

A Test of the Function of Drip Tips¹

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DRIP TIPS, OR THE ACUMINATE APICES OF LEAVES, are a common feature of understory plants in the humid tropics (Richards 1996). Perhaps the most persistent hypothesis for their function is that they facilitate the rapid channeling of water from leaves, which decreases the drying time for the leaf surface (Stahl 1893, Lightbody 1985). Retention of water on leaves may be favorable for the colonization or growth of epiphylls (*e.g.*, lichens and bryophytes) and fungi (Richards 1996). These organisms may reduce the photosynthetic potential of leaves through shading or necrosis (Coley & Kursar 1996). Water more rapidly flushed from leaves may also help to dislodge debris, such as dead plant material or soil, the presence of which could shade leaves and provide favorable sites for colonization by epiphylls or fungi.

These ideas have been tested a few times (Dean & Smith 1978, Williamson 1981, Lightbody 1985, Monge-Najera & Blanco 1995), but rarely with real (non-artificial) leaves under natural conditions. We experimentally studied the role of drip tips on leaves of saplings in the tropical forest understory. Specifically, we tested the hypotheses that drip tips reduce the occurrence of fungi, epiphylls, and debris on leaf surfaces. We also tested the hypothesis that drip tips reduce the volume of water retained on leaves.

We examined the function of drip tips between 23 November and 2 December 1998, during the rainy season in tropical wet forest at the La Selva Biological Field Station in the Caribbean lowlands of Costa Rica. La Selva receives an average of 3962 mm of rain annually (Sanford *et al.* 1994); rainfall during the study was over twice the average (T. Brenes, pers. comm.). We used multiple species of saplings, including *Faramea parviflora* (Rubiaceae), *Cassipourea elliptica* (Rhizophoraceae), *Eugenia casipourea* (Myrtaceae), *Ocotea meziana* (Lauraceae), *Rourea* sp. (Connaraceae), *Protium* sp. (Burseraceae), *Zygia gigantifolia* (Fabaceae), and *Stemmadenia robinsonia* (Apocynaceae). To help isolate the effects of drip tips from other variations in leaf morphology, we chose species that had glabrous, similarly sized leaves with entire margins and similar drip tip length. All individuals included in the study occurred in the same habitat: older secondary, closed-canopy forest. Epiphylls were present on the older leaves of all study plants.

On 23 November, we selected 28 saplings that were 1.0–1.5 m tall and chose three of the youngest, fully expanded leaves within each that had no visible signs of fungi, epiphylls, or debris and were relatively horizontal to the surface of the ground. To reduce unseen propagules and debris on leaves, each leaf was wiped on its upper surface with a soft cloth. Each leaf was then assigned one of three treatments: (1) unmanipulated; (2) apices of leaves trimmed to leave the drip tip shape intact, as a control for effects of cutting (“modified drip tips”); or (3) drip tips removed, leaving smooth, rounded leaf apices (“cutoff drip tips”). Each plant received all three treatments, for a total of 84 leaves in the experiment. On 1 and 2 December, using a headlamp to improve visibility, we measured fungi (including only what were probably fungal fruiting bodies; see below), epiphylls (lichens and bryophytes), and debris (particles of humus and leaf litter) occurring on leaf surfaces. To estimate occurrence, we placed a transparent plastic sheet with a 5- × 5-mm grid on each leaf and counted the number of squares containing epiphylls, fungi, or debris. Total leaf area was recorded as the total number of squares that were at least half filled with leaf surface. Percent occurrence of each category was calculated by multiplying the proportion of squares containing fungi, epiphylls, or debris by 100.

We also compared the amount of water retained on leaves among treatments, using three leaves (one from each treatment) from each of seven plants ($N = 21$ leaves). Leaves were removed from their branches, and petioles were embedded in plasticine so that the leaf surfaces were horizontal. We dripped 5 ml of water on dry leaf surfaces for 20 to 30 sec using a pipette, and collected all the water that dripped off the leaf in a 10-ml graduated cylinder. We waited at least 20 sec for the last drop to fall from each leaf. Volume of water remaining on the leaf was calculated as 5 ml minus the volume of water recovered in the graduated cylinder.

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TABLE 1. Back-transformed means (SE) for percent occurrence of fungi, epiphylls, and debris; mean (SE) ml of water retained on the leaf surface for three experimental treatments testing the function of drip tips; and results of ANOVAs comparing treatments. Means followed by the same letters are not significantly different at $\alpha = 0.05$ by a Tukey's studentized range test. See text for description of treatments.

	Unmanipulated	Modified drip tip	Cutoff drip tip	<i>F</i>	df	<i>P</i>
fungi	13.2 (2.7) b	11.5 (2.4) b	20.8 (2.9) a	7.93	2, 54	0.001
epiphylls	3.8 (1.1) a	5.3 (1.9) a	7.3 (1.8) a	1.26	2, 54	0.3
debris	3.4 (1.3) a	2.4 (0.8) a	3.4 (1.1) a	0.24	2, 54	0.8
water	0.21 (0.08) b	0.14 (0.05) b	0.41 (0.03) a	7.24	2, 12	0.009

To compare treatments with respect to occurrence of the three categories (fungi, epiphylls, and debris), we used mixed-model ANOVA, including individual plant as a random effect. To correct for heteroscedasticity, proportions of leaf area containing fungi, epiphylls, and debris were arcsine-square root transformed prior to analyses (Snedecor & Cochran 1989). We did not include sapling species as a factor in the models; this may have obscured differences among treatments by increasing unexplained variance in the models. We also used mixed-model ANOVA to compare volume (ml) of water collected among treatments, including individual plant as a random effect. Residuals for the untransformed values of water (ml) retained on leaves were normally distributed (Wilk-Shapiro test, $W > 0.95$) and conformed to the equal variance assumption for ANOVA (Snedecor & Cochran 1989); thus we used untransformed data for this analysis. We found no significant relationship between leaf area and water collected from leaves ($r_s = 0.23$, $P = 0.31$), and there were no differences in leaf area among treatments (two-way ANOVA: $F_{2,12} = 1.99$, $P = 0.2$); thus we did not include leaf area as a variable in this analysis. Percent occurrence and water retained on leaf were compared among the three treatments using Tukey's studentized range tests (HSD). All statistical analyses were performed using SAS (SAS 1996).

