
The Direct Effects of Rainfall on Hygrophilous Vegetation

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PLATE XIII

Phot. 18. The vegetation of a rock showing in a rough way the dry exposed parts covered with crustaceous lichens, the more sheltered and ledged portions with foliaceous lichens and mosses, and finally the deep valley down the middle where we find that the lichens are being replaced by mosses and even flowering plants.

NOTE. The above reproductions are from photographs taken with Zeiss Microplanars. The specimens used for Photos 1—5, 7, 8 and 10 are in the Father Reader Herbarium, now in the possession of the Botany Department of the University of Bristol. All the other specimens are from my own collection.

THE UNIVERSITY, BRISTOL.

THE DIRECT EFFECTS OF RAINFALL ON HYGROPHILOUS VEGETATION

By FORREST SHREVE

(*With Plate XIV*)

INTRODUCTION

The botanists and zoologists who visited the tropics in the decades immediately following the general acceptance of the principle of natural selection were impressed with the presumed adaptational value of many structures and many features of habit or behaviour that are common in tropical nature or striking in the eyes of those to whom they are new. During the later period in which physiological work was carried into the tropics a number of attempts were made to determine the present functional importance of some of these adaptational features, with the result that many of them were found to have no value of the sort that casual observation and a vivid imagination had indicated. The importance of the structures in *Cecropia* which Schimper alleged to serve indirectly to protect the plant from the ravages of leaf-cutting ants has been disavowed by the latest workers, many supposed cases of remarkable protective mimicry in insects have been found to be fallacious, and other cases of the kind might be mentioned. Indeed, the general attitude of mind with regard to the functional value of very many of the striking features of tropical plant and animal life is extremely sceptical at the present time. Without wishing to minimise unduly the value of work on the "biological factors" which influence the activities of tropical animals and plants, I feel that a much surer road to the understanding of the fundamental features of tropical plant activity and the operation of evolutionary processes in the tropics lies in a study of the normal physiology of tropical plants and in a study of the influence on them of the physical factors by which they are most profoundly affected and through which the "biological factors" exert their work. In the observation and experimentation reported in this paper I have endeavoured

to determine the physiological value of some striking rain-forest "adaptations," with results which I think will do nothing to lessen the scepticism alluded to above.

In a paper which is now in the press I have described the climatic conditions and vegetation of the rain-forest which clothes the upper slopes of the Blue Mountains of Jamaica. This body of forest lies between 1375 m. and 2260 m. elevation, and receives a well-distributed rainfall which increases from 266.7 cm. at the lower altitudes to 426.7 cm. at the highest summits. In addition to the liberal rainfall the prevalence of a fog blanket over the northern slopes, which face the trade wind, contributes to the making of an extremely hygrophilous environment.

Anyone who visits at frequent intervals so pronounced a rain-forest as this will not fail to be impressed with the almost continual wetness of the foliage of the herbaceous and shrubby vegetation of the forest interior. This is a condition which is capable of influencing the activities of the plants concerned in several ways, and it has led me to examine into the validity of what has been reported from other rain-forest regions regarding the occurrence of dripping points, velvet surfaces, epiphyllae¹ and hydathodes. Our knowledge of these features of tropical hygrophilous vegetation is due chiefly to Stahl and Haberlandt who worked at Buitenzorg (rainfall 499 cm.), Jungner who worked in the mountains of the Kamerun (rainfall 388 cm.), and Holtermann who worked in the mountains of Ceylon (rainfall from 240 to 384 cm.). The amounts of rainfall in these localities are of the same order as that in the Jamaican mountains, but the fall is somewhat more violent in all of them than it commonly is in Jamaica. While the region in which I have worked may be slightly different from those studied in the eastern hemisphere, not only in respect to the violence of the fall, but its daily and seasonal distribution, I am nevertheless sure that the conditions of wetness and sustained high humidity in the Jamaican forests can not be greatly exceeded elsewhere. The conditions, in other words, are just such as would give the action of hydathodes and dripping points their supposed service in the physiological economy of rain-forest plants.

My examination of the Jamaican forests has revealed a very weak representation of such features as the hydathode, the dripping point, the velvet surface, the variegated leaf, drooping juvenile foliage, etc. The experiments which I have undertaken have been for the object of determining the physiological value of the dripping point, and some of the actual effects of wetness on foliage.

Wettability

I can confirm Wiesner and Miyoshi with regard to the wettability of the rain-forest foliage, as mature leaves of all the plants with one exception are of this character. In several trees (*Alchornea latifolia* Sw., *Guarea swartzii* DC. and *Sciadophyllum brounei* Spreng.) the young leaves are non-wettable, and their under sides retain that condition after reaching maturity. The one unwettable plant is the papaveraceous *Bocconia frutescens* L., a shrub with large pinnatifid

¹ Under the term "epiphyllae" are comprised various epiphyllous plants—epiphytes growing on the surfaces of leaves; they are chiefly algae, lichens and liverworts.

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leaves, which grows continuously throughout the year, and sometimes attains to a height of 3 m. *Bocconia* is never found in the deep forest, but grows only in open situations on the leeward slopes of the Blue Mountains. Its leaves have a glaucous scurfy appearance, and shed water readily until they are old, discoloured and about to fall.

