Water permeability of plant cuticles: permeance, diffusion and partition coefficients

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Summary. Using isolated cuticular membranes from ten woody and herbaceous plant species, permeance and diffusion coefficients for water were measured, and partition coefficients were calculated. The cuticular membranes of fruit had much higher permeance and diffusion coefficients than leaf cuticular membranes from either trees or herbs. Both diffusion and partition coefficients increased with increasing membrane thickness. Thin cuticles, therefore, tend to be better and more efficient water barriers than thick cuticles. We compared the diffusion coefficients and the water content of cuticles as calculated from transport measurements with those obtained from water vapor sorption. There is good to fair agreement for cuticular membranes with a low water content, but large discrepancies appear for polymer matrix membranes with high permeance. This is probably due to the fact that diffusion coefficients obtained from transport measurements on membranes with high permeance and water content are underestimated. Water permeabilities of polyethylene and polypropylene membranes are similar to those of leaf cuticular membranes. However, leaf cuticles have much lower diffusion coefficients and a much greater water content than these synthetic polymers. This suggests that cuticles are primarily mobility barriers as far as water transport is concerned.

Key words: Cuticular transpiration — Diffusion coefficients — Plant cuticle — Water content — Water permeability

Introduction

Permeability coefficients are composite quantities, depending both on the mobility of a species (diffusion coefficient) and its concentration in the membrane (Crank 1975). Water permeability coefficients determined for plant cuticles in the past (Schönherr 1976a, b, 1982; Schönherr and Schmidt 1979; Schönherr and Lendzian 1981; Schönherr and Mérida 1981; Schönherr et al. 1979) could not be analysed in terms of properties of the membranes studied, as neither diffusion nor partition coefficients were known. By using an electrolytic method we were able to measure both the permeability and mobility of water through cuticles. From these data partition coefficients can be calculated.

Materials and methods

Cuticular membranes

Cuticles were isolated enzymatically as described earlier (Riederer and Schönherr 1984; Schönherr and Riederer 1986). Astomatous cuticles were obtained from mature leaves of trees or herbaceous plants (*Citrus aurantium* L.; *Clivia miniata* Reg.; *Ficus elastica* Roxb. var. *decora*; *Hedera helix* L.; *Nerium oleander* L.; *Pyrus communis* L. cv. Bartlett, *Schefflera actinophylla* (Endl.) Harms) and from mature fruits (*Capsicum annuum* L.; *Lycopersicon esculentum* Mill.; *Solanum melongena* L.).

Isolated cuticles will be referred to as cuticular membranes (CM). Extraction of CM with chloroform/methanol removes the soluble cuticular lipids (SCL) and yields the polymer matrix membranes (MX-membranes). The thickness of the membranes was estimated from their mass and area using a specific gravity of 1100 kg/m³ (unpublished results). For tomato and pepper fruit cuticles corrected gravimetric thicknesses were obtained as described by Riederer and Schönherr 1985.

