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Pachepsky, L. B.
Duke University Phytotron

Ferreyra, R. A.
CEPROCOR | Facultad de Cciencias Agropecuarias Universidad Nacional de Cordoba

Collino, D.
IFFIVE-INTA

Acock, B.
RSML USDA-ARS

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TRANSPIRATION RATES AND LEAF BOUNDARY LAYER PARAMETERS FOR PEANUT ANALYZED WITH THE TWO-DIMENSIONAL MODEL 2DLEAF

L. B. PACHEPSKY[1,2], R. A. FERREYRA[3,4], D. COLLINO[5], and B. ACOCK[1]

[1]*RSML, USDA-ARS, Beltsville, MD 20705, USA*
[2]*Duke University Phytotron, Durham, NC 27705, USA*
[3]*CEPROCOR, Córdoba, Argentina*
[4]*Facultad de Cciencias Agropecuarias, Universidad Nacional de Córdoba, Córdoba, Argentina*
[5]*IFFIVE-INTA, Córdoba, Argentina*

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PACHEPSKY L. B., FERREYRA R. A., COLLINO D. and ACOCK B. *Transpiration rates and leaf boundary layer parameters for peanut analyzed with the two-dimensional model 2DLEAF.* BIOTRONICS **28**, 1–12, 1999. Rates of leaf transpiration and photosynthesis are both affected by the thickness of the boundary layer (BL) and by the rates at which gases diffuse through it. These BL properties are currently impossible to measure and must be estimated by using models in conjunction with measured rates of transpiration. Transpiration rates and BL for two Argentine peanut (*Arachis hypogaea* L.) cultivars, Florman INTA, Virginia type, and Manfredi 393 INTA, Spanish type, were studied with the two-dimensional model 2DLEAF which accounts for leaf anatomy, i. e. for leaf internal structure and stomatal density. Measurements on leaf cross-sections and leaf surface images demonstrated a significant difference between two cultivars. Published transpiration rates for peanut of Virginia and Spanish types measured in controlled environment and field conditions were used to determine two parameters of the leaf BL, its thickness, d, and the ratio of diffusion coefficients in the BL and in the intercellular space, B. Both parameters were different for two cultivars. Transpiration rate was presented (a) as a function of BL parameters d and B with four empirical parameters which depended on cultivar and stomatal aperture, and (b) as a function of stomatal aperture and d. Dependence (b) showed that the transpiration rate of Manfredi 393 INTA is higher than that of Florman at the same environmental conditions, and that this is completely due to the difference in leaf anatomy. It was shown that the values of BL thickness, d, grow with increasing stomatal aperture. For amphystomatous leaves of peanut, two empirical parameters, d and B, are necessary and sufficient to quantitatively describe the effect of the BL on transpiration.

Key words: transpiration; leaf boundary layer; diffusion; two-dimensional modeling; leaf anatomy; peanut; *Arachis hypogaea* L.

INTRODUCTION

Although peanut (*Arachis hypogaea* L.) has a potential for high rates of photosynthesis as compared with other C_3 species (*12*) in both controlled environment (*13*) and field (*14*) studies, peanut yields are comparatively low (*15*). Pallas *et al.* (*15*) also indicated that while there are many possible explanations for the low yeilds, studying peanut leaf anatomy, which is different from that of other species, and which could cause differences in leaf gas exchange, seems to be very useful in understanding the physiological processes governig higher yields. Wright and Bell (*18*) in a series of field studies in subtropical Australia, showed, in particular, that crop water deficit of varying duration and intensity can decrease peanut yield. At the same time, Bhagsari *et al.* (*1*) and Klepper (*7*) indicated that peanut photosynthesis is not reduced as drastically by water stress as it is in some other crops. Peanut maintained a higher leaf water content than barley, wheat, and soybean leaves in relatively dry soil. Transpiration rates of peanut plants in soil at wilting water contents were reported to be about 66% of the maximum and the plants had their stomata partially open (*19*).

All studies of peanut leaf anatomy (see for example, *12* and *17*) show that peanut leaves contain a subepidermal layer of large water storage cells adjacent to the abaxial side; these cells may help compensate for water loss during water stress. Therefore, leaf anatomy effect on transpiration needs to be studied in peanut.