The unwettable character of young leaves is sometimes due to their short close-set pubescence, or in other cases (e.g. *Alchornea*) to a thin wax coating which manifests itself in a highly polished surface rather than in a bloom, or in *Bocconia* to a fine scurfiness, which becomes worn off as the leaves grow old. The examination of a number of West Indian and American cacti and agaves which proved to be unwettable indicated that the condition is due to the minute roughness of the cuticular coat, by means of which cushions of air are retained beneath drops of water which fall upon the surface. I take it as true in general that the particular structural features by virtue of which leaves happen to be wettable or non-wettable have no significance whatever with regard to the wettability itself. The degrees of pubescence, or of polished waxiness, or of cuticularisation in leaves have their most important physiological rôle in relation to water conservation, and it is by the merest chance that these features have to do with wettability.

The Occurrence of Hydathodes

There is no feature of foliage leaves that appears to give greater promise of having concrete utility under rain-forest conditions than does the hydathode. With conditions of soil moisture and soil temperature highly favourable to water intake at the roots, and with atmospheric conditions extremely unfavourable to water loss at the foliage, the excretion of liquid water by hydathodes might well be anticipated as serving to prevent injection of the intercellular spaces and to aid in maintaining a balance between water intake and water loss.

I have made a careful examination of the entire rain-forest flora with a view to determining the prevalence of hydathodes, only to find that outside the Gramineae and Cyperaceae there are but four common flowering plants in which they are found—one of these probably being introduced—and but two species of ferns in which they are functional, although a larger number appear to possess non-functional hydathodes. *Heterotrichum patens* (Sw.) DC. is a small melastomaceous tree in which the upper surface of the leaves is covered with two sorts of hairs, the longer of which have glandular tips and function as hydathodes. The leaf of *Lobelia assurgens* L. (see Plate XIV, Phot. 1) has a denticulate margin, the tips of the teeth being surmounted by water-excreting pores. *Hedyosmum arborescens* Sw. is a small tree with thick dentate leaves; at the ends of the teeth there are hydathodes of the pore type. *Fragaria vesca* L. (which may or may not be native) has hydathodes which function vigorously in the manner so familiar in it elsewhere. *Diplazium altissimum* (Jenm.) C. Chr. is a large fern found in the most moist situations in the rain-forest, and it possesses functional hydathodes at the angles between the teeth of its margin.

In all of the above forms the hydathodes function most vigorously at night. In the commonest herbaceous plants of the most moist habitats there are no

hydathodes, and in the numerous ferns which give anatomical evidence of having functional hydathodes I have never seen them in action.

Under the normal conditions of the rain-forest I have never seen naturally injected leaves in any of the forms which are without hydathodes. I was sceptical as to the possibility of any considerable amount of injection taking place naturally until I had the unusual opportunity in the Blue Mountains of witnessing a violent and uninterrupted rainfall of five days' duration, with a total fall of 201 cm. On visiting the rain-forest at the immediate close of this rain I discovered that all of the thin-leaved ferns and flowering plants were partly injected, and on many of the plants a majority of the leaves were completely injected, so that when laid on a newspaper the print could be read through them as plainly as though the leaves had been dehydrated and cleared in xylol. This condition had probably been somewhat more general immediately after the cessation of the rain, as seven hours had elapsed before I reached the rain-forest. It is probable that some individual leaves had been totally injected for two or three days, but there was no evidence of any deleterious effects following the injection, and a complete remedying of the condition was only a matter of hours. I was not able to find any leaves that were even partially injected in any of the trees or shrubs, and even in the herbaceous *Pilea nigrescens* Urb., one of the commonest terrestrial plants, I was not able to find any completely injected leaves. The phenomenon was chiefly confined to the ferns which possess thin and lightly cutinised epidermal walls, and did not fail to include the one species possessed of functional hydathodes. I endeavoured to obtain a similar completeness of injection in the leaves of *Diplazium celtidifolium* Kze. by several laboratory methods, without any success whatever. I was not able, by any means at my command, to imitate the strong, continued impact of rain drops which had been the principal factor in causing the natural injection.

Haberlandt (2, p. 372) reports having caused partial injection of leaves by poisoning their hydathodes during the time of their activity, and Wiesner (10, p. 7) speaks of having completely injected the leaves of *Tradescantia zebrina* by subjecting them to 45 days of artificial rainfall. I do not, however, know of any previously reported cases of leaf-injection taking place in nature. I have been in the Jamaican rain-forest at times when there was rainfall of as great duration as that which I have mentioned, but much less in violence of fall and in amount, without finding traces of injection, which, together with my failure to produce it experimentally, points to the strength of the impact of the rain as the most important cause of injection. That such conditions are rare even in the rain-forest region is evinced by the fact that there had not been a rainfall of such duration and amount between 1815 and 1909. The exceptional nature of the conditions necessary to cause injection is therefore evident, and it is particularly significant that under these conditions the one form possessing hydathodes was not saved from injection by their activity.

Both on this evidence and on that of the rarity of hydathodes in the flora as a whole, I am compelled to maintain that their physiological importance has been overestimated.

