Zeitschrift: Berichte der Schweizerischen Botanischen Gesellschaft = Bulletin de la Société Botanique Suisse

Herausgeber: Schweizerische Botanische Gesellschaft

Band: 89 (1979)

Heft: 3-4

Artikel: Transpiration types in montane rain forest

Autor: Wanner, Hans / Soerohaldoko, Soetomo

DOI: https://doi.org/10.5169/seals-63118

Ber. Schweiz. Bot. Ges. *89* (3/4), 193–210 (1979)

Transpiration types in montane rain forest

Hans Wanner and *Soetomo Soerohaldoko*

Institut für Pflanzenbiologie, Universität Zürich
Zollikerstrasse 107, CH-8008 Zürich

Pusat Penelitian Botani (Laboratorium Treub),
LBN, LIPI, Kebun Raya, Bogor, Indonesia

Manuscript received June 20, 1979

Introduction

The microclimates of the different „strata" in tropical rain forest have been repeatedly investigated and characterised (Richards 1966, Walter 1973, Longman and Jenik 1974). During daytime relative humidity in the upper canopy may fall to 60% or less. On the other hand the lowest stratum of vegetation near ground level may never experience humidities lower than 95% r.h. It may therefore be expected that the plants belonging to these different synusiae are adapted to the corresponding temperature and humidity regime. Leaves from the upper canopy have been described as xeromorph (sclerophyllous, „Laurel" type of Warming) in contrast to the hygromorphic structure of the leaves of ground herbs and small trees. It is still not possible to explain the preponderance of megasclerophyllous leaves of rain forest trees nor for that matter the other leaf forms occurring in the lower strata. Since Richards stated „the crude teleological explanations put forward in the last century . . . no longer seem satisfactory, but, our present knowledge does not allow a convincing alternative view to be suggested" no new experimental findings have been brought forward which could contribute to our understanding of the ecophysiology and structure of rain forest leaves. A connection between the sclerophyllous nature of the tree leaves and a diurnal water „stress" when the leaves are heated up by solar radiation suggests itself. However it is not at all known whether the canopy leaves of ombrophilous rain forest trees suffer periodically from water stress. Our knowledge of the water relations of rain forest plants is still very meagre, in spite of the statements to the contrary of Stocker (1935). Stocker's publication bears the title „Ein Beitrag zur Transpirationsgrösse im javanischen Regenwald". The three trees investigated by him (*Cassia fistula, Calophyllum* *inophyllum, Cassine glauca)* however are not at all representative for the typical ombrophilous forest. The shade plants of Stocker's transpiration experiments (*Cyrtandra pendula, Begonia isoptera* and an „Acanthaceae") on the other hand are indeed frequent components of the montane rain forest in West-Java. Stocker found a weak midday transpiration depression of the tree leaves, but he did not believe this was a sign of any serious water shortage. Coster (1937) measured the transpiration of many trees in Java with Stocker's method, i.e. by quickly weighing cut leaves and shoots. Although his observations are probably the most extensive in respect of number of species investigated and embrace much information on the water economy of forest and plantation trees, Coster's work has been overlooked by textbook writers on tropical rain forest. Some of his results and conclusions will be discussed later.

The most recent measurements of transpiration in rain forest plants have been performed as part of the vast research program conducted by Howard T. Odum at El Verde, Puerto Rico (1970). In contrast to all earlier experiments, transpiration was measured with an open air-flow system around the leaves, humidity sensors allowing a continuous monitoring of the transpiration concomitant with CO_2-exchange and radiation measurements. Transpiration was a function of insolation and varied sharply from day to day depending on light and humidity. Odum and his collaborators did not experiment with plants of different strata and synusiae.

In view of this scarcity of data we found it useful to investigate the transpiration of different rain forest leaves under comparable conditions. Though the method employed – quick weighing of cut leaves – is open to some objections, the procedure allows one to characterize the ability of different leaf types to regulate transpiration (Hygén 1953, Pisek and Berger 1938).

Methods

The experiments were performed at the mountain station of the Botanic Garden Bogor at Cibodas (formerly written Tjibodas), approximately 1400 m altitude, West-Java. The plants investigated were young and adult trees belonging to different strata of the montane rain forest, some shrubs and herbs occurring at the same site (with the exception of *Gaultheria fragrans,* growing at 2200 m). Table 1 sumarizes the names and some characteristics drawn from Backer (1963). A very detailed description and ecological analysis of the vegetation in the same area is given by I. Yamada (1975–1977).

Branches or leaves were cut in the afternoon or early morning and at once enclosed in plastic bags, the cut end submerged in water. The plastic bags were hung up by the windows of the work room, they were always protected from direct insolation. The following morning the leaves were cut and weighed at short intervals. Several leaves of the same or different species could be weighed almost simultanesously with a torsion balance. Between the weighings the leaves were exposed to diffuse light by the window. Light intensity, wet and dry bulb temperature were measured frequently during the experiment. Temperature and relative humidity remained often very nearly constant for 1–3 hours. Leaf area and dry weight (90^0) were obtained at the end of the weighing period.

During the daily measuring periods in August 1975 the average temperature in the experimental room was $20,3^0 \pm 3,6^0$. The leaves were exposed near a window between the weighings, with some ventilation from the adjacent door. Diffuse light intensity varied more than temperature and r.h. because of the frequent appearance of clouds: 1949 ± 662 Lux.

Table 1:

List of plants from which leaves were taken for transpiration measurements at Cibodas, West-Java (Nomenclature and data from Backer 1963).

