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Pima cotton leaf transpiration analysis using the WALL model that accounts for liquid water movement

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A b s t r a c t. Leaf transpiration of eight genotypes of Pima cotton was measured in the field of the Maricopa Agricultural Center in August 1994. Photomicrographs of leaf cross-sections and of the leaf surfaces were scanned and analyzed with the image analysis software. The data were used to parameterize the new WALL model, developed in this study to analyze the leaf transpiration with a special emphasis to liquid water movement inside the leaf. The transpiration stream was assumed to go from vein endings in two directions, towards the upper and lower leaf surfaces. These fluxes were presented as two parallel currents driven by the water vapour concentration difference between the atmosphere and the open surface of the vein endings and on the mesophyll and epidermis (inner parts) cells' surfaces as a flow in thin films of water. Simulations were run to estimate quantitatively the contribution of the cuticular transpiration to the total amount of leaf transpiration stream, to evaluate the role of the mesophyll cell walls' surfaces in the water transfer inside the leaf, and to calculate the dependence of transpiration and its components on temperature. Simulation results showed (1) a major role of the cuticular transpiration as a leaf cooling mechanism and (2) that the cell wall properties can affect water film characteristics that also affect the transpiration course.

K e y w o r d s: *Gossipium barbadense* L., cuticular transpiration, mesophyll cell walls, electric analogy, the WALL model

INTRODUCTION

Transpiration mediated water flow in plants is a passive process that occurs in response to physical forces. Its effects are multiple, including water loss, leaf temperature changes, and transport of nutrients and signaling substances. However, the ability of plants to control transpiration is mostly limited to stomatal movements and/or changing the water permeability of the cuticle.

In 1993 Canny wrote, 'Flow of the transpiration stream in the lumen apoplast of the xylem appears hydrodynamically orthodox in being approximately described by the Hagen-Poiseuille Law, and by Murray's law for branching pipes' and demonstrated it using experimental data on the veins' radii. In 2003 McCulloh *et al*. showed that the Murray's law (Murray, 1926) that states that the optimal design of the brunching pipes for cardiovascular system 'equalizes the sum of all radii cubed (Sr^3) at all points along the flow path if the volume flow (Q) of the blood is conserved within the vascular system and the flow is laminar' is applicable to the plant vein system with certain conditions and it describes the experimental data better than other vein branching hypotheses. Recent results, for example, by Steudel (2002) also indicate that to some extent, plants behave 'like 'hydraulic machines' and that water flow within plants may be described by just a few physical principles'. Steudel's paper also points out our lack of knowledge regarding resistances to transpiration flow in liquid phase, the complexity of the liquid-phase water flow regulation mechanisms inside leaves and plants in general, and the difficulty in making the corresponding measurements. Mathematical models accounting for the major mechanisms seem to be the efficient way to overcome these difficulties as it was demonstrated in numerous studies (Jones, 1992; Nobel, 2005) just to name a few most important ones.

Cuticular transpiration and its role have traditionally received far less attention than the stomatal variety, although the structure and chemical composition of plant cuticles have been extensively studied (Bondada *et al.*, 1996; Oosterhuis

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et al., 1988; Šantrůček *et al.*, 2004; Schreiber and Riederer, 1996; Schreiber *et al*., 2001). Some measurements have showed that cuticular transpiration varies in a range from 10 to 70% of the total (Antipov, 1971; Burghardt and Riederer, 2003; Kim *et al*., 2007; Šantrůček, 1991). Riederer and Schreider (2001), studying astomatous cuticular membranes, found no significant correlation between cuticular permeability and the thickness of the cuticle or of the wax layer. However, these authors estimated that the cuticular conductance increased approximately two-fold when leaf surface temperature rose from 15 to 35°C.

Pima cotton (*Gossypium barbadense* L.) is grown in the hottest areas of the Southwestern United States (Cornish *et al*., 1991). It was bred for irrigated production (Radin *et al*., 1994) and many new genotypes of Pima cotton respond well to irrigation (Radin, 1992). They have very high transpiration rates at high temperature, and the corresponding cooling of the leaves provides a protection against heat damage. Radin (1989) and other authors observed how transpiration worked as a heat avoidance mechanism for both upland and Pima cotton. Burke and Upchurch (1989) studied transpiration of upland cotton as related to its estimated thermal kinetic window, TKW, (the temperature range allowing normal enzyme function in plants) of 23.5-32°C and presented a relationship between air and leaf temperatures and plant water uptake. They found that transpirational cooling occurs when leaf temperature exceeds the lower bound of the TKW. No quantitative data have been found on TKW for Pima cotton, but accounting for its more intensive transpiration, it could be assumed that its minimum and maximum are higher than those for the upland cotton.