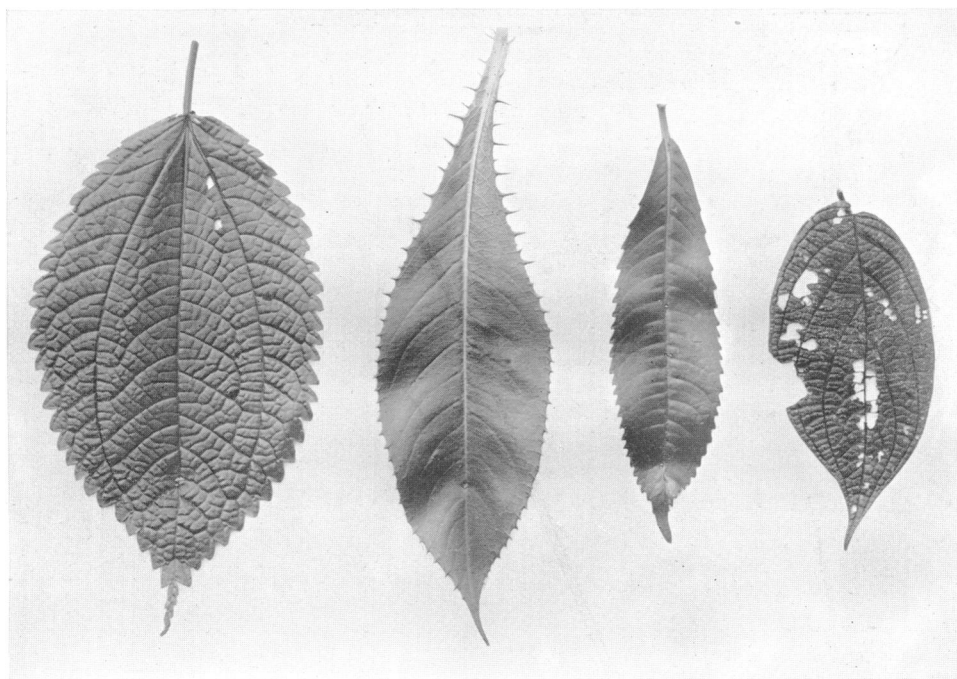
The Occurrence of Dripping Points and Epiphyllae

The matter of deciding whether the apex of a leaf in a particular species is sufficiently pointed to be considered as falling within the definition of a dripping point as made by Stahl, or whether it is only such a point as is extremely common in foliage leaves is a difficult one to decide, apart from all consideration of the function of the points. I have seen no forms in the Jamaican rain-forest with such pronounced points as are figured by Stahl (8) for *Ficus religiosa*, *Boehmeria urticaefolia* and *Elatostema cuspidiferum*. The commonest broad-leaved Jamaican forms which show a pronounced elongation of the apex (see Plate XIV) are *Pilea grandifolia* (L.) Blume (herb), *Boehmeria caudata* Sw. (small tree), *Lobelia assurgens* (herb), *Piper geniculatum* Sw. (shrub), *Besleria lutea* L. (shrub), *Guarea swartzii* DC. (tree), *Alchornea latifolia* (tree), *Heterotrichum patens* (small tree), and *Hedyosmum arborescens* (tree). In *Alchornea* there is a marked difference between sun and shade leaves (Plate XIV, Phot. 2). The former are smaller, blunt tipped and convex as a whole, as well as also being bullate or inflated between the veins. The shade leaves are larger, provided with a long dripping point, and are flat. The petiole of the youngest leaves is placed at an angle of about 45° to the stem and the lamina droops. In the later development shade leaves take a nearly horizontal position, sun leaves remaining turned down in their original position.

A number of the above species have gutters traversing the leaf surface, due to the sunken position of the veins, the gutters being so situated as to aid in drainage. These forms are *Pilea grandifolia*, *Boehmeria caudata*, *Piper geniculatum* and *Besleria lutea*. In some of the species possessing dripping points there is as much drainage from the basal as from the apical end, due to the position of the leaf on the stem, the forms of which this is true being *Hedyosmum arborescens*, *Besleria lutea* and *Lobelia assurgens*. Dripping points capable of functioning quite as effectively as those in the above-named broad-leaved species are to be found in some of the narrow-leaved trees and shrubs, as *Hedyosmum nutans*, *Eugenia biflora* var. *wallenii*, and species of *Tamonea*.

Jungner (4) states that species possessing dripping points predominate in the vegetation of the Kamerun mountains. Stahl (8) makes no statement as to their abundance in Java, but Holtermann (3) speaks of their occurrence in the mountains of Ceylon, saying (p. 222), "Allerdings fehlen auch nicht Sträucher und Bäume, deren Blätter keine Träufelspitze zeigen; aber die Laubblätter mit ausgezogener Spitze sind unbedingt in der Uebersahl." I can only say of the Jamaican rain-forests that the dripping point is a distinctly inconspicuous feature in the vegetation as a whole, particularly as regards the largest of the forest trees.

Jungner considers the ready drainage of water from the surface of leaves as of the greatest importance in cleansing them of the spores of epiphyllous hepatics, mosses, etc., and in preventing the presence on the surface of the leaf of a film of water which would be favourable to the growth of epiphyllae. In the Kamerun he has found the leaves with dripping points to be free of epiphyllae unless injured, and the leaves with blunt apices to be full of epiphyllae soon after reaching mature size. He has also observed that dripping points are absent from plants of the strand and other open situations.



Phot. 1. Leaves of four species possessing the most pronounced dripping points in the Jamaican montane rain-forests. From left to right: *Pilea grandifolia*, *Lobelia assurgens*, *Hedyosmum arborescens*, *Piper geniculatum*.



Phot. 2. Sun leaves (left) and shade leaves (right) of *Alchornea latifolia*, showing the presence of dripping points on the latter.

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VEGETATION (pp. 82—98).