Apparatus and methods

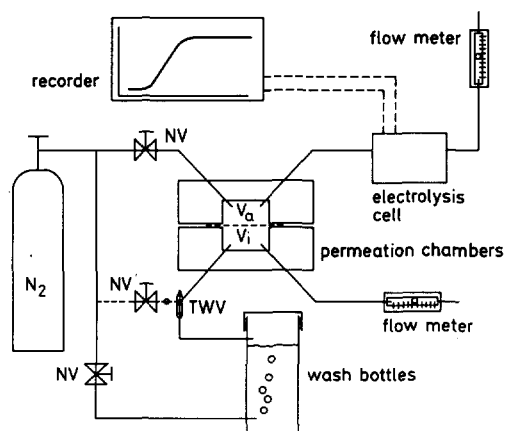The transport apparatus was made of brass and consisted of two half-cells, separated by the membrane to be studied
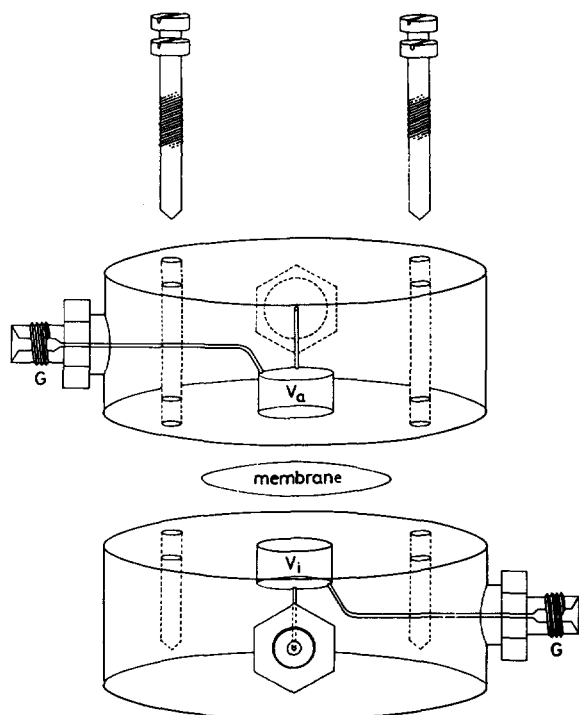
Fig. 1. Drawing of the permeation chambers between which the membrane is sandwiched. V_a and V_i are the gas volumes of the outer and the inner chambers respectively; G are the inlets and outlets for the N_2 streams

Fig. 2. Diagram of experimental arrangement. NV, needle valve; TWV, three-way valve; V_a and V_i are the gas volumes of the outer and inner chambers of the permeation chambers, respectively

(Fig. 1). To obtain an air-tight seal, the surfaces of the half-cells were lightly coated with silicon grease (Wacker, Munich, FRG) before the membrane was inserted and the half-cells screwed together. The gas volume of the half-cell facing the outer surface of the cuticle (V_a) will be referred to as the outer chamber. The volume facing the inner surface of the cuticle (V_i) will be called the inner chamber.

Initially, the outer and inner chambers were flushed with dry nitrogen gas to remove all water from the membrane and chambers. The experiment was started by flushing the inner chamber with moist N_2 of a predetermined water vapour concentration. The outer chamber was constantly flushed with dry N_2 to carry the water molecules penetrating the cuticles to the electrolysis cell developed by Keidel (1959). In this cell the water is trapped by P_2O_5 and then electrolytically cleaved to form O_2 and H_2. The current needed for electrolysis is proportional to the amount of water cleaved. This current is recorded. A current of 1 μA is equivalent to 9.34×10^{-14} kg water/s. For further details the reader is referred to the paper by Rust and Herrero (1969) in which the theory of the method as well as its use and limitations are discussed.

The experimental set-up is shown in Fig. 2. The N_2 was dried using Sicapent (Merck, Darmstadt, FRG) or molecular sieve 4 Å (Merck, FRG) and passed through a copper coil submerged in a thermostated water bath maintained at $25° \pm 0.1$ °C before entering the permeation chambers. Flow rates of N_2 were adjusted using flow meters positioned at the exit of the inner permeation chamber and at the exit of the electrolysis cell of the WDD Aquanat (NATEC, Hamburg, FRG). The electrolysis current is recorded continuously.

In most experiments the inner chamber was flushed with N_2 saturated with water vapour, which was obtained by bub-

bling the N_2 through two wash bottles maintained at $25° \pm 0.1$ °C. Humidities below 100% were obtained by the dew point method, i.e. passing the N_2 through wash bottles in a second thermostat maintained at the desired temperatures.

This type of arrangement could be used for membranes having a permeance up to 9×10^{-4} m/s. Water flow rates greater than this limit would damage the electrolysis cell; thus with some *Citrus* MX-membranes it was necessary to split the N_2-stream coming from the outer chamber. The split ratio was determined using two bubble flow meters.

