. In each bark section and its control bark peeling behaviour was estimated with paint on the trees (solid bars), plastic tubes on trees (empty bars) and plastic tubes on the pinewood control (grey bars). For the proportion of peeled bark, only the upper limit is shown.

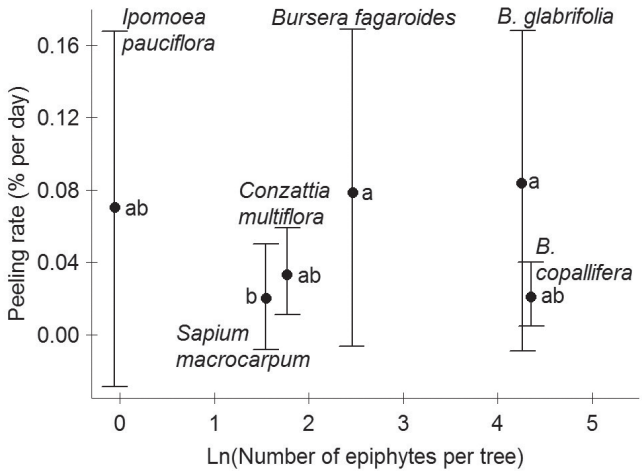

Figure 4 – Mean bark peeling rate (% per day) of six tree species of the tropical dry forest of San Andres de la Cal, Central Mexico. On the x axis, tree species are ordered by the logarithm of the mean number of epiphyte individuals per tree (Vergara-Torres et al. 2010). Solid circles indicate the mean values and dispersal lines are standard deviation. Letters indicate if means were significantly different: a mean marked with an "a" is statistically different than a mean marked with a "b", and means marked with "ab" are not statistically different from those marked with "a" or "b" (Tukey test, $P < 0.05$).

The rate of paint loss differed between tree species ($f = 4.1$, $p < 0.01$). *Bursera fagaroides* (a limiting species) and *B. glabrifolia* (a preferred species) had the highest peeling rates (fig. 4), but these differed only from the peeling rate of *Sapium macrocarpum* (a limiting species) (Tukey test, $p < 0.05$), which had the lowest peeling rate. The rest of tree species had peeling rates that did not differ statistically from either the fastest or slowest peeling rates (fig. 4) (Tukey test, $p < 0.05$). These differences did not match between preferred and limiting host (preferred phorophytes with low peeling rate and limiting phorophytes with high peeling rate) and the correlation between peeling rate and epiphyte abundance (mean number of epiphytes per tree) was therefore low ($\tau = 0.20$) and non-significant ($p > 0.05$).

There was no generalized effect of strata in the peeling rate ($f = 1.2$, $p > 0.05$). The effect of strata depended on the tree species, since the species-strata interaction was significant ($f = 3.3$, $p < 0.01$). Multiple comparisons (Tukey, $p < 0.05$) showed that in *Bursera copallifera*, *Conzattia multiflora* and *Sapium macrocarpum*, the peeling rate was similar among strata (fig. 5A, D & E). In *Bursera fagaroides* (outer branches, fig. 5B), *B. glabrifolia* (trunk, fig. 5C) and *Ipomoea pauciflora* (inner branches, fig. 5E), the maximum rate of peeling was observed in one stratum, but the peeling rate did not differ in the other two. Among the tree species in which epiphytes are highly concentrated (Vergara-Torres et al. 2010), *Bursera copallifera* had a low peeling rate and *B. glabrifolia* had one of the highest. Among the species with low epiphyte load, *B. fagaroides* had a bark peeling rate 2.4 times higher than *Conzattia multiflora*.