There is abundant data on upland cotton leaf morphology in the literature, but very little on that of Pima cotton. A comparison between the Pima cotton study by Pachepsky *et al.* (2000) and morphological studies on upland cotton (Van Volkenburgh and Davis, 1977) suggests the two species have very similar leaf internal structures, with quantitative differences (not exceeding 20%) in some characteristics such as leaf thickness and stomatal density. This offers the opportunity to use upland cotton data in some cases when there is a shortage of Pima cotton measurements.

The objectives of this study were: (1) to formulate a model of transpiration explicitly accounting for liquid-phase water movement in the leaf, with a special reference to cuticular transpiration; (2) to parameterize this model with experimental data on Pima cotton; (3) to quantify the dependence of leaf transpiration and its components on leaf temperature; (4) to quantify the role of the cuticle as a cooling mechanism for Pima cotton; and (5) to attempt an explanation of Pima cotton's water deficit tolerance from the perspective of liquid water movement in the leaf.

MATERIALS AND METHODS

Transpiration measurements and other experimental studies were carried out in 1994 at the Maricopa Agricultural Center of the University of Arizona (33.07°N, 111.98°W, elevation 358 m ASL) at an experimental farm of approximately 400 ha located in the midst of an irrigated agricultural area. Surrounding fields are planted predominantly with cotton and alfalfa, with an equal area of fallow land interspersed. Large uncultivated areas surrounding the agricultural belt support Sonoran desert vegetation. Rainfall is usually below 100 mm during the growing season, whereas potential evapotranspiration is about 1 000 mm.

Eight Pima cotton (*Gossipium barbadense* L.) cultivars were studied (Pima: 32, S-1, S-2, S-3, S-4, S-5, S-6, and S-7). These eight lines represent a selection gradient in a breeding program conducted with Pima cotton for the last 50 years (Feaster *et al*., 1967). Seeds were planted in plots 13.7 m long and 1 m wide on April 14, 1994 on fine-loamy, mixed, hyperthermic Typic Haplargid soil. After seedling establishment, plants were thinned to a uniform spacing of 15 cm between plants. Air temperature was around 43/25°C (day/night), relative humidity averaged around 35%, and maximum PAR intensity reached 2000 μmol $m^{-2}s^{-1}$ during the generative stages. Modal management practices for the region were followed for irrigation scheduling, fertilization, and insect control.

Measurements of transpiration (and photosynthesis) rates and leaf area were made on August 13-16, 1994, during the fruit maturation period. The first fully-expanded main stem leaves of 10 individual plants were used for all measurements. Leaf temperature from three individual plants of each cultivar was measured continuously with copper-constantan thermocouples (OMEGA TT-T-40), attached to the lower side of the leaf surface and connected to a CR21 Micrologger (Campbell Scientific Inc., Logan, UT, USA). Air temperature was measured with a shaded thermocouple positioned 10-15 cm above the canopy. During the transpiration measurements, air temperature was 44/25°C (day/night), relative humidity was around 31% and PAR was around 2 000 μmol $m^{-2}s^{-1}$ at noon. All measurement days were clear and sunny. Measurements started 3 days after irrigation with no water stress observed. Photosynthesis rates were measured between 1:00 and 4:00 p.m. with a portable steady-state gas-exchange system (Analytical Development Co., Ltd, Hoddesdon Herts, UK). Transpiration rates were measured with a Li-Cor steady-state porometer (LI-COR Inc., Lincoln, NE, USA). Individual leaf area was calculated from observations of leaf length and width. Stomatal density was measured on August 28, 1994, and the same day the first fully expanded leaf was taken for the cross-sectional microscopic analysis. Additional information about the experiments was reported by Lu *et al*. (1997) and Pachepsky *et al*. (2000).

RESULTS

Most of the leaf characteristics did not differ significantly among genotypes. Therefore, we used averaged values to parameterize the WALL model. Detailed experimental data can be found in previous studies (Lu and Zeiger, 1994; Lu *et al*., 1993, 1997; Pachepsky *et al*., 2000). Average leaf area was equal to 199 ±13.9 cm^2 determined on 120 samples. Leaf thickness was different in the morning, 304 ± 21.4 μm, and in the afternoon, 325 ±23.0 μm (determined on 160 samples) but there was no significant difference among the various cultivars. Stomatal density on the abaxial side was 2.5-fold of that on the adaxial side and ranged from 400 to 450 stomata per mm^2 (measured on approximately 160 samples). Figure 1 shows photographs of the abaxial and adaxial leaf surfaces and photomicrographs of these surfaces and of the leaf cross-section.