Equations and calculations

The water flow (F in kg/s) across cuticles was calculated from the electrolysis current (I in μA) using Eq. (1):

$$F = \Delta I \times 9.34 \times 10^{-14} \text{ kg μA}^{-1} \text{ s}^{-1} \qquad (1)$$

where ΔI is the difference between the steady-state electrolysis current [$I(t_i)$] and the background current [$I(t_o)$] recorded when both chambers were flushed with dry nitrogen gas (Fig. 3).

Permeance coefficients (P in m/s) are obtained as the ratio of flow (F in kg/s) per unit area (A in m^2) and driving force (ΔC in kg/m^3):

$$P = \frac{F}{A \Delta C} \qquad (2)$$

In Eq. (2) the concentration of the water vapour (C) in the inner chamber may be used instead of ΔC, since the vapour concentration in the outer chamber is essentially kept at zero by properly adjusting the flow rate of N_2.

At 25 °C and 100% humidity (partial pressure of water vapour, p/p_o is unity) C in the inner chamber amounts to 23.05×10^{-3} kg/m^3.

The permeability coefficient (p in m^2/s) is the permeance of a 1-m-thick cuticle and is calculated as the product of permeance and membrane thickness (l in m).

Diffusion coefficients (D in m^2/s) were obtained by the method of Rust and Herrero (1969) and Felder et al. (1975):

$$D = \frac{I(t_i) \, l^2}{6 \int_{t_0}^{t_i} [I(t_i) - I(t_0)] \, dt} \qquad (3)$$

$$\int_{5}^{47}\left[I(t_1) - I(t_0)\right]\,dt = 4.42 \cdot 10^{-2}\,\text{As}$$
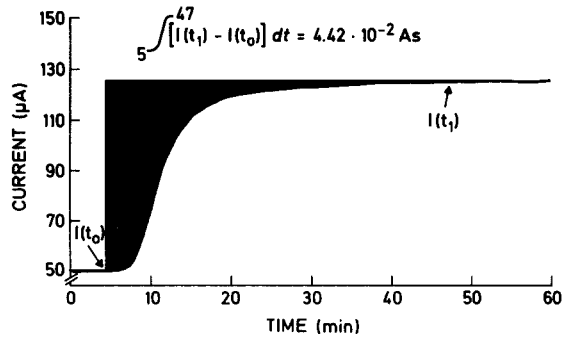
Fig. 3. Current vs time plot obtained for water permeation across a polyethyleneterephthalate membrane

The integral in the denominator represents the area above the permeation curve (electrolysis current vs time) from the start of the experiment until steady state is reached (Fig. 3). The numercial value of the integral was obtained by the cut and weigh method. In cases where D depends on C, the value of D represents an average diffusion coefficient.

With p and D known, the partition coefficient (K) can be calculated (Crank 1975; Rust and Herrero 1969; Yasuda and Stannett 1962):

$$K = \frac{p}{D} = \frac{\bar{C}}{C} \tag{4}$$

K is the ratio of the equilibrium water concentration in the cuticle ($\bar{C}$ in kg/m^3) and the water vapour concentration in the nitrogen atmosphere (C in kg/m^3).

Testing the apparatus

At low flow rates of N_2 in the outer chamber, the water permeability of membranes was dependent on flow rates due to unstirred layers over the membrane surface. Flow rates ranging from 0.8 to 1.5 l/h were sufficient to obtain permeance coefficients in CM that were independent of N_2-flow rates. This amounts to one to two changes in carrier gas volume per second. Due to the much higher permeability of MX-membranes, N_2-carrier gas flow rates up to 16 l/h were necessary to achieve permeances independent of flow. In these cases the carrier gas coming from the outer chamber was split before entering the electrolysis cell. This was necessary since the efficiency of the electrolysis cell decreases when carrier gas flow rates exceed 6 l/h (Rust and Herrero 1969).