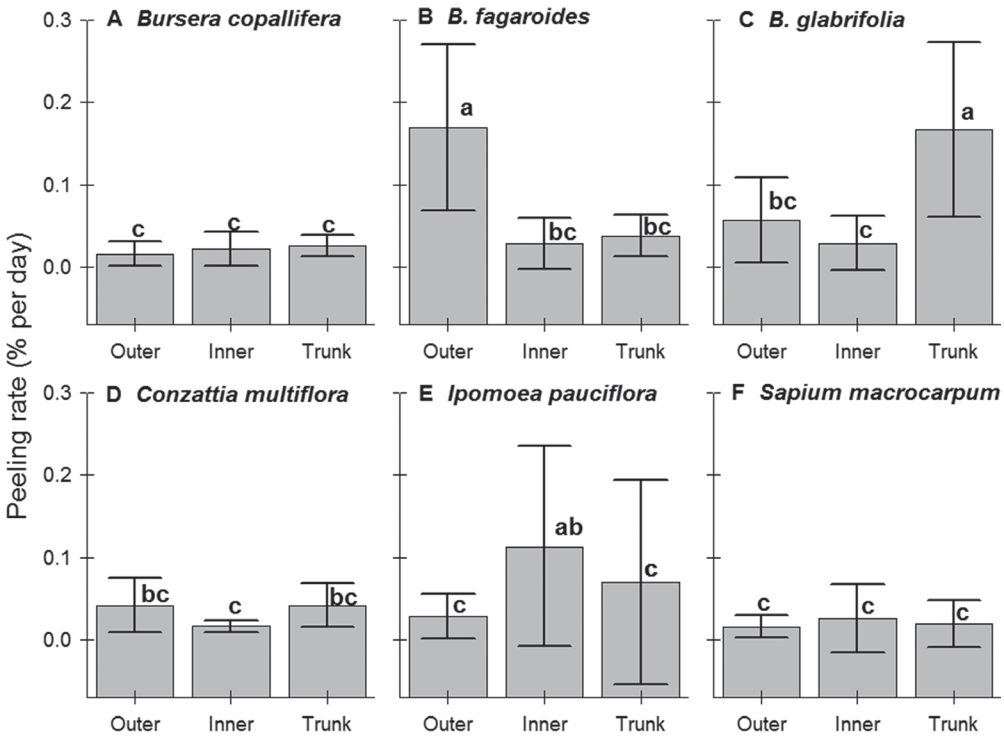

Figure 5 – Mean bark peeling rate (% per day) measured in three canopy strata (outer branches, inner branches and trunk) of six tree species of the tropical dry forest of San Andres de la Cal, Central Mexico. Bars indicate the mean values and the dispersal lines are standard deviation. Different letters indicate significant differences between mean values (Tukey test, $P < 0.05$).

Time to the first peeling event differed among tree species ($f = 23.7$, $p < 0.0001$), strata ($f = 4.5$, $p < 0.05$) and with the interaction species-strata ($f = 6.1$, $p < 0.00001$). The shortest time to first peeling events occurred in *Bursera fagaroides* and *B. glabrifolia* (Tukey test, $p < 0.05$; fig. 6A); in these species, the first peeling event occurred in less than three months, while in the rest of the species the first evidence of peeling was observed after three months (fig. 6A).

Among the strata, the first peeling events occurred soonest on the trunk (fig. 6B), while time to the first peeling event was similar between the outer and inner branches (fig. 6B). The previous pattern was only repeated in *B. fagaroides*; in this species, the fastest time to first peeling occurred on the trunk (fig. 7).

Time to reach maximum peeling did not differ between tree species ($f = 0.6$, $p > 0.05$) or strata ($f = 2.0$, $p > 0.05$), but did differ in the interaction species-strata ($f = 2.6$, $p < 0.05$). Nevertheless, in the interaction species-strata, time to reach maximum bark peeling differed between trunk (slower) and the inner branches (faster) in *B. glabrifolia* only (fig. 8).

