

Drip-tips are Associated with Intensity of Precipitation in the Amazon Rain Forest

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ABSTRACT

Drip-tips are a common feature of the leaves of rain forest trees, but their functional significance remains contested. The most widely accepted hypothesis is that drip-tips assist drainage of the lamina thereby aiding drying of the leaf surface and reducing the rate of colonization and abundance of epiphyllic organisms. The drying action of drip-tips may also enhance transpiration and reduce the need for investment in support structures. Furthermore, drip-tips may help prevent splash erosion around the base of the tree. Data from 130 forest Amazonian plots are used to investigate the abundance and distribution of drip-tips and, through regression methods that incorporate spatial autocorrelation, seek to identify associations between the frequency of drip-tips and a range of climatic variables. The average frequency of species and trees with drip-tips across all plots was 32 and 33 percent, respectively. Trees and species with drip-tips were significantly more prevalent in the Central-East Amazon than the other regions. Drip-tips were also associated with tree species that have smaller maximum heights and with trees with smaller trunk diameters. The proportion of species and individuals with drip-tips was more strongly correlated with precipitation of the wettest trimester than with total annual precipitation or length of the dry season. Our results extend and provide support for both existing hypotheses for the functional benefit of possessing a drip-tip. Moreover, the currently unrecognized macrogeographic association between the frequency of drip-tips in trees of the tropical forest understory and areas of heavy precipitation suggests a new function for this trait.

Abstract in Portuguese is available in the online version of this article.

Key words: acuminate tips; adaptation; Amazonia; functional traits; macroecology; RAINFOR.

LEAVES WITH LONG ACUMINATE TIPS, OFTEN REFERRED TO AS DRIP-TIPS, ARE A COMMON FEATURE OF TROPICAL RAIN FORESTS AND CLOUD FORESTS (Givnish 1987, Richards 1996). The strong association of drip-tips with tropical rain forests has even led to them being used as an archetypal rain forest characteristic in paleoecological research, where they are regarded as a ‘semi-reliable’ indicator of rain forest presence if they occur in more than 25 percent of dicotyledonous angiosperm species in a sample (Burnham & Johnson 2004).

Despite the widespread use of drip-tips in reconstructing past climates, their functional significance remains a subject of active debate (L cking & Bernecker-L cking 2005, Burd 2007). The earliest and most thoroughly investigated hypothesis is that rain forest plants have evolved drip-tips as a strategy to enhance the rate of drainage from leaves. In support of this hypothesis, several authors have experimentally demonstrated that leaves with

drip-tips drain water at a faster drainage rate than similar leaves without an elongated tip (reviewed in Lightbody 1985, see also Dean & Smith 1978, Burd 2007, Richards 1996). Lightbody (1985) extended this reasoning to argue that if drip-tips were an adaptation to the high humidity and rainfall of tropical forests, they should be more apparent in plants that live in microhabitats of relatively higher precipitation. She went on to test this in two different ways. First, she compared the size of drip-tips of an undetermined species of *Piper* across 18 sites along a simple five-point ordinal gradient of ‘wetness’. Secondly, she compared the ability of leaves to drain drops of water by experimentally manipulating the size of tips. The results of both studies provided strong support for the drainage hypothesis. Leaves from wet regions had significantly longer tips than those with a similar surface area from dry regions, and experimentally shortened tips shed water significantly more slowly than intact specimens (Lightbody 1985). This experiment, however, was criticized by Williamson (1986) who argued that Lightbody did not account for differences in the size of water drops (which increase in

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proportion to the width of the leaf tip—Williamson 1981). As a possible alternative, Williamson (1986) suggested that the rate of water removal might be constant for a given leaf and position. Lightbody's (1986) response was that even if the study did not explicitly account for drop size, her general conclusions were still valid. Farji-Brener *et al.* (2002) have also found evidence that microclimate can influence the occurrence of drip-tips. In a study on rain forest trees in Costa Rica, they found that drip-tips were less represented in canopy species where environmental conditions favor the natural drying of leaves such as high solar radiation, strong winds, and low relative humidity.

There are several possible ecological advantages to the rapid drainage facilitated by drip-tip leaves, but perhaps the most widely cited is that rapid water removal reduces the rate of colonization and abundance of epiphyllic organisms such as mosses, lichens, and fungi (Richards 1996). Ivey and DeSilva (2001) experimentally tested this hypothesis by reducing the size of drip-tips on a range of species with similar leaf morphologies and comparing their effectiveness at reducing epiphyll colonization against two control groups (untrimmed and trimmed, but retaining drip-tip). Leaves with their drip-tips cut off had ~1.7 times higher percent occurrence of fungi and retained ~2.3 times as much water as the two control groups (Ivey & DeSilva 2001). On the other hand, no evidence was found that drip-tips reduced the occurrence of epiphylls or that drip-tips help shed debris from the leaf surface. More recently, Burd (2007) found no evidence that experimental removal of the drip-tips of *Faramaea occidentalis* or *Psychotria marginata* influenced the extent of epiphyll cover (or tissue loss) after 11 mo *in situ*. Similarly, a comparison of artificial leaves with and without drip-tips revealed no differences in the presence of epiphyllous lichen communities, and the development of lichen communities at the apex of the leaves was actually greater in those with drip-tips (Lücking & Bernecker-Lücking 2005).