Transpiration was measured on August 13 and 16, 1994, days with different air temperature 36 and 35°C and 50 and 45% RH, respectively, the differences quite significant for these areas with high temperature and low humidity since it affects noticeably the transpiration rates. During the measurements on August 13 (2:00-4:00 p.m.), the average air temperature was around 36.13°C, with a very low coefficient of variation (CV), 1.3%. At the same time, leaf temperature ranged around 32.82°C, CV = 2.1%. The mean value of atmospheric water vapour concentration (VPA) was 2.0465 mol m^{-3}, CV = 3.75, and water vapour concentration in the leaf (VPI) was 1.0238 mol m^{-3}, CV = 3.1%. Transpiration rate was 0.041 g m^{-2} s^{-1}, CV = 12.8. During the August 16 measurements (2:00-4:00 p.m.), the average air temperature was around 35.55°C, CV = 1.25%. At the same time, leaf temperature ranged around 33.85°C, CV = 1.9%. The mean value of atmospheric water vapour concentration (VPA) was 2.093 mol m^{-3}, CV = 3.8, and water vapour concentration in the leaf (VPI) was 1.1411 mol m^{-3}, CV = 2.4. Transpiration rate was not significantly different for the various genotypes, and ranged around 0.03 g m^{-2} s^{-1}, CV = 12.8.

The WALL model is a modified classic conductance-based model (Nobel, 2005) that accounts, in addition, for (1) hydraulic flux in, and water supply from, leaf microtubes (veins); (2) thin film water transport on the surfaces of epidermal and mesophyll cells; and (3) flow through a microporous medium, the cuticle (Fig. 2). Resistances to both liquid and gaseous water flow on the path of the transpiration stream from the saturated conditions at the vein endings, P_{sat}, to atmospheric water vapour concentration, P_{atm} are shown in Fig. 3. The left branch of the circuit represents the path downward and through the abaxial leaf surface and the adjacent boundary layer (indices '*l*') and the right branch corresponds to the path upward and through the adaxial leaf surface and the adjacent boundary layer (indices '*u*'). Resistances to the flow are: r_{bl} for the boundary layer, r_{cut} for the cuticle, r_{film} for the water films on the cell surfaces, r_{st} for stomata, and r_{ias} for the intercellular spaces.

To determine the cell wall resistance to water movement, we used the methodology developed by Toledo *et al*. (1990). The mesophyll tissue was considered as a porous

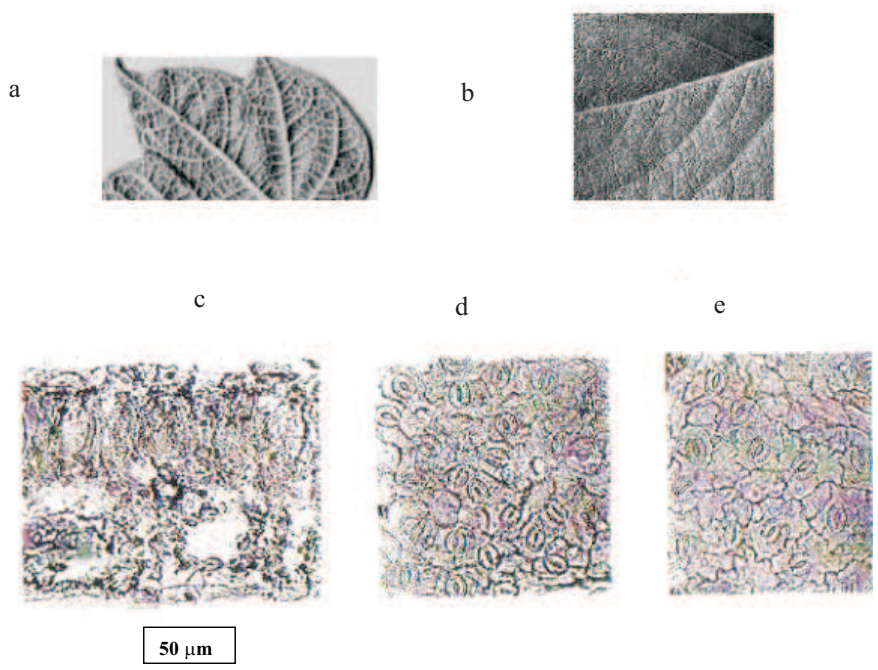

Fig. 1. Lower (a) and upper (b) Pima cotton leaf surfaces, leaf cross-section (c), and photomicrographs of the abaxial – upper (d) and adaxial - lower (e) leaf surfaces.

