

Assessing the adaptive significance of plant architectural adaptations to elevated temperature

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February 26, 2010

1 Introduction

Plants growing in natural environments are exposed to fluctuating ambient temperatures. Photosynthetic activity and metabolism are, however, optimal within specific temperature ranges. Plants have therefore evolved a variety of temperature-mediated developmental adaptations to enhance productivity and promote survival. For example, when the plant is challenged by drought or heat it may alter its physiology to reduce water loss [3, 6, 8], or it may alter its shape. Models of the physical and physiological effects of temperature variation on plant processes are therefore valuable tools in enhancing our understanding of the interaction of plants with their microenvironments.

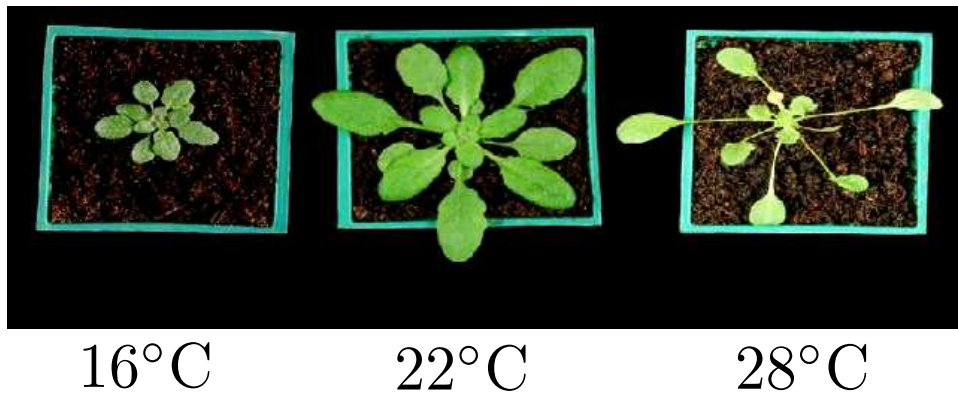


Figure 1.1: Adult *Arabidopsis* plants grown at three different temperatures.

Plants display a range of dramatic phenotypes when grown at elevated temperatures (see Figure 1.1). These include elongation of stems and petioles (leaf stems), and increased leaf angles from the soil surface (hyponasty), as seen for adult *Arabidopsis* in Figure 1.2. At high photon irradiances of light, these adaptations are accompanied by a small increase in leaf area.



Figure 1.2: Adult *Arabidopsis* plants grown at 22°C (top) and 28°C (bottom). The elongation of the stems and the increased leaf elevation of the plant grown at 28°C compared to the one grown at 22°C is clear.

Despite the striking nature of these phenotypes, their potential adaptive significance remains speculative. High air temperature likely imposes two major physiological stresses on plants: heating of plant tissues and increased loss of water through pores (stomata) on the surface of leaves (transpiration) [1]. Stomatal movements are essential for photosynthetic gas exchange, and ultimately for plant survival [9, 10]. Closure of the stomata can therefore only provide a limited water conservation solution during conditions of increased evaporative water loss.

High temperature-mediated leaf elevation has been postulated to reduce heat damage through decreasing direct exposure of leaves to sunlight [7]. The adaptive significance of axes elongation growth at elevated temperatures remains unknown.

Water use efficiency is a priority area in plant science research, particularly with regard to growth at elevated temperatures associated with global climate change [3]. Transpiration has been modelled in a number of crops and trees to provide predictions of water usage within canopies (eg. [2]). None of these models incorporate temperature-mediated alterations in plant architecture. It has been hypothesised that stem elongation and leaf elevation may both facilitate leaf cooling and limit the water supply to leaf stomata and hence reduce water loss. Figure 1.3 shows a thermal image of two *Arabidopsis* specimens, one grown at 22°C and the other at 28°C, the latter (with its modified architecture)

displays enhanced leaf cooling whereas the former does not. *Arabidopsis* provides a suitable model organism to assess the adaptive significance of such architectural changes given their speed of growth and adaptation, and the ease with which experiments are performed.

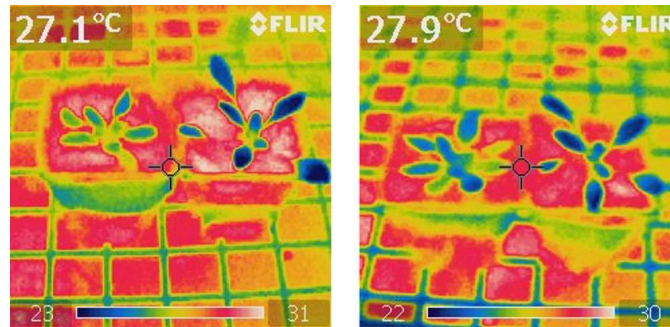


Figure 1.3: Thermal imaging of two *Arabidopsis* plants, one grown at 22 C (left plant) and the other at 28 C (right plant) exposed to high temperature. It is clear that the plant grown at 28 C displays more efficient cooling.

The purpose behind the structural change in *Arabidopsis* after prolonged heat stress remains unclear. The use of mathematical models may help to explore the relationship between plant geometry, water flow and leaf temperature.

Experimental data for use in validating and tuning the mathematical models is available from the Franklin laboratory, including water-loss time course data and results from thermal imaging studies (as in Fig. 1.3).

2 Study group questions and goals

The questions asked at the start of the study group were:

1. Do architectural adaptations to high temperature increase water use efficiency through reducing transpirational loss from leaves?
2. Do architectural adaptations to high temperature facilitate plant cooling?

Any progress towards answering these questions would provide components towards a model which would predict optimum plant architectures to maintain transpirational rate and leaf temperature over a range of growth temperatures.

3 Modelling ideas

The week began with the team discussing a number of possible modelling ideas and directions.

Addressing the questions of water efficiency, water conservation and control of the transpirational loss from leaves requires models incorporating:

1. Water flow in soil and uptake at roots.
2. Water flow through the plant stem.
3. Water flow through the leaf stems and leaves to stomata.
4. Transpiration processes.
5. Evaporative boundary layers around leaves.
6. Regulation of stomatal opening.
7. Air flow around leaves and stems.
8. Evaporation at soil surface.