Another potential advantage to rapid drainage and drying is more directly related to the expected reduction in the span of time that the leaf lamina is covered in a film of water. The presence of a thin layer of water on a leaf may, over a period of time, significantly reduce the photon flux that reaches the chloroplasts (Richards 1996). Furthermore, Leigh (1975) suggested that a film of water on the leaf may reduce transpiration and thereby reduce nutrient uptake, and that retaining more water on the leaf surface may increase the required investment in physical support tissue. Edmisten (1970) has also suggested that a layer of water could result in the loss of inorganic nutrients (leaching) from the leaf tissue via diffusion, although this loss may be limited, given the relatively impermeable nature of most leaves.

There is at least one alternative hypothesis for the adaptive function of drip-tips that is not based on their ability to drain water rapidly. Williamson (1981) suggested that the advantage of long acuminate tips might be related to their function during rainfall rather than to their capacity to facilitate drying afterwards. He reasoned that as the size of droplets falling from drip-tips is smaller than from less elongated tips, drip-tips might function to reduce splash erosion of soil around the base of the tree. Such

avoidance of local erosion could be particularly important in low nutrient soils where rainfall is intense and prolonged (Williamson 1981). This hypothesis is consistent with the observation that drip-tip width increases with decreasing height of leaf from the ground (Williamson *et al.* 1983) as splash erosion will be less intense where shed water droplets do not reach terminal velocity prior to impact. Rebelo and Williamson (1996) also demonstrated that drip-tips are more prevalent in tree communities from erosion-prone clay soils as compared with more erosion-resistant sandy soils from the central Amazon. In most cases, however, shed droplets fall onto the leaf litter layer rather than directly onto bare soil, and hence it is unclear whether soil erosion under forest canopies is significantly affected by direct droplet impact.

We set out to describe and analyze the distribution and abundance of the drip-tip phenotype in Amazonian tree species in relation to bioclimatic gradients and soil in the Amazon rain forest. Following Malhado *et al.* (2009a, b, 2010), we use a combination of detailed information on species composition from permanent botanical plots with data extracted from herbaria (in this case leaf tip characteristics). We use this information to investigate the spatial (macrogeographic) associations between contemporary climatic variables, soil types, and occurrence of drip-tips. Based on previous studies (discussed above), our specific hypotheses are that the frequency of drip-tips will be found to be (1) correlated with a range of bioclimatic variables that may influence the ecological importance of leaf drying/drainage; (2) negatively correlated with the nutrient status of soils; and (3) lower in canopy (taller) species than in (shorter) understory species. Previous approaches to understanding drip-tip form and function have mostly been local or experimental, and our hope was that taking a macroecological approach would yield new insights into the adaptive significance of this fascinating and widespread trait (*cf.* McLachlan & Ladle 2011).

METHODS

Our main research tool and principal source of data for exploring spatial variation in leaf tip morphology within the Amazonian rain forest (Amazon basin and Guiana Shield) is the RAINFOR forest plot database (Peacock *et al.* 2007—<http://www.rainfor.org>), to which we added 26 data plots from Guyanas and Suriname compiled by the ATDN network (ter Steege *et al.* 2003). Our final dataset was constructed using information from 130 permanent plots distributed across eight South American countries (*cf.* Malhado *et al.* (2009a, b, 2010)). It should be noted that the required diameter at breast height (dbh) data are unavailable for ATDN plots and, consequently, they were not included in some analyses. The complete database used in this study (date of extraction: August 2006) contained 95,761 individual trees from 3324 species. The plots used spanned local and regional environmental gradients that naturally occur in Amazonia, including mature forests that are seasonally flooded, water-logged, and non-flooded lowland *terra firme* forests on both clay-rich and white-sand substrates (80% *terra firme*). All sites consisted of an apparently mature forest with natural gap-phase dynamics and a

canopy dominated by non-pioneer species and, furthermore, none of the plots is believed to have experienced any recent anthropogenic disturbance. The individual plots range in size from 0.25 to 9 ha (mean \pm SD = 1.1 ha \pm 0.9; median = 1) and in total encompass 142.5 ha of forest. The number of stems per plot ranged from 265 to 1307 per ha (mean \pm SD = 672 \pm 164; median = 667).

Information on leaf tip characteristics was added for as many as possible of the 3324 species in the database, using images from floras and herbaria (details in Table S1). Records were only excluded if the tree species was undetermined (475 species) or if the phenotypic information could not be found (63 species). In total, data for 83,868 individual trees and 2786 species were collated for analysis. Dbh data were available for 55,472 trees from 100 plots and was used as a simple surrogate for tree height.

Categorization of leaf tip characteristics can be problematic given a continuous gradation of form within and between species (Gentry 1969). To maximize our ability to detect shifting geographical trends in morphology, leaf tips were classified into five ordinal categories: (1) retuse; (2) rounded; (3) acute; (4) small tip; and (5) drip-tip (Fig. 1). Retuse and rounded tips were combined for the analysis as neither shows any apical protuberances. To reduce variability caused by the subjective and qualitative nature of the tip categorization process, all images were assessed solely by the lead author (ACMM).