Occurrence of fungi on experimental leaves was higher overall than for epiphylls or debris (Table 1). We did not identify the fungi, but the most common type had the appearance of small black spots. These may have been the fruiting bodies of a more extensive hyphal growth (Gilbert *et al.* 1997). The most common epiphylls were white, gray-white, or greenish white foliose lichens; liverworts or other bryophytes were also occasionally present. Debris primarily consisted of senesced leaflets of *Pentaclethra macroloba*, the dominant canopy tree, and humus particles.

Leaves with cutoff drip tips had *ca* 1.7 times higher percent occurrence of fungi (Table 1). Percent occurrence of epiphylls and debris did not differ among treatments (Table 1). Individual plants differed significantly in percent occurrence of fungi ($F_{27,54} = 3.84$, $P = 0.0001$) and debris ($F_{27,54} = 3.19$, $P = 0.0001$), but not epiphylls ($F_{27,54} = 1.49$, $P = 0.1$). Leaves with cutoff drip tips retained *ca* 2.3 times more water on their surface than those in the other two treatments (Table 1). Differences among individual plants did not explain variation in water retention ($F_{6,12} = 1.37$, $P = 0.3$).

These results support the hypothesis that drip tips play a role in reducing fungi on leaves of understory trees and in facilitating efficient drainage of water from leaf surfaces. Most of the fungi we observed occurred near the midvein, base, and tips of the leaves, which were also the regions of the leaf that retained the most water following the water retention experiment. Although some have suggested that epiphylls may increase the chance of fungal colonization on leaves (Coley & Kursar 1996), we found no significant relationship between percent occurrence of epiphylls and percent occurrence of fungi ($r_s = 0.09$, $P = 0.4$).

Over the duration of this experiment, we found no evidence that drip tips reduced occurrence of epiphylls or that drip tips helped to shed debris from leaf surfaces. Elsewhere, support for this relationship has been equivocal, both observationally (Shreve 1914, Bien 1982) and experimentally (Monge-Najera & Blanco 1995, Coley & Kursar 1996). Interestingly, we observed that epiphylls occurred most frequently on the drier regions of the leaves (away from the midveins, bases, and tips of the leaves), which may indicate that humidity is less of a limiting factor for the establishment of epiphylls than for fungi. Although debris on leaf surfaces could carry epiphyll or fungal propagules or provide a favorable microclimate in which such propagules could become lodged and establish, we did not find evidence that drip tips facilitate washing debris from leaf surfaces.

A high percent coverage by epiphylls can shade leaves, thus reducing plant photosynthetic potential

(Coley *et al.* 1993, Coley & Kursar 1996). Many epiphylls, however, grow fairly slow, and therefore may not significantly compromise photosynthetic capacity until leaves approach senescence. In contrast, leaf-colonizing fungi may have a more immediate impact, since they are more likely to establish on young leaves (P. D. Coley, pers. comm.), and in our study, appeared to grow about three times faster than epiphylls. Moreover, some leaf-colonizing fungi can induce leaf senescence, at least in some crop plants (Jachmann & Fehrmann 1989). If pathogenic fungi behave similarly to the fungi we observed, drip tips in understory rain forest plants may represent the result of selection to reduce fungi rather than epiphylls. Ellenberg (1985) argued that the presence of drip tips was environmentally or ontogenetically determined and that drip tips therefore should have no adaptive significance. Indeed, some of the species we studied have drip tips only as saplings in the humid understory (Gentry 1993); when they reach the more exposed canopy at maturity, their leaves do not form drip tips. Nonetheless, if trees possessing drip tips while in the understory “sapling bank” (Richards 1996) are able to reduce fungi on their leaves, they may increase their chance of surviving to adulthood (Gilbert 1995).

Past studies have found, as we did, that drip tips increase the rate of water shedding or leaf drying (Stahl 1893, Dean & Smith 1978, Lightbody 1985). These findings suggest that this may be a mechanism by which drip tips reduce fungal growth or colonization. Others, however, have suggested that increased rates of water shedding and leaf drying may increase transpiration rates (Stahl 1893, Leigh 1975), reduce nutrient leaching from the leaf (Edmisten 1970), and decrease reflectance of sunlight (Lightbody 1985). Drip tips also reduce the size of droplets falling from leaves, which may help minimize soil disturbance beneath a plant (Williamson 1981, Williamson *et al.* 1983, Rebelo & Williamson 1996) or reduce the spread of fungal pathogens among leaves within plants (J. O'Brien, pers. comm.).

To our knowledge, this study was the first to distinguish the role of drip tips in reducing leaf fungi from any role in reducing epiphylls. Similar experiments measuring the effects of drip tips on accretion of fungi and epiphylls over the full life of leaves will help to further clarify the role of this defining element of the wet tropics.

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