Modelled Influences of Non-exchanging Trichomes on Leaf Boundary Layers and Gas Exchange

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The two main resistances in the exchange of gases between plants and the atmosphere are stomatal and boundary layer resistances. We modeled boundary layer dynamics over glabrous and pubescent leaves (assuming non-exchanging trichomes) with leaf lengths varying from 0.01 to 0.2 m, and windspeeds of $0.1–5.0 \text{ m s}^{-1}$. Results from theoretical and semi-empirical formulae were compared. As expected, boundary layer thickness decreased with decreasing leaf length and increasing windspeed. The presence of trichomes increased leaf surface roughness, resulting in lowered Reynolds numbers at which the boundary layer became turbulent. This effect is especially important at low windspeeds and over small leaves, where the Reynolds number over glabrous surfaces would be low. We derived a new simple dimensionless number, the trip factor, to distinguish field conditions that would lead to a turbulent boundary layer based on the influence of trichomes. Because modeled rates of CO_2 and H_2O_v exchange over turbulent boundary layers are one or more orders of magnitude faster than over laminar boundary layers, a turbulent boundary layer may lead to increased carbon uptake by plants. The biological trade-off is potentially increased transpirational water loss. However, in understory habitats characterized by low windspeeds, even a few trichomes may increase turbulence in the boundary layer, thus facilitating photosynthetic gas exchange. Preliminary field data show that critical trip factors are exceeded for several plant species, both in understory and open habitats.

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Introduction

Transport of CO_2 and water vapor (H_2O_v) between plants and the environment takes place mostly via stomatal pores since the waxy cuticle covering the leaf epidermis is highly impermeable to water and other gases (Kerstiens, 1994). A trade-off in conditions favorable for CO_2 uptake from the atmosphere is the loss of water to the environment. In both C_3 and C_4 plants, stomates are generally open during daytime and closed at night, resulting in lowered daytime resistance to gas exchange (Aphalo & Jarvis, 1993; Meinzer *et al.*, 1995). An additional resistance to the exchange of CO_2 and H_2O_v is the boundary layer, the layer of air over the leaf surface in which the windspeed is below that of the ambient windspeed. Typically, stomatal resistance is considerably higher than boundary layer resistance (Nobel, 1991).

The thickness and character of the boundary layer are influenced by factors such as windspeed, shape and size of the leaf, and leaf surface roughness. Airflow in the boundary layer can have either a laminar or turbulent character. While turbulent air flow patterns are more complicated

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to describe, diffusion across a laminar boundary layer is described mathematically by Fick's first law of diffusion (Campbell, 1986). Determining whether airflow is laminar or turbulent is complicated in systems at the scale of leaves in wind. Grace (1978) suggested that the boundary layer over leaves is mostly turbulent, and turbulent flow in the boundary layer has been observed over poplar leaves studied in wind tunnel conditions. However, at low windspeeds, boundary layers may be laminar even if the ambient airflow is turbulent (Vogel, 1994). The rate of gas transport in turbulent boundary layer flow conditions is an order of magnitude or more faster than diffusion in laminar conditions (Schwarzenbach *et al.*, 1993).

Leaf surfaces of many plants are covered with trichomes during some or all stages of their life (Johnson, 1975; Brewer & Smith, 1997). Reported functions of trichomes include reduction of absorbed solar radiation (Eller & Willi, 1977), reduction of leaf temperature and rates of transpiration (Ehleringer & Mooney, 1978), defense against herbivory and parasites (Neal *et al.*, 1989; Bodnaryk, 1996), reduction in water films on leaves that can inhibit gas exchange (Brewer & Smith, 1994, 1997), and decoupling leaf temperature from changes in solar radiation (Meinzer & Goldstein, 1985).

Depending on density, trichomes may increase leaf surface roughness, which can change air flow in the boundary layer from laminar to turbulent. Moreover, increased surface roughness can lead to increased heat exchange across surfaces of leaves (Chen *et al.*, 1988) due to increased turbulence. Others have reported that changes in boundary layer characteristics can alter the response of plants to ambient CO_2 concentrations (Aphalo & Jarvis, 1993). Influences on boundary layer conditions could be particularly important for plants in low wind environments, such as forest understories. In the understory, large leaf areas presumably facilitate light capture (compared to leaves of similar plants in open habitats; e.g., Parkhurst & Loucks, 1972). However, there is a trade off because larger leaves have thicker boundary layers than small leaves.

