SOME MEASUREMENTS OF LEAF TEMPERATURES OF TROPICAL AND TEMPERATE PLANTS AND THEIR INTERPRETATION

PH. STOUTJESDIJK

Instituut voor Oecologisch Onderzoek, Biologisch Station "Weevers' Duin", Oostvoorne.

SUMMARY

Leaf temperatures of tropical rain forest plants, weeds, crops, as well as temperate beach and dune plants, were measured by contact with fine ribbon thermocouples and by a non-contact thermal radiation method. With strong solar radiation, non-transpiring leaves (covered with vaseline) in the tropics usually have temperatures of more than 10 °C above air temperature. Temperature differences of up to 20 °C were measured. The highest temperature differences leaf-air of temperate plants are only a few degrees centigrade below those of tropical plants. The temperatures of fresh leaves (both tropical and temperate) may vary in full sunshine from somewhat below air temperature to virtually the same temperature as the vaseline covered leaf.

The question was asked whether the strong transpiration cooling observed on leaves of *Saccharum officinale*, *Calotropis gigantea* and *Phragmites communis* and the extreme transpiration cooling (13 °C below air temperature) observed by Lange in the Sahara had to be explained by special properties of the leaf or rather by the dryness of the atmosphere.

From the temperature measurements on the leaves and the vapour pressure of the air it is possible to calculate a factor n which is the ratio of the total resistance of the leaf to water loss and the external resistance. For weeds and production crops typical values of n are between 3 and 6. Similar values were found for the sclerophyllous *Eryngium maritimum* and for *Aster tripolium*. For some species a high n (> 50) seems to be normal. The data indicate that strong transpiration cooling is not due to an abnormally low water loss resistance but to the extreme dryness of the air.

1. INTRODUCTION

The leaves represent the most important part of most plants, both by mass and by the processes that take place in them. This alone justifies to consider their temperature accurately.

Leaf temperatures also give an insight into the water relations of the plant. Furthermore the leaf also is the habitat of insects, fungi, lichens, mosses and in the tropics even higher plants that live inside or on the surface of the leaf: the phyllosphere (RUINEN 1961).

In the tropics measurements of leaf temperatures with reliable methods are still rare, be it true that the most detailed and fundamental study of the physical processes on which leaf temperature depends was made in India by RASCHKE (1956). From an ecological viewpoint it is certainly worth while to produce more extensive data.

With regard to the measurements available from other areas the remark can be made that there is a certain tendency to over-emphasize plants from extreme climates or habitats (*cf.* WALTER 1960).

The present paper gives measurements under conditions of strong insolation made on tropical and temperate plants with leaves of various type and size. The role of transpiration cooling was studied as well.

Many of the measurements on tropical plants were made in or near the mountain garden Tjibodas situated on the slope of the volcano Gedeh (W. Java) at 1400 m above sea level. Some measurements were made in the humid tropical lowland and some in East Java where the dry season is very pronounced.

The measurements on temperate plants refer to dune and beach plants on the Dutch coast.

2. METHODS

To measure leaf temperatures, two methods were used. The simplest method is to touch the surface of the leaf with one junction of a fine thermocouple, while the other junction is suspended in the air surrounding the leaf. Constantane and manganine wire (0.06 mm diameter) was flattened to make a fine ribbon and of this ribbon a manganine-constantane-manganine thermocouple was made. One of the junctions was pressed against the leaf, the other was suspended freely in the air. This method has the advantage that it measures straightforward the temperature difference leaf – air. However when leaves have an irregular or hairy surface it is often difficult to maintain a good contact between thermocouple and leaf.

In most cases a more complicated method was used which measures the heat radiation emitted by the leaf. The theoretical background of this method and the construction of the instrument (called "radiometer") was described in an earlier paper (STOUTJESDIJK 1966). In spite of the more complicated procedure it gives more constant results than the thermocouple. However, the leaf must fill the field of view of the instrument, a circle with a diameter of 2,5 cm. This means that the method cannot be used for small or narrow leaves like those of grasses. In these cases a thermocouple was used.