I have found epiphyllae to be very common in certain situations in the Jamaican rain-forest, they being mostly Hepaticae of the now subdivided genus *Lejeunea*. The situations in which epiphyllae are commonest are the beds and lower slopes of ravines and narrow valleys, and the gaps of the main ridge—just those situations, that is, in which the humidity is most constantly high and in which the sunlight has the least play in drying the foliage. On the ridges and peaks epiphyllae are exceptional, although crustaceous lichens are occasionally found on leaves. In the situations where they are most abundant the epiphyllae are naturally found in greater numbers on the leaves of the herbaceous plants and undershrubs, but they are by no means absent from the leaves of trees when these are shaded by higher foliage. In the undergrowth of deep ravines I have found large colonies of *Lejeunea* growing on the leaves of *Boehmeria caudata*, *Piper geniculatum*, *Piper fadyenii* and *Pilea grandifolia*, the very species in which there are the most pronounced dripping points. In more open situations I have found very minute *Lejeunea* growing abundantly on the leaves of *Boehmeria caudata*, and at a distance of 6 to 8 m. from the ground I have found rich growths of epiphyllae on the leaves of *Solanum punctulatum* Dun., *Guarea swartzii* and *Eugenia biflora* var. *wallenii*. The occurrence on the herbaceous *Pilea grandifolia* is not so frequent as on shrubs of similar leaf form, which I attribute to the shorter life of the leaves of *Pilea* rather than to the efficacy of its dripping points, for they are not more frequent on the smaller and similar but blunt-tipped leaves of *Pilea nigrescens*, which is commoner than the former species in the most moist situations. The leaves of the orchid *Cranichis* sp. have a velvet sheen due to the conical projection of the outer walls of the epidermal cells. Stahl considers that this anatomical feature serves to hasten the evaporation of standing water from the surface, but I have nevertheless frequently found the older leaves of *Cranichis* covered by epiphyllous hepatics. I have not seen epiphyllae on the leaves of *Lobelia assurgens* nor on *Heterotrichum patens*, which is not due to their both being provided with pronounced dripping points, but rather to the fact that they grow only in relatively open places.

There is no questioning the fact that the continual wetness of leaves favours the occurrence of epiphyllae, as witness their abundance on the leaves of two filmy ferns which demand constant wetness (*Trichomanes rigidum* Sw. and *T. radicans* L.), and they are undoubtedly harmful in shading the chlorenchyma and bearing down the leaf by the weight of the water which they hold. The occurrence of epiphyllae, however, is not a function of the shape or character of surface in a leaf so much as it is of the conditions of the immediate environment of the plant. Wherever the humidity is high and constant, fog prevalent, and condensation of moisture common, those plants which are sheltered from breeze or subjected to drip from higher layers of foliage bear epiphyllae regardless of whether or not they possess dripping points. Plants of open situations, on the other hand, are devoid of epiphyllae regardless of their form.

Draining Power of Dripping Points

Although the wetness of foliage favours the growth of epiphyllae, it remains to be questioned whether the dripping point lessens materially the duration of the wetness of leaves in the most moist habitats—a matter which I have endeavoured to determine experimentally.

Sound leaves of average size were taken from plants which possess the most pronounced dripping points, and while still fresh were fastened by a single pin to a board at a slope of 40° to the horizontal. These were then wetted thoroughly by spray from a watering-pot and their drainage observed. Two trials were made with the entire leaves and a third with the same leaves after removing the tips

TABLE I

To show the transpiration behaviour of a shoot of Heterotrichum patens wetted and allowed to grow dry

Time p.m.	Temp. of air (° F.)	Humidity of air	Potometer reading	Rate per 5 minutes	Remarks
1.25	66	80	0	—	Leaves dry
1.30	66	80	115	115	
1.35	66	80	224	109	
1.40	66	80	334	110	
1.45	66	80	446	112	
1.50	66	80	560	114	
1.52	66	80	0	—	
2.00	66	80	185	115	
2.05	66	81	300	115	
2.10	67	82	0	—	
2.15	67	82	114	114	
Leaves wetted on upper surfaces					
2.20	67	77	240	126	
2.25	67	77	330	90	
2.30	67	77	403	73	
2.35	67	77	468	65	
2.40	67	77	527	59	Thin film of water left
2.45	67	77	587	60	
2.47	67	77	0	—	
2.52	67	77	65	65	Dry spots appearing
2.57	66	80	135	70	
3.02	66	80	204	69	
3.07	66	80	270	66	Surfaces nearly dry

and cutting the ends to a rounded form with scissors. The data from these three tests are designated A, B and C respectively in the following summary of their behaviour. The test was carried out in a building with jalousies on all four sides and there was a slight air movement during all three tests. The time of day was from 2.23 to 3.47 p.m., the temperature being nearly uniform at 66° to 67° F. (19° C.), the humidity averaging 73 % during A and B, falling to 68 % at the beginning of C and to 63 % by the end of it. The time at which each condition is noted is reckoned from the moment the spray ceased to fall :

Pilea grandifolia.

- A. Dry on the protuberances 9 min.; still wet in the gutters 24 min.
- B. Drying on the protuberances 2 min.; more than half dry on the protuberances 7 min.; dry except at the bottom and sides 13 min.; still wet in the gutters and at the bottom 29 min.
- C. Drying on the protuberances 3 min.; still wet in the gutters and at the bottom 22 min.

Alchornea latifolia (a full-grown shade leaf).

- A. Dry in spots 1 min.; almost completely dry 22 min.
- B. Dry in spots 1 min.; almost completely dry 17 min.
- C. Dry in spots 1 min.; water remaining in spots 14 min.; dry 22 min.

Besleria lutea.