The objective of this study was to evaluate influences of trichomes on boundary layer conditions for photosynthetic gas exchange. We predicted

that even widely spaced trichomes (i.e., low density) might act to enhance gas exchange at the leaf surface by facilitating the onset of turbulent gas exchange in the boundary layer, and that this influence could be particularly important for plants in low wind or still environments. Using a modeling approach, we addressed the following questions: (1) how do trichomes influence the thickness and flow characteristics in the boundary layer; and (2) what are the potential implications of boundary layer thickness and flow pattern on exchange of CO_2 and H_2O_v? While the results we present are based on model predictions, they increase our understanding of potential influences of leaf pubescence on photosynthetic gas exchange and, thus, lead to new avenues of investigation.

Methods

To understand the influences of trichomes on boundary layer dynamics, we modeled characteristics of the boundary layer, the influence of trichomes on leaf surface roughness, and the resulting effects on gas exchange. For all analyses, we assumed non-exchanging (dead, dry) trichomes, with an even spacing across the leaf surface. Definitions of symbols and a list of assumptions are found in Appendices A and B.

DESCRIBING THE LEAF BOUNDARY LAYER

Because air speed in the boundary layer approaches free stream asymptotically, the outer limit of the boundary layer is generally defined as the distance from the leaf surface at which the local windspeed is 99% of the free stream wind velocity (Vogel, 1994). Several methods have been developed to estimate the thickness of the boundary layer, which usually is assumed to be laminar. Vogel (1994) reported a formula to estimate the boundary layer thickness at distance from the leading edge of the leaf as a function of the leaf length (L) and the Reynolds number (Re_L):

$$\delta = 5 \frac{L}{\sqrt{Re_L}}. \tag{1}$$

Equation (1) assumes laminar flow in the boundary layer, which is reasonable if the thickness of

the boundary layer is much smaller than the width of the leaf and $6 \times 10^2 < Re < 1 \times 10^5$ (Vogel, 1994).

To estimate total gas exchange over a leaf surface, an expression of average boundary layer thickness is useful. Assuming a laminar boundary layer, eqn (1) can be rewritten to estimate the average boundary layer thickness (Monteith & Unsworth, 1990):

$$\delta = 1.72 \frac{L}{\sqrt{Re_L}}. \qquad (2)$$

A major limitation for these theoretically derived formulae is that they tend to overestimate boundary layer thickness at higher windspeeds and at high Re, for both leaf models and real leaves (Vogel, 1994). As a compromise between theoretical and purely empirical estimates, semi-empirical equations have been developed. For example, Nobel (1991) reported a semi-empirical formula to estimate the boundary layer thickness over flat, leaf-like objects at $3 \times 10^2 < Re < 16 \times 10^3$:

$$\delta = 1.03 \frac{L}{\sqrt{Re_L}}. \qquad (3)$$

Note that the numerical factor in eqn (3) has the units m s$^{-0.5}$. The units of boundary layer thickness and leaf length in eqns (1–3) are meters, and apply to laminar boundary layer conditions. However, at higher Reynolds numbers the boundary layer becomes turbulent, and these equations can no longer be used. A theoretical formula to estimate the thickness of a turbulent boundary layer is given by Vogel (1994):

$$\delta = 0.376 \frac{L}{\sqrt[5]{Re_L}}. \qquad (4)$$

While the boundary layer may be laminar at the leading edge of a leaf, at some distance downwind, the boundary layer may become turbulent due to the length of the leaf or presence of trichomes. In our study, in this case the leaf surface was partitioned into laminar and turbulent parts for modeling. Even if the upper part of the boundary layer is turbulent, a thin laminar layer of air may exist at the leaf surface (e.g., Grace, 1978; Vogel, 1994).

To generally characterize leaf boundary layers, we compared estimates of the boundary layer thickness using eqns (1–4) for leaves 0.01, 0.025, 0.05, 0.10 and 0.20 m long (orientation in the direction of the wind), and at ten different wind-speeds ranging from 0.10 to 5.0 m s^{-1}. The range of leaf lengths is representative for those found in nature (e.g., Campbell, 1986; Barbour et al., 1987), although shorter and longer leaf lengths are not uncommon. For modeling purposes, leaves were treated as flat, smooth plates, although we acknowledge that boundary layers over leaf models and real leaves behave differently (Grace, 1978; Vogel, 1994).