The model 2DLEAF, that accounts for leaf anatomy in simulating leaf transpiration and photosynthesis, has been developed and used to study leaf photosynthesis and transpiration for a number of plant species (*10, 11*). The problem with using 2DLEAF in transpiration studies is the leaf boundary layer (BL), a part of the atmosphere near the leaf surface with special gas transport characteristics, which affects transpiration rate drastically (*9*). Even measuring the leaf BL thickness doesn't seem possible currently, and modeling the leaf BL appears to be the only way to study transpiration at the mechanistic level. Description of the leaf BL with two parameters, thickness d and the ratio of the coefficient of diffusion in the BL and in the intercellular space, B, used to study transpiration of hypostomatous potato leaves both normal and transgenic (*11*), allows the quantitative description of the leaf BL in two-dimensional leaf gas exchange model.

The objectives of this work were (i) to determine the values of the leaf BL parameters with the data on leaf anatomy for two peanut cultivars and the data on transpiration in field and controlled environment conditions and (ii) to estimate the effect of leaf anatomy on transpiration.

MATERIALS AND METHODS

Plant materials

Two peanut (*Arachis hypogaea* L.) cultivars, Florman INTA and Manfredi 393

INTA, of different botanical types, Virginia and Spanish, respectively, were grown at the experimental station of the IFFIVE–INTA (31°28' S; 64°08' W, 474 m above sea level), Córdoba, Argentina, in 1997/98 growing season: Some researchers consider Manfredi 393 INTA an intermediate between Spanish and Virginia. The seeds were sown on November 19th, 1997, using seeds previously treated with the fungicide carboxin (Vitamax: Uniroyal Quimica S. A., Argentina); row spacing was 0.7 m, with a plant density of 14.28 plants/m^2. Weed control was done manually, and diseases were controlled applying the fungicide tebuconazole (Folicur: Bayer Argentina S. A., Argentina) and the insecticide abamectin (Vertimec: Merck, Sharp & Dohme Argentina S. A., Argentina). The soil in which the crops grew is a deep silt loam Entic Haplustoll, with supplementary drip irrigation until 45 days after planting.

The Florman INTA cultivar was obtained in 1985 as a result of selection from the Florunner cultivar (INTA, 1986). Its development cycle is 140–155 days long. Leaves usually have four small to medium leaflets, dark green in color; very occasionally they present five or six leaflets. Very high photosynthetic rates, up to 55 μmol m^{-2} s^{-1}, were observed for cultivars originated from Florunner at high light intensities and favorable water conditions (*13*). Observed transpiration rates for these cultivars varied in a wide range of values, up to 46.3 mmol m^{-2} s^{-1} (*15*). The cultivar Manfredi 393 INTA was obtained in 1994 through a genealogical selection introduced from ICRISAT (India) in 1982, originated from a crossing between the Robut 33–1 and Nc. Ac 2698 lines. Its development cycle is 135–145 days long. In general, for peanut cultivars of the Spanish type, photosynthetic rates are in average 10% lower than those of the Virginia type (*12*), whereas transpiration rates are very variable and different in field and closed environmental conditions.

Leaves for the anatomical analysis were collected from both crops at the 120 th day of the crop cycle for cross–section analysis (10 leaves for each cultivar) and at 90th day for studying leaf surfaces, both adaxial and abaxial (11 leaves from each cultivar). One leaflet from the first fully expanded and fully developed leaf (usually the second or third from the apex) on the main stem of randomly selected plants were collected. Leaf epidermis samples were obtained by mechanical peeling from the adaxial and abaxial surfaces of the leaflets. Samples of leaf cross–sections were obtained without a microtome, by pressing leaf samples between sheets of plastic foam and extracting samples with razor. Slides were prepared and observed under a magnification of 200X under a microscope with imaging capabilities, which was also used to digitize the resulting images. Dimensions on the images were obtained by comparing with a known reference viewed under the same conditions.