Comparative measurements showed that there was a good accordance between the leaf temperatures measured by means of the radiometer and those obtained with a thermocouple when the latter were based on the highest differences leaf – air measured in a short series of readings. Consequently each measurement with the thermocouple consisted of a quick series (1 minute) of readings of which the highest value was used.

Usually both the temperature of a normal leaf attached to the plant in a horizontal position (if not mentioned otherwise) and of a non-transpiring leaf covered with vaseline were measured. The influence of the vaseline cover on radiation reflectance and absorption was neglected in the present study.

SEYBOLD & VAN DER WEY (1929) and RASCHKE (1956) have shown that temperatures at the tip and the margin of a leaf can be considerably lower than those

at the centre. To make the measurements comparable all leaf temperatures were measured at the centre of the leaf.

3. DISCUSSION OF RESULTS

3.1. The temperature measurements

A selection of typical and comparable results is given in the diagram (*fig. 1*) and *table 1*. The data given are usually mean values of several measurements.

In the diagram and the table instead of leaf temperatures the differences leaf temperature – air temperature (Δ t) are given which makes the measurements more comparable.

The Δ t values of the vaseline covered leaves are the most simple case as here the influence of transpiration is absent which can be very great as a glance at the diagram shows. Even without the effects of transpiration there is a considerable variation of the Δ t. Variation in solar radiation, wind velocity and size of the leaves can be considered as the main causes.

The relations can be written as follows:

$$R_{net} = 2 \alpha \Delta t... \tag{1}$$

in which R_{net} is the net absorbed radiation per cm^2 of leaf (cal/cm^2 min), α is the heat transfer number (cal/cm^2 min °C). The factor 2 is due to the fact that the leaf gives off heat at the upper and the lower side.

The relation of α with leaf size and wind velocity is given by different authors (*cf.* RASCHKE 1956) in expressions of this form:

$$\alpha = C\ U^{0,5}\ b^{-0,3}$$

in which U is wind force and b is the diameter of the leaf.

Thus the highest Δ t values are measured when R_{net} is high and α is low *i.e.*, with strong sunshine on big leaves in sheltered places. In open spots in the forest the big leaves of *Musa, Hornstedtia, Passiflora* reach temperatures of up to 20°C above air temperature when transpiration is stopped.

Lower Δ t values are measured when the leaves are small or narrow (*Oryza sativa, Imperata cylindrica*) or when the wind is somewhat stronger (*Calotropis, Saccharum officinale*).

The temperature of the fresh leaves under tropical conditions can be frequently more than 10°C above air temperature and Δ t may even be close to 20°C. The Δ t values of temperate plants come close to these values. Absolute leaf temperatures of up to 48°C. were measured on *Plumeria acuminata*, an Apocynacea from S. America with sclerophyllous leaves (air: 30°C, vaseline covered leaf: 51°C). Leaves of the crater fern (*Polypodium*) reach 40°C on the top of the vulcano Papandajan where air temperature was 20°C. On the other hand sugar cane and *Calotropis* leaves in full sunshine may have a temperature which is even below air temperature. The same applies to *Phragmites* leaves.

Apparently these leaves use all the net absorbed radiation energy for tran-spiration or even slightly more, which means that part of the transpiration energy is drawn as sensible heat from the air.

As was discussed in an earlier paper (STOUTJESDIJK 1966) the diagram quickly gives an estimate of the part of the net absorbed radiation energy that is used in transpiration. This fraction is with a good approximation:

$$\frac{\Delta\,t_{dr} - \Delta\,t_{tr}}{\Delta\,td_r}$$

The suffixes dr, resp. tr, refer to non-transpiring resp. normal leaves. The dia-gram shows that it varies between virtually nothing and over 100%. This applies both to the tropical plants and the temperate species.

For comparison we mention the measurements of LANGE (1963) in S. Spain. Lange measured Δ t values of vaseline-covered leaves up to 20 °C and of fresh leaves up to 14 °C.