INFLUENCE OF TRICHOMES

We predicted that the presence of trichomes on leaf surfaces would increase surface roughness and change flow patterns in the boundary layer from laminar to turbulent. A set of equations that estimates the minimum height of an intrusion into a laminar boundary (sub)layer at which the layer becomes turbulent is given by (Goldstein, 1938):

$$\varepsilon \leqslant k \frac{L}{\sqrt[4]{Re_L^3}}. \qquad (5)$$

In eqn (5), ε is the minimum intrusion height (m) for a projection, L is the length of the leaf (m), and Re_L represents the Reynolds number at the trailing edge of the leaf. The values of the constant, k, are 9.5 and 12.2 for pointed and rounded projection, respectively (Goldstein, 1938). Equation (5) is based on the assumption that flow was unaffected if $Re \leqslant 30$ for a pointed projection, or $Re \leqslant 50$ for rounded projections, because flow is dominated by viscous forces at these low Re values (e.g., see Vogel, 1994). We will refer to the minimal intrusion height as the critical trichome height, i.e., the height at which trichomes "trip" the boundary layer, changing it from laminar to turbulent flow.

In this study, we assumed that the boundary layer over leaves was laminar unless $Re_{critical}$ was exceeded at some point downwind. $Re_{critical}$ can be exceeded for both glabrous and pubescent

leaves due the length of the leaf (e.g., Dryden, 1959). Moreover, the boundary layer over a pubescent leaf can become turbulent when the critical trichome height is exceeded, as described by eqn (5) (Goldstein, 1938).

Note that eqn (5) does not take into account the density or the diameter of the trichomes, and is applicable only over a specific range of trichome heights. This is illustrated by reexpressing eqn (5) in the form $Re_L = (kL/\varepsilon)^{4/3}$ where k is defined as either 9.5 or 12.2. In this form, the equation specifies $Re_{critical}$ (i.e., Re where flow changes from laminar to turbulent) in a boundary layer containing protrusions. The problem is that as values for protrusion height ε tend toward zero, $Re_{critical}$ approaches infinity, which cannot be so. Thus, while these equations are suitable for making empirical predictions of what happens over a limited range of L/ε, they are not reliable near the glabrous limit.

We estimated a representative trichome height based on reported values, varying from 0.12–5 mm (Neal *et al.*, 1989; Brewer, unpublished data). In practice, the effective height of the trichome layer may be less than the trichome length due to the bending of trichomes. Thus, we used the effective height of the trichome canopy in our analyses rather than trichome length.

FLUX OF GASES

The diffusion rate across a laminar boundary layer is described by Fick's law of diffusion (Campbell, 1986):

$$F_j = -D_j\left(\frac{(C_{in}) - (C_{out})}{\delta}\right). \qquad (6)$$

Under laminar conditions, the diffusion coefficient of CO_2 in air, D_j, is about 14.7×10^{-6} m^2 s^{-1} at 20°C (Monteith & Unsworth, 1990). In this study, we assumed an ambient CO_2 concentration of 350 ppm, and a ratio of C_{in}/C_{out} of 0.8. Depending on the case, CO_2 fluxes were calculated for different boundary layer conditions (fully laminar, fully turbulent, and partially laminar/turbulent). Equation (6) also applies to turbulent boundary layers. Under turbulent conditions, the diffusion coefficient is replaced by the eddy diffusion coefficient, E_j. In this study, E_j was

assumed to be 10 times larger than the diffusion coefficient under laminar conditions, i.e., $E_j = 10D_j$ (Schwarzenbach *et al.*, 1993). This is a conservative assumption since the eddy diffusion coefficient is at least one or more orders of magnitude higher than the diffusion coefficient in laminar conditions (Schwarzenbach *et al.*, 1993).