The performance of the apparatus was checked using a polyethyleneterephthalate (PETP) membrane. The water permeance of the membrane ($l = 26 \times 10^{-6}$ m; $A = 0.5 \times 10^{-4}$ m^2) as determined gravimetrically (Schönherr and

Table 1. Parameters describing water permeability of astomatous cuticular membranes

Species	l (μm)	P (m/s)	p (m^2/s)	D (m^2/s)	K	$\bar{C}$ (kg/kg)
Leaves						
Schefflera	2.96	8.19×10^{-7} [a] $(5.19-11.19)$ [b]	2.43×10^{-12} [a] $(1.49-3.39)$ [b]	1.57×10^{-15} [a] $(0.99-2.17)$ [b]	1 578 [a]	0.032
Clivia	6.50	1.14×10^{-6} $(0.67-1.61)$	7.42×10^{-12} $(4.27-10.5)$	9.14×10^{-15} $(4.32-13.96)$	812	0.017
Hedera	4.33	2.66×10^{-6} $(1.45-3.87)$	1.16×10^{-11} $(0.60-1.73)$	3.35×10^{-15} $(2.38-4.33)$	3 463	0.073
Nerium	12.81	3.25×10^{-6} $(1.55-4.95)$	4.17×10^{-11} $(1.84-6.50)$	2.85×10^{-14} $(1.41-3.75)$	1 612	0.034
Ficus	5.68	4.25×10^{-6} $(3.21-5.20)$	2.41×10^{-11} $(1.89-2.91)$	1.05×10^{-14} $(0.88-1.22)$	2 295	0.048
Citrus	2.87	1.20×10^{-5} $(1.04-1.38)$	3.44×10^{-11} $(2.60-4.32)$	5.20×10^{-15} $(2.80-7.50)$	6 615	0.139
Pyrus	3.12	1.22×10^{-5} $(0.68-1.77)$	3.80×10^{-11} $(2.11-5.50)$	2.95×10^{-15} $(1.85-4.05)$	12 881	0.270
Fruits						
Solanum	6.47	2.23×10^{-5} $(0.68-3.79)$	1.26×10^{-10} $(0.63-1.85)$	1.08×10^{-14} $(0.28-1.88)$	11 666	0.240
Capsicum	8.03	9.28×10^{-5} $(4.47-14.1)$	7.44×10^{-10} $(3.40-11.5)$	2.98×10^{-14} $(2.16-3.80)$	24 966	0.523
Lycopersicon	8.00	1.42×10^{-4} $(1.10-1.84)$	1.13×10^{-9} $(0.86-1.40)$	4.96×10^{-14} $(3.37-6.18)$	22 783	0.477
Maximum/Minimum	4.46	173	465	32	31	31

[a] Means of four (Lycopersicon) or six membranes; [b] 95% confidence interval

Water content ($\bar{C}$) was calculated for cuticular membranes in equilibrium with air containing 23.05×10^{-3} kg/m^3 water. A specific gravity of cuticles of 1100 kg/m^3 was used in calculations

Table 2. Parameters describing water permeability of synthetic polymer membranes of low water permeability

Polymer	p (m^2/s)	D (m^2/s)	K	$\bar{C}$ (kg/kg)	Density (kg/m^3)
Polyethylene	6.04×10^{-11}	8.20×10^{-12}	7.36	0.185×10^{-3}	920
	3.29×10^{-11}	1.22×10^{-12}	26.97	0.654×10^{-3}	950
Polypropylene	1.87×10^{-11}	4.90×10^{-13}	96.99	0.970×10^{-3}	907
Polyethyleneterephthalate	1.27×10^{-10}	2.70×10^{-13}	470.00	7.810×10^{-3}	1389

Data taken from Rust and Herrero (1969)

Lendzian 1981) was 6.85×10^{-6} m/s. The coefficient of variation of repeated determinations was less than 4%.