Leaf cross–sections and leaf surfaces images (examples for both cultivars are presented in Fig. 1) were scanned and the SigmaScan software package was used to measure the sized of cells of different tissues, as well as the leaf thickness and the volume of the leaf and different tissues within it. The results of these measurements were summarized in leaf cross–section schematization (Fig. 2) which were used as domains for calculating with the 2DLEAF model. Table 1

presents the results of some leaf surface measurements.

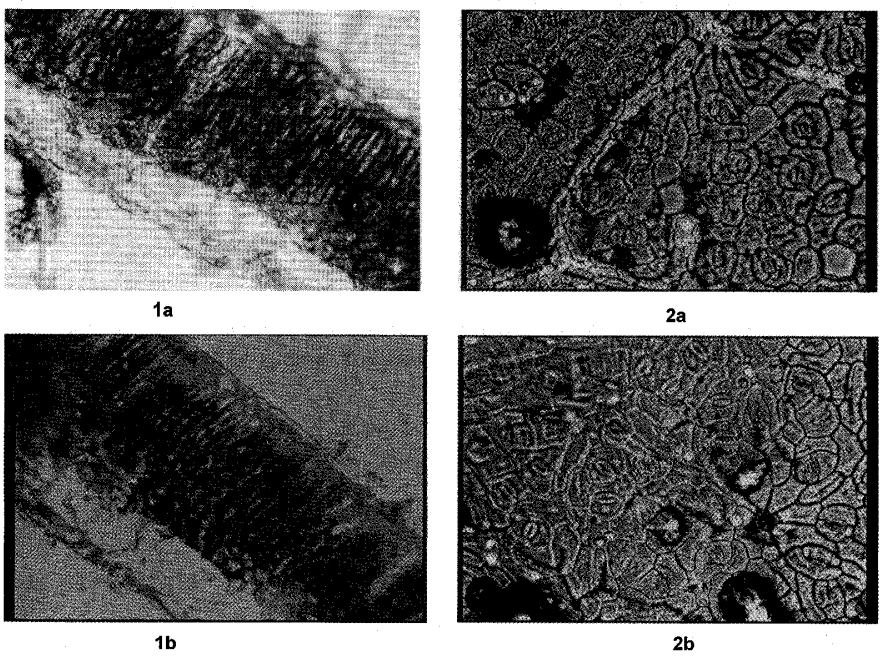

Fig. 1. Peanut leaf cross-sections, 1a-Florman INTA, 1b-Manfredi 393 INTA, and 2a-abaxial leaf surface of Florman INTA and 2b-adaxial leaf surface of Manfredi 393 INTA

Table 1. Surface characteristics for leaves of two peanut cultivars with standard errors.

Parameter	Florman INTA		Manfredi 393 INTA	
	Abaxial side	Adaxial side	Abaxial side	Adaxial side
Stomatal density, mm^{-2}	254±47	260±31	250±48	325±58
Length of stomate, μm	19.7±1.6	18.4±1.4	17.1±1.3	15.2±0.8
Stomatal aperture, μm	12.3±1.3	12.6±0.6	10.7±0.4	10.6±0.7