Name and Family	Height	Occurrence in Java
A. Trees		
Altingia excelsa Norona Hamamelidaceae	15–60 m	W., humid forest, 200–1700 m
Brassaiopsis glomerulata (Bl.) Regel, Araliaceae	up to 10 m	W., humid forest, local ± 1400 m
Castanopsis argentea (Bl.) DC. Fagaceae	20–30 m	W., humid mixed forest, 200–1400 m
Dysoxylum excelsum Bl Meliaceae	10–50 m	W.C.E., forest, 90–1600 m
Ehretia javanica Bl. Boraginaceae	10–30 m	W.C.E., forests, 700–2100 m
Flacourtia rukam Z. & M. Flacourtiaceae	5–15 m	W.C.E., evergreen forest, 5–2100 m
Lithocarpus indutus (Bl.) Rehd. Fagaceae	20–45 m	W-half of Java, humid forest, 50–1600 m
Persea rimosa (Bl.) Kosterm. Lauraceae	15–40 m	W.C.E., mixed forest, 400–1200 m
Platea latifolia Bl. Icacinaceae	20–45 m	W.C.E., forests, 1000–1600 m
Saurauia pendula Bl. Saurauiaceae	4–13 m	W.C.E., shady, wet forest, 100–1500 m
Viburnum lutescens Bl. Caprifoliaceae	crooked tree or shrub, up to 10 m	W.C.E., open forest, 900–1700 m
B. Shrubs		
Cestrum aurantiacum Lindl. Solanaceae	2– 5 m	from Central America, naturalized in forest edges, above 1000 m
Gaultheria punctata Bl. Ericaceae	0,25–3 m	W.C.E., open stony localities, 1900–2900 m
C. Herbs		
Cyrtandra grandis Bl. Gesneriaceae	up to 2 m	W., forest, 1700–2300 m
Peristrophe hyssopifolia (Burm. f.) Merr., Acanthaceae	0,35–1,3 m	W.C.E., brushwood, not too dark forest, 90–1700 m
Molineria capitulata (Lour.) Herb., Hypoxidaceae	0,35–1,5 m	W.C.E., humid mixed and bamboo forest, 50–2200 m

Water saturation deficit was measured as described by Slavik (1974, p. 145). The weighing data for the water loss by the cut leaves were standardised by the method of Hygén (1951): all weights were expressed as per mill of the initial weight immediately after cutting (= 1000) and the logarithms ($\log_{10}$) of these numbers used for graphic analysis. In view of the constant environment during the transpiration measurements we did not deem it necessary to reduce these values to standard conditions (atmospheric pressure 760 mm and saturation deficit 5 mm Hg) as proposed by Hygén.

Results

1. Water saturation deficit.

Whenever the water balance of a plant is under stress a water saturation deficit is expected to develop. Although this useful indicator of the state of water balance is easily measured we are not aware of published data from rain forest plants.

The results of two series of measurements are summarised in the tables 2, 3 and 4. During the first period of measurements in March and April 1972 it rained nearly every day (3 mm to 20 mm). As expected, plants of the ground and shrub layer in the mountain rain forest did not develop significant water deficits under these conditions (Table 2). *Cestrum aurantiacum,* with the highest deficit of 5,8% is not indigenous, but a naturalized small tree of Central American origin. Relative humidity at the sampling area varied between 99% and 92%.

August is the least wet month in Cibodas (approximately 2% of yearly precipitation of 3500 mm). In 1975 we measured during a 9 day uninterrupted dry period not only water deficits from the lower layers of vegetation but also from the highest canopy at different times of the day. Again it was found that leaves from the lowest strata of vegetation had no water deficit between 08.00 and 09.00 hr when relative humidity within the forest was 93%. Leaves from the same plants had mostly a slight water deficit in the early afternoon at 14.00 to 14.30 hr (Table 3).

Table 2:
Water deficit of ground herbs, epiphytes and small trees in the rain forest of Cibodas, 27 March – 7 April 1972. Time 1140–1215, relative humidity 92% (minimum of day).

Cyrtandra grandis		3,3%
Cyrtandra picta		0
Amomum coccineum		0
Selaginella opaca		4,6%
Humata sp. (epiphytic fern)		1,5%
Elaphoglossum callifolium (epiphytic fern)		1,3%
Cestrum auranticacum		5,8%
Brassaiopsis glomerulata		2,3%
	at 0900	0
	at 1400	0
Dysoxylum excelsum (small tree, lm)		0
Flacourtia rukam (adult and young leaves)		0
Viburnum lutescens		0

Table 3:
Water deficit of leaves from the ground and shrub laver during a dry season at Cibodas, 5 August 1975.

Measurements between 0800 and 0830:	no water deficit
Measurements between 1400 and 1430:	
Amomum coccineum	2,8%
Brassaiopsis glomerulata	2,8%
Cyrtandra arborescens	2,2%
Cyrtandra grandis	0
Cestrum aurantiacum	6,7%
Peristrophe hyssopifolia	0,9%
Rubus moluccanus	10,5%

Leaves from the upper canopy had a small water deficit already at 08.30 hr, which seemed to increase somewhat during the morning, but began to decrease around noon. The regular appearance of clouds at this time of day even during the driest period of the year may be responsible for this lowering of the water deficit. In two species, *Lithocarpus indutus* and *Ehretia javanica,* we found that the young leaves had a smaller water deficit than adult leaves.

Our data show clearly that even after a relatively long dry period, canopy leaves develop only small water deficits. *Lithocarpus indutus* was the only tree where water deficits higher than 5% could be observed under these conditions.

2. Transpiration of cut leaves.

It is still disputed whether the initial weight loss of a cut leaf corresponds exactly to the transpiration of the intact leaf. There are a number of observations by different authors demonstrating that the method of quick weighing of cut leaves or shoots may give good results. This method is certainly suitable for comparative purposes under standard conditions. As proposed by Hygén (1951) we began each experiment with fully saturated leaves, which is in any case the normal state of the plants's water relations in the morning at our mountain rain forest site. When such a saturated leaf is severed and brought into a room at 80% relative humidity it will loose water by evaporation through stomata and cuticle. A relative humidity of 80% is lower than the minimum relative humidity of 90% to which the ground vegetation is ever exposed. On the other hand relative humidity may sink to 70% at the height of the canopy, somewhat lower than in our experimental conditions.