- A. Dry spots 3 min.; nearly dry 12 min.; dry 22 min.
- B. Dry spots 1 min.; more than half dry 6 min.; dry 14 min.
- C. Dry spots 1 min.; more than half dry 9 min.; dry excepting at the extreme tip 13 min.

Hedyosmum arborescens.

- A. Dry spots 1 min.; nearly dry 15 min.; dry 22 min.
- B. Dry spots 1 min.; more than half dry 6 min.; almost entirely dry 14 min.
- C. Dry spots 1 min.; half dry 8 min.; dry 22 min.

Tamonea sp.

- A. Drying uniformly over the whole surface 12 min.; lower part still wet with thin film of water 19 min.
- B. Drying uniformly 9 min.; wet at lower part 17 min.
- C. Drying uniformly 16 min.; all standing water gone from tip 21 min.; dry 22 min.

Guarea swartzii (leaflet).

- A. Dry spots 1 min.; nearly dry 16 min.; dry 22 min.
- B. Dry spots 1 min.; more than half dry 6 min.; dry 14 min.
- C. Dry spots 1 min.; dry except on the midrib 13 min.

Eugenia biflora var. *wallenii*.

- A. Dry spots 1 min.; nearly dry 14 min.; dry 22 min.
- B. Dry spots 1 min.; more than half dry 6 min.; dry 14 min.
- C. Dry spots 1 min.; more than half dry 5 min.; dry except at tip 13 min.; dry 22 min.

The general indication of the above tests is that the cutting off of the tips does not greatly, if at all, delay the drainage and drying off of all but the very tip of the leaf. Recognising the source of error in the unavoidable fall of humidity during the last test, I repeated the experiment on the following day, using pairs of fresh leaves of the same size, from one of which the tip had been removed. A different selection of species was made for the sake of comparison. In this case

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the leaves were wetted by a sharp shower of rain and then removed to shelter, where the temperature was 65° F. (18° C.) and the humidity remained constantly at 80 %, there being no movement of the air.

Data under A refer to the leaves with tips, under B to those without them :

Pilea grandifolia.

- A. Dry areas appear at once; gutters wet nearly half-way up, and one-third of the leaf surface accordingly wet 51 min.; lower ends of gutters and one-sixth of leaf surface still wet 68 min.
- B. Dry areas appear at once; standing water at the end and in one gutter half-way up, the others scarcely one-eighth of the way up, and about one-seventh of the leaf surface wet 51 min.; water still standing at the tip, one-seventh of the surface wet 68 min.

Piper geniculatum.

- A. Small dry areas at top of leaf 15 min.; drying rapidly at the top 23 min.; dry except at extreme tip 70 min.
- B. Small dry areas at top 15 min.; drying rapidly at the top 23 min.; more water standing in the gutters than on the leaf with its dripping point, and a larger area thus kept wet 51 min.; dry except at the tip and about one-fifth of the surface near it 70 min.

Cestrum hirtum.

- A. Small dry areas appear at once; no standing water, the whole end drier than in leaf B 45 min.; merely damp over about one-fifteenth the area, at the tip 65 min.
- B. Small dry areas at once; water standing at the tip and one-fifth the area wet 65 min.

Lobelia assurgens.

- A. Small dry areas at once; water standing at the tip and one-half the area wet 46 min.; practically dry 66 min.
- B. Small dry areas at once; water standing at the tip and one-third the area wet 46 min.; standing water at the tip and one-third the area wet 46 min.; standing water at the tip, a very small area wet above it 66 min.

Boehmeria caudata.

In the open, water flows copiously from the tips of this form during showers, yet the leaves do not show a tendency to drain off, possibly due to the short, scattered hairs. At the end of 70 min. both leaves looked much the same as at the start, being covered with a thinner but still unbroken water film.

Piper and *Cestrum* show some indication that the removal of the tip delays the drying of the surface. A little water will stand about as long at the end of a dripping point as it will at the rounded end of a leaf that has been trimmed, but in the latter case there is a broader area of standing water and from it a film will be maintained by capillarity in the gutters and over the general surface adjacent to the standing water. However, in *Pilea grandifolia*, which has very pronounced

gutters, the removal of the tip did not appear to delay drying, neither did it do so in *Lobelia assurgens*, in which the surface is glabrous and flat.

The method which I employed in my tests was the same as that used by Stahl (8, p. 108) when he found that the time necessary for drainage in leaves from which the tips had been cut was to that necessary in whole leaves as 3 to 1 in *Justicia picta*, as 8 to 1 in *Coffea arabica*, and nearly as 4 to 1 in *Piper nigrum*. The dripping points on the species with which I have experimented are certainly as pronounced as they are on any leaves of *Coffea arabica* which I have ever seen, and Stahl does not appear to have tested the leaves which he figures as having the longest points, nor does he give any details as to the behaviour of the leaves on which he made his experiments. In view of my results with *Piper geniculatum* and *Cestrum hirtum* Sw., I can not deny the efficacy of the dripping point in preventing the standing of water in the lowest third of the gutters and the lowest fifth of the leaf surface. Yet in view of my results with nine other forms I am forced to believe that the efficacy of the dripping point as a means of hastening the drying of the general surface of the leaf has been overestimated. As far as concerns the favouring of the growth of epiphyllae, I might believe that it would be to the advantage of leaves to have even the small amount of water at the tip and in the gutters removed if it were not that I have found the epiphyllae to be situated usually over the upper and middle portions of leaves, at least rarely to be filling the gutters and covering the tip except in leaves already well overgrown.