For the interpretation of the leaf temperatures measured it is important to realise that they were generally measured on leaves in a horizontal position. This often is a good approximation of the normal position of at least a consi-derable part of the leaves. However, many plants have a tendency to carry the leaves more vertical like for instance the sugar cane. In the dry savanna wood of East Java it is even a conspicuous feature of the trees to have the leaves or leaflets either hanging or standing upright. The growth habit can be doubtless of great importance to avoid excessive temperatures during the middle of the day.

As a special case we mention the *Nymphaea* leaf. This leaf uses only an unex-pectedly small fraction of R_{net} for transpiration. Remarkable as well are the high temperature differences between the leaf and the water on which it rests. This temperature difference can probably be maintained by means of an iso-lating layer of air at the lower side of the leaf. At this side the leaf has many protruding ribs. In the depressions between the ribs air bubbles are anchored. The leaf is even warmer than a black copper foil resting on the water.

GESSNER (1956) gives maximal transpiration rates of *Nymphaea alba* which also indicate a rather weak transpiration as compared with the energy absorbed.

3.2. Interpretation of leaf temperatures and transpiration cooling

For the observer who suffers from the heat of the sun in the dry savanna country of East Java it is astonishing that a plant like *Calotropis gigantea* can keep its leaf temperature even below air temperature.

The question arises in how far the high fraction of R_{net} used and the strong transpiration cooling observed here depend upon properties of the leaf which facilitate transpiration, and in how far upon the dryness of the atmosphere. The same applies, *mutatis mutandis* to *Phragmites communis*.

LANGE (1963) puts the same question with regard to the extreme transpira-tion cooling he observed on leaves of *Citrullus colocyntha* in the desert of Maure-tania. In full sunlight Lange observed leaf temperatures of 37 °C when the air

temperature was 50 °C. The fact that the same species does not reach temperatures below air temperature in Spain is considered by Lange as a strong argument that the dry air rather than special anatomical properties of the leaf cause the extreme transpiration cooling in the desert. To answer this question from the available data we proceeded as follows.

In an earlier paper (STOUTJESDIJK 1966) a relation was given between leaf temperature, wet bulb temperature, air temperature, temperature of a non transpiring leaf and a factor n, the reciprocal value of the 'Wasserbedeckungsfaktor' introduced by Raschke. The assumption was made (not completely correct) that n expresses the resistance against water loss of the leaf independent from environmental factors. The factor n is calculated from the energy balance of a leaf as follows.

Heat transfer (H in cal/cm² min) from a surface which is Δ t °C warmer than the air is expressed by:

$$H = 2 \alpha \Delta t$$

The expression for evaporation (E) known as Dalton's law is similar:

$$E = C (e_{surf} - e_{air}), \tag{2}$$

as evaporation can be understood as a diffusion of water vapour through a thin boundary layer of still air and heat transfer as a conduction of heat through the same boundary layer, α and C are proportional. When we express E in energetic units we get

$$E = \frac{\alpha}{\gamma} (e_{surf} - e_{air}) \text{ in cal/cm}^2 \text{ min} \tag{3}$$

γ is the psychrometric "constant", e_{surf} is the vapour pressure at the evaporating surface.

For a leaf the energy balance is:

$$\frac{2(e_{leaf} - e_{air}) \alpha}{n \gamma} + 2 \alpha (t_{leaf} - t_{air}) = R_{net (tr)}$$

e_{leaf} is the saturation vapour pressure at the temperature of the leaf, n (RASCHKE) is the factor by which the transpiration of the leaf is reduced as compared with a water surface of the same temperature under the same environmental conditions as the leaf, i.e. the depth of the boundary layer and the vapour pressure of the ambient air must be the same.

When we put as a first approximation the net absorbed radiation of a transpiring leaf ($R_{net (tr)}$) equal to that of a non-transpiring leaf ($R_{net (dr)}$) we get:

$$R_{net (tr)} = R_{net (dr)} = 2 \alpha (t_{dry\ leaf} - t_{air})$$

or:

$$\frac{2(e_{leaf} - e_{air})\, \alpha}{n\qquad\gamma} + 2\,\alpha\,(t_{leaf} - t_{air}) = 2\,\alpha\,(t_{dry\ leaf} - t_{air})$$

dividing by $2\,\alpha$ gives:

$$\frac{(e_{leaf} - e_{air})}{n\gamma} = t_{dry\ leaf} - t_{leaf}$$

$$n = \frac{(e_{leaf} - e_{air})}{\gamma\,(t_{dry\ leaf} - t_{leaf})} \qquad (4)$$

γ has the theoretical value of the psychrometer "constant" which was also found experimentally (STOUTJESDIJK 1961). For the normal range of temperature and atmospheric pressure at sea level, γ has a value between 0,42 and 0,44 (VAN DER HELD 1937).