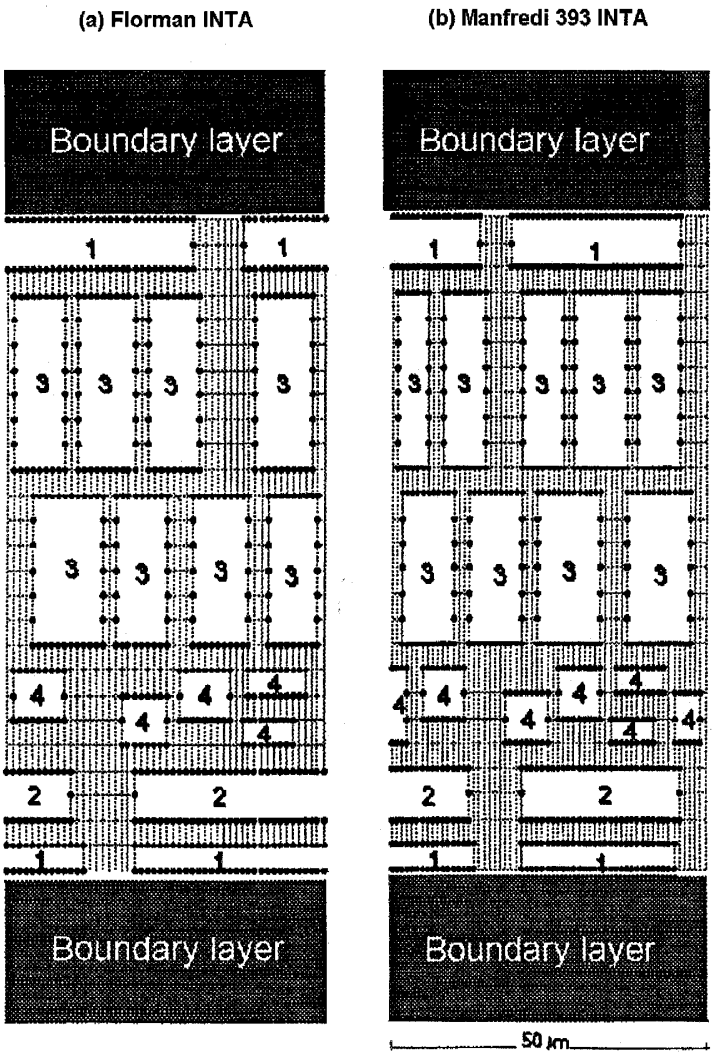

Fig. 2. Domains created to run the 2DLEAF model by schematizing the leaf cross sections of Florman INTA (a) and Manfredi 393 INTA (b). Rectangles represent cells and tissues, the rectangles marked "1" show the epidermis, the rectangles marked "2" represent the water storage cells, all the rest represent the mesophyll cells. A grid was used for numerically solving the diffusion equations of the model. Dark points represent the sites from which evaporation takes place.

The 2DLEAF model

The 2DLEAF model was described in detail by Pachepsky and Acock (*10*). The model simulates the transport of three gases: water vapor, carbon dioxide, and oxygen as a two-dimensional flow in a domain which extends through the leaf cross-section and the boundary layer. The 2DLEAF model can be used for both amphystomatous and hypostomatous leaves. The 2DLEAF model (*10*) simulates (a) transport of CO_2 and water vapor in the intercellular spaces and in the boundary layer adjacent to a leaf, (b) fluxes of CO_2 across cell surfaces due to assimilation, and (c) fluxes of water vapor from the cell surfaces due to the

difference between atmosphere and intercellular water vapor pressure.

Assimilation of CO_2 and evaporation of water are simulated on the surfaces of the polygons representing palisade and spongy mesophyll cells. No gas movement and/or assimilation is modeled within cells. Values of CO_2 concentration ($[CO_2]$) at outer edge of the BLs are equated to the ambient $[CO_2]$ value. Water vapor pressure at the cell surfaces is set to the saturated value for the specific leaf temperature.

The system of equations of the model includes three diffusion equations for CO_2, O_2, and water vapor, and five algebraic carbon assimilation equations as boundary conditions for CO_2 transport, according to a CO_2 assimilation model based on Rubisco kinetics (*2, 3*). Boundary conditions are defined also by constant values of $[CO_2]$, $[O_2]$, and water vapor pressure at the outer borders of the BLs. Temperature, air humidity, $[CO_2]$, and light intensity must be known to calculate the coefficients in the system of equations and to set the boundary conditions (*10*). The system of equations was solved in the complex domain representing intercellular space and the BLs as shown in Fig. 2. A two-dimensional grid is superimposed on the leaf intercelluar space and the adjacent BLs. Gas concentrations are defined at the nodes of this grid. The system of equations is solved numerically using a Galerkin-type finite element scheme (*5*). Grid generation and flow domain selection must be completed before the calculations. This was done using the measured leaf anatomy.

Leaf BL parameters

Transpiration was the major object of the current study, therefore the emphasis in modeling was placed on water vapor transport. It was shown both experimentally and theoretically (see a brief review in (*11*)) that the BL characteristics drastically affect transpiration rates. In our previous work for a hypostomatous potato (*11*), it was shown that two parameters, BL thickness, d, and the ratio of the coefficient of diffusion in the BL to the coefficient of diffusion in the intercellular space, B, which can be determined with transpiration data, are necessary and sufficient to account for the BL effect in leaf gas exchange models. For the amphystomatous peanut leaf, we assumed that the parameters of the adaxial BL are equal to those of the abaxial BL.