Both from the evidence, then, of the occurrence and distribution of epiphyllae in nature and from that of experiment, I may say that I do not consider the dripping point to be functional as a structure which reduces the probability of the overgrowing of leaves with epiphyllae. Neither do elongated tips show a capacity for hastening the drying of leaves which is marked enough or general enough to be of importance in this connection.

Wetness as affecting Leaf Temperature

Stahl rejects the view of Jungner that dripping points are a feature serving to lessen the growth of epiphyllae on leaves, saying: "Etwas sicheres über die Gründe des Vorkommens oder Mangels von Epiphyllen wissen wir also zur Zeit nicht." He attributes to them, rather, a function in preventing the cooling of leaves by evaporation of water from the upper surface and the consequent fall in transpiration rate.

It is obvious that the depression of the temperature of leaves by the evaporation of water from their surfaces must be of about the same order of magnitude as the depression of the temperature of a wet bulb thermometer at the same humidity. In the rain-forest, under the conditions of humidity which have been described this depression would not be great. Desiring to measure the depression of temperature in leaves due to wetting, and having no more satisfactory method for the determinations, I wrapped a single thickness of leaf around the bulb of a thermometer and took readings directly. The figures given in Table II show the behaviour of *Pilea grandifolia*. The humidity was read from a Lambrecht polymer which had just been set in agreement with a sling psychrometer. The

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figures for wet-bulb depression are the amounts indicated by psychrometric tables for the humidity and temperature observed.

TABLE II

To show the influence of wetting on leaf temperature in Pilea grandifolia

Time p.m.	Condition of leaf	Temp. of air (° F.)	Temp. of leaf	Humidity of air	Depression of wet bulb (° F.)	Depression of leaf temp. (° F.)
1.30	Dry	68.9	68.9	78	4.7	0.0
1.32	Wet	68.9	67.5	78	4.7	1.4
1.34	Wet	68.9	66.7	78	4.7	2.2
1.36	Thin layer of water	68.9	66.4	78	4.7	2.5
1.38	Thin film of water	68.9	66.2	79	4.5	2.7
1.40	Thin film of water	68.9	66.2	79	4.5	2.7
1.42	Very thin film	68.9	65.8	79	4.5	3.1
1.44	Nearly dry	68.9	66.4	79	4.5	2.5
1.46	Dry	68.9	66.9	79	4.5	2.0
1.48	Dry	68.9	66.9	79	4.5	2.0
1.50	Dry	68.9	67.1	79	4.5	1.8
2.00	Dry	68.9	68.9	79	4.5	0.0
2.02	Made wet again	68.9	66.9	79	4.5	2.0
2.04	Kept wet	68.9	66.7	79	4.5	2.2
2.06	Kept wet	68.9	66.2	79	4.5	2.7
2.08	Kept wet	68.9	66.0	79	4.5	2.9
2.10	Kept wet	68.9	66.0	79	4.5	2.9
2.12	Kept wet	68.9	65.8	79	4.5	3.1
2.14	Kept wet	68.9	65.5	79	4.5	3.4
2.16	Kept wet	68.9	65.3	79	4.5	3.6
2.18	Kept wet	68.9	65.3	79	4.5	3.6
2.20	Kept wet	68.9	65.3	79	4.5	3.6
2.52	Average of 16 readings while kept wet	68.9	65.1	78	4.7	3.8
2.54	Not re-wetted	68.9	64.6	77	5.0	4.3
2.56	Drying rapidly	68.9	64.4	76	5.8	4.5
2.58	Drying rapidly	68.8	64.4	75	5.4	4.5
3.00	Nearly dry	68.9	64.6	75	5.4	4.3
3.02	Dry	68.9	64.8	75	5.4	4.1

This test shows there is an appreciable lowering of the leaf temperature due to wetting, but that this is at no time as great as the depression of the wet bulb temperature. As might be expected, the evaporation of the last remaining film of water sometimes depresses the temperature more than wetness for a prolonged period. The occasions when leaves are drying off rarely fail to be occasions when the humidity is high, and I doubt if as great a depression of leaf temperature as that obtained in the latter part of the above test (4.5° F., 2° C.) often occurs in nature, because of the relatively low humidity (75 % to 79 %) at which the experiment was carried out.

In order to determine directly the influence of wetting on the rate of water intake in severed shoots, several tests were made by the potometer method, in which the rates of intake in a shoot before and after wetting, but under otherwise identical conditions, were contrasted. The wetting was done with a watering-pot, and was found not to wet the under sides of the leaves, as only a few seconds were necessary to completely wet the upper surfaces. The apparatus was moved after each wetting to a dry place on the laboratory tables in order to avoid a rise of humidity. The data given in Table III are for a shoot of *Pilea grandifolia* bearing eight leaves, and show the normal rate of intake, together with the effect produced on the rate by wetting the leaves and allowing them to dry off. Fifteen minutes after wetting, the intake had fallen to 30 % of its normal, this being coincident with the maximum evaporation of the water film, with no apparent lag in the effect of the wetting. As soon as the leaf began to have large dry areas the rate of intake rose very rapidly to the normal.