The curves resulting from frequent weighing of cut leaves have been analyzed by several authors. Most often a first phase with a linear decrease in weight with time is followed by a second phase with a lower rate of transpiration. The transition from the first to the second phase has mostly been ascribed to the closing of the stomata. The second phase of slower weight decrease would thus be interpreted as being due to cuticular transpiration, the first phase („stomatal phase“) to the sum of cuticular and stomatal transpiration. As shown by Hygén (1951) the product of

Table 4:
Water deficit of leaves from the canopy tree laver of the mountain rain forest at Cibodas, 12 August 1975, after nine days without rain.

		time	water deficit
Altingia excelsa		0820	2,4%
		0930	2,7%
		1430	2,1%
Castanopsis argentea		0840	1,8%
		1450	0,7%
Ehretia javanica		0900	4,9%
		1500	1,9%
	young leaves	1502	0
Lithocarpus indutus			
high tree,	young leaves	0830	6,6%
	adult leaves	0840	14,1%
small tree (2,5 m),	young leaves	1115	7,5%
	adult leaves	1120	10,1%
Platea latifolia (free standing tree in park at Cibodas)		0945	4,2%
		1200	4,7%
		1445	3,9%

the rate of transpiration during the stomatal phase E_S and the rate of „cuticular“ transpiration E_C, named by him „standard product“ = $E_S \cdot E_C$ can be used as an index of xerophytism. Xeromorphic plants should have a smaller standard product compared with mesomorphic and hygromorphic individuals of the same species. The immediate reason for this difference is the observation that xeromorphic plants have a slightly lower transpiration in the stomatal phase and a considerably lower cuticular transpiration than hygromorphic plants.

Hygén found these regularities with temperate plants, mainly different *Vaccinium* species in Scandinavia. He found the differences in transpirational behaviour to be „fairly closely correlated to differences in morphological structure and leaf anatomy“. We are not aware that this line of research on the ecophysiology of transpiration has been followed by other investigators, although Williams and Amer (1957) recommended the use of the „standard product“ in their critical re-examination of Hygén's transpiration equation. The same authors also found that it is not necessary to standardize and to convert weighings to logarithms for the evaluation of E_S, E_C and their products. This was the procedure we followed: the slopes of the first and second portion of the transpiration curve were obtained by fitting straight lines to the data (not always possible). For a graphic comparison only the curves were standardized, i.e. the weighings expressed as per mill of the initial weight and then logarithms taken.

The results of our transpiration measurements are summarized in table 5. This table contains also the dimensions of the leaves used for the experiments and the corresponding dimensional quotients.

The transpiration characteristics of the leaves from the different vegetation layers can easily be seen in table 5 and figure 1.

Table 5:

Dimensions and transpiration of cut leaves of rain forest plants at Cibodas.
F area (cm^2); FWt fresh weight (mg); DWt dry weight (mg); W water content (mg); E_s stomatal, E_c cuticular phase transpiration ($mg \cdot g^{-1} FWt \cdot min^{-1}$); $E_s \cdot E_c$ standard product; leaf age: a adult, y young

species	leaf position	leaf age	F	FWt	DWt	W	DWt/F	W/F	F/FWt	E_s	E_c	$E_s \cdot F_c$
Altingia excelsa	upper canopy	a	44.5	1598	582	1016	13.1	22.8	.028	.377	.155	.058
	canopy park tree	a	51.9	1495	515	980	9.9	18.9	.035	.698	.197	.138
Brassaiopsis glomerulata	small tree (3 m)	a	110.3	2336	474	1862	4.3	16.9	.047	1.688	.134	.226
Castanopsis argentea	upper canopy	a	51.0	1569	658	911	12.9	17.9	.033	.268	.205	.055
Dysoxylum excelsum	small tree (85 cm)	a	56.2	1374	–	–	–	–	.041	1.952	.742	1.448
Ehretia javanica	upper canopy	a	68.5	2049	609	1440	8.9	21.0	.033	.741	.158	.117
Flacourtia rukam	small tree (2.5 m)	y	40.0	647	–	–	–	–	.062	1.397	.321	.448
		a	60.5	1087	–	–	–	–	.056	1.430	.679	.971
Lithocarpus indutus	young tree (2.5 m)	a	158.9	3435	1340	2095	8.4	13.2	.046	1.587	.249	.395
	high tree	y	56.9	2093	405	1688	7.1	29.7	.027	1.670	.712	1.189
		a	118.0	3171	1473	1698	12.5	14.4	.037	.287	–	–
Persea rimosa	young tree (1.5 m)	y	37.6	1088	165	923	4.4	24.6	.035	.746	.550	.410
		a	59.8	1789	600	1189	10.0	19.9	.033	.808	.427	.345
	upper canopy	y	33.9	960	199	761	5.9	22.4	.035	.433	–	–
		a	19.8	704	321	383	16.2	19.3	.028	.302	.216	.065
Platea latifolia	high tree park	a	107.1	3900	1530	2370	14.3	22.1	.027	.230	.066	.015
Saurauia pendula	10 m approx.	a	107.5	3848	1028	2820	9.6	26.2	.028	1.408	.424	.597
Viburnum lutescens	shrub 60 cm	a	55.0	1214	276	938	5.0	17.1	.045	1.442	.672	.969
Cestrum aurantiacum	3 m	a	62.9	1131	181	950	2.9	15.1	.056	2.650	.356	.946
Gaultheria punctata	shrub 1.5 m	a	28.4	1364	552	812	19.4	28.6	.021	1.078	.677	.729
Cyrtandra grandis	herb	a	238.2	9765	1008	8757	4.2	36.8	.024	1.060	–	–
Peristrophe hyssopifolia	herb	a	69.5	1166	196	970	2.8	14.0	.060	3.919	2.558	10.025
Molineria capitulata	herb	a	393.0	8462	1496	6966	3.8	17.7	.046	1.990	.201	.400