The plot of electrolysis current vs time for the PETP membrane is shown in Fig. 3. After a short hold-up time the current increased sigmoidally and finally reached a plateau, the steady-state current (127 µA), after approximately 47 min. The background current (46 µA) is due to residual moisture in the carrier gas. The net current resulting from flow of water across the membrane was 81 µA in the steady state. The integral has the calue of 4.42×10^{-2} A s.

In this experiment $C = 23.05 \times 10^{-3}$ kg/m^3 and the permeance (Eq. 2) and diffusion coefficients (Eq. 3) were 6.56×10^{-6} m/s and 1.91×10^{-13} m^2/s, respectively. The coefficients of variation for repeated determinations using the same membrane were 1% and 7%, respectively. There is good agreement between the permeances measured gravimetrically and those obtained electrolytically, and the diffusion coefficient is similar to values taken from the literature (Table 2).

Permeance coefficients calculated using the gradient of water vapour concentration (Eq. 2) as the driving force have the same dimension (m/s) as those obtained using the gradient of water (vapour) activity (Schönherr and Schmidt 1979) or the gradient of radioactivity (THO) (Schönherr 1976a), but they are not numerically identical. At 25 °C permeances calculated from Eq. 2 are larger by a factor of 43384 than the coefficients of previous papers from this laboratory. For temperatures other than 25 °C the conversion factor can be calculated as the ratio of density of liquid water and density of water vapour.

A further difference in nomenclature compared with our earlier work should be pointed out. The nomenclature adapted here is that used by Hartley and Graham-Bryce (1980). What we are now calling permeance (flow per unit area and driving force) used to be referred to as permeability coefficient (m/s), and the permeability coefficient of this paper (permeance of a 1-m thick membrane) was previously referred to as specific permeability (Schönherr 1982).