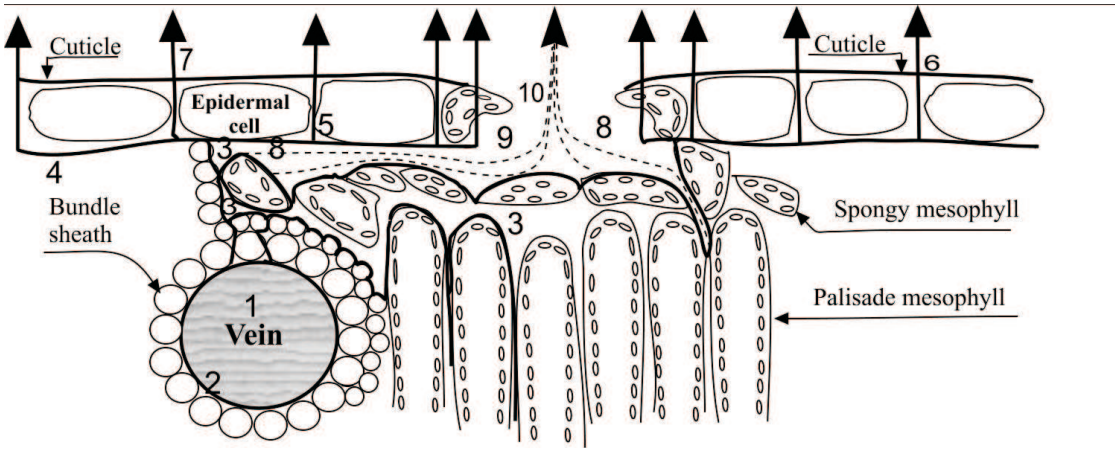

Fig. 2. Water pathways in the leaf as presented by the WALL model (liquid phase flows are shown as solid lines with arrows; vapour phase flows are shown as dashed lines): (1) transport in veins; (2) leakage through vein walls; (3) movement as films over (a) bundle sheaths and (b) palisade and spongy mesophyll; (4) lateral movement as water films on the inner side of the epidermal cells; (5) movement between epidermal cells towards cuticle; (6) diffusion through cuticle; (7) evaporation from the outer cuticle surface into the atmosphere; (8) evaporation from water films on cell surfaces into the intercellular spaces and substomatal cavities; (9) gas-phase diffusion in the intercellular spaces and substomatal cavities; and (10) transport of water vapour through stomata into atmosphere.

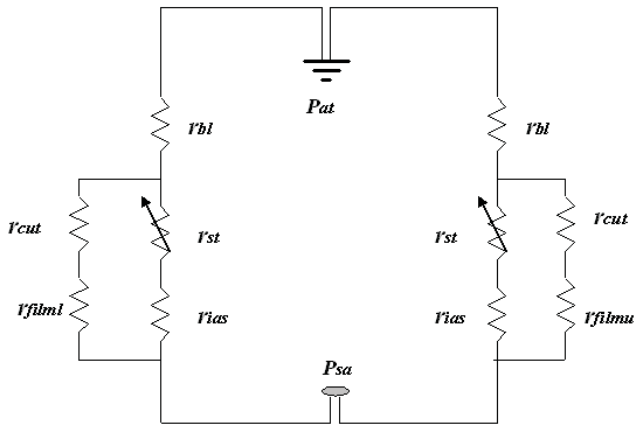

Fig. 3. Resistances to both liquid and gaseous water flow on the path of the transpiration stream, from vein ending to atmosphere, where the vapour concentration are P_{sat} and P_{atm}, respectively. The left branch of the circuit represents the path downward, through the abaxial leaf surface and the adjacent boundary layer (indices '*l*'); the right branch corresponds to the path upward and through the adaxial leaf surface and the adjacent boundary layer (indices '*u*'). Resistances: r_{bl} is for the boundary layer, r_{cut} is for the cuticle, r_{film} is for the water films on the cell surfaces, r_{st} is for stomata, and r_{ias} is for the intercellular spaces.

medium in which no filled pores exist in the mean direction of flow. Under these conditions, flow is restricted to thin films.

The hydraulic conductance of a cylindrical pore segment of radius r containing a thin film of non-dimensional thickness $h^* = h/r$ is:

$$K(h^*,r) = (pr^4 / 8\mu_w)\left\{1+(1-h^*)^4\left[3-4\ln(1-h^*)\right]-\right.$$
$$\left.-4(1-h^*)^2\right\}, \quad (1)$$

where: μ_w is the viscosity of water, and h is the thickness of the film (Toledo *et al*., 1990, p. 676, eq. 14). Toledo *et al*. deduced this equation from the Navier-Stokes equations assuming rectilinear flow and zero shear stress between the water film and the air and applied it to non-cylindrical pores such as the ones comprising intercellular air spaces. In our case, we assumed pore radius to be equal to the mean distance between mesophyll cells, or approximately 1μm, as obtained from our photomicrograph-derived anatomical measurements. The film thickness was estimated as 0.1 μm.