Results

THE LAMINAR BOUNDARY LAYER

In general, thickness of the boundary layer decreased with increasing windspeed and decreasing leaf length (Fig. 1a and b). Estimated
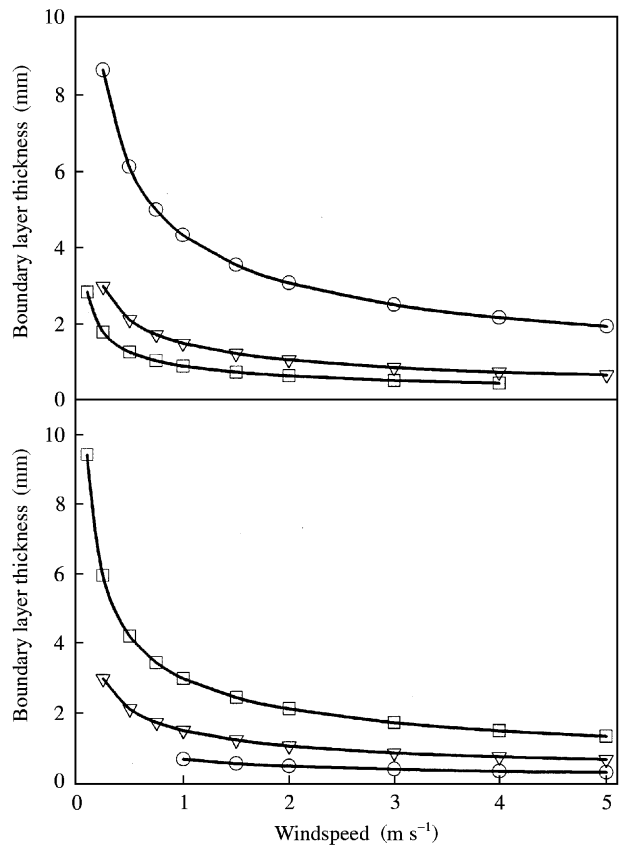

FIG. 1. The laminar boundary layer thickness over a leaf of 0.05 m long, calculated according to three different methods as a function of windspeed [Panel 1(a)]: at the trailing edge of a leaf (Vogel, 1994), and the average boundary layer thickness using a theoretical equation (Monteith & Unsworth, 1990) and a semi-emperical equation (Nobel, 1991). (–⊖–) Trailing edge; (–▽–) average, theoretical; (–☐–) average, semi-empirical. Panel 1b shows the boundary layer thickness over three different leaf sizes as a function of windspeed, calculated according to Monteith & Unsworth (1990). $L = 0.01$, (–⊖–); $L = 0.05$, (–▽–); $L = 0.20$, (–☐–).

boundary layer thickness was dependent on the method of calculation (Fig. 1a). Differences in boundary layer thickness across a leaf were largest between the boundary layer at the trailing edge and the average boundary layer (from the leading to the trailing edge). Likewise, estimates of average boundary layer thickness differed between the semi-empirical method [eqn (3)] and the theoretical averaging method [eqn (2)]. Boundary layer thickness increased with increasing leaf length (Fig. 1b).

TRICHOME EFFECTS AND THE TURBULENT BOUNDARY LAYER

Critical trichome height decreased with increasing windspeed (Fig. 2a) due to the influence of windspeed on Re, resulting in thinner boundary layers. Using trichome canopy heights observed in nature (Table 1), the curves in Fig. 2a suggest that critical trichome heights are exceeded for most plant species at wind speeds above $2\,\mathrm{m\,s^{-1}}$. An exception is *H. Albiflorum*, with expected effects of trichomes on boundary layer flow between windspeeds of 0.25 and $1.0\,\mathrm{m\,s^{-1}}$. Moreover, critical trichome height was higher for rounded trichomes compared to pointed trichomes, as was expected based on the difference of values for the constant (k) in eqn (5).

A measure of the effect of trichomes on airflow in boundary layer is given by the ratio of the critical windspeed for a leaf with trichomes to the critical windspeed for a leaf without trichomes (Table 2). If this ratio < 1, turbulence occurs at a lower windspeed for pubescent than glabrous leaves. From this ratio, we derived a simple method to assess the influence of trichomes on turbulence in the leaf boundary layer, the trip factor (TF). This is a dimensionless ratio of the height of the trichome canopy to the length of the leaf (Fig. 2b):