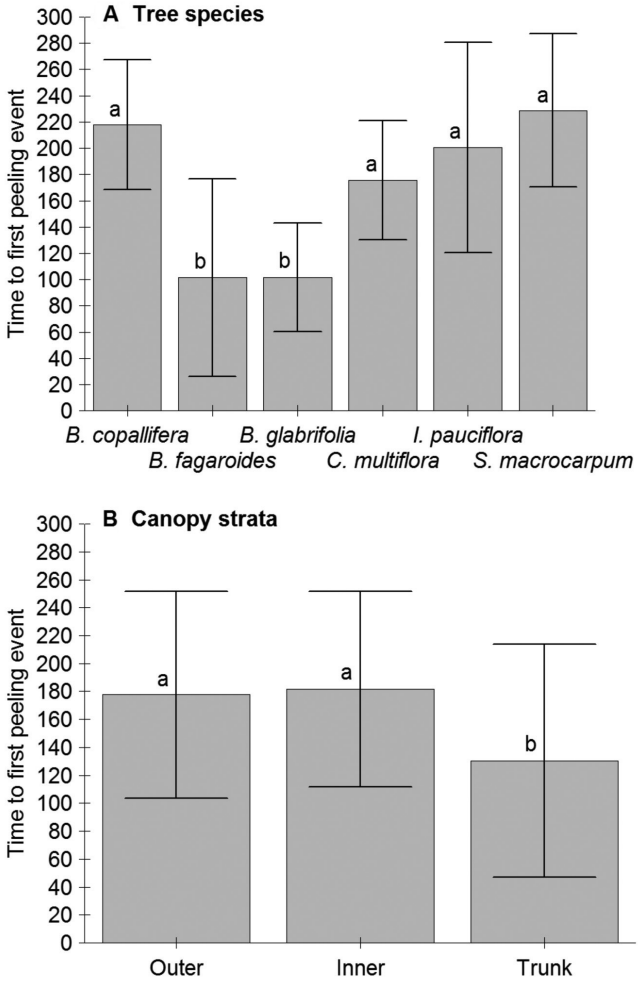

Figure 6 – Mean time to the first peeling event in six tree species of the tropical dry forest of San Andres de la Cal, Central Mexico (A), and in three canopy strata (outer branches, inner branches and trunk) of these tree species (B). Bars indicate the mean values and dispersal lines are standard deviation. Different letters indicate significant differences between mean values (Tukey test, $P < 0.05$).

DISCUSSION

Bark peeling behaviour is an important tree trait that has been associated with a lower abundance of epiphytes and vines (e.g. Zimmerman & Olmsted 1992, Talley et al. 1996). However, there is little experimental evidence regarding peeling rates and most studies have determined peeling simply from the appearance of the bark, ignoring the actual bark peeling rate. Here we have shown that, in a tropical dry forest, peeling occurs in all of the surveyed trees (regardless of bark appearance), but the estimated rate differs according to the method employed, among both tree species and strata. Contrary to expectation, peeling behaviour was not related to epiphyte abundance.

Previous studies have estimated bark peeling rates with painted dots (Callaway et al. 2002b) or small painted sections of the bark (López-Villalobos et al. 2008). However, these procedures have not included a control treatment or an alternative method of estimating the peeling. We added a control treatment and an alternative method of estimation (plastic tubes); however, the alternative method proved to overestimate the bark peeling because, in the majority of the tube-plots, (1) tubes began to fail in the first month, (2) most plots reached their maximum peeling in less than three months, and (3) most of the plots produced peeling values in excess of 90 % by the end of the experiment. These factors suggest that the bark peeling values estimated with the plastic tube method could have been seriously inflated by the failure of the glue to firmly attach the tubes to both the bark and the pinewood of the control treatment. The paint method could provide a more cautious estimate and one that more closely reflects the actual peeling rate, since no paint coverage was lost in the control treatment, suggesting that any paint loss from the painted area of bark was not simply the paint flaking off the bark but was the result of bark peeling.

A previous study with one tree species of a tropical dry forest, *Bursera fagaroides*, suggests that the bark peeling rate decreases from the trunk to the upper branches (López-Villalobos et al. 2008). In accordance with this trend, the time to the first peeling event was shorter on the trunk among all of the tree species, but this difference was only obvious in *B. fagaroides* when the species-strata interaction was observed. In *Bursera glabrifolia*, maximum peeling rate was observed on the trunk; however, most of the evidence was actually against a faster peeling rate on the trunk stratum; for most species, time to the first peeling event, time to reach maximum peeling and the peeling rate were similar between strata. In *B. fagaroides*, the bark peeling rate was fastest on the outer branches but, in *Ipomoea pauciflora*, this was recorded on the inner branches. The different trend may have been observed in *B. fagaroides* because we followed the peeling rate over the entire year while the previous study (López-Villalobos et al. 2008) only did so for three months during the dry season.