The viscosity of water, μ_w, depends strongly on temperature (Fig. 4a); we used the following formula to estimate it (CRC Handbook of Chemistry and Physics, 2008-2009, F-51):

$$\log_{10}(\mu_w / \mu_{20}) =$$
$$= (1.3272(20-T) - 0.001053(T-20)^2 \Big/ (T+105), \quad (2)$$

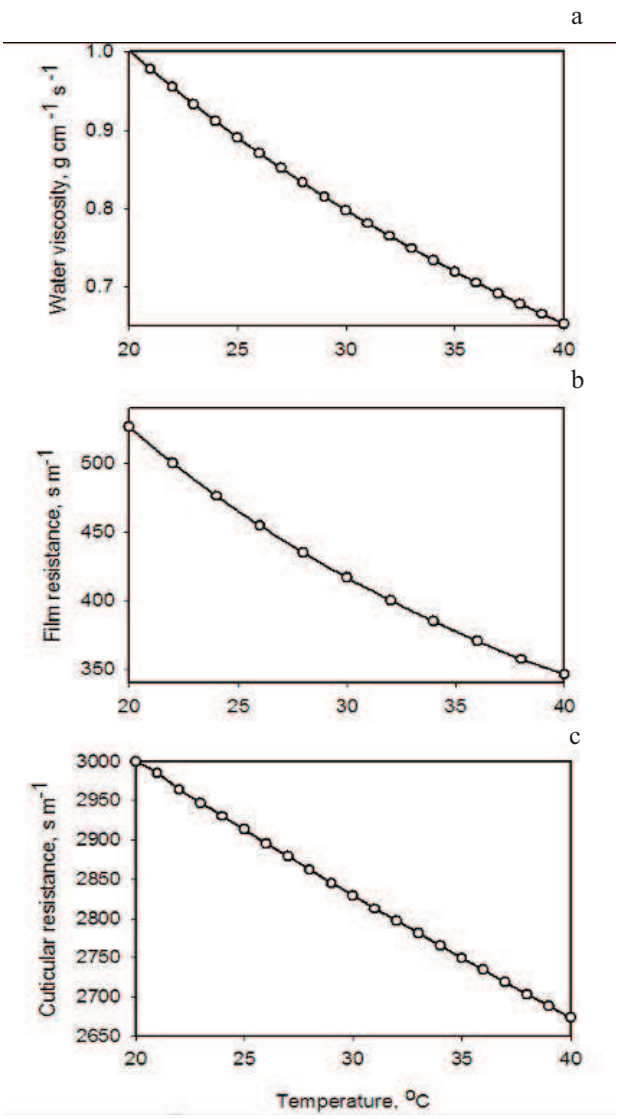

Fig. 4. Dependence on temperature of water viscosity (a), film (b), and cuticular (c) resistances.

obtaining the value of water viscosity at 20°C, μ_{20}, from the Handbook of Chemistry and Physics. We then calculated the resistance as the reciprocal of the hydraulic conductance K (Eq. (1)). The results are shown in Fig. 4b.

We calculated cuticular resistance according to Hall (1982), also as a function of leaf temperature. Hall (1982) stated that cuticular resistance is also affected by atmospheric pressure, but we assumed pressure effects to be constant for this study. The resulting expression for r_{cut} is:

$$r_{cut} = q r_0 / (T / T_0)^{1.75} , \quad (3)$$

where: r_0 is the resistance at 20°C, which we estimated from published values for cuticular membranes (Schönherr, 1982) and cuticles of various plant species (Table 1); q is a coefficient to account for dimensions; T and T_0 are the ambient and 293.15°K (20°C) temperatures, respectively. Figure 4c shows the dependence of r_{cut} on temperature, it decreases by 10% across the range of 20-40°C. Values for boundary layer, r_{bl}, and intercellular air space, r_{ai}, resistances were taken from estimates by Nobel (2005), and considered constants.

Stomatal resistance depends strongly on stomatal aperture that, in turn, depends on both temperature and relative air humidity, RH, provided that light conditions do not change. We assumed that when stomata are fully closed, r_{st} is equal to r_{cut}, and estimated the values for open stomata with our experimental data. We assumed that, at an air temperature of 40°C and 30% RH, stomata were closed and that there is a linear dependence of stomatal transpiration on stomatal aperture. For a mild drought, at 50% RH, we set the stomatal resistance for 40°C to 1 000 s m^{-1} on both leaf surfaces. For 90% RH, we considered r_{st} equal to 450 s m^{-1} on the adaxial side and 300 s m^{-1} on the abaxial leaf surface based on the observed stomatal density data.

Intercellular air space resistance also had different values for the upper and lower parts of the leaf. The upper part contains mostly densely packed palisade cells and air spaces have less volume than those in the lower part of the leaf, which

T a b l e 1. Cuticular, r_{cut}, boundary layer, r_{bl}, and stomatal, r_{st}, resistances (s m^{-1}), measured for various plants

Plants	r_{cut} x 10^{-3}	r_{bl}	r_{st}	References
Acer platanoides	8.5	69	470	Holmgreen *et al*. (1965)
Betula verrucosa	8.3	80	92	Holmgreen *et al.* (1965)
Quercus ribur	38.0	69	670	Holmgreen *et al*. (1965)
Circaea lutetiana	9.0	61	1 610	Kramer (1983)
Lamium galeodolon	3.7	73	1 060	Kramer (1983)
Mesophytes	2.0- 5	–	–	Cowan and Milthorpe (1968)
Xerophytes	5.0-40	–	–	Cowan and Milthorpe (1968)
Crops	2.5-10	13-130	31-1 000	Nobel (2005)
Many trees	5.0-20	13-130	1 000	Nobel (2005)
Xerophytes	10.0-100	13-130	1 000	Nobel (2005)