For lower atmospheric pressures (B) the reduction factor for γ is not $\dfrac{B}{760}$ but somewhat higher. The error made by substituting $R_{net\ (dr)}$ for $R_{net\ (tr)}$ can be estimated as follows.

When the non-transpiring leaf is 10 °C warmer than the fresh leaf it emits in the normal temperature range about 0,08 cal/cm² min more heat radiation. When $R_{net\ (tr)}$ is e.g. 1 cal/cm² min then $R_{net\ (dr)} = 0,92$ cal/cm² min.
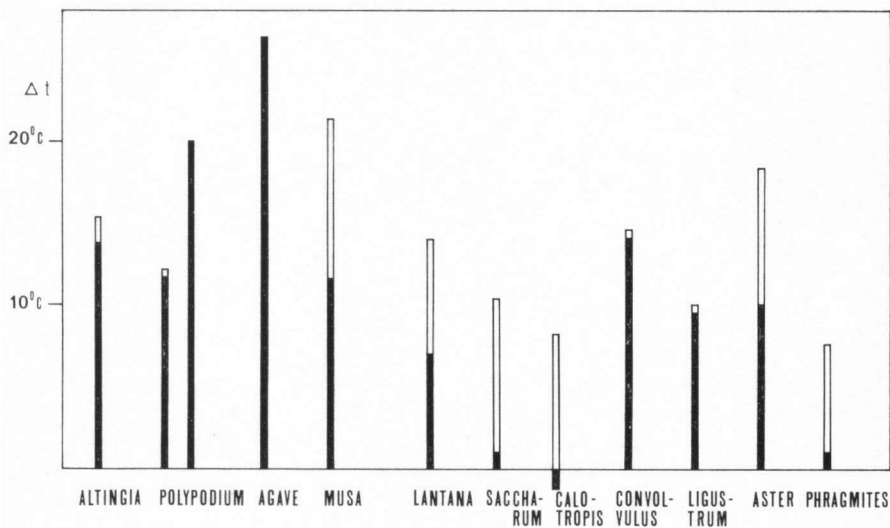

Fig. 1. Temperature differences leaf air of transpiring and vaseline covered leaves, showing different types of thermal behaviour of tropical and temperate plants.
White column: Δt of vaseline covered leaf.
Black column: Δt of transpiring leaf.
Full names of plants in *table 1*.

378

When Δ t of the non-transpiring leaf is 15 °C it should be replaced in the calculation by $\dfrac{1,0}{0,92} \times 15\,°C = 16,3\,°C$. Consequently in expression (4) $t_{dry\ leaf}$ $-t_{leaf}$ should be: 11,3 °C instead of 10 °C.

Corrections of this kind were applied when calculating the values of n. As the correction term is always relatively small, even big errors in estimating R_{net} do not affect the calculation of n seriously, doubtless less than the error in the temperature measurements.

IMPENS (1966), by a somewhat different treatment of the energy budget equation arrives at virtually the same expression for the factor n as given here. The correction factor contains a heat transfer term instead of an estimate of the energy budget.

The values of n (table 1) range from 2,1 (Hornstedtia) to 100 or more. The very high n numbers are of course quite sensitive to small errors in the temperature measurements.

Quick growing crops and weeds have low n values. This could be expected as CO_2 has to enter through the same stomata by which water vapour disappears. The table also shows that the cooling of the Calotropis leaves below air temperature is only partly due to a low transpiration resistance but as much to

Table 1. Temperature differences leaf-air (Δt) for fresh leaves and vaseline covered leaves in the same position. The factor n gives the resistance of the leaf against water loss as compared with a wet surface under the same conditions.