The studied tree species constitute key elements of this forest; altogether, they constitute 66 % of the individuals present (Vergara-Torres et al. 2010) and, overall, they present a

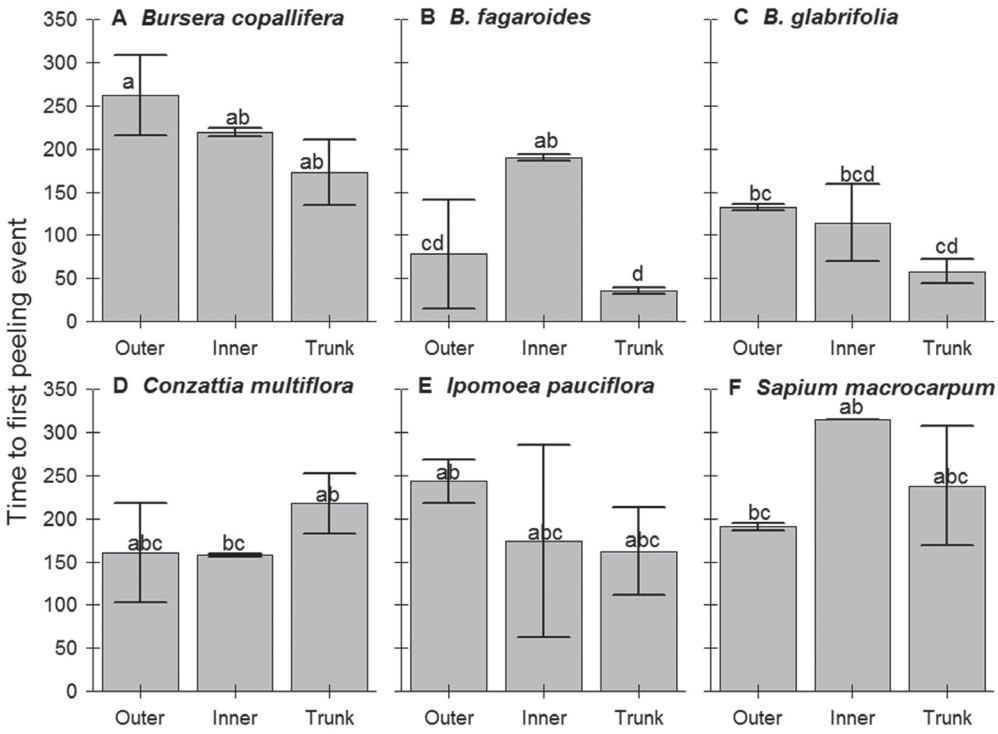

Figure 7 – Mean time to the first peeling event in three canopy strata (outer branches, inner branches and trunk) of six tree species of the tropical dry forest of San Andres de la Cal, Central Mexico. Bars indicate the mean values and dispersal lines are standard deviation. Different letters indicate significant differences between mean values (Tukey test, $P < 0.05$).