Results

The cuticular membranes studied had permeances ranging from 8.19×10^{-7} *(Schefflera)* to 1.42×10^{-4} m/s *(Lycopersicon)*. Generally, fruit cuticles were more permeable than leaf cuticles and permeances differed by a factor of 173 (Table 1). Differences between species are even larger when comparisons are made on a unit thickness (1 m) basis, as permeability coefficients differed by a factor of 465. *Schefflera* CM had the lowest
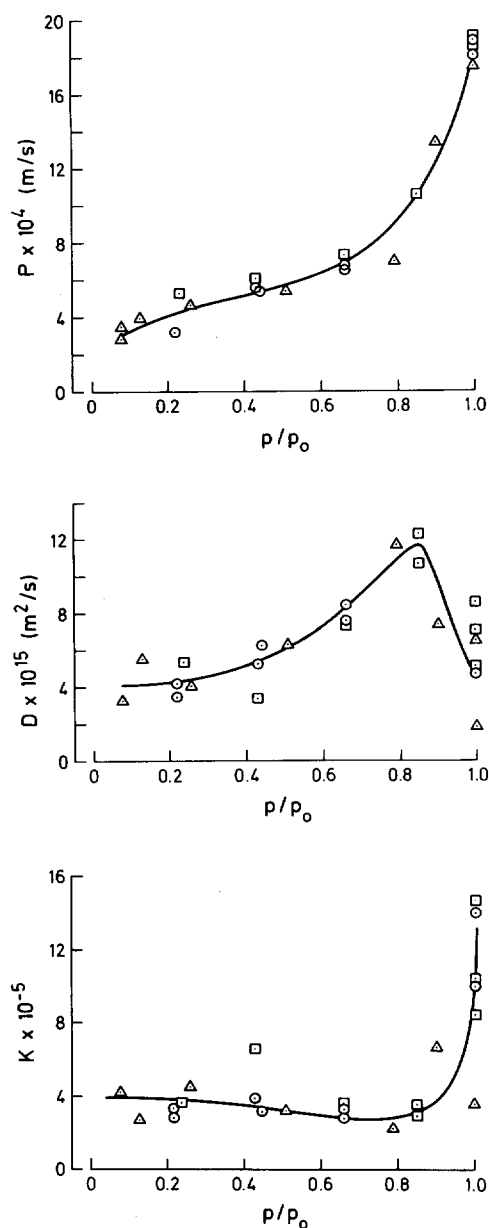
Fig. 4. The effect of driving force (partial pressure of water vapor, p/p_o) on water permeability parameters for three *Citrus* polymer matrix membranes
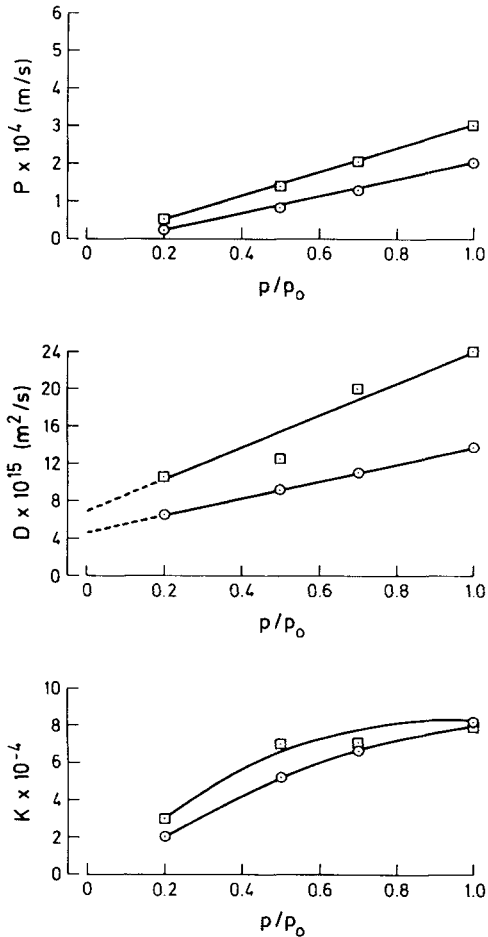
Fig. 5. The effect of driving force (partial pressure of water vapor, p/p_o) on water permeability parameters of two *Ficus* polymer matrix membranes

diffusion cofficient $(1.57 \times 10^{-15} \text{ m}^2/\text{s})$, but the CM having the highest D *(Lycopersicon)* differed only by a factor of 32. A similar range was observed for the partition coefficients and water content of CM (Table 1).

The effect of the magnitude of the driving force *(C)* on permeance and diffusion coefficients was studied using polymer matrix membranes from *Citrus* and *Ficus* leaves. Permeance increased in both cases with increasing driving force (Figs. 4, 5), but the shapes of the graphs differ. At maximum driving force $(p/p_o = 1)$ permeance coefficients of MX-membranes were about 2 orders of magnitude larger than those for CM.

Diffusion coefficients for water in MX-membranes were only slightly larger than in CM and they increased with increasing driving force (p/p_o). With *Citrus* MX-membranes a sudden decrease in D was observed at $p/p_o = 1$ (Figs. 4, 5).

Discussion

Cuticles function to minimize passive water loss from plant to the atmosphere. The permeances of this rather arbitrary selection of species differed by a factor of 173. Transpirational water fluxes can be calculated from the data by multiplying permeance coefficients with the driving force. Assuming the absence of unstirred air layers, and humidities of 0% at the outer surface and 100% at the inner surface of the cuticles (or pure water), maximum transpiration rates at 25 °C are obtained by multiplying P with $23.05 = 10^{-3} \text{ kg/m}^3$.

For fruit cuticles maximum transpiration rates range from 44 (aubergine) to 283 g water m^{-2} day^{-1} (tomato). These are fairly high transpiration rates (and in reality water loss will be considerably smaller due to unstirred layers and higher humidities of the atmosphere), but since developing fruits depend on the transpiration stream for their supply of mineral nutrients, these high rates appear to be functional. To reduce transpiration to a minimum level (as found for leaves) would not be meaningful for such fruits, which have no stomata to regulate their water status.