Table 2 presents the transpiration rates we found in the literature for several peanut cultivars in controlled, field, and greenhouse conditions. We simulated the maximum transpiration rates for the conditions of the experiments.

The 2DLEAF model was used to calculate transpiration rates for Florman INTA and Manfredi 393 INTA cultivars leaf anatomy (Fig. 2) for all possible combinations of values of d and B in a range of values considered reasonable at two values of stomatal aperture, maximal (12 μm for Florman INTA and 10 μm for Manfredi 393 INTA) and minimal, 1 μm (for both cultivars). Peanut leaves are strictly amphystomatous; numerous publications reviewed, for example by Ramanatha Rao and Murty (*17*), indicate that there are as many stomata on the abaxial as on the adaxial. For some cultivars, the stomatal density on the adaxial side is about 5–10% higher than on the abaxial side. The values of the

Table 2. Published peanut leaf transpiration data used in this study

#	Transpiration, mmol m^{-2} s^{-1}	Air relative humidity, %	Leaf temperature, ℃	Cultivars	Experimental conditions	Source
1	0.3–4.0	72	25	Florigiant	Controlled environment	(*13*)
2	0.5–4.1	50	32.5–35.1	McCubbin Early Bunch	Australia, field experiment with various plant densities	(*18*)
3	0.5–7.7	Variable	30	Florunner Tang	Greenhouse and outside in pots	(*1*)

BL thickness, d, were varied over the range 100–2000 μm for both cultivars. This range is based on estimates by Nobel (*9*) for leaves 5 cm long. Parameter B can be greater or less than 1 reflecting the relative thickness of the turbulent (caused by fast air convection, wind, etc.) and laminar (caused by the roughness of various kinds of leaf surfaces) sub-layers in the BL. If the laminar sublayer dominates, as can happen in controlled conditions, then $B<1$. In field and even greenhouse conditions, the turbulent sub-layer dominates, and then $B>1$. Based on the estimations made in our previous work (*11*), the calculations for peanut were made with B in the range 0.5–5. The leaf surface of both cultivars was not especially rough (Fig. 1) and we assumed that the value 0.5 is a reasonable minimal value for the parameter B. At the value of 5 the calculated transpiration rates were much higher than the measured ones (Fig. 3 and 4).

RESULTS AND DISCUSSION

Figs. 3 and 4 present the dependencies of the transpiration rates on the BL thickness, d, and on the ratio of coefficients of diffusion in the BL and in the intercellular space, B, for Florman INTA and Manfredi 393 INTA, respectively. The lower surfaces present this dependence at a stomatal aperture of $a=1\,\mu$m, and the transparent upper surfaces present this dependence at $a=12\,\mu$m for Florman and $a=10\,\mu$m for Manfredi.

For both cultivars, calculated transpiration rates are higher for the maximal stomatal aperture than for the minimal one at all values of the BL parameters (Figs 3 and 4). Transpiration rate increases when the thickness of the BL decreases, at all values of the parameter B. Transpiration rate is higher for the greater values of the parameter B. All these qualitative dependencies are consistent with the known mechanisms of transpiration.

All four surfaces shown in Fig. 3 and 4, can be well approximated with the function