TABLE III

*To show the transpiration behaviour of a shoot of Pilea grandifolia
wetted and allowed to grow dry*

Time a.m.	Temp. of air (° F.)	Humidity of air	Potometer reading	Rate per 5 minutes	Remarks
9.30	68	78	100	—	Before wetting
9.40	67	80	158	29	„ „
9.45	67	80	187	29	„ „
9.50	67	80	217	30	„ „
9.55	67	81	247	30	„ „
Leaves made wet					
9.58	67	81	100	—	Leaves entirely wet
10.03	67	81	123	23	Thin film
10.08	67	82	135.5	12.5	Thin film
10.13	67	82	144.5	9	Protuberances dry, gutters full
10.20	68	82	159.5	10.7	Leaves half dry
10.25	68	81	173.5	14	Still wet at bottom and edges
10.30	68	81	192.5	19	Nearly dry
10.35	68	80	215.0	22.5	Tips only wet
10.42	69	80	253	28	Some tips wet
10.45	69	80	272	31.5	Leaves dry

In order to determine the effect of continuous wetting the same shoot of *Pilea* was used again, and the leaves were kept wet by putting water on them with a fine pipette. The resulting data are given in Table IV. Twenty minutes after wetting the intake had been reduced to 37 % of its normal amount, but then rose slightly and remained rather constant an hour after wetting at a rate which was 44 % of the normal.

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TABLE IV

To show the transpiration behaviour of a shoot of Pilea grandifolia wetted and kept wet

Time a.m.	Temp. of air (° F.)	Humidity of air	Potometer reading	Rate per 5 minutes
10.50	69	80	78	—
10.55	69	79	118	40
11.00	70	80	156	38
11.05	70	79	195	39
11.10	70	78	240	45
Leaves wetted				
11.12	70	77	200	—
11.17	70	78	230	30
11.22	70	77	250	20
11.27	70	76	267	17
11.32	70	77	282	15
11.37	70	77	298	16
11.42	70	77	315	17
11.47	70	77	332	17
11.52	70	76	351	19
11.57	71	76	369	18
12.03	71	76	387	18
12.08	70	76	405	18
12.13	70	76	423	18

For comparison a similar test was made with *Heterotrichum patens*. A shoot bearing four pairs of leaves gave the result shown in Table I (p. 88). The average of the readings for the surface-dry shoot from 1.35 to 2.15 p.m. was 113 mg. per 5-minute period; after wetting it fell to an average of 68.5 mg. for the interval from 2.25 to 3.07 p.m.—a fall to 61 % of the normal rate. The lowest 5-minute rate was 53 % of the normal, but this was reached before the maximum evaporation of the water film had begun, and before the leaf was entirely dry the rate had risen to 62 % of the normal.

The results indicate that the wetting of foliage by rain lowers the water intake in severed shoots. To what extent the potometer results indicate an actual lowering of the transpiration rate, as contrasted with a lowering of intake (due to the cuticular absorption of water), will be discussed presently.

Wetness as affecting Water Intake

Regarding the effect of wetness on the rate of intake, it is natural to believe that at least a portion of the fall demonstrated is due to the stoppage of cuticular transpiration, which is slightly more than half of the total water loss in leaves of rain-forest hygrophytes. In order to determine the fall due to stopping the cuticular loss without at the same time producing the cooling effect of the water film, a shoot of *Pilea grandifolia* was run on the potometer long enough to secure its normal rate of intake, after which the upper surfaces of its leaves were coated with vaseline and it was again run for an hour. The results are shown in Table V. The rate for the first 30 minutes after vaselining was 77 % of the former rate, and

for the succeeding 30 minutes was 72 %, at a time of the day when there is a tendency for the rate to fall in untouched plants. It has been known for a long time (Comes, 1878) that stoppage of the cuticular transpiration increases that from the stomata, but this is an effect which I shall have to consider for the present purpose as being the same whether the stoppage is due to water or to some non-volatile substance.

TABLE V

*To show the transpiration behaviour of a shoot of Pilea grandifolia
with upper surfaces of leaves vaselined*

Time p.m.	Temp. of air (° F.)	Humidity of air	Potometer reading	Rate per 5 minutes
12.58	69	79	79	—
1.03	69	79	106	27
1.08	69	79	132.5	26.5
1.13	69	79	159.5	27
1.18	69	79	184	24.5
1.23	69	78	208	24
Leaves vaselined on upper surfaces				
1.28	69	78	228	—
1.33	69	78	249.5	21.5
1.38	69	79	270	20.5
1.43	69	79	290	20
1.48	69	79	309	19
1.53	69	79	319	20
1.58	69	79	349	20
2.03	69	79	368	19
2.08	69	79	387	19
2.13	69	79	406	19
2.18	69	79	424	18
2.23	69	79	442.5	18.5
2.28	69	77	460	17.5

The fall in the rate of entry of water to shoots of *Pilea* which were kept wet continually (see Table IV) was shown to be down to a rate which was 44 % of the normal. Speaking then in general terms we may say that in *Pilea* the rate in wet leaves is from 40 to 50 % of the normal and that in vaselined leaves it is from 70 to 80 % of the normal; which is to say that approximately half of the fall is due to the stoppage of cuticular transpiration.

A determination of the same nature carried out on *Heterotrichum patens* is given in Table VI. The normal rate of 84.7 mg. per 5-minute period was cut down to an average of 79 % after the first 30 minutes—to an amount, that is, of the same order shown by *Pilea*.