$$TF = \frac{TH}{L}. \qquad (7)$$

In eqn (7) TF represents the trip factor (dimensionless), TH the trichome height (m), and L the leaf length (m). The trip factor can be empirically derived from data on critical windspeed, leaf length and trichome canopy height (Table 2). The
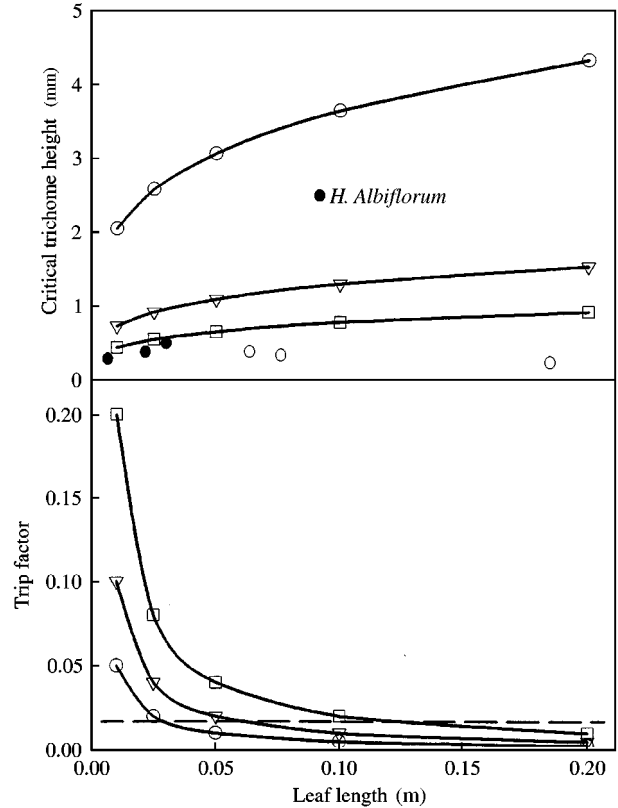

FIG. 2. The dependency of critical trichome height on leaf length and windspeed [Panel 2(a)]. Data on leaf length and trichome height are indicated for selected plant species (Table 1) with $TF < 0.02$ (open symbols) and $TF > 0.02$ (filled symbols). (–⊖–) $0.25\,\mathrm{m\,s^{-1}}$; (–▽–) $1.0\,\mathrm{m\,s^{-1}}$; (–⊟–) $2.0\,\mathrm{m\,s^{-1}}$. Panel 2b shows the Trip Factor (TF), ratio of trichome height to leaf length, as a function leaf length and trichome height. Values for trichome canopy height are 0.5 mm (open circles), 1.0 mm (open triangles), and 2.0 mm (open squares). TF values above 0.02 (see dashed reference line) indicate that the onset of turbulence is enhanced by the presence of trichomes: (–⊖–) $TH = 0.5\,\mathrm{mm}$; (–▽–) $TH = 1.0\,\mathrm{mm}$; (–⊟–) $TH = 2.0\,\mathrm{mm}$.

critical value for the TF also can be derived theoretically by rewriting eqn (5) in the form $TF = \varepsilon/L = k/Re_L^{3/4}$, where k is either 9.5 or 12.2 (Goldstein, 1938). Based on our modeling results, a trichome canopy height $\sim 2\%$ of the leaf length ($TF \geqslant 0.02$; see reference line in Fig. 2b) decreased the critical windspeed and enhanced the onset of turbulence in the boundary layer. The enhancement of turbulence by trichomes increased with trichome height and decreased with leaf length (Fig. 2b).

Interestingly, potential influences of trichomes on boundary layers can be predicted with

TABLE 1

Morphological characteristics for leaves of selected plant species in the Compositae family, in open (OP), semi-open (SO), or understory (US) habitats. Leaf sides are designated as adaxial (AD) and abaxial (AB). Mean values are shown for leaf length (n = 5), trichome density and height of the trichome canopy (n = 15), and Trip Factor (n = 5). TF values above the critical value of 0.02 are indicated in bold and italics

Family and species	Habitat	Leaf length (m)	Trichome density (number mm^{-2})		Trichome canopy height (mm)		Trip Factor	
			AD	AB	AD	AB	AD	AB
Achillea millefolium L. B&H	OP	0.007	18.0	18.2	0.23	0.24	***0.03***	***0.03***
Anaphalis margaritacea L.	US	0.065	14.1	> 25.0	0.28	0.37	< 0.01	0.01
Antennaria alpina L. Gaertn.	SO	0.028	18.8	> 25.0	0.30	0.54	0.01	***0.02***
Arnica cordifola Hook.	US	0.075	2.6	3.6	0.29	0.33	< 0.01	0.01
Balsamorhiza sagittata Pursh	SO	0.180	15.3	> 25.0	0.13	0.13	< 0.01	< 0.01
Heterotheca villosa Pursh	OP	0.020	11.1	12.8	0.32	0.44	***0.02***	***0.02***
Hieracium albiflorum Hook.	SO	0.091	15.4	14.7	2.46	2.34	***0.03***	***0.03***