Lowest permeances were observed for adaxial leaf cuticles. Maximum transpiration rates ranged from 1.63 *(Schefflera)* to 24.3 g m^{-2} day^{-1} (pear leaf). For leaves a strategy which aims at keeping cuticular transpiration rates as low as possible appears meaningful, because water status can be regulated via stomata.

Although the physiological implications of the large differences in permeance coefficients observed are interesting, we shall not discuss this aspect further. Instead, we shall focus on the question of how these permeances and their differences come about.

In homogeneous membranes water permeability coefficients depend only on the mobility of water in the membrane (D) and on the water content of the membrane (Crank 1975), since

$$p = DK \qquad (5)$$

where the partition coefficient (K) relates the equilibrium water concentrations of the membrane to that of the surrounding atmosphere (Eq. 4). It follows that cuticles of low water permeability should have both low diffusion and low partition coefficients. For a homogeneous membrane of a given p and given driving force, the water flow will be inversely proportional to membrane thickness.

Most xeromorphic plant species have relatively thick cuticles; this is usually interpreted as an
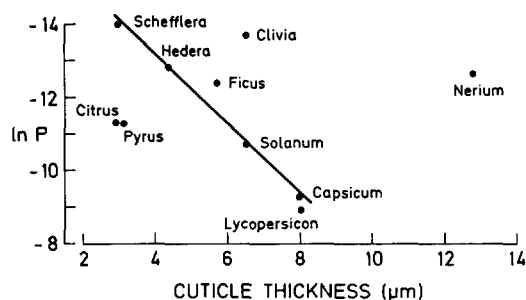
Fig. 6. Dependence of the logarithm of the permeance coefficient (ln P) on thickness of cuticles

adaptation to water stress. However, Kamp (1930) and Schönherr (1982) found that thick cuticles are not necessarily better water barriers than thin cuticles. Our present study confirms these findings (Table 1). The thickest cuticle studied was that of *Nerium*. It was 4.3 times thicker than that of *Schefflera* but 4 times more permeable to water. *Hedera* and *Ficus* CMs were less than half as thick as that of *Nerium* but their water permeabilities were similar.

A good linear correlation was found, when ln D was plotted vs the thickness of cuticles (ln D = 0.49 l − 35.08; r = 0.92; l in μm). This implies that diffusion coefficients increase with increasing thickness of cuticles. Only *Nerium* did not fit the equation.

As D is a determinant of p (Eq. 5), one might expect that water permeability would decrease with decreasing thickness of cuticles. However, the correlation coefficient was only 0.58 (*Nerium* not included) and inspection of the graph ln P = al+b (Fig. 6) shows that in addition to *Nerium, Citrus, Pyrus* and *Clivia* do not fall on the line. With the remaining six species water permeability increased with increasing thickness of cuticles, in contrast to the common believe that thick cuticles are better water barriers than thin ones.

The second determinant of water permeability is the partition coefficient, that is, the water content of the membranes. By reference to Table 1 it can be seen that the departure of *Citrus* and *Pyrus* from the line is due to a much higher water content when compared with *Schefflera*, which has cuticles of similar thickness. *Clivia* cuticles, on the other hand, have an exceptionally low water content and therefore a much lower water permeability than *Solanum* cuticles, which are of similar thickness.

Looking at all the species tested (except *Nerium*), there is a significant correlation between D and K (r = 0.80). D tends to increase as K increases. This type of dependence has also generally been observed with most synthetic polymer membranes (Yasuda and Stannett 1962).