As drip-tip incidence may vary with leaf size, leaves were also placed into seven size categories using the geometric leaf-size classification of Raunkiaer (1934) as modified by Webb (1959). We used the methodology and data developed by Malhado *et al.* (2009b) for this analysis. Furthermore, to assess the hypothesis that drip-tips are less abundant in canopy species, we obtained published data on maximum height (Baker *et al.* 2009) for all the

studied species and, as an alternative approach, we also assessed dbh (a simple surrogate for tree height) for all individuals in our plots.

The spatial distribution of drip-tips was investigated at two different scales. First, simple comparisons of leaf tip metrics were made at a regional level. Recent studies (*e.g.*, Malhi *et al.* 2004, ter Steege *et al.* 2006; Malhado *et al.* (2009a, b, 2010)) have demonstrated consistent ecological differences in tree characteristics among different regions of the Amazon. Here, to aid direct comparisons, we split the Amazon forest biome into four main regions: Region 1, North Amazonia, containing plots from Guyana, Suriname and Venezuela; Region 2, North–West Amazonia, containing plots from Ecuador, Colombia, and North Peru; Region 3, Central-East Amazonia, all Brazilian plots (states of Amazonas and Pará only); Region 4, South–West Amazonia, containing plots from Bolivia and South Peru.

Secondly, a detailed investigation of the spatial patterns of variation in leaf tip morphology was made through the use of several simple metrics, which acted as dependent variables within the OLS (Ordinary Least Squares) regressions. The primary metrics used are: the proportion of individual trees in each plot that displayed drip-tips (hereafter called drip-tips_{ind}) and the proportion of species in each plot that displayed drip-tips (hereafter called drip-tips_{sp}). Potential predictor variables were chosen to reflect the main hypotheses for the functional significance of drip-tips. As the main hypotheses are related to leaf drying and the ability of leaves to shed water, we used a series of metrics of precipitation and temperature retrieved from the weather-station interpolated BIOCLIM (Bioclimate Prediction System, Hijmans *et al.* 2005) datasets which include annual mean temperature ($^{\circ}$ C); annual temperature range (maximum temperature of warmest month—minimum temperature of coldest month); mean temperature of wettest trimester ($^{\circ}$ C); annual precipitation (mm/yr); precipitation of wettest month; and precipitation of coldest trimester (mm). The BIOCLIM data were used to explore and identify the variables that are most likely to predict drip-tip frequency and, sequentially, a time-series (1998–2005) of cumulative monthly rainfall derived from the Tropical Rainfall Measuring Mission (TRMM 3B43-V6) at 0.25 $^{\circ}$ spatial resolution was used for an in-depth analysis of the rainfall patterns in Amazonia. The TRMM combines multiple data sources including satellite information on rainfall with ground precipitation gauge adjustment (Huffman & Bolvin 2007). The TRMM dataset has been shown to accurately represent the rainfall patterns over the Amazonian region (Aragão *et al.* 2007). For each month of the years 1998–2005, we calculated the average cumulative rainfall. The monthly surfaces (one for each month of the year) were then used to estimate for each pixel: (1) the cumulative annual precipitation (mm/yr), based on the sum of the monthly values; (2) the length of the dry season, as the number of months with rainfall <100 mm/m; (3) the wettest trimester (mm precipitation); and (4) the driest trimester (mm precipitation) (see Malhado *et al.* 2009b for figure).

Here, we make the *de facto* assumption that current climate provides a sufficient approximation of historical climate to pick up any sufficiently strong environment-trait associations. How-

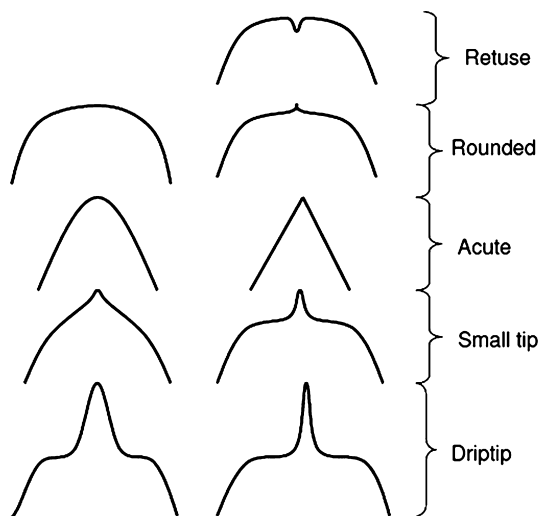


FIGURE 1. Diagram of drip-tip ordinal categories. Figure represents a qualitative generalization derived from several sources and was used as a guide in classifying species in this study.

ever, it should be recognized that the 7 yr climate time series of the TRMM data represents a small sample of current climate that may not necessarily represent the historical environment within which a given Amazonian tree species evolved, hence we should be cautious in inferring causal processes from such analyses (McLachlan & Ladle 2011).