TABLE 2

Critical windspeed and tripfactor for glabrous leaves (TH = 0 mm) and pubescent leaves with trichome canopy heights of 0.5 and 2 mm. The critical windspeed is defined as the windspeed at which boundary flow changes from laminar to turbulent flow. Note that TF ⩾ 0.02 (indicated in bold font) coincide with lower critical windspeed for pubescent leaves compared to glabrous leaves

Leaf size (m)	Critical windspeed, m s^{-1}			Trip Factor, $TF = TH/L$	
	$TH = 0$ mm	$TH = 0.5$ mm	$TH = 2$ mm	$TH = 0.5$ mm	$TH = 2$ mm
0.010	6.00	1.61	0.25	**0.05**	**0.20**
0.025	2.40	2.18	0.34	**0.02**	**0.08**
0.05	1.20	2.74	0.43	0.01	**0.04**
0.10	0.60	3.44	0.54	0.005	**0.02**
0.20	0.30	4.33	0.68	0.0025	0.01

a simple dimensionless number, from field data on leaf length and trichome canopy height for leaves in different habitats or microenvironments. Actual field data show that TF is higher that the critical value for several species, in both open and understory habitats (Table 1). However, the windspeed at which the critical trichome height is exceeded depends on the plant species (Table 2).

FLUX OF GASES OVER THE LAMINAR AND TURBULENT BOUNDARY LAYER

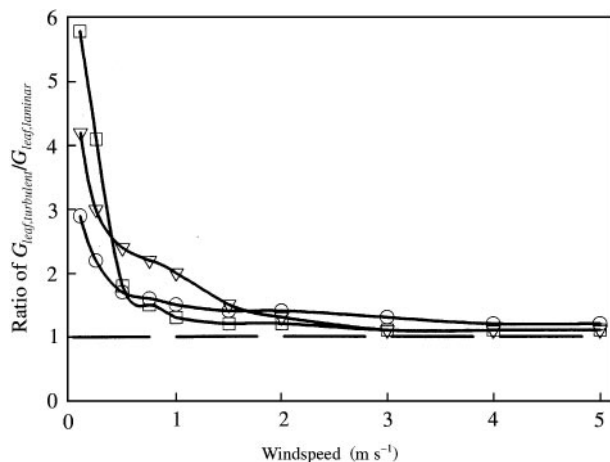We found a pronounced increase in photosynthetic gas exchange over pubescent leaves due to the higher leaf conductance to CO_2 gas, especially at low windspeeds (Fig. 3). Leaf conductance, $[(G_{bl,CO_2})^{-1} + (G_{s,CO_2})^{-1}]^{-1}$, over the turbulent boundary layer was greater for bigger leaves at low windspeed, as indicated by a higher ratio of leaf conductance over turbulent compared to laminar boundary layers (Fig. 3).

Discussion

To our knowledge, there has been very little work predicting the influence of trichomes on boundary layer dynamics. These results show that the presence of trichomes can greatly enhance the transition from laminar to turbulent

FIG. 3. The ratio of leaf conductance to CO_2 gas $[(G_{bl,CO_2})^{-1} + (G_{s,CO_2})^{-1}]^{-1}$, assuming turbulent versus laminar boundary layer flow, as a function of windspeed and leaf length. Stomata are assumed open, $G_{s,CO_2} = 1.2 \text{ cm s}^{-1}$. (–⊖–) $L = 0.01$ m; (–▽–) $L = 0.05$ m; (–⊟–) $L = 0.20$ m.

flow in the leaf boundary layer, and increase photosynthetic gas exchange rates. Using the dimensionless "trip factor" (TF), we can predict when the presence of trichomes enhances turbulence in the boundary layer. Preliminary field data (Table 1) suggest that the presence of trichomes may enhance gas exchange of CO_2 and H_2O_v ($TF > 0.02$) for plant species in both open and understory habitats, depending on the windspeed.

THE LAMINAR BOUNDARY LAYER

Boundary layer thickness decreased with increasing windspeed and decreasing leaf length, as expected from the physical character of the boundary layer. However, estimates of boundary layer thickness differed considerably (Fig. 1a). Thus, assumptions must be considered carefully when choosing a specific method to calculate boundary layer characteristics (McNaughton, 1994). Theoretical formulae tended to give higher estimates of the thickness of the laminar boundary layer compared to semi-empirical formulae, similar to reports by Nobel (1991) and Vogel (1994).