	Air temp.	Wet bulb temp.	Δt fresh leaf	Δt vaseline covered leaf	n	Remarks
Plants from montane rainforest						
Castanopsis argentea	22,0	19,2	10,7	11,7	53	
Altingia excelsa	21,3	19,0	13,8	15,3	43,5	
Passiflora ligularis	19,3	17,5	15,8	20,1	16	$\perp$ sun (normal position)
Musa acuminata	20,6	19,4	13,4	14,5	53	less turgescent
Musa acuminata	19,6	17,3	11,6	21,4	5,0	turgescent leaf
	22,5	18,8	13,1	15,9	25,0	same leaf getting less turgescent
Musa acuminata	17,7	17,0	14,2	18,6	11,5	
Hornstedtia spec.	18,8	18,0	14,4	18,3	14,5	
Hornstedtia spec.	19,5	18,0	4,4	11,9	2,1	old leaf
Hornstedtia spec.	19,5	18,0	6,8	11,4	5,7	young leaf
Asplenium nidus	19,5	18,5	10,0	9,8	–	
Rhododendron javanicum	21,8	18,2	9,1	17,2	5,6	terrestrial, cultivated in garden Tjibodas
Crater fern						
Polypodium feei	22,7	20,3	10,8	11,1	182	Gedeh
	22,7	20,3	14,4	15,9	–	,,
	17,8	16,1	16,4	–	–	,,
	20,9	–	19,9	–	–	Papandajan

Table 1. Continued

	Air temp.	Wet bulb temp.	Δt fresh leaf	Δt vaseline covered leaf	n	Remarks
Nymphaea						
Nymphaea spec.	23,4	20,4	7,7	7,8	–	water 26,9 °C
	20,4	18,0	7,4	9,6	–	water 23,6 °C copper foil: $\Delta t = 6,8$
Production crops						
Saccharum officinarum	31,3	26,2	4,6	12,5	5,5	Pasuruan
	31,7	25,4	1,6	9,8	5,2	Pasuruan
	31,8	25,5	–1,2	–	–	Pasuruan. Leaf upright (normal position)
Zea mays	30,0	25,2	4,0	7,9	9,3	Bogor, measurements Puspa Dewi Natalia
	25,2	21,0	7,1	11,7	8,9	Tjipanas
Zea mays	22,4	16,1	4,3	10,8	5,7	Tjibodas 9–9.30
	23,9	16,7	8,1	13,2	8,5	Same leaf 9.30–10.30
Oryza sativa	22,3	19,2	6,6	12,0	6,3	Tjidodas
Oryza sativa	28,1	25,3	3,1	7,6	5,2	Bogor, measurements Ida Ismail
Tropical weeds						
Imperata cylindrica	20,8	17,7	7,0	14,0	4,8	Tjibodas
	29,3	25,6	4,2	7,9	9,5	Surabaja
Saccharum spontaneum	25,3	18,5	6,0	11,6	8,9	Tjibodas
Lantana camara	22,6	20,5	7,6	14,3	4,4	
Plants from Savanna vegetation E. Java						
Calotropis gigantea	30,8	25,1	2,2	10,7	3,7	May
	33,6	21,9	–1,0	8,1	5,9	October
Schleichera oleosa	31,1	26,9	8,0	14,7	9,6	
Zizyphus jujuba	30,2	25,6	3,1	8,1	7,3	leaves ⊥ sun
Azadirachta indica	31,2	26,5	4,5	8,5	11,3	leaves ⊥ sun
Plants from dunes and seacoast (Netherlands)						
Rhamnus cathartica	20,4	16,4	8,0	16,3	4,2	
Salix cinerea	20,4	16,4	5,7	13,2	2,6	
Verbascum nigrum	23,9	19,8	5,8	17,0	2,8	
Cynoglossum officinale	21,0	16,2	5,7	11,1	5,7	
Crataegus monogyna	24,3	15,7	8,5	9,0	128	
Ligustrum vulgare	24,3	15,7	9,5	10,0	138	leaf ⊥ sun
Hippophaë rhamnoides	22,1	17,2	7,7	11,0	12,8	leaf ⊥ sun
Convolvulus arvensis	18,1	14,6	14,2	14,6	255	
Eryngium maritimum	18,0	14,4	5,9	13,6	3,2	leaf slightly S-exposed
Aster tripolium	18,0	14,5	10,1	18,4	4,5	leaf slightly S-exposed
Phragmites communis	23,0	16,9	1,0	7,6	3,5	
Plants from desert and S. Spain (Lange)						
Citrullus colocynthis	27,5	20,2	7,5	15,5	7,3	S. Spain
	50,0	24,0	–13,0	10,0	3,5	Sahara