Table 2. Values of component resistances r_{bl} is for the boundary layer, r_{cut} is for the cuticle, r_{film} is for the water films on the cell surfaces, r_{st} is for stomata, and r_{ias} is for the intercellular spaces and of total cotton leaf resistance r_{leaf} calculated as described in 'The WALL Model' section at various leaf temperatures and 50% air humidity (s m^{-1}); indices '*l*' and '*u*' refer to the lower and upper leaf surfaces, respectively

Component resistances	Leaf temperature (°C)										
	20	22	24	26	28	30	32	34	36	38	40
r_{blu}	130	130	130	130	130	130	130	130	130	130	130
r_{stu}	450	555	660	765	870	975	1 080	1 185	1 290	1 395	1 500
r_{iau}	195	195	195	195	195	195	195	195	195	195	195
r_{cutu}	3 000	2 964	2 930	2 895	2 862	2 829	2 797	2 765	2 734	2 703	2 673
r_{filmu}	526	500	476	455	435	417	400	385	370	357	346
r_{bll}	195	195	195	195	195	195	195	195	195	195	195
r_{stl}	300	370	440	510	580	580	720	720	860	930	1 000
r_{ial}	130	130	130	130	130	130	130	130	130	130	130
r_{cutl}	3 000	2 964	2 930	2 895	2 962	2 829	2 797	2 765	2 734	2 703	2 673
r_{filml}	526	500	476	455	435	417	400	385	370	357	346
r_{leaf}	312	342	371	399	425	450	473	495	516	535	553

contains more sparsely-distributed spongy cells (Fig. 1). Table 2 shows all the resistance values calculated for Pima cotton for the WALL model in a leaf temperature range from 20 to 40°C. Some resistances are different for upper and lower leaf surfaces (Nagarajah, 1975).

We explored, using sensitivity analysis, how leaf temperature and various leaf resistance components affect the total leaf resistance estimated by WALL. For these calculations, we assumed that values of the resistances are equal on both sides of the leaf to those on the upper side (Table 2, upper part). The results of this numerical experiment with WALL (Fig. 5), suggest that Pima cotton leaf resistance is very sensitive to leaf temperature. When leaf temperature grows from 20 to 40°C, r_{leaf} changes from 276 to about 500 s m^{-1}, almost two-fold, in a slightly nonlinear way (Fig. 5a).

Boundary layer resistance also strongly affected the total leaf resistance (Fig 5b). When r_{bl} changes from 1 to 900 s m^{-1} the total leaf resistance grows linearly from 400 to 900 s m^{-1} (Fig. 5b). This range is unrealistic for cotton, and boundary layer resistance should not reach the high values shown considering cotton's leaf morphology. However, for other species, having leaf surfaces with trichomes, hair, and other formations, with curled leaves, leaf folding, paraheliotropic behavior, and so forth, r_{bl} could conceivably reach such high values. Stomatal resistance r_{st} on both sides of the leaf has a major effect on r_{leaf} (Fig. 5c). Stomatal resistance can change dramatically during the day driven by environmentally-mediated changes in stomatal apertures; in our calculations, we varied r_{st} from 10 to 1 200 s m^{-1}, and the total leaf resistance r_{leaf} changed from 155 to 545 s m^{-1}, almost three fold (Fig. 5c).

Resistance of air spaces affects total leaf resistance less than the abovementioned variables, albeit significantly. When r_{ias} changed from 1 to 550 s m^{-1}, r_{leaf} grows from 380 to 535 s m^{-1} (Fig. 5d). Air space resistance can be really high depending on how densely the mesophyll cells are packed; the mesophyll of plant leaves growing in dry and sunny conditions, usually occupies a higher relative volume than that of the leaves of plants growing in wet and shady conditions (Pachepsky and Acock, 1998).

Figure 5e presents a significantly nonlinear dependence of the total resistance on the cuticular resistance. When r_{cut} is relatively low that happens at higher temperatures, it affects the total resistance more than when it's high, at lower temperatures.

Variations in film resistance affect the total leaf resistance much less than other components. While r_{film} changes from 100 to 600 s m^{-1}, total leaf resistance grows only 3%, from 428 to 441 s m^{-1} (Fig. 5f). That allowed us to set r_{film} to equal values on the upper and lower parts of the cotton leaf, although mesophyll cells, and their quantitative surface characteristics, are quite different in these parts.