The character of free stream airflow is an important factor in determining the flow character in the boundary layer. Even in closed canopies (e.g., crops, some forests), the free air stream is

generally turbulent (Shaw *et al.*, 1974; Grace, 1978; Hollinger *et al.*, 1994). Even if the free air stream is turbulent, the boundary layer at the leaf surface may remain laminar because of low windspeeds near leaves in many habitats (Grace, 1978). However, the resulting leaf boundary layer is unsteady, which is one of the reasons why the engineering formulae, such as those used here do not provide accurate estimates.

INFLUENCE OF TRICHOMES

The presence of trichomes decreased the *Re* at which the boundary layer becomes turbulent ($Re_{critical}$). Assuming leaf lengths of 0.01–0.2 m, and turbulent boundary layers at $Re \sim 3500$ in field conditions (Grace, 1978), the windspeed at which the transition from laminar to turbulent boundary layer occurs varied from 1.6–4.3 m s^{-1} ($TH = 0.5$ mm) to $0.3 - 0.7$ m s^{-1} ($TH = 2$ mm) (Table 2). The influence of trichomes on the boundary layer of larger leaves is less pronounced than the influence on small leaves (Fig. 2). Yet, in understory habitats where low windspeeds (e.g., $U < 0.5$ m s^{-1}) are common (Sigmon *et al.*, 1984; Brewer & Smith, 1997; Morecroft *et al.*, 1998), the presence of even a few trichomes may play a role in how leaf boundary layer dynamics influence gas exchange. However, the wind speed at which trichomes may enhance turbulence in the boundary layer varies by species (Fig. 2a).

Because ε is calculated at the trailing edge of a leaf, the effect of trichomes on the boundary layer actually may have been underestimated. This bias could be addressed by calculating ε at a distance halfway between the leading and trailing edge of the leaf, assuming that boundary layer thickness will be the average of the two edge positions. Other assumptions made in this study also were conservative (e.g., flat, glabrous leaf surface, trichomes of simple shapes, $E_j = 10 \times D_j$). Thus, the potential effect of trichomes on boundary layer dynamics may be more pronounced than indicated by our calculations. Yet, in field conditions, leaves do not always comply with the assumptions made (Appendix B), and turbulence may occur at much lower *Re* than predicted on the basis of theoretical and semi-empirical models (Grace, 1978; Vogel, 1994).

Consequently gas fluxes over real pubescent leaves may be higher than expected, even under laminar boundary layer conditions (Grace & Wilson, 1976; Vogel, 1994).

While we assumed either rounded or pointed trichomes, the variety of trichome types and shapes found in nature is large (e.g., Mauseth, 1988). Moreover, we would predict that the distribution (even versus patchy) and density of trichomes, varying from the absence of trichomes to 100–200 trichomes per mm^2 for montane and subalpine plant species (Brewer et al., 1991; Brewer & Smith, 1997), also would have important influences on airflow in the boundary layer. However, the combined effects of trichome shape, distribution, and density are hard to quantify and have not been considered in this or other recent models.

GAS EXCHANGE AND ECOLOGICAL IMPLICATIONS OF BOUNDARY LAYER CONDITIONS

Many studies report important influences of trichomes on photosynthetic gas exchange in open habitats (e.g., Eller & Willi, 1977; Ehleringer & Mooney, 1978; Brewer & Smith, 1994). Leaf conductance, $[(G_{bl,CO_2})^{-1} + (G_{s,CO_2})^{-1}]^{-1}$, over turbulent boundary layers was considerably higher than over laminar boundary layers (Fig. 3), especially at low windspeed. This is because Eddy diffusion coefficients are at least one to three orders of magnitude higher than diffusion coefficients in laminar conditions (Jones, 1992; Schwarzenbach et al., 1993). In scenarios where stomates were partially or fully open (i.e., the most relevant for photosynthetic gas exchange), $[(G_{bl,CO_2})^{-1} + (G_{s,CO_2})^{-1}]^{-1}$ was up to 6 times higher for turbulent compared to laminar boundary layer conditions (Fig. 3). The influence of turbulence on leaf conductance decreased with increasing windspeed. In this study, the effect of trichomes was similar for all leaf sizes, except at low windspeed. However, the transition from laminar to turbulent boundary layer conditions has much greater significance for gas exchange rates over smaller versus larger leaves, because boundary layers over large leaves are often turbulent due to leaf size, even if a leaf surface is glabrous. Therefore, leaf size rather than trichomes, may be the factor that triggers the onset of turbulence in a boundary layer over large leaves.