dry air and probably also to a somewhat stronger wind. The same applies to the very strong transpiration cooling of *Citrullus* leaves in the desert. A calculation using the data of Lange shows that *Citrullus* falls within the normal range of strongly transpiring leaves as Lange already supposed it would. It is true that for *Citrullus* in Spain a higher n number was calculated, but the same leaf would have a temperature of 7°C below air temperature under desert conditions. The value of n enables to predict the behaviour of a leaf in a completely different environment than where the measurements were made, as is supported by data given by STOCKER (1954): under desert conditions *Phragmites communis* transpires as strongly as *Citrullus colocynthis*.

The lowest value of n was measured on *Hornstedtia* occurring in openings in the forest. However, as the table shows, much higher values were measured here as well.

Measurements on *Musa acuminata* leaves show that a loss of turgescence is accompanied by an increase of n from 5 to 25.

The morphology of the leaf is a poor guide for an estimation of its transpiring potential, as is again demonstrated by the low n values of *Rhododendron javanicum* and of the temperate beach plant *Eryngium maritimum*. Both have scleromorphic leaves. *Phragmites* could also be called somewhat xeromorphic. The somewhat succulent salt marsh species *Aster tripolium* also has a low n, as have *Cynoglossum* and *Verbascum nigrum* growing in the dry dunes, be it true that the latter two species are not xeromorphic.

We mention in this connection data cited by ADRIANI (1956) showing that among salt marsh plants, *Aster tripolium* has the highest transpiration per unit of leaf surface.

MAXIMOV (1929) and VASSILJEV (1931) have shown that xeromorphic plants in arid areas can have a very strong transpiration per unit of leaf surface.

On the other hand Lange found low transpiration and high leaf temperatures for sclerophyllous mediterranean species. Naturally when the stomata are closed a scleromorphic leaf can reduce its transpiration more effectively than a mesomorphic one. Is it not known whether the sclerophylls studied by Lange can have a high transpiration under conditions of sufficient water supply or have a low transpiration all the year round.

The trees from the dry savanne country in East-Java, *Schleichera*, *Zizyphus* and *Azadirachta* show n numbers which are not among the lowest measured but not very high either. In the same habitat low n numbers were measured on *Calotropis gigantea*.

The leaves of the two forest trees *Altingia* and *Castanopsis* as well as *Polypodium*, the craterfern have high transpiration resistances as have, among others, the temperate plants *Ligustrum vulgare* and *Crataegus monogyna* with more or less scleromorphic, *Convolvulus arvensis* with typically mesomorphic leaves.

In the literature few n values (or their reciprocal values) are given explicitly. Impens found for bean leaves values between 4 and 6 when measurements were made under conditions comparable with ours. Raschke found much higher values (n = 29) for *Canna indica* and *Alocasia indica* but incidentally very low

values were measured (2,2 and 4). Raschke calculated from data by MARTIN (1943) n-values of 3 and less for *Helianthus annuus* leaves.

As mentioned, the value of n is not completely a property of the leaf as such but still somewhat influenced by the environment. It has, however, the advantage that its meaning is easy to grasp.