Since it is impossible to measure the actual rate of transpiration by the potometer method, and since it is obviously impossible to use the weighing method when the leaves must be made wet, I have been unable to determine experimentally how much of the fall in rate of water intake not already accounted for is to be attributed to lowering of the leaf temperature and how much to the absorption of water through the epidermis of the wet surfaces. It would have been possible

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for me to place shoots on the potometer and then to wet them completely or to submerge them, but under the conditions of such an experiment I should not have considered failure of the potometer bubble to move backward as evidence that the leaf surfaces were not absorbing water. It is conceivable that water might be absorbed by the leaf surfaces at the same time that it was entering the cut end of the shoot from the potometer tubing, the excess going to fill vessels

TABLE VI

*To show the transpiration behaviour of a shoot of *Heterotrichum patens* with upper surfaces of leaves coated with vaseline*

Time p.m.	Temp. of air (°F.)	Humidity of air	Potometer reading	Rate per 5 minutes
1.47	63	83	407	—
1.52	63	83	476	69
1.57	63	82	558	82
2.01	63	81	5	—
2.06	63	80	105	100
2.11	63	80	195	90
2.21	63	80	364	85
2.26	63	81	449	85
2.31	63	81	531	82
Upper surfaces vaselined				
2.42	63	81	6	—
2.47	63	81	127	121
2.52	63	81	202	75
2.57	63	83	285	83
3.02	63	84	370	70
3.07	63	83	422	65
3.12	63	84	490	72
3.17	63	84	558	68
3.20	63	84	21	—
3.25	63	84	93	72
3.30	63	84	160	67
3.35	63	84	225	65
3.40	62	84	290	65
3.45	62	83	354	64
3.50	62	82	420	66

or intercellular spaces, or to increase the turgidity of cells already filled. I have, however, already reported (7) on an experiment of this nature with one of the filmy ferns, in which the absence of intercellular spaces made it possible to demonstrate the absorption of water by the leaf surface through a retreat of the potometer bubble. The anatomical character of the epidermal cells of *Pilea* is such as to indicate that the entrance of water to its leaves would be nearly, if not quite, as easy as in the filmy ferns, and such entrance of water is apparently responsible for the remaining fall of water intake in wet shoots which can not be accounted for by interference with cuticular transpiration.

The lowering of leaf temperature due to wetting which is shown in Table II was obtained at a humidity of 75 % to 79 %. In the rain-forest, under the

conditions that obtain when leaves become wet by rainfall or drip, the humidity is usually near 95 %, and is never below 90 %. At air temperatures between 68° and 76° Fahr. (20° and 24.5° C.) the depression of the wet bulb temperature is 1.5° to 3° F. As shown in Table II the depression of the leaf temperature is never as low as that of the wet bulb of the psychrometer. In other words, 2° F. is probably the maximum natural depression of leaf temperature due to wetting. I have no experimental evidence of the influence which such small changes of temperature as this may exert on transpiration or intake, but such influence would undoubtedly be extremely small, if possible of detection. It would not, therefore, account for the difference in reduction of intake between wetted and vaselined leaves, a difference which amounts to 30 % of the intake of dry shoots.

The principal physiological effect of rainfall upon the leaves of rain-forest plants appears, therefore, to be the reduction of water intake through the shoot, which is partly due to the stoppage of cuticular transpiration (as has been shown in *Pilea*), and partly to the entrance of water through the leaf surface (as has been shown to occur in the Hymenophyllaceae). Both the stoppage of cuticular transpiration and the entrance of water through the epidermal surface would result in a lowering of the intake of the leaf from the conducting tissues of the petiole and stem. The lowering of leaf temperature due to wetting is too slight to affect the rate of transpiration appreciably.

Distinct physiological effects may also be exerted by the epidermal intake of water which is free, or nearly free, of inorganic salts, especially in a region of prevailing low transpiration. The cell sap of the Hymenophyllaceae has been shown (7) to possess a low osmotic pressure, which is undoubtedly correlated with the low intake of soil water and the high intake of rain water by the leaves of these plants, which are so constantly in a condition of wetness.

SUMMARY

1. Plants possessing hydathodes are very infrequent in the montane rain-forests of Jamaica. Exceptionally prolonged and heavy rain causes injection of the intercellular spaces in thin-leaved herbaceous plants, including one of the forms with hydathodes.

2. Plants possessing dripping points are relatively uncommon in the rain-forest, as are also those with velvet surfaces, variegated foliage, and drooping juvenile leaves. Experimental evidence fails to confirm the view of Stahl as to the utility of the dripping point in drying the leaf surface.

3. Epiphyllae (epiphyllous algae, lichens, etc.) are abundant on leaves of every type, including the few with dripping points; their occurrence being dependent solely on the moisture conditions which surround the plant.

4. Surface wetness does not lower the temperature of leaves sufficiently, under rain-forest conditions, to affect their transpiration rate.

5. Surface wetness of leaves lowers their intake of water from the stem, partly through the stoppage of cuticular transpiration and partly through the absorption of water by the lightly cuticularised epidermis. The substitution of

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the intake of root-absorbed, salt-containing water by the intake of leaf-absorbed, salt-free water is the most important effect of rainfall on hygrophilous vegetation.

6. Hydathodes, dripping points and other supposedly adaptational structures in hygrophilous foliage fail to perform the functions which have been attributed to them, and are poorly represented in the Jamaican rain-forest.

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VEGETATION OF THE WYE GORGE AT SYMONDS YAT

By ELEANORA ARMITAGE

(*With Plate XV and one Figure in the Text*)

INTRODUCTION

The remarkably rich oak-beech association (*Querco-fagetum*) of the wooded Carboniferous Limestone gorge of the Wye, where this river forms for a short distance the boundary between the counties of Herefordshire and Gloucestershire, and the very distinctive grouping of vegetation which is found in this area, appear to have hitherto escaped the attention of British ecologists, though considerable work has been done on the vegetation of the Carboniferous Limestone in other parts of England—see Tansley (**2**, pp. 49, 146—161) and the literature there