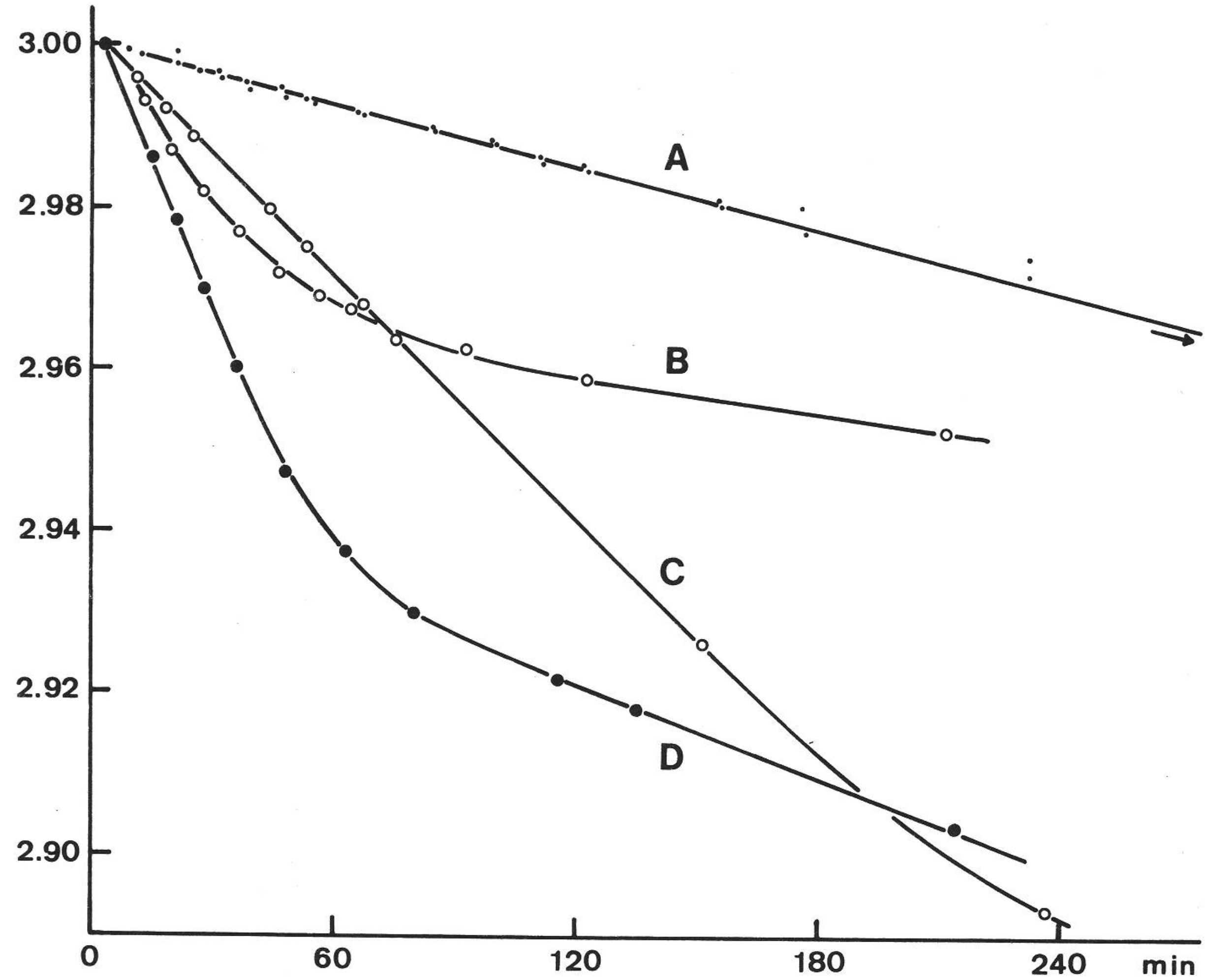

Figure 1:
Standardized transpiration curves of cut leaves. Ordinate: logarithm of permill fresh weight, initial weight = 1000.
A Castanopsis argentea; B Brassaiopsis glomerulata; C Cyrtandra grandis; D Cestrum aurantiacum.

2.1. Stomatal phase transpiration.

Some well-definable patterns are discernible:

a) Leaves from the upper canopy in the forest have a rather low transpiration (E_s) mostly smaller than 0.5 mg · g^{-1} · min^{-1}. Examples are *Altingia excelsa, Castanopsis argentea* (Fig. 1, curve A), *Persea rimosa, Lithocarpus indutus.* To the same group belongs a tall tree of *Platea latifolia,* which is however free-standing in the park area of Cibodas. A tree of *Altingia excelsa* from the park, situated on the border of a large pond, has a somewhat higher transpiration. The leaves from *Ehretia javanica* are from a tree which does not reach the height of *Altingia.* Their transpiration is on the average still considerably smaller than 1 mg · g^{-1} · min^{-1}.

b) Leaves from smaller trees and shrubs have generally a transpiration value E_s which is higher than 1 mg · g^{-1}: *Brassaiopsis glomerulata* (Fig. 1, curve B), *Dysoxylum excelsum, Flacourtia rukam, Lithocarpus indutus, Saurauia pendula, Viburnum lutescens, Cestrum aurantiacum* (Fig. 1, curve D), *Lithocarpus indutus.*

c) The highest transpiration has been found with the leaves of *Peristrophe hyssopifolia,* a soft-leaved herb of the undergrowth. Two other herbs, *Molineria capitulata* and *Cyrtandra grandis* (Fig. 1, curve C) lose their water less quickly. The soft leaves of the shrubs *Viburnum lutescens* and *Cestrum aurantiacum* show also a high transpiration but not quite equal to that of *Peristrophe.*

The leaves of a young and an adult tree of *Lithocarpus indutus* and *Persea rimosa* have been used for a comparison of the effect of aging at different heights in the forest. It can be seen that adult leaves from the small tree (circa 2.5 m), of *Lithocarpus indutus* have approximately the same transpiration as young leaves from the canopy. Adult leaves from the latter position behave like those of group.

Persea rimosa is another species used for a comparison of the properties of adult and young leaves from a small tree (1.5 m) and a high tree (canopy approximately 30 m). The leaves of the young tree showed a considerable variation of E_S, the two young leaves cannot be clearly differentiated from the adult leaf (19) in respect of the transpiration characteristics. The leaves from the canopy not only lose their water much slower than the leaves from a small tree, but also show that here a young leaf has a higher transpiration rate than adult leaves. The difference is however much smaller than with the corresponding leaves from the canopy of a *Lithocarpus indutus* tree. This quantitative difference between the two species does not mask the (probably) general rule, that

1) under identical conditions young leaves lose water faster than similarly positioned adult leaves.
2) Leaves from small individuals of canopy forming tree species have a similar transpiration to other shade plants of the lower vegetation strata.