Through the work of GRADMANN (1928), VAN DEN HONERT (1948) and BANGE (1953) the transport of water through the plant can be understood as to take place via a chain of resistances placed in series. The last two of these resistances are the internal resistance of the leaf (r_l) against water vapour transport (stomata) and the external resistance of the boundary layer on the surface of the leaf. For a wet surface only the external (r_a) resistance exists. Therefore

$$n = \frac{r_a + r_l}{r_a}$$

r_a is inversely proportional to α, *i.e.* it is partly a property of the leaf (size), partly depends upon wind velocity. So it can be understood that the lowest n-values are measured under calm conditions and on big leaves (*Hornstedtia*). The somewhat higher values measured for *Calotropis* and sugar cane must be due to a somewhat stronger air movement.

In literature some data are given on the internal resistance of the leaf against water loss (r_l). The relation between r_l, r_a and n is given by (5). r_a is contained in the constant C in our relation (2) as follows (*cf.* SLATYER, p. 247):

$$C = 590 \cdot \frac{273}{PT} \rho v \cdot \frac{1}{r_a} \text{ cal/cm}^2 \text{ min mm Hg}$$

or

$$C \sim \frac{590 \cdot 10^{-6}}{r_a}$$

as

$$C = \frac{\alpha}{\gamma} \text{ (compare eq. (2), (3))}$$

$$r_a = \frac{\gamma}{\alpha} \cdot 590.10^{-6} \text{ (min/cm)}$$

By estimating α from $R_{net\ (dr)}$ and Δt_{dry} (compare eq. (1)), r_a can be calculated and via n also r_l, eg. for cane sugar $R_{net} \sim 0.9$, $\Delta t_{dry} = 10°C$.

$$\alpha = \frac{0,9}{2.10} = 0,045 \text{ cal/cm}^2 \text{ min °C.}$$

$$r_a = \frac{0,44}{0,045} \cdot 590.10^{-6} = 58.10^{-4} \text{ min/cm}$$

when n = 5

$$r_l = 4r_a = 232.10^{-4} \text{ min/cm}$$
$$= 0,14 \quad \text{sec/cm}$$

Impens found similar values for bean leaves. Slatyer cites values from 0,5 sec/cm upwards, considerably higher than the present values.

It must be realised that an increase in water loss resistance by e.g. a factor 2 does not mean a reduction of transpiration by the same factor, as the following example shows. When a leaf in full sun is at air temperature, e.g. 30 °C, and the vaseline covered leaf has a temperature of 40 °C, a reduction of transpiration to half the original value will mean a temperature rise of the leaf to about 35 °C. When e_{air} is 20 mm Hg, this means that $e_{leaf} - e_{air}$ has risen from 11.8 mm to 22.2 mm. Thus resistance against water loss must have increased by about a factor 3.8. As CO_2 uptake is by the same pathway as transpiration we also see that a reduction of transpiration results in a much stronger increase of the resistance against uptake of CO_2.

The considerations about the mechanism of transpiration also make it possible to estimate the influence of wind and leaf size. On this point many contradictory statements are given in literature (cf. STOCKER 1956).

Wind reduces r_a (which is inversely proportional to α) but it does not influence r_l. Decreasing leaf size also reduces r_a as it increases α.

With a leaf in still air with high n (e.g. 50) transpiration will be weak and leaf temperature considerably above air temperature when insolation is strong. Increasing air movement to a value which reduces r_a to half its original value will reduce the total resistance $r_a + r_l$ with only 1 %. As, however, α is doubled Δt_{tr} is halved. The reduced leaf temperature will reduce $(e_{leaf} - e_{air})$ to a higher degree than $r_a + r_l$, hence there is a reduction of the already low transpiration.

When n is low, e.g. 3, then $r_l = 2$ and $r_a = 1$ in relative units. When r_a is reduced to half its original value there is a total resistance of 2,5. Transpiration would increase with a factor 3/2,5 but this is partly counteracted by the decreased leaf temperature. A calculation along these lines showed that for the case of the *Verbascum nigrum* leaf (*table 1*) indeed an increase in windspeed with a factor 4 (meaning about a doubling of α) would decrease transpiration by about 10 %. When this line of reasoning is correct a small increase of transpiration is possible with increased air movement when leaf temperature is below air temperature or only slightly above it.