While trichomes may increase CO_2 uptake due to their influences on turbulence in the boundary layer, a possible cost is increased transpirational water loss. Obviously stomatal control plays a key role in the dynamics of gas exchange for such leaves in open habitats. Stomata are likely to close where increases in turbulence in the boundary layer leads to higher VPD. The shape, height, and density of trichomes will determine their effectiveness in increasing turbulent boundary layer conditions. Pubescence may be particularly advantageous for smaller leaves because the length of trichomes relative to leaf length will be greater compared to larger leaves (as indicated by higher values of TF, Fig. 2b; Table 1), thereby increasing the influence on $Re_{critical}$.

Wind tunnel studies have shown that the spatial distribution of protrusions into the boundary layer has a significant effect on the turbulent drag over a surface (Sirovich & Karlsson, 1997). A leaf surface with a dense trichome canopy may have an "effective" surface for gas exchange above the epidermis (e.g., Jones, 1992). For especially dense trichome layers, i.e. $> 60\ mm^{-2}$ (Brewer et al., 1991; Brewer & Smith, 1997), two boundary layers may influence diffusion of gases. An extra boundary layer resistance for gas diffusion may exist under a dense trichome canopy, which could decrease gas exchange with the environment considerably. The effective depth of the trichome canopy in this case will be approximately the length of the trichomes (Jones, 1992) and be characterized by still air conditions. Boundary layer conditions on top of such a dense trichome layer would be considerably different than near the leaf epidermis. The relative trade offs between potentially lowered rates of gas exchange, influences on leaf temperature (e.g., via higher reflectance), and the vapor pressure gradient are not well understood at this time.

Conclusion

Trichomes play an important role in determining the thickness and flow character of the boundary layer over leaves and, thus, have a significant effect on photosynthetic gas exchange of plants. This influence may be particularly

important in low wind environments, such as forest understories where, even at low densities, the presence of trichomes may lower the onset of turbulence in the boundary layer, thus enhancing photosynthetic gas exchange. Preliminary field data suggest that this influence on the boundary layer may be relevant in open, semi-open, and understory habitats. However, the wind speed at which trichomes may enhance turbulence in the boundary layer varies by species. To test some of the predictions resulting from this work, experimental studies are needed that explore the effects of trichomes on photosynthetic gas exchange and boundary layer flow. Moreover, additional studies that apply the trip factor, the new dimensionless number derived in this study, will be important for testing the influence of trichomes on the character of the boundary layer under field conditions.

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Re	Reynolds number (dimensionless)
Re_L	local Reynolds number (dimensionless)
$Re_{critical}$	Reynolds number at which boundary layer flow becomes turbulent
TF	trip factor (dimensionless)
TH	trichome height (m)

APPENDIX A

List of Symbols

C_{in}	gas concentration in stomatal cavity (g m^{-3})
C_{out}	gas concentration in ambient air (g m^{-3})
D_j	diffusion coefficient of a gas in air under laminar conditions $(\text{m}^2\,\text{s}^{-1})$
E_j	diffusion coefficient of a gas in air under turbulent conditions $(\text{m}^2\,\text{s}^{-1})$
δ	boundary layer thickness (m)
ε	critical trichome height (m), minimum height of a vertical projection into the undary layer, at which the layer becomes turbulent
F_j	gas flux per unit of surface area $(\text{g m}^{-2}\,\text{s}^{-1})$
G_{s,CO_2}	Stomatal conductance to CO_2 (cm s^{-1})
G_{bl,CO_2}	Boundary layer conductance to CO_2 (cm s^{-1})
k	constant
L	length of the leaf (or plate) in direction of the wind (m)

APPENDIX B

List of Assumptions and Definitions

1. The outer limit of the boundary layer is defined as the distance from the leaf where the local windspeed is 99% of the free stream wind speed (Vogel, 1994).

2. Laminar flow is assumed when $\delta \ll L$ (m).

3. The surface of a glabrous leaf is assumed to be flat and smooth.

4. Trichomes have simple shapes, either rounded or pointed; they are dead, dry, and non-exchanging.

5. Laminar flow will be affected when (according to Goldstein, 1938):
   $Re^* > 30$ (rounded trichomes) or
   $Re^* > 50$ (pointed trichomes)

6. At low windspeeds ($< 0.25\,\text{m s}^{-1}$), the boundary layer is laminar, unless trichomes change the flow pattern.

7. The long axis of the leaf is parallel to the direction of airflow.

8. The critical trichome height (ε) is calculated at the trailing edge of the leaf.