Figure 6 shows estimates of the contribution of cuticular transpiration to the total leaf transpiration. Calculations were made for five different values of RH from 50 to 90% in a range of leaf temperature from 20 to 40°C. This contribution did not depend on the RH and significantly depended on temperature changing from 23 to 40% RH. At the 35°C that occurred in our experimental field at the moment of measurements, this contribution was around 35%.

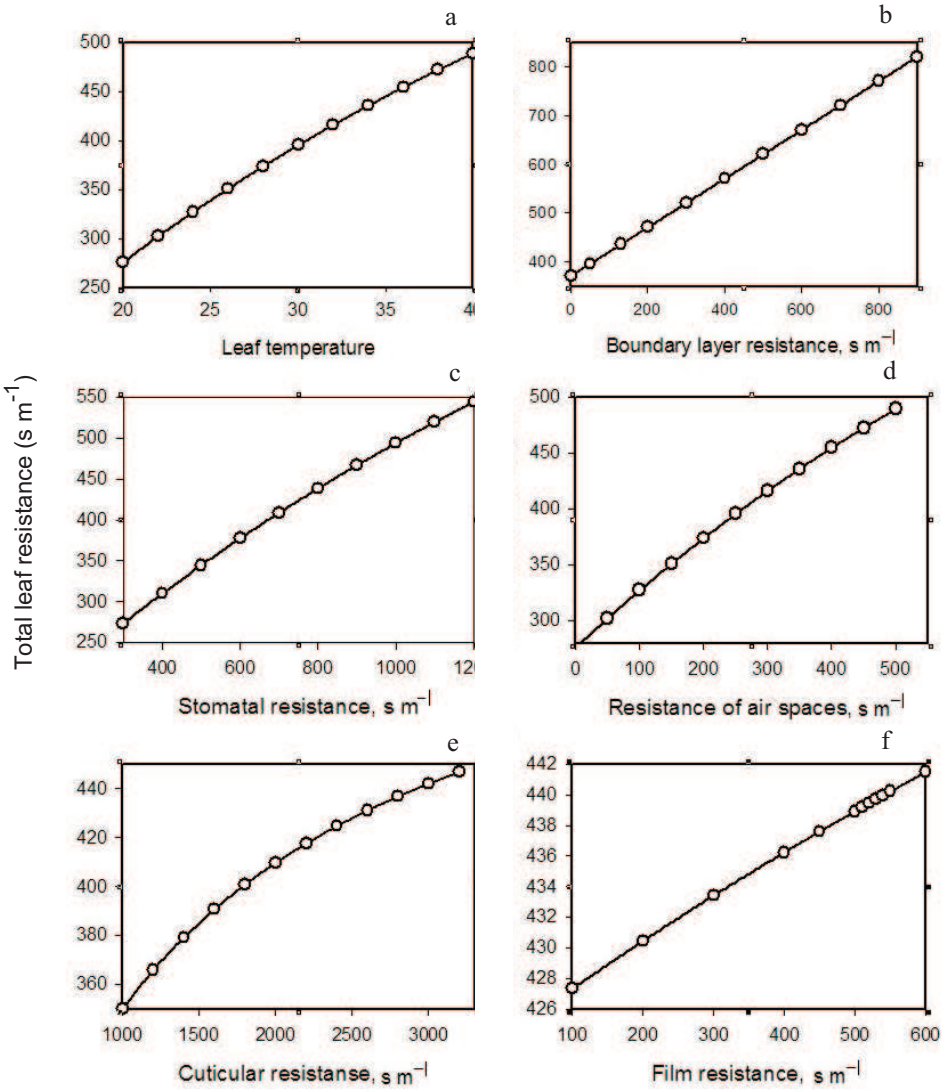

Fig. 5. Dependence of the total leaf resistance on leaf temperature (a) and on the resistances of various components: on the boundary layer resistance, r_{bl} (b), stomatal resistance, r_{st} (c), resistance of the intercellular air spaces, r_{ias} (d), cuticular resistance, r_{cut} (e), and water films on the mesophyll cell surfaces, r_{film} (f).

DISCUSSION

Plants of upland cotton grown under field conditions have about 100-160 stomata on the adaxial side and 220-330 stomata on the abaxial side (Morey *et al.*, 1974; Van Volkenburgh and Davies, 1977). This is quite different from the values we obtained for Pima cotton that were around 140-165 on the adaxial, and 400-460 on the abaxial side. Therefore, the values of stomatal resistance and in cooling the cuticular transpiration contribution into the total one for Pima cotton should be different for two types of cotton.

Cotton has an internal cuticle that covers the guard cells (Wullschleger and Oosterhius, 1989). It extends from the outer stomatal edge to the epidermal cells bordering the substomatal cavity. Pesacreta and Hasenstein (1999) also reported an internal cuticle for thistle (*Cirsium horridulum*) leaves; they noted that although the internal cuticle is not sufficiently studied, its existence 'has profound implications for the path of water movement'. These observations confirm a vital importance of the cuticular transpiration that defends not only mesophyll but also guard and epidermis cells from heat damage.