It has been suggested that drip-tips may function to reduce splash erosion of soils during rainfall (Rebello & Williamson 1996) that may therefore be favored in erosion-prone low nutrient soils. Therefore, the distribution of drip-tips in relation to soil type for each plot was analyzed, first, using the simple ordinal classification system of Malhi *et al.* (2004) and, second, using data on soil fertility (sum of bases), where available (54 plots, Quesada *et al.* 2009). Soil sampling for the sites was carried out in accordance with a standard protocol (see <http://www.geog.leeds.ac.uk/projects/rainfor/projdocs.html>). Soil pits were situated at representative locations for the dominant soil and topographic positions, usually located a few meters outside the permanent sample plots to reduce potential disturbance. All soil samples were analyzed and exchangeable Ca, Mg, K, Na and Al determined by the silver thiourea method (Pleysier & Juo 1980). The sum of bases (SB) was calculated as: $[SB] = [Ca] + [Mg] + [K] + [Na]$.

STATISTICAL ANALYSIS.—Leaf tip characteristics vary considerably both within and between taxonomic groups. All families with more than five species in the database were characterized by two or more leaf tip categories. Moreover, from the 235 genera that had three or more species, 213 genera had two or more leaf tip categories. In face of such variation, it was deemed unnecessary to control for phylogeny. RAINFOR plots do show a degree of spatial clustering, however, and ecological and physical variables may therefore be more similar (or dissimilar) because of spatial proximity, and it is therefore appropriate to account for spatial autocorrelation (Legendre 1993; Malhado *et al.* (2009a, b)). The use of spatial filters based on Principal Coordinates of Neighbour Matrices (PCNM) is recommended when seeking to partition the effects of spatial and environmental components on the response variable (Borcard *et al.* 2004). In PCNM, statistically significant eigenvectors describing the relationship between samples (in the current study, permanent plots) can be entered into a partial regression model as predictor variables along with the environmental variables of interest (Diniz-Filho & Bini 2005).

In the current study, the first test was for the presence of spatial autocorrelation in the residuals through the use of Moran's *I* index (using Gabriel connectivity) and Moran's *I* correlograms. Second, because of the evidence of spatial autocorrelation, PCNM was used to generate spatial eigenvectors that were then tested for significance against the response variable (following Diniz-Filho & Bini 2005). Finally, statistically significant eigenvectors and climate metrics were entered as explanatory variables into OLS regression models. This approach treats the environmental predictors as partial effects, taking space explicitly into account (Rangel *et al.* 2006). The association of sum of bases and drip-tip abundance was tested using the Dutilleul (1993) method

for adjusting the degrees of freedom. All spatial analyses were performed using the software Spatial Analysis in Macroecology (SAM v2; Rangel *et al.* 2006).

In addition to the spatial clustering analyses, we repeated the TRMM analyses using sub-dataset (see Appendix S1) to identify if our results were robust in relation to the uncertainty associated with estimates of the proportion of individual trees (and the proportion of species) in plots of different sizes.

Differences in the mean height and mean dbh between species that possessed and did not possess drip-tips were investigated using independent sample *t*-tests. Differences in soil types (using the ordinal ranking system) were assessed using an ANOVA and Tukey *post-hoc*. Analyses, unless otherwise stated above, were performed using SPSS 14.0 (SPSS Inc., Chicago, IL, USA).

RESULTS

DISTRIBUTION AND ABUNDANCE.—The frequency of species with drip-tips per plot varied from 13 percent up to 52 percent (Fig. 2): the six highest species-level drip-tip abundances (> 40% of tree species possessing drip-tips) were in Brazil (five plots) and Guyana (one plot) (Fig. 2). The frequency of individual trees with drip-tips varied in a broader range from 1 to 62 percent.

The average frequency of species with drip-tips (drip-tips_{sp}) across the 130 plots was 31.9 ± 0.4 percent (mean \pm SE) and the frequency of trees with drip-tips (drip-tips_{ind}) was 33.0 ± 1.0 percent. There was no significant difference between the proportion of drip-tips_{sp} and drip-tips_{ind} within plots ($t = -1.24$, $df = 129$, $P = 0.22$). Trees with drip-tips made up an average of 28.8 ± 1.0 percent of total basal area (BA-tips) for all trees in all plots with available data combined ($N = 100$). Plot level analyses of contributions of drip-tips_{ind} and BA-tips showed that drip-tip trees are on average slightly smaller (using BA as the size metric) than non-drip-tip trees ($t = 5.54$, $df = 99$, $P = 0.001$).

There was substantial variation in relative frequency of the four tip size categories: trees with retuse/rounded leaves and acute tips being far less numerous than trees with small tips or drip-tips (Fig. 3). Indeed, drip-tips accounted for 33.1 percent (trees) and 31.9 percent (species) in the dataset and more than 70 percent of all trees and species in the sample were classified as possessing small tips or drip-tips (Fig. 3). Drip-tips occurred predominantly in leaves in the microphyll, notophyll, and mesophyll categories (Fig. 4). They were absent in tree species in the sample that possess very small leaves and were relatively less abundant in tree species with the largest leaves (macrophyll) (Fig. 4). There were only two species in the Megaphyll category, both with rounded tips.

There was a significant difference between the frequencies of drip-tips_{sp} by regions ($F = 9.198$, $df = 3$, $P < 0.001$). Tukey *post-hoc* analysis revealed that the Central-East region had a significantly higher incidence of drip-tips_{sp} per plot than all other regions (Fig. 5), a pattern repeated in the data for drip-tips_{ind} ($F = 22.738$, $df = 3$, $P < 0.001$).