2.2. Transpiration of the „cuticular phase“.

In contrast to Hygén's and other authors' results we could not always distinguish clearly the „cuticular“ from the initial „stomatal“ phase. Unfortunately we were not able to observe the closing movement of the stomata simoultaneously with the transpiration measurement. The low transpiration of adult high canopy leaves lasted in most cases for hours without any conceivable diminution (Fig. 1, curve A: *Castanopsis argentea*). In most cases however, a linear phase at the beginning of the experiment was followed by a more ore less extended transition (Hygén's „closing“) phase (Fig. 1, curves B and D). It seems not possible however, to correlate the duration of this phase with any particular ecological leaf type. With some leaves (i.e. *Cyrtandra, Peristrophe*) the high speed of water loss remained nearly constant until the leaves had lost their turgescence. In several experiments the „transition“ phase with a decreasing rate of transpiration lasted for some hours till the end of the observation period. It is evidently impossible to define a clear-cut „cuticular“ phase transpiration rate E_S in such cases. The „standard products“ ($E_S \cdot E_C$) in table 5 therefore are with some species approximate values only. It is interesting to note that the values of this product in the last column of the table 5 nevertheless show a more or less regular correlation with the ecological leaf type. Small standard products are found with leaves from the upper canopy, higher values with the leaves from smaller trees and shrubs, the highest values being shown by *Peristrophe hyssopifolia.* If Hygén's interpretation is adopted canopy leaves are „xeromorphic", while leaves in the lower strata are increasingly „hygromorphic". A comparison with Hygén's values for the standard product of scandinavian herbs and small shrubs (chamaephytes) show however a characteristic difference to the tropical rain forest leaves. The range for the standard products for the latter is generally smaller and the minimal values for the canopy leaves are much smaller than for example Hygén's xeromorph Ericaceae, where the smallest values are found with *Vaccinium Vitis-idaea* (average 0.30). Our results appear to confirm and extend the usefulness of the „standard product" for the characterisation of ecological leaf types to those of the tropical rain forest.

3. Dimension quotients of leaves: surface development, degree of succulence and sclerophylly.

The 3 dimension quotients are

degree of sclerophylly:	dry weight (g) / surface (dm^2)
degree of succulence:	saturation water content (g) / surface (dm^2)
surface development:	surface (dm^2) / fresh weight (g)

These quotients have frequently been used by plant ecologists to characterise leaves of different ecological types. In order to compare our results with published data we recalculated the values of Table 5 which are based on leaf area, surface assumed to be twice the area of the leaf.

3.1. Sclerophylly:

When the data from our measurements are ordered according to the degree of sclerophylly (Table 7) it can clearly be seen that the order corresponds rather well to the position of leaves in the different layers of the forest. The highest degree of sclerophylly is shown by the leaves from the upper canopy and the lowest values by ground herbs. It is especially instructive to compare the values obtained for *Lithocarpus indutus* and *Persea rimosa.* In both species adult leaves from the highest crowns are most sclerophyll, young leaves at the same height much less, while least sclerophyll are young leaves from young, small trees. The range of values for the mountain rain forest extends to higher degrees of sclerophylly than those found by Stocker (1935), due to the fact that he failed to include high rain forest trees in his investigation. Within a vertical profile in the rain forest the whole known range of degrees of sclerophylly can be found. At the top are leaves corresponding to the „Hartlaubpflanzen" of extratropical areas, in the ground layer of vegetation the leaves have the same low degree of sclerophylly as those

Table 6:
Stomatal phase transpiration of montane rain forest plants at Cibodas.

Species	E_s (mg · g^{-1}FWt · min^{-1}) adult leaves	s.d.	young leaves
A. high trees			
1. Platea latifolia	0.230		
2. Castanopsis argentea	0.268	± 0.068	
3. Lithocarpus indutus			1.670
4. Persea rimosa	0.302		0.433
5. Altingia excelsa, forest	0.377	± 0.088	
6. Altingia excelsa, park	0.698	± 0.100	
7. Ehretia javanica	0.741	± 0.185	
B. trees of intermediate height, young trees, shrubs			
8. Persea rimosa (young tree)	0.808		0.746
9. Cyrtandra grandis	1.060		
10. Gaultheria punctata	1.078		
11. Saurauia pendula	1.408		
12. Flacourtia rukam	1.430		1.397
13. Viburnum lutescens	1.442		
14. Lithocarpus indutus	1.587		
15. Brassaiopsis glomerulata	1.688		
16. Dysoxylum excelsum	1.952		
17. Cestrum aurantiacum	2.650		
C. Herbs			
18. Molineria capitulata	1.990		
19. Peristrophe hyssopifolia	3.919		

of shade plants in forests of temperate climatic regions. A hint that even higher degrees of sclerophylly may be found at high altitudes is indicated by the value for *Gaultheria fragrans,* a ericaceous shrub occurring in open stony localities at 1900–2900 m altitude. With increasing altitude the vegetation on the slope of Mt. Pangerango appears to be more sclerophyllous.

3.2. Succulence.

Compared with the degree of sclerophylly the saturation water content per unit of surface (Table 7, B) does not show any clear correlation with the position of the leaf. Maximal values are shown by the leaves of a ground herb *Cyrtandra grandis,* and the young leaves of the high crown of *Lithocarpus indutus.* The lowest values of succulence have been found with another ground herb, *Peristrophe hyssopifolia,* and the adult leaves of a very small tree of *Lithocarpus indutus.*
As the data of *Lithocarpus indutus* and *Persea rimosa* show, young leaves are more succulent than adult ones.

Table 7:

Dimension quotients of leaves.

A sclerophylly = dry weight (g) / surface (dm^2)
B succulence = saturation water content (g) / surface (dm^2)
C surface development = surface (dm^2) / fresh weight (g)
Except were noted, the measurements were taken on adult leaves.

Name	A	B	C
Gaultheria punctata, ericaceous shrub, growing in a rocky area at 2000 m altitude	0.97	1.42	0.42
Persea rimosa, high tree	0.81	0.96	0.56
Platea latifolia, high tree, park	0.72	1.11	0.54
Altingia excelsa, high tree	0.66	1.14	0.56
Castanopsis argentea, high tree	0.63	0.89	0.65
Lithocarpus indutus, high tree	0.62	0.72	0.74
Persea rimosa, young tree	0.50	0.99	0.67
Altingia excelsa, park tree	0.49	0.94	0.71
Saurauia pendula, small tree	0.48	1.31	0.55
Ehretia javanica, high tree	0.44	1.05	0.67
Lithocarpus indutus, young tree	0.43	0.66	0.92
Lithocarpus indutus, high tree, young leaves	0.40	1.52	0.52
Persea rimosa, high tree, young leaves	0.29	1.12	0.71
Viburnum lutescens, small tree	0.25	0.85	0.91
Brassaiopsis glomerulata, small tree	0.21	0.84	0.94
Cyrtandra grandis, ground herb	0.21	1.84	0.49
Persea rimosa, young tree, young leaves	0.21	1.22	0.70
Molineria capitulata, ground herb	0.19	0.88	0.93
Cestrum aurantiacum, shrub	0.14	0.75	1.12
Peristrophe hyssopifolia, ground herb	0.14	0.69	1.20
Flacourtia rukam, young leaves	–	–	1.24
Flacourtia rukam	–	–	1.13
Dysoxylum excelsum, young tree	–	–	0.82