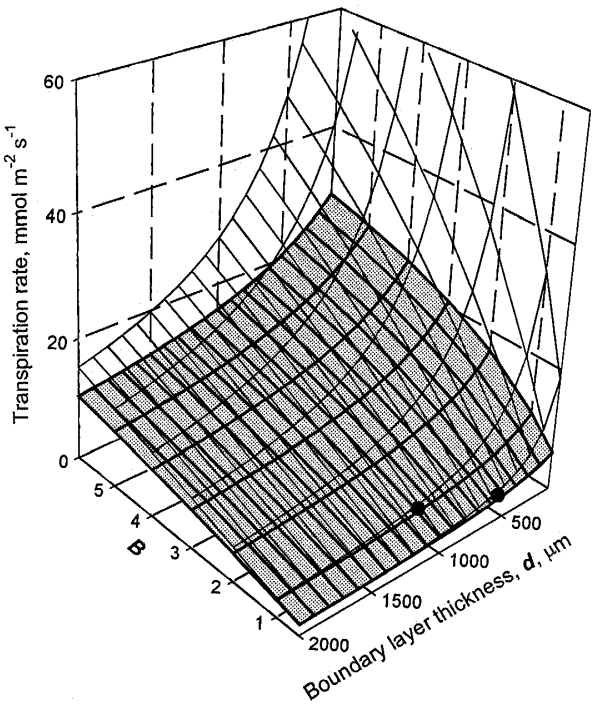

Fig. 3. Leaf transpiration rate as a function of the boundary layer parameters for Florman INTA. Stomatal aperture, a=1 (gray surface) and 12 μm (transparent surface). Points represent the transpiration rate, 4.1 mmol $m^{-2} s^{-1}$, measured in controlled conditions for the cultivar Florigiant, Virginia type (Pallas et al., 1974).

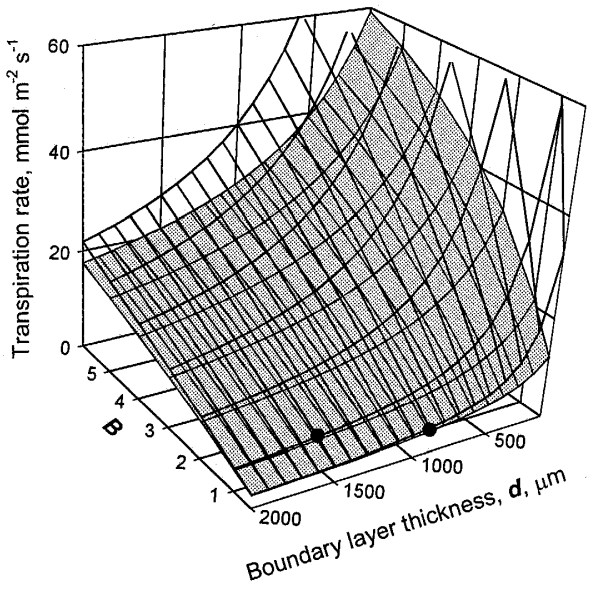

Fig. 4. Leaf transpiration rate as a function of the boundary layer parameters for Manfredi 393 INTA. Stomatal aperture, a=1 (gray surface) and 10 μm (transparent surface). Points represent the transpiration rate, 4.0 mmol $m^{-2} s^{-1}$, measured in the field for the cultivar McCubbin, Spanish type (Wright and Bell, 1992).

Table 3. Empirical parameters for the formula (1) of transpiration on the BL parameters, d and B, a is a stomatal aperture.

	Florman INTA		Manfredi 393 INTA	
	$a=1\,\mu m$	$a=12\,\mu m$	$a=1\,\mu m$	$a=10\,\mu m$
k_1	5483.44	4805.27	7416.6	7632.52
k_2	25.43	111.36	79.53	25.51
k_3	38.60	280.4	183.89	6.08
k_4	0.30	0.72	0.82	0.72

$$Tr=\frac{k_1B}{d+k_2B+k_3}+k_4 \qquad (1)$$

where Tr is the transpiration rate, k_1, k_2, k_3, and k_4 are empirical parameters depending on the cultivar and the stomatal aperture, determined separately for every surface fitting the calculated data to the formula (1), Table 3. Formula (1) shows that the transpiration rate is inversely proportional to the BL thickness. The dependence of transpiration rate on B is not so clear, but for the cultivars Florman INTA and Manfredi 393 INTA, k_1, values for the maximal and minimal stomatal apertures are about two orders of magnitude higher than k_2 values. This means that the contribution of B in the numerator is bigger than in the denominator. This means, in turn, that transpiration increases with growing values of B.