The species in the dataset with drip-tips had significantly lower mean maximum published heights than species without

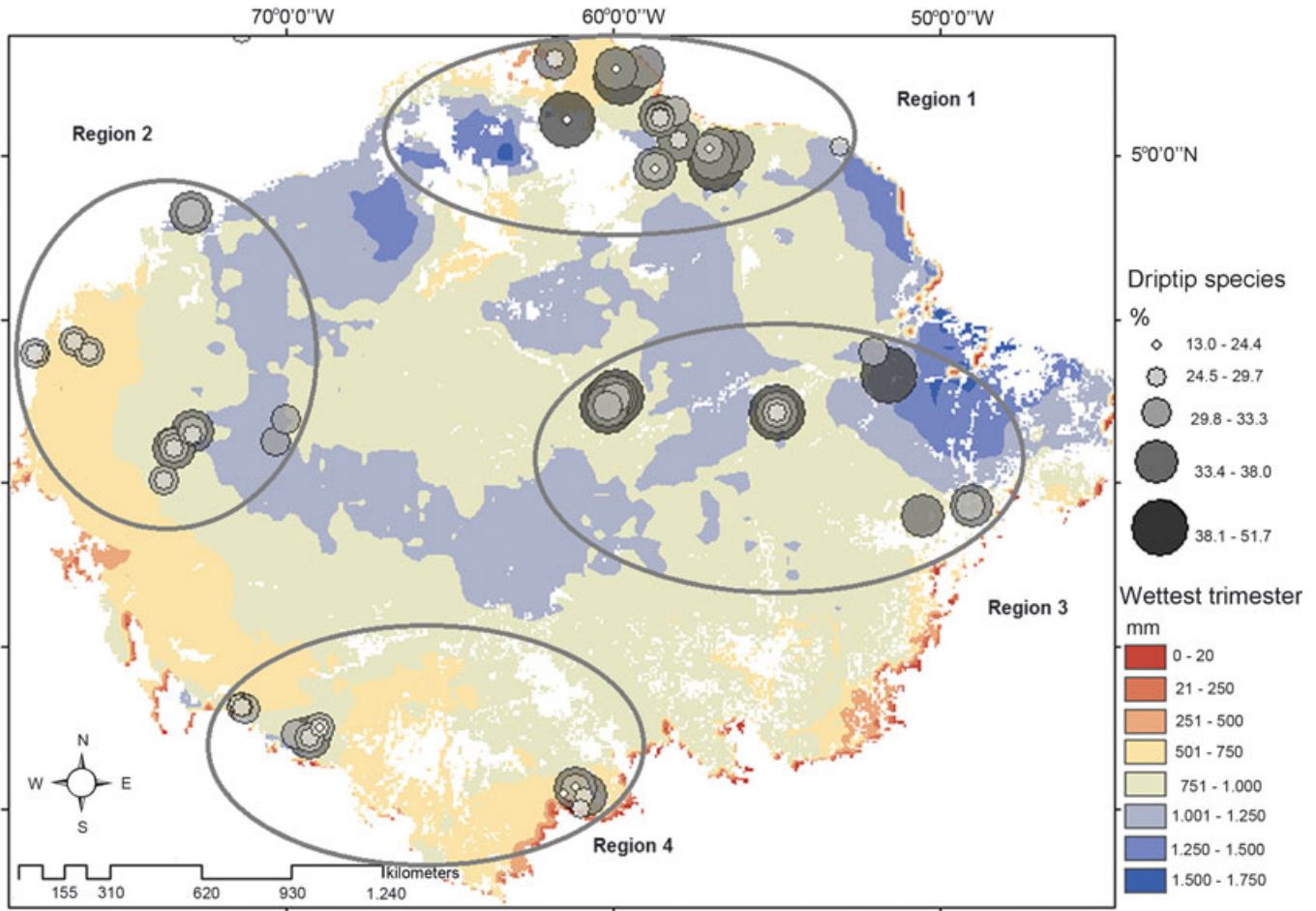


FIGURE 2. Map of the incidence of drip-tip_{sp} in each plot ($N = 130$) organized by frequency categories and regions (Region 1 = North; Region 2 = North-West; Region 3 = Central-East; Region 4 = South-West). For the purposes of clear visualization, the positions of some plots within clusters have been adjusted, and thus may not correspond to exact geographic location.

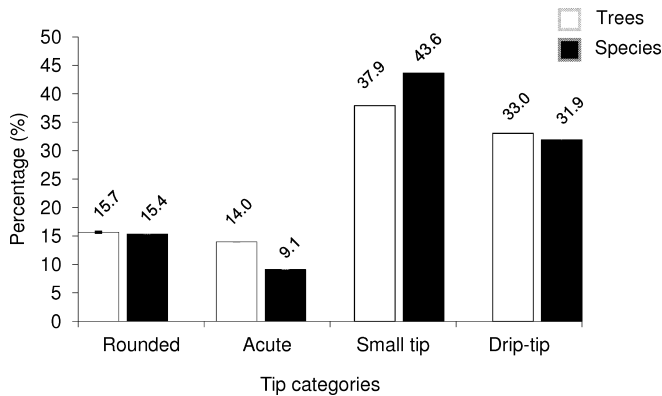


FIGURE 3. Percentage of individual trees (all species combined, $N = 83,868$) and species ($N = 2,786$) in different tip size categories (rounded, acute, small tip, drip-tip).