3.3. Surface development

Leaves of shade plants in temperate climates have generally a large surface development. Tables 5 and 7 seem to confirm this rule, however with exceptions. *Cyrtandra grandis* as a ground herb, and *Saurauia pendula,* as an understorey tree, have both a low surface development. The statement of Stocker that the shade plants of rain forest have a very low surface development is not corroborated by our list. It seems to be true, however, that the high values of some typical shade plants of extratropical areas, such as *Oxalis acetosella* cannot be found with phanerogamous ground herbs in the rain forest. The leaves of the upper canopy are all caracterised by a low surface development. *Gaultheria fragrans* behaves also in this respect like its ericaceous relatives, chamaephytes of extratropical areas.

Discussion

Evolution in land plants has led to a stabilisation of their internal water relations, achieved by long term constitutional and short term physiological regulation of their water economy. The adaptive value of this relative „homoiohydry" can easily be deduced from the strong correlation between water potential and growth or for that matter between precipitation and plant productivity. The adaptation to a variable and sometimes extreme water regime in the plant environment will be determined in form and extent by the frequency of extremes of the water potential in soil and atmosphere. In rainforest the range of extremes in radiation, temperature and water potential is largest around the crowns of the highest tree and least near the ground.

Our experiments with leaves under identical conditions, from all layers of vegetation show that such an adaptation exists. Leaves from the upper canopy invariably lose water by transpiration more slowly than any other leaf type in the forest. The ground layer vegetation consists of hygrophytes with a high evaporative power. The overall *resistance* against transpirational water loss is clearly highest in the uppermost leaves and decreases gradually towards the ground. It should be evident however that this conclusion from our experiments must not be interpreted as meaning a higher transpiration in the ground vegetation layer under *natural* conditions. The generally very low saturation deficit within the forest will depress transpiration to much smaller values than we found under our experimental conditions. As has been repeatedly pointed out, an intermittent increase in transpiration may be favorable for plants living in a constantly near saturated atmosphere. The ability to increase the transpiration rapidly to a high level (sunspots!) must be regarded as a definite advantage, even if this response may be lethal under special circumstances such as when a gap is created in the forest following the death of a high tree.

For the leaves of canopy trees a somewhat higher transpiration than observed here may be expected under the actual conditions in this leaf layer during direct insolation. Using the quick weighing method and working in a similar environment in West Java, Coster (1937) found in fact with the same species a higher transpiration for leaves exposed to direct sun light. His results with potted plants from the ground vegetation maintained under natural conditions *within* the forest may give reasonable approximate values for the transpiration of the ground vegetation. Despite the somewhat doubtful extrapolations by Coster his values for the transpiration of different layers of vegetation in the montane rain forest seem to be still the only estimate as to its order of magnitude. Another interesting observation by Coster is his comparison of lowland rain forest trees with those from montane rain forest under similar conditions. He found that trees from the latter have generally a lower transpiration than lowland rain forest trees. When the same species were used for the transpiration measurements at two different altitudes (Bogor, Java 250 m, and Leuweung Cai, Java, 1750 m) the difference was even greater. It seems necessary to confirm and extend these and other pertinent observations by Coster. His interpretation of the higher transpiration in the lowland as due to the higher saturation deficit at higher temperatures is certainly an oversimplification. Internal factors resulting in an adaptation to the prevailing conditions would again be expected to play an important role.

The most important question which remains to be answered is the nature of the different transpiration resistances. Why do the sclerophyll leaves of the canopy layer under identical conditions transpire less than the hygrophyll leaves of the ground vegetation or the shade leaves of the same or a younger tree? While the sclerophylly coincides completely with the transpiration, the degree of succulence and the surface development do not. Sclerophylly, the amount of dry substance per unit surface of the leaf, means primarily the mass of cell wall substances.

This is readily confirmed by examining transverse sections of different types of leaves. This provides the leaf with the typical rigidity, compared with the soft leaves of lower strata. Since they also possess a thick cuticula sclerophyll leaves would be expected to have a lower cuticular transpiration than hygrophyll leaves. This has been proved for plants of temperature climates (i.e. Pisek and Berger 1938) and our results though somewhat irregular for the cuticular phase bear out the same general relationship. The main and most consistent difference between the sclerophyll and hygrophyll leaves lies in the rate of the first or stomatal (+ cuticular) phase of the evaporation curve. We have as yet no satisfactory explanation for this difference. More detailed and comparative studies on the anatomical structure, and especially the stomatal path of evaporation are needed.

One consequence of sclerophylly is certainly a decrease in cell wall elasticity and a greater resistance to changes in volume. One important implication of this higher rigidity must be a smaller hydraulic capacitance (change in volume per unit applied pressure) of the leaf. On the other hand, the soft and often somewhat succulent leaves of the lowest strata most probably have a higher hydraulic capacitance. When sclerophyll leaves are exposed to direct radiation the resulting increased transpirational water loss cannot be compensated by the leaf's water capacitance. Hence it must be replaced by water from the conducting tissues against the combined resistance of the conducting and absorbing system. Leaves of the undergrowth and expecially those of the ground vegetation are only sporadically exposed to direct sunlight when a sunspot moves across them. Because of the low evaporative resistance of such leaves transpiration will rapidly incrase to high values. These leaves are able to react quickly to the sudden increase in radiation by their presumed high hydraulic capacitance. This type includes the different species of *Cyrtandra, Begonia* and many other more or less succculent herbs, as well as low climbers such as *Agalmyla parasitica.* There are however, other kinds of ground herbs with a very thin leaf blade, namely *Rubus moluccanus* and *Peristrophe hyssopifolia.* They do not seem to have a high hydraulic capacitance. Indeed the leaves of *Peristrophe* droop rapidly when exposed to direct sun light for a few minutes. The leaves of *Rubus moluccanus,* however, are supported by a strongly developed net of veins projecting on the underside of the leaf blade. Further research is needed to discover whether these different morphological types, reflected also in the degree of succulence and the surface development, react differently to saturation deficits of the atmosphere.