Calculations with the WALL model showed that cuticular transpiration can be quite high and plays a significant role in protection leaves from overheating. The cuticle occupies about 96-99.5% of the leaf area, far more than the stomata do. Although stomatal transpiration can reach high values that are never observed for cuticular transpiration, the amount of water crossing the cuticle is comparable with that passing through the stomata. This amount is also independent

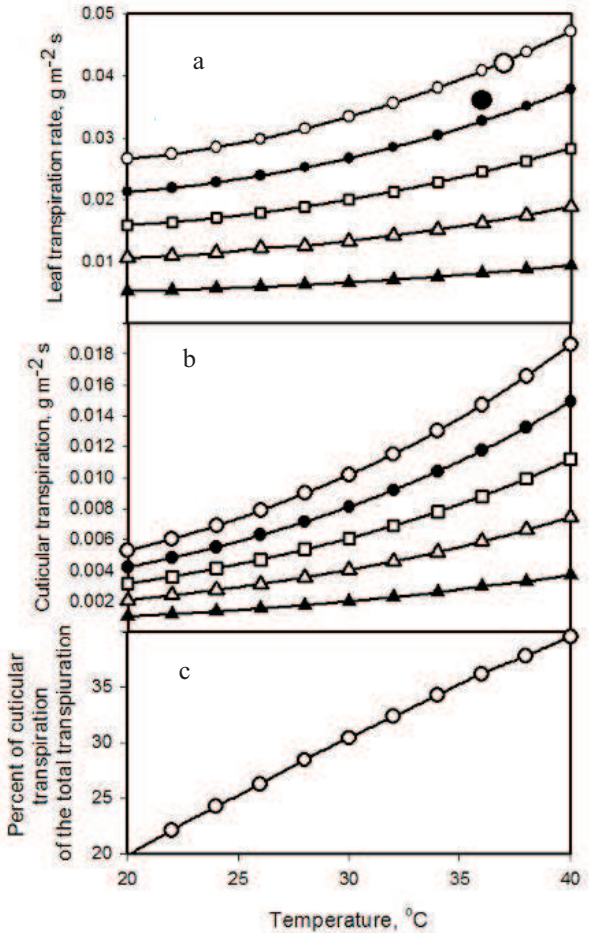

Fig. 6. Dependence on temperature of leaf transpiration (a), cuticular transpiration (b), and cuticular transpiration as a percentage of total leaf transpiration (c) at various levels of atmospheric relative humidity: 50% (open circles), 60% (closed circles), 70% (squares), 80% (open triangles), and 90% (closed triangles); two big circles represent measured transpiration rates on August 13 (open circle) and on August 16 (closed circle).

of whether stomata are closed or open. Therefore, cuticular transpiration provides permanent cooling of mesophyll cells going on independently on whether stomata are closed or open. This is especially important for Pima cotton growing in an extreme heat, at very high light levels, usually at low relative air humidity. Stomata close sometimes completely for a while before irrigation, to prevent a leaf from a complete drying. During these periods, the cuticular transpiration that cannot be stopped maintains life conditions for assimilating cells, preventing important proteins like Rubisco from coagulation and loss of its structure.

Kramer (1983) considered cell walls as a very important component 'in any discussion of plant water relations'. The volume of water occurring in the cell walls is important with respect to the possible role of the wall as a pathway for water movement outside the xylem. Water in plants is described as existing in two systems: apoplastic water occurring in the cell walls and xylem elements, and symplastic water occurring within the protoplasts. The former is equivalent to the apparent free space of Butler (1953), Briggs and Robertson (1957), and the outer space of Kramer (1957). This is the part of cell or a tissue into, and out of which, water and solutes can move freely by diffusion. In a tissue such as the mesophyll, this is almost completely water of hydration of the cell walls (Jarvis and Slatyer, 1970; Tyree and Jarvis, 1982). Symplastic water flow contributes insignificantly to water exchange between cells (Fricke, 2000). From 5 to 40% of the water in a cell occurs in the walls; more than half of the volume of some cell walls is occupied by water. It is generally assumed that water movement from veins to the evaporating surface occurs mainly via the cell walls (Kramer, 1983). The buffering capacity of the wall water may be the factor in 'hardening off' of plants when exposed to dry conditions. This may occur through an increased production of hemicellulose and pectic substances, coupled with a decrease of protein synthesis (Prusakova, 1960).

CONCLUSIONS

1. The WALL model of leaf transpiration has been developed that accounts for liquid water movement inside the leaf.

2. The model was parameterized and validated with the field data on Pima cotton leaf transpiration

3. The results of simulation with the WALL model showed a major role of the cuticular transpiration as a leaf cooling mechanism.

4. Modeling with the WALL has also shown that the cell wall properties can affect water film characteristics that, in turn, affects the transpiration stream.

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