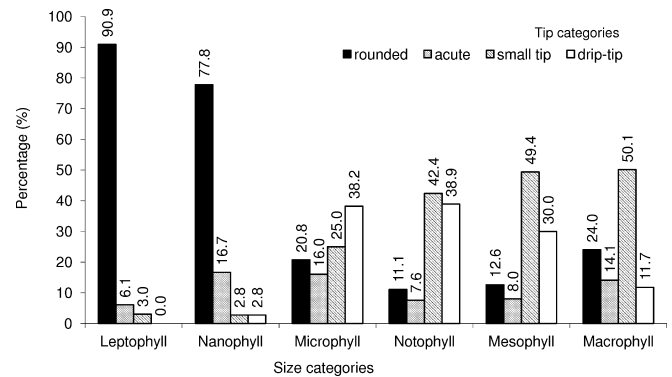


FIGURE 4. Percentage of tree species ($N = 2,709$) with different leaf tip categories grouped by leaf size category (leptophyll = leaves up to 0.25 cm^2 in area; nanophyll = $0.25\text{--}2.25 \text{ cm}^2$; microphyll = $2.25\text{--}20.25 \text{ cm}^2$; notophyll = $20.25\text{--}45.0 \text{ cm}^2$; mesophyll = $45.0\text{--}182.25 \text{ cm}^2$; macrophyll = $182.25\text{--}1640.25 \text{ cm}^2$).

drip-tips ($t = 4.488$, $df = 2119$, $P < 0.001$; Fig. 6) and a significant difference in mean maximum published height was also found across the four tip morphology categories ($F = 21.036$,

$df = 3$, $P < 0.001$). Tukey *post-hoc* tests revealed that the differences are driven by species with rounded leaves having taller maximum published heights than trees with leaves that have

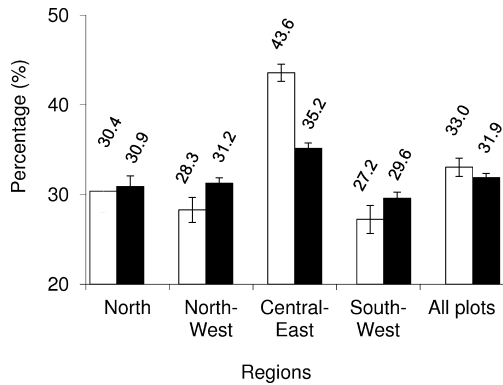


FIGURE 5. Average percentage of species (black, $N = 2786$) and individual trees (white, $N = 83,868$) with drip-tips in the four Amazonian regions (130 plots). Error bars represent one standard error of the mean.

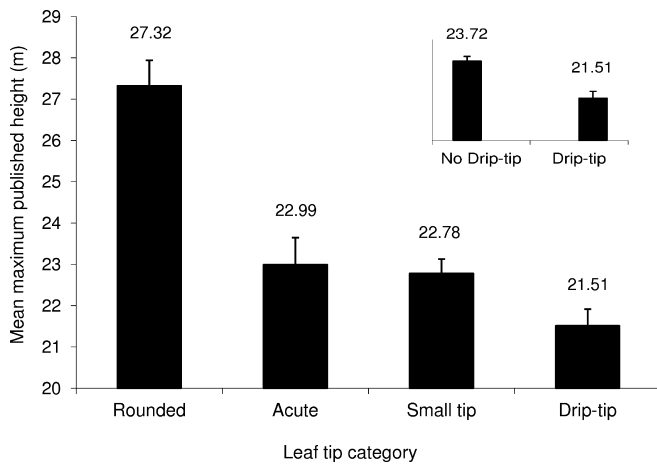


FIGURE 6. Mean maximum published height for species ($N = 2121$) identified as possessing different leaf tip categories. Error bars represent one standard error of the mean.

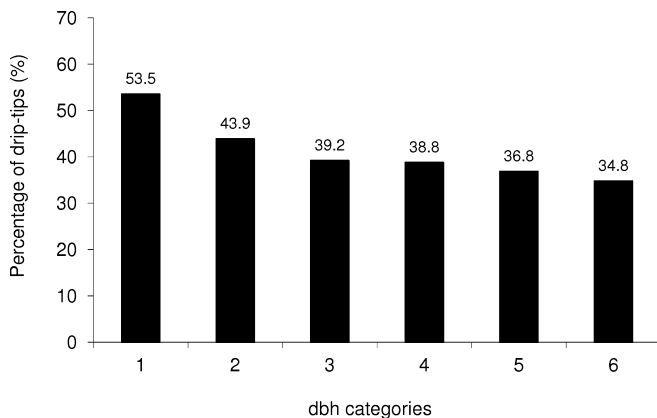


FIGURE 7. Percentage of individual trees with drip-tips in relation to those without drip-tips ($N = 54,912$) across 6 dbh (diameter at breast height) size categories (1 = 100–200 mm, 2 = 200–300 mm, 3 = 300–400 mm, 4 = 400–500 mm, 5 = 500–600 mm, 6 = >600 mm).

more acute tips (Fig. 6). Trees with drip-tips also had a significantly smaller mean dbh than those without ($t = 13.801$, $df = 40,398$, $P < 0.001$; Fig. 7) and a significant difference in mean dbh was also found across the four tip morphology categories ($F = 21.036$, $df = 3$, $P < 0.001$). Tukey *post-hoc* tests revealed that all tip categories are significantly different in mean dbh from each other.