All adult leaves of the high canopy are characterized by a low transpiration. They transpired less than younger leaves as well as adult and young leaves of smaller or younger trees. We interprete this as an adaptation to their low hydraulic capacitance caused by sclerophylly. In our view sclerophylly is not an *adaptation* to water stress as has often been postulated, but rather a *consequence* of the special microclimatic environment on the growth processes and development of the leaves at the top of the canopy. These leaves must adapt to their low hydraulic capacitance by reducing both stomatal and cuticular transpiration, so that a serious water stress cannot develop during the relatively short dry periods. As the soil is always wet in our area of investigation, the internal resistance to water transport is most probably the limiting factor for the water supply to the leaves of high trees.

Even the adult leaves of young trees of the same species at the upper canopy behave like shade leaves. Thus, adaptation to the changing light climate at higher levels is possible through more or less continuous leaf change and a limited life expectancy of the leaves of not more than 1,5 years (Longman and Jenik 1974).

Summary

1. Transpiration measurements were performed by weighing water saturated cut leaves under near constant conditions at Cibodas, West Java.

2. Leaves were taken from all layers of vegetation within the montane rain forest. Besides the transpiration of the cut leaves under „standard“ conditions the following characteristics were evaluated: water saturation deficit, degree of succulence, degree of sclerophylly, degree of surface development.

3. Water saturation deficits were rarely observed with leaves from the ground vegetation and they were in any case small, even during a dry spell of 9 days in August 1975. Leaves from the upper canopy developed a small water deficit during the morning which, however, was compensated by noon.

4. Transpiration was measured at 20^0 and 80% r.h. with all leaves. This r.h. is lower than the minimum r.h. at 50 cm height in the forest (> 90%), but higher than the minimum at the height of the upper canopy (around 70%).

5. The curves for the weight-decrease with time after cutting do not always show the „standard“ pattern of two more or less linear phases as described by many authors.

The xeromorphic leaves from the upper canopy generally exhibited a weak transpiration which decreased slightly or not at all over several hours. In sharp contrast to this type of transpiration curve was the rapid decrease in weight of the hygromorphic leaves from ground herbs. A linear stomatal phase was often not observed with this type of curve. Leaves from young trees or smaller trees and shrubs showed an intermediate behaviour. Young leaves of a particular species generally had a higher transpiration rate than adult leaves from the same layer of vegetation.

The „standard product“ (s.p.) of Hygén (1951): „intensity of stomatal phase transpiration times intensity of cuticular phase transpiration“ derived from our measurements is well correlated to the ecological leaf type. The xeromorphic leaves had a smaller s.p. than the leaves of the ground layer. Intermediate values were obtained for the other strata.

6. Sclerophylly (g dry wt/dm^2 surface) (Table 5) is highest in the leaves from the upper canopy, decreasing in lower strata to minimum values for the ground herbs. Succulence (g saturation water content/dm^2 surface) was in order of decreasing values: *Cyrtandra grandis* (a small shrub with large leaves), young tree leaves, adult tree leaves, ground herbs and adult leaves of a small young tree of *Lithocarpus indutus.* The ground vegetation contains plants with broad variations in succulence. The degree of surface development follows roughly an inverse order to that of succulence.

7. It is pointed out that the sclerophylly of the upper canopy is probably not an adaptation to water stress conditions. Such conditions are in any case rare or nonexistant under the local climatic conditions. Sclerophylly develops as a result of the effect of microclimatic conditions on leaf growth and development. Sclerophylly probably reduces the hydraulic water capacitance of the leaves. An internal resistance in the water supply to the transpiring surfaces might be the reason for their relatively low evaporative capacity and its adaptive value. The contrasting high transpiration from the cut leaves of ground herbs along with the intermediate values for leaves from higher strata and for young leaves might also have an adaptive value. Namely to maintain and accelerate a generally slow water transport whenever the light conditions permit it. Ground herbs are either more or less succulent with probably a high hydraulic capacitance or they have a high surface development with a small water capacitance.

Zusammenfassung

Transpirationstypen im montanen Regenwald

1. Die Transpiration abgeschnittener, wassergesättigter Blätter wurde in Cibodas (1400 m ü.M.) Westjava, mit der Wägemethode gemessen.

2. Blätter aller Schichten des montanen Regenwaldes wurden untersucht. Neben der Transpiration ermittelten wir noch folgende Grössen: Wassersättigungsdefizit, Sukkulenzgrad, Sklerophylliegrad, Oberflächenentwicklung.

3. Wassersättigungsdefizite wurden bei Blättern der Bodenvegetation selten beobachtet. Sie waren in jedem Fall sehr klein, auch während einer Trockenperiode von 9 Tagen im August 1975. Blätter der Kronenschicht entwickelten am Vormittag ein geringes Wassersättigungsdefizit, das jeoch gegen Mittag wieder verschwand.

4. Die Transpiration wurde meist in einem Raum bei 20^{0}C und 80% relativer Feuchtigkeit in diffusem Licht gemessen. Diese Luftfeuchtigkeit ist niedriger als die minimale Feuchtigkeit bei 50 cm Höhe über dem Boden ($>$ 90%), jedoch höher als die minimale Feuchtigkeit in der Kronenschicht (um 70%).

5. Die Kurven für die Gewichtsabnahme der Blätter nach dem Abschneiden entsprechen nur teilweise dem Standardmuster mit 2 deutlich getrennten, linearen Phasen. Die xeromorphen Blätter der oberen Baumschichten zeigten eine schwache Transpiration ohne oder mit nur einer geringen Abnahme der Transpirationsintensität während mehrerer Stunden. Die hygromorphen Blätter der Bodenschicht verhielten sich entgegengesetzt. Eine lineare, stomatäre Phase konnte bei diesem Blattyp oft nicht beobachtet werden. Blätter kleinerer oder junger Bäume aus mittleren Schichten verhielten sich intermediär. Junge Blätter einer Art hatten allgemein eine höhere Transpiration als ältere Blätter der gleichen Vegetationsschicht. Das „Standardprodukt" (s.p.) von Hygén (1951): Intensität der Transpiration in der stomatären Phase multipliziert mit der Transpirationsintensität in der kutikulären Phase, korreliert gut mit dem ökologischen Blattypus: Xeromorphe Blätter haben ein kleineres Standardprodukt als hygromorphe Blätter, mit intermediären Werten für die übrigen Schichten.