Fig. 5 presents the calculated leaf transpiration rate as a function of stomatal aperture and boundary layer thickness for Florman INTA (gray surface) and Manfredi 393 INTA (transparent surface) with $B=1$ and the same external conditions. Transpiration rate of Manfredi 393 INTA is always higher than that of Florman. This is completely due to the quantitative difference in leaf anatomy, that is due to different stomatal densities and different cell surface area per unit of leaf area; there is no other factor affecting the transpiration rate. Transpiration rate increases with increasing stomatal aperture, but this dependence is much more pronounced when BL thickness is less than $1000\,\mu m$.

Isolines for the observed transpiration rates are shown for both cultivars in Fig. 5. Every point on any isoline presents a pair of d and B values corresponding to the same transpiration value. For all three isolines, when stomatal aperture increases, the thickness of the BL grows, as was also shown by Parlange and Waggoner (*16*).

In Figs. 3 and 4 points are the experimental transpiration values which were plotted on the surfaces and the corresponding values of the BL parameters were found. It was assumed that the leaf interior schematization which we obtained for the cultivar Florman can be used to calculate leaf gas exchange for the genetically close cultivars, i. e. for Florigiant, Early Bunch, and Florunner, which also belong to the same botanical type of peanut, Virginia. The cultivars Mc

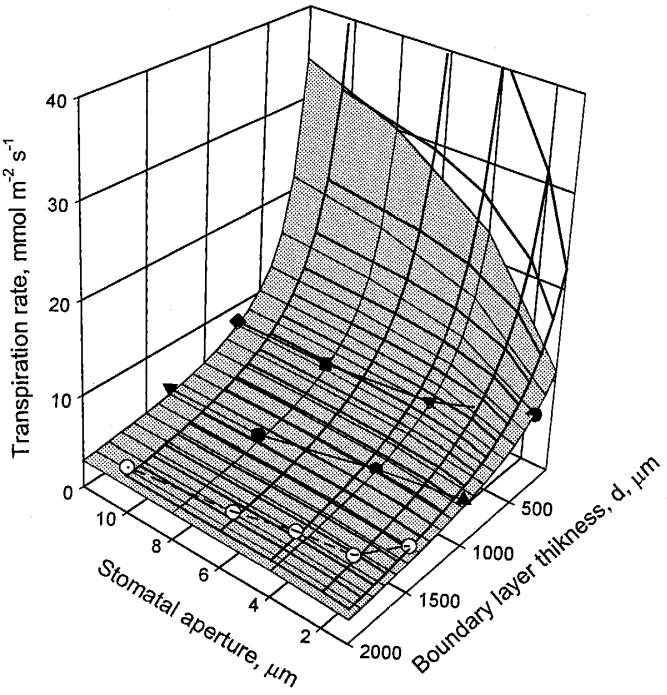

Fig. 5. Leaf transpiration rate as a function of stomatal aperture and boundary layer thickness for Florman INTA (gray surface) and Manfredi 393 INTA (transparent surface) ; $B=1$, temperature 25℃, and relative humidity 70%. Two sets of black points connected with solid lines represent the transpiration rate for the cultivars of the Virginia type, and the set of white points connected with the dashed line represent the transpiration isoline for the Spanish type cultivar.

Cubbin belongs to the Spanish type, and leaf anatomy analogous to that of Manfredi 393 INTA was assumed. For transpiration rates observed in field and greenhouse conditions, the BL thickness is higher than for the transpiration observed in controlled conditions (Fig. 5), at all values of stomatal aperture. Measured points plotted in Figs. 3 and 4 show that for these values of transpiration rates, the value of the parameter B cannot be greater than 1.

Using formula (1), the combinations of BL parameters values, d and B, possible for the measured transpiration rates were analyzed. Fig. 6 presents these combinations for transpiration rates of 4.1 and 7.7 mmol $m^{-2} s^{-1}$ for Florman INTA at the maximal and minimal stomatal apertures. At the lower transpiration rate (Fig. 6a) in controlled conditions, the BL parameter values very much less (d lies in a range 300–1000 μm and B varies between 0.5 and 1) than at higher transpiration rates in field conditions, Fig. 6b (d varies from 300 to 2000 μm and B grows up to 3), for the same anatomical properties. For Manfredi 393 INTA with a different leaf anatomy and a transpiration rate 4.0 mmol $m^{-2} s^{-1}$, the range of the B values (Fig. 6c) is approximately the same as for Florman INTA at the close value of transpiration rate, Fig. 6a, but the range of the BL thickness, d, is much larger. For Manfredi INTA, the stomatal aperture also affects much stronger the BL parameters than for Florman INTA