ENVIRONMENTAL CORRELATIONS.—Spatial autocorrelation is present in our dataset as measured by Moran’s I index (Moran’s $I = 0.171$, $SE = 0.076$; Expected = -0.008 , $P = 0.019$ for frequency of species with drip-tips; and Moran’s $I = 0.365$, $SE = 0.077$; Expected = -0.008 , $P < 0.001$ for frequency of individuals with drip-tips) and therefore we used spatial eigenvectors in all the environmental correlation analyses. The initial exploratory analyses, using the BIOCLIM data, indicated that the frequency of drip-tips_{sp} was significantly correlated with precipitation of the coldest trimester and that drip-tips_{ind} was associated with the precipitation of the wettest month (Table 1). The in-depth analyses of rainfall using TRMM data indicated that frequency of drip-tips_{sp} across plots was significantly positively correlated with the precipitation of the wettest trimester (Table 1) and proportion of drip-tips_{ind} was associated with the precipitation of the wettest trimester and cumulative annual precipitation. Our subset analyses (grouping plots to control for possible plot-size effects) produced very similar results to those reported above—a correlation with precipitation of the wettest trimester (Table S2).

No significant relationship was found between drip-tips_{sp}/drip-tips_{ind} and soil type as characterized with the simple ordinal classification system ($df = 4$, $F = 0.440$, $P = 0.780$). A significant association, however, was found between drip-tips_{sp} and soil fertility, with lower nutrient soils possessing a higher frequency of the trait ($r = -0.403$, $N = 52$, corrected $df = 23.1$, corrected $P = 0.045$). It should also be noted that when soil fertility was assessed while statistically accounting for the effects of rainfall, this relationship disappeared—although because of the underlying structure of the data it is difficult to do this test while effectively controlling for any impacts of spatial autocorrelation.

DISCUSSION

DISTRIBUTION AND ABUNDANCE OF DRIP-TIPS.—Drip-tips are a common feature of wet rain forests (reviewed in Givnish 1987) and the results of this study are broadly in line with other published work in this area. It was found that 32 percent of species and 33 percent of individual trees possessed drip-tips across the study plots. Burnham and Johnson (2004) define archetypal tropical rain forest (ATR) as having > 25 percent of drip-tips.

Richards (1996) noted that drip-tips vary with the size of the tree being studied. In the present study, it was found that trees with drip-tips were generally smaller than those with other types of leaf-tip. This was true for both individual trees (those with drip-tips having lower average measured dbh than those without) and for species (those with drip-tips having significantly

TABLE 1. Partial regression coefficients of the OLS regression, *t* statistics, and associated P-values of species with drip-tips and individual trees with drip-tips, indicating the contribution of climatic variables and taking into account spatial autocorrelation in explaining the proportion of drip-tips in permanent plots. Spatial structure was accounted for in the regressions by adding eigenvectors filters produced with PCNM (these eigenvectors filters are omitted from the table). All dependent variables were transformed. (A) Data derived from Bioclimate Prediction System. (B) Data derived from the Tropical Rainforest Measurement Mission.

	Species with drip-tips			Individuals with drip-tips		
	Coefficient	<i>t</i>	<i>P</i>	Coefficient	<i>t</i>	<i>P</i>
(A) BIOCLIM						
Annual mean temperature	−0.516	−0.845	0.4	0.853	1.473	0.144
Annual temperature range	−0.268	−1.586	0.116	0.006	0.03	0.976
Mean temperature of the wettest trimester	0.456	0.922	0.359	−0.584	−1.241	0.218
Annual precipitation (PPT)	−0.056	−0.452	0.652	−0.151	0.882	0.38
PPT wettest month	−0.126	−1.038	0.302	0.259	2.125	0.036*
PPT of the coldest trimester	0.505	2.491	0.014*	−0.27	−1.053	0.295
(B) TRMM						
Cumulative annual PPT	−0.522	−1.23	0.221	−1.025	−2.619	0.01*
Dry season length	−0.327	−1.028	0.306	−0.393	−1.418	0.159
PPT wettest trimester	0.528	2.196	0.03*	0.79	3.404	<0.001*
PPT driest trimester	−0.012	−0.058	0.953	0.055	0.267	0.79

*Significant environmental variables.

lower maximum published heights than those without). This supports the anecdotal observations of Leigh (1975) and the more recent studies of Rollet (1990) and Zhu (1997). Leigh (1975) had noticed that drip-tips were more prevalent among the saplings of understory trees in the neotropics than among fallen leaves on the forest floor, an observation recently confirmed by Panditharathna *et al.* (2008) in trees from a Sri Lanka rain forest. This suggestion also gains some support from a study by Zhu (1997) who observed that leaves with drip-tips in 17 rain forest plots from South Yunnan, China, varied with tree age (a potential surrogate for size). Elongated tips were more common in saplings and seedlings of mega and mesophanaerophytes, while leaf apex becomes acuminate and obtuse in mature trees (Zhu 1997). In the current study, we only used data from trees with dbh >10 cm so it is unlikely that we underestimated the total proportion of individual trees with drip-tips due to the trait being assigned on the basis of the mature specimens that exist in herbaria and floras. However, it should be noted that our estimate is only for the proportion of drip-tips on larger trees—seedlings and saplings often possess drip-tips that are lost as the tree gets larger (Richards 1996).