Equation (5) was derived for homogeneous membranes, which obey Henry's law (C = KC). In heterogeneous membranes D values calculated from Eq. (3) represent a form of average, and their magnitude depends on the type of structural heterogeneity and on the diffusion coefficients within the individual components (Barrer 1968). These D values may still be used to characterize mobility of water in the membranes but application of Eq. (5) to calculate C will lead to erroneous values (Yasuda and Stannett 1962).

To test the assumptions inherent in Eq. (5), the D and C values obtained from transport measurements should be compared with D and C values obtained from water vapour sorption. We do not have such data but some preliminary results were made available to us by Drs. Chamel, Escoubes and Pineri (Grenoble, France). These show that sorption isotherms (25 °C) for *Citrus* and *Ficus* CMs are not linear, and at p/p_0 = 1 the water contents of approximately 150 g/kg and 60 g/kg were obtained, respectively. These figures agree well with ours (Table 1). Diffusion coefficients measured at low water content (p/p_0 = 0.03) were 1.2 × 10^{-14} m²/s and 9 × 10^{-15} m²/s for *Ficus* and *Citrus* CMs, respectively. Again, these values are not too far from ours obtained from transport studies (Table 1). However D values obtained from sorption studies increased with increasing water content (with increasing p/p_0); with a higher water content of CM, agreement between our D values and those from the sorption experiments is no longer good. Thus, by using our D values (which appear to be too low) the water content estimated from Eqs. (4) and (5) are likely to be overestimates.

Water permeance of MX-membranes increased with increasing partial pressure (Figs. 4, 5). Diffusion coefficients increased as well, but this increase could not completely account for the effect of p/p_0 on P. Diffusion coefficients were not much larger than those calculated for CMs (Table 1; Figs. 4, 5), and they were between 8 *(Citrus)* and 29 *(Ficus)* times higher than those obtained from sorption studies.

Therefore, all partition coefficients calculated for MX-membranes are unrealistically high (Figs. 4, 5). Our data give no hint as to why diffusion coefficients in MX-membranes are so grossly underestimated. Structural heterogeneity and deviations from Henry's law very likely play a role. Again, complete sorption data are required before

an attempt can be made to analyse this problem.

In spite of these difficulties it is clear that diffusion coefficients in cuticles are extremely low, even in the polymer matrix, where figures of 3×10^{-13} to 3×10^{-14} m²/s were calculated from sorption experiments. These D values are one to two orders of magnitude smaller than those for synthetic polymer membranes of low water permeability (Table 2). Permeability coefficients, however, are similar to those of leaf cuticular membranes (Table 1) because of the extremely low water content of synthetic polymers.

A water content as low as that of polyethylene cannot be realized by plant cuticles, as cutin always contains a considerable number of polar groups. For example, a polyester made up of C_{16}-hydroxy-fatty acid residues (monomer molecular weight 269) will contain 3.72 mol of ester bonds/kg cutin. If only 1 mol water is sorbed per mole of ester linkage the polyester will contain 67 g/kg water. This calculation neglects free hydroxyl groups and other polar constituents of cutin (Holloway 1982), but it results in a water content similar to that found for leaf CM (Table 1).

Since polar groups in cutin are unavoidable, cuticles of low water permeability must have very low diffusion coefficients. Plant cuticles are mainly mobility barriers as can be seen by comparing diffusion coefficients in cuticles with those of water in a liquid hydrocarbon membrane (hexadecane) where a value of 4×19^{-9} m²/s was measured (Schatzberg 1965). This value is 4 to 5 orders of magnitude larger than D in MX-membranes and up to 6 orders of magnitude larger than in cuticular membranes.

These differences can be attributed in part to the fact that cuticles are solid-state membranes with a high degree of cross-linking. Crystalline, soluble, cuticular lipids associated with the cutin polymer reduce water permeance by 2 to 3 orders of magnitude (Schönherr 1982). However, this effect still cannot be analysed, since diffusion coefficients in MX-membranes calculated from transport measurements greatly underestimate the mobility of water in the polymer matrix.

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