Generally speaking a very strong influence of wind on transpiration is rarely to be expected as the bigger part of total leaf resistance is situated inside the leaf and is unaffected by windspeed. The situation becomes different when r_l is affected by the wind, *i.e.*, when there is a pumping effect as some authors suppose (BERNBECK 1924). Leaf temperature measurements combined with measurements of transpiration in a windtunnel would enable to decide by which mechanism wind influences transpiration.

I am very grateful to the Director and staff of the National Biological Institute at Bogor (Java) for their help and hospitality and to my pupils (of which I want to mention in particular Miss Puspa Dewi Natalie and Miss Ida Ismail) for their assistance.

REFERENCES

ADRIANI, M. J. (1956): Der Wasserhaushalt der Halophyten. *Handb. Pflanzenphysiol.* **III**: 902–914. Springer.

BANGE, G. G. J. (1953): On the quantitative explanation of stomatal transpiration. *Acta Bot. Neerl.* **2**: 255–298.

BERNBECK, O. (1924): Wind und Pflanze. *Flora N. F.* **17**: 293–300.

GESSNER, F. (1956): Der Wasserhaushalt der Hydrophyten und Helophyten. *Handb. Pflanzenphysiol.* **III**: 853–901. Springer.

GRADMANN, H. (1928): Untersuchungen über die Wasserverhältnisse des Bodens als Grundlage des Pflanzenwachstums. *Jahrb. Wiss. Bot.* **69**: 1.

HELD, E. F. M. VAN DER (1937): De psychrometerconstante. *Warmtetechniek* **8**.

HONERT, T. H. VAN DEN (1948): Watertransport in plants as a catenary process. *Disc. Faraday Soc.* **3**: 146.

IMPENS, I. I. (1966): Leaf wetness, diffusion resistances and transpiration rates of bean leaves (Phaseolus vulgaris L.) through comparison of "Wet" and "Dry" leaf temperatures. *Oecol. Plant.* **1**: 327–334.

LANGE, O. L. (1959): Untersuchungen über Wärmehaushalt und Hitzeresistenz mauretanischer Wüsten- und Savannenpflanzen. *Flora* **147**: 595–651.

— & LANGE, R. (1963): Untersuchungen über Blattemperaturen, Transpiration und Hitzeresistenz an Pflanzen mediterraner Standorte. (Costa Brava, Spanien). *Flora* **153**: 387–425.

MARTIN, E. V. (1943): Studies of evaporation and transpiration under controlled conditions. *Carnegie Inst. Wash. Publ.* **550**.

MAXIMOV, N. A. (1929): *The plant in relation to water.* Allen and Unwin, London.

RASCHKE, K. (1956): Ueber die physikalischen Beziehungen zwischen Wärmeübergangszahl, Strahlungsaustausch, Temperatur und Transpiration eines Blattes. *Planta* **48**: 200–238.

RUINEN, J. (1961): The phyllosphere, an ecologically neglected milieu. *Plant and Soil* **15**: 81–109.

SEYBOLD, A, & H. G. VAN DER WEY (1929): Untersuchungen über iso- and heterokalorische Laubblätter. *Rec. Trav. bot. Néerl.* **26**: 97–127.

SLATYER, R. O. (1967): *Plant-water relationships.* Academic Press, London and New York.

STOCKER, O. (1954): Der Wasser- und Assimilationshaushalt südalgerischer Wüstenpflanzen. *Ber. Dtsch. Bot. Ges.* **67**: 289–299.

— (1956): Die Abhängigkeit der Transpiration von den Umweltfaktoren. *Handb. Pflanzenphys.* **III**: 436–488. Springer.

STOUTJESDIJK, Ph. (1961): Micrometeorological measurements in vegetations of various structure. *Proc. Kon. Ned. Ak. Wet.* C. **64**: 171–207.

— (1966): On the measurement of the radiant temperature of vegetation surfaces and leaves. *Wentia* **15**: 191–202.

VASSILJEV, J. M. (1931): Ueber den Wasserhaushalt von Pflanzen der Sandwüste im südöstlichen Kara-Kum. *Planta* **14**: 225–309.

WALTER, H. (1960): *Einführung in die Phytologie III, Teil I: Standortslehre.* Ulmer, Stuttgart.