The present finding of lower maximum published heights for tree species with drip-tips supports the observations of Farji-Brener *et al.* (2002) in Costa Rican rain forest where drip-tips were less frequent in canopy species. These data also lend support to their contention that high solar radiation, strong winds and low relative humidity favor the natural drying of leaves, rendering the possession of a drip-tip largely ‘unnecessary’ (Farji-Brener *et al.* 2002) and perhaps even disadvantageous in these circumstances.

ADAPTIVE SIGNIFICANCE.—The frequency of drip-tips (species and individuals) across plots was significantly correlated with precipitation metrics. This supports a supposition of Grubb (1977) that drip-tips are effective under conditions of alternating heavy storms and sunny spells, but ineffective and occurring in low abundance in montane rain forests where the moisture is supplied by persistent fog and drizzle. It should be noted, however, that montane plots were excluded from the current study. Interestingly, several authors (Rundel & Gibson 1996, Schneider *et al.* 2003) have suggested that drip-tips are an advantage under humid conditions *per se* based on the near absence of this trait in tree-line or early successional forests. However, it was found that the drip-tips_{sp} within a plot were most strongly associated with wet season precipitation rates, implying that it is intensity of precipitation rather than atmospheric humidity or the duration of the wet season that may account for the distribution of this trait in the Amazon. This finding lends credence to Williamson’s (1981) hypothesis that the adaptive function of drip-tips is to reduce splash erosion during heavy rainfall, although it is still not clear how the presence of leaf litter would moderate the relative costs and benefits of smaller water droplets.

Interestingly, although no clear evidence was found of any associations between tip structure and soil type (*sensu* Malhi *et al.* 2004), there was a significant negative relationship between the drip-tips_{sp} and the nutrient level of soil within a plot (for the subset of plots where such data were available). As Chapin (1980) notes, any factor that reduces water contact with the surface of the leaf lamina (*e.g.*, drip-tips, well-developed smooth cuticle, certain types of pubescence, erect leaf angle, etc.) reduces leaching loss. Leaching of this nature would be expected to be especially

important in low nutrient soils where the ability of trees to retain their nutrients would be at a premium. No support was found, however, for Rebelo and Williamson's (1996) observation that drip-tips are more prevalent in tree communities from erosion-prone clay soils (possibly because of the poor resolution of the rather crude soil data used herein). Furthermore, the significant relationship between soil fertility and drip-tips might be affected by the spatial clustering of low-fertility sites in Central-East Amazon—where we also found a higher frequency of drip-tips. Furthermore, when we statistically account for rainfall patterns, we found no support for this soil nutrient hypothesis although, in this case, complications in the structure of the data such as the low number of plots with soil data available (54) make it difficult to draw any definitive conclusions.

CONCLUSIONS

The (previously unreported) strong correlation between abundance of drip-tips and maximum seasonal precipitation in Amazonia clearly supports the hypothesis drip-tips are an adaptation for removing water quickly and efficiently from the leaf surface. Moreover, the data imply that drip-tips may also function to reduce the effects of splash erosion. The latter interpretation, however, should be cautiously accepted, as we found no strong evidence of an association between drip-tips and erosion-prone soils. If the avoidance of splash erosion is only advantageous in a limited number of ecological circumstances (very erosion-prone soils, low levels of leaf litter, etc.), then our study implies that drip-tips might confer previously unrecognized advantages during heavy precipitation, such as reducing 'splash-damage' to leaves lower on the tree—a possibility that could be investigated experimentally.

More generally, while the frequency of drip-tips in Amazonia is clearly environmentally determined to a certain extent within the dataset, none of the associations are particularly strong, reflecting a high degree of variability in this trait. This finding suggests that the selective advantages of an Amazonian tree either possessing (or not possessing) drip-tips are not very high, at least within the environmental boundaries of Amazonia.

From a methodological context, this study demonstrates that traits-based macrogeographic/macroecological approaches can play an important role in the identification and assessment of adaptations (McLachlan & Ladle 2011). Specifically, macrogeographic studies have at least three advantages over smaller-scale manipulative experiments: they can uncover previously unrecognized environment-trait correlations revealing ecogeographic patterns that would be weak or invisible at finer spatial scales, they have the potential to discriminate between strong and weak selective pressures, and they may suggest new avenues for research. With respect to the results of the current study, we would encourage experimental approaches aimed specifically at analyzing the function of drip-tips during heavy precipitation focusing on ecological consequences over a range of time scales.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

APPENDIX S1. Additional analyses to assess the potential influence of variation in plot size on the relationship between the proportion of individual trees in each plot with drip-tips and the TRMM variables.

TABLE S1. *List of floras and herbaria used as information sources and number of species retrieved from each source.*

TABLE S2. *Partial regression coefficients of the OLS regression, *t* statistics, and associated *P*-values of species with drip-tips and individual trees with drip-tips.*

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