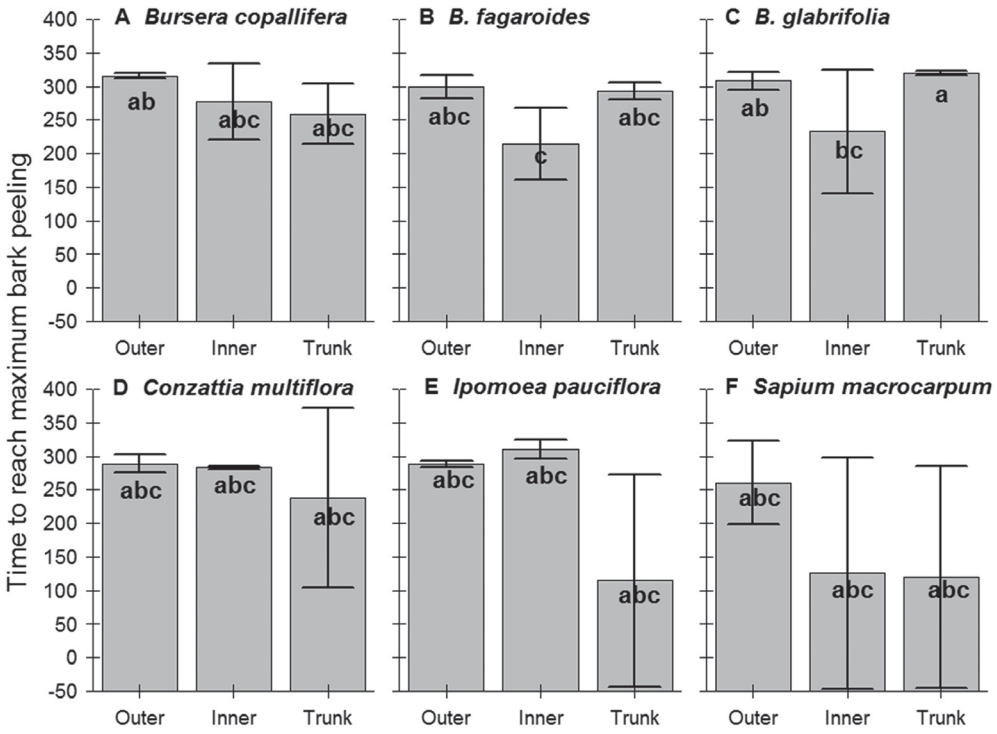

Figure 8 – Mean time to reach maximum bark peeling in three canopy strata (outer branches, inner branches and trunk) of six tree species of the tropical dry forest of San Andres de la Cal, Central Mexico. Bars indicate the mean values and dispersal lines are standard deviation. Different letters indicate significant differences between mean values (Tukey test, $P < 0.05$).

higher peeling rate that that observed previously (Callaway et al. 2002b). Of the species surveyed, *Sapium macrocarpum* (7.3 % per year) and *Bursera copallifera* (7.7 % per year) had a peeling rate lower than 10 % per year; while *Conzattia multiflora* (12.1 % per year), *Ipomoea pauciflora* (25.7 % per year), *B. fagaroides* (28.7 % per year) and *B. glabrifolia* (30.6 % per year) had bark peeling rates higher than 10 %. These numbers suggest that the mean peeling rate for the trees of the studied forest is 18.7 % per year, the highest rate documented to date. For example, in the temperate forest of Sapelo Island, the average of the yearly peeling rates of *Ilex opaca* (0.0 % per year), *Liquidambar styraciflua* L. (1.1 % per year), *Quercus nigra* L. (1.1 % per year), *Q. virginiana* (2.2 % per year), *Magnolia grandiflora* L. (2.2 % per year), *Celtis laevigata* (3.3 % per year), *Juniperus virginiana* (10.9 % per year) and *Pinus taeda* (18.0 % per year) produces a joint mean peeling rate for these species of 4.8 % per year (Callaway et al. 2002b).

One possible explanation for the high bark peeling rate observed among the tree species of the studied tropical dry forest is the lack of a cork cover (phellem) (Trockenbrodt 1990). Most species surveyed have green barks that lack phellem. *Sapium macrocarpum* was the only species that can have a well-developed phellem, but only on the trunk. In contrast, tree species from temperate forests have a thick phellem layer.

The observed bark peeling rates do not explain the abundance of epiphytes among the surveyed tree species. In general, the tropical dry forest is considered an environment with low epiphyte abundance and low species richness. The main explication for this pattern is the long dry season (Gentry & Dodson 1987, Vergara-Torres et al. 2010) but our data suggest that epiphytes that inhabit the tropical dry forest must also be adapted to colonize trees with high bark peeling rates.

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