6. Die *Sklerophyllie* (g Trockengewicht / dm^2 Oberfläche) ist am stärksten ausgeprägt bei Blättern der Kronenschicht und nimmt mit abnehmender Höhe ab bis zu minimalen Werten in der Krautschicht. Die stärkste *Sukkulenz* (g Sättigungswassergehalt / dm^2 Oberfläche) fanden wir bei Cyrtandra grandis, einem wenig verholzten „Strauch" der Bodenschicht mit grossen Blättern. Darauf folgten junge und adulte Blätter von Bäumen. Minimale Werte fanden wir bei einem Kraut der Bodenschicht und adulten Blättern eines kleinen, jungen Baumes von Lithocarpus indutus. Die Bodenvegetation enthielt Vertreter mit extrem verschiedener Sukkulenz.

Der Grad der *Oberflächenentwicklung* verhält sich annähernd umgekehrt wie die Sukkulenz.

7. Es wird hervorgehoben, dass die Sklerophyllie der oberen Baumschichten wahrscheinlich *nicht* eine Adaptation an einen zeitweise angespannten Wasserhaushalt ist. Ein solcher ist auf jeden Fall sehr selten oder tritt überhaupt nie ein. Wir betrachten die Sklerophyllie als Ergebnis der Einwirkung mikroklimatischer Bedingungen auf das Blattwachstum und die Blattentwicklung. Die Sklerophyllie verringert offenbar die hydraulische Wasserkapazität der Blätter. Ein innerer Widerstand gegen die Wasserversorgung der transpirierenden Oberflächen dürfte die Ursache der geringen evaporativen Fähigkeit der oberen Blätter sein. Die hohe Transpiration der abgeschnittenen Blätter von Bodenpflanzen und jungen Bäumen dürfte ebenfalls eine adaptive Bedeutung haben. Sie erlaubt eine rasche Beschleunigung des meist langsamen Wassertransportes sobald die Belichtungsverhältnisse es gestatten. Kräuter der Bodenschicht sind mehr oder weniger sukkulent mit einer wahrscheinlich hohen Wasserkapazität (Volumen*änderung* pro Einheit angewendeten Druckes) *oder* sie haben eine hohe Oberflächenentwicklung mit geringer Wasserkapazität.

We would like to thank Dr. Setijati Sastrapradja, Director of the National Biological Institute, Bogor, Indonesia, and the other staff members for their help.

Thanks are due to Prof. Dr. Soeratno Partoatmodjo, former Director of the Biotrop, Bogor, Indonesia, and Dr. Soetrisno Hadi, program manager forest biology of Biotrop, Bogor. Indonesia, who have given a fellowship to the second author to make these studies; our gratitude to Pak Nurta and Mr. Idjun of the Botanical Gardens Cibodas for their assistance.

References

Backer C.A. and R.C. Bakhuizen van den Brink Jr. 1963. Flora of Java. N.V.P. Nordhoff, Groningen, 3 Vols.
Coster Ch. 1937. De Verdamping van verschillende Vegetationsvormen op Java. Tectona *30,* 1–104.
Faber F.C. von, 1915. Physiologische Fragmente aus einem tropischen Urwald. Jahrb. wiss. Bot. *56,* 197.
Hygén G. 1951. Studies in plant transpiration I. Physiologia Plantarum *4,* 57–183.
– 1953. Studies in plant transpiration II. Physiologia Plantarum *6,* 106–133.
Longman K.A. and J. Jenik, 1974. Tropical forest and its environment. London. 196 p.
Odum H.T., A. Lugo, G. Cintron and C.F. Jordan, 1970. Metabolism and evapotranspiration of some rain forest plants and soil. In Odum, H.T.: A tropical rain forest. A study of irradiation and ecology at El Verde, Puerto Rico. U.S. Atomic Energy Commission. p. I 103–164.
Pisek A. und Edith Berger, 1938. Kutikuläre Transpiration und Trockenresistenz isolierter Blätter und Sprosse. Planta *28,* 124–155.
Richards P.W. 1952. The tropical rain forest. Cambridge University Press. 450 p.
Slavik B. 1974. Methods of studying plant water relations. Ecological Studies 9. Springer Verlag, Berlin. 449 S.
Stocker O. 1929. Das Wasserdefizit von Gefässpflanzen in verschiedenen Klimazonen. Planta *7,* 382–387.
– 1939. Transpiration und Wasserhaushalt in verschiedenen Klimazonen. III. Ein Beitrag zur Transpirationsgrösse im javanischen Regenwald. Jahrb. wiss. Bot. *81,* 464–496.
– 1976. The water-photosynthesis syndrome and the geographical plant distribution in the Saharan Deserts. In O.L. Lange, L. Kappen and E.D. Schulze: Water and plant life. Ecological Studies 19. Springer Berlin. p. 506–521.
Walter H. 1973. Die Vegetation der Erde in ökophysiologischer Betrachtung. Bd. 1. Die tropischen und subtropischen Zonen. G. Fischer, Stuttgart. 743 S.
Williams W.T. and F.A. Amer, 1957. Transpiration from wilting leaves. J. exp. Bot. *8,* 1–19.
Yamada Isamu, 1975. Forest ecological studies of montane forest of Mr. Pangrango, West Java. I. Stratification and floristic composition of the montane rain forest near Cibodas. The Southeast Asian Studies, Kyoto University *13,* No. 3.
– 1976. Forest ecological studies of montane forest of Mt. Pangrango, West Java. II. Stratification and floristic composition of the montane rain forest vegetation of the higher part of Mt. Pangrango. ibid. *13,* No. 4.
– 1976. Forest ecological studies of montane forest of Mt. Pangrango, West Java. III. Litter fall of the tropical montane forest near Cibodas. ibid. *14,* No. 2.
– 1977. Forest ecological studies of montane forest of Mt. Pangrango, West Java. IV. Floristic composition along the altitude. ibid. *15,* No. 2.

Hans Wanner
Institut für Pflanzenbiologie
der Universität Zürich
Zollikerstrasse 107
CH-8008 Zürich

Soetomo Soerohaldoko
Pusat Penelitian Botany
(Laboratorium Treub)
Kebun Raya, Bogor, Indonesia