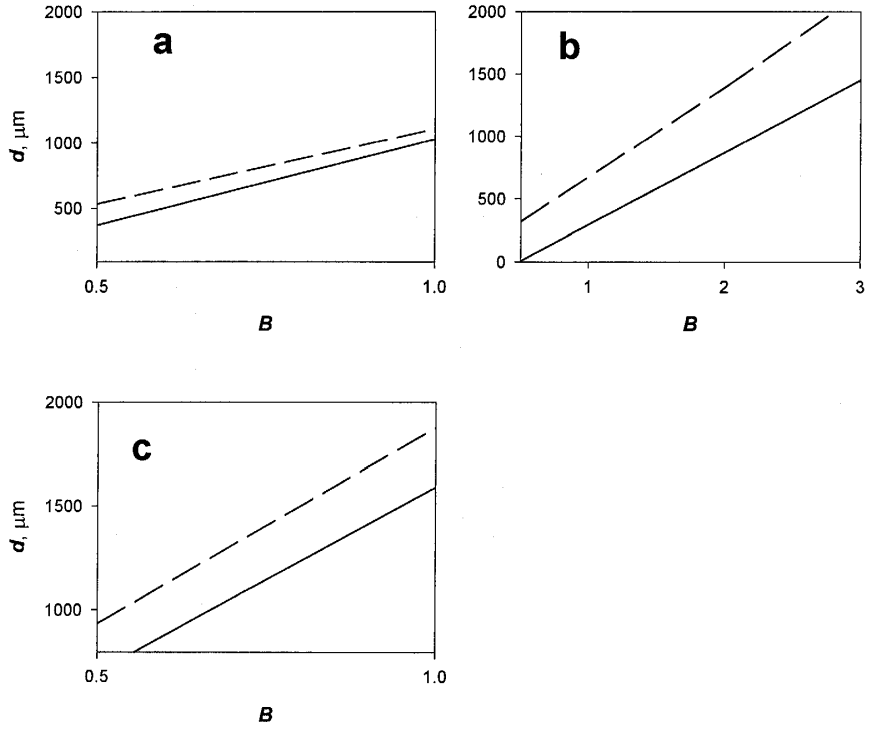

Fig. 6. Leaf boundary layer parameter values at the same transpiration rate, Florman INTA–Tr=4.1 mmol m^{-2} s^{-1} at controlled environment conditions (a) and Tr=7.7 mmol m^{-2} s^{-1} in the field (b) ; Manfredi 393 INTA, Tr=4 mmol m^{-2} s^{-1} (c). Upper lines are for stomatal aperture a=1 μm, lower lines are for stomatal aperture 12 μm (Florman INTA) and 10 μm (Manfredi 393 INTA).

(cf. Fig. 6c and 6a), lines for 1 and 12 μm of stomatal aperture lie much close to each other for Florman INTA than for Manfredi 393 INTA.

Therefore, the comparison of the leaf anatomical structure for two peanut cultivars of different botanical types demonstrated a significant quantitative difference between them. Two-dimensional modeling based on the analysis of leaf anatomy showed the differences in transpiration processes for these cultivars that were expressed as different dependencies of the transpiration rates on the boundary layer parameters, different ranges of the BL parameter values. For amphystomatous leaves, as well as for hypostomatous (*11*), two empirical parameters, BL thickness d and the ratio of the coefficients of diffusion in the intercellular space and in the BL, B, are necessary and sufficient to quantitatively describe the effect of the boundary layer on the transpiration rate. For amphystomatous plants, at $d>1000$ μm, the dependence of transpiration on stomatal aperture is much weaker than that for hypostomatous plants, as the comparison of the results of this study and of the article (*11*) show.

Pallas (*12*) emphasized the uniqueness of the assimilation process for peanut as compared with other species. The study of peanut transpiration with a two-dimensional diffusion model allows us to see the specific properties of the boundary layer and its effect on transpiration, which is especially important in water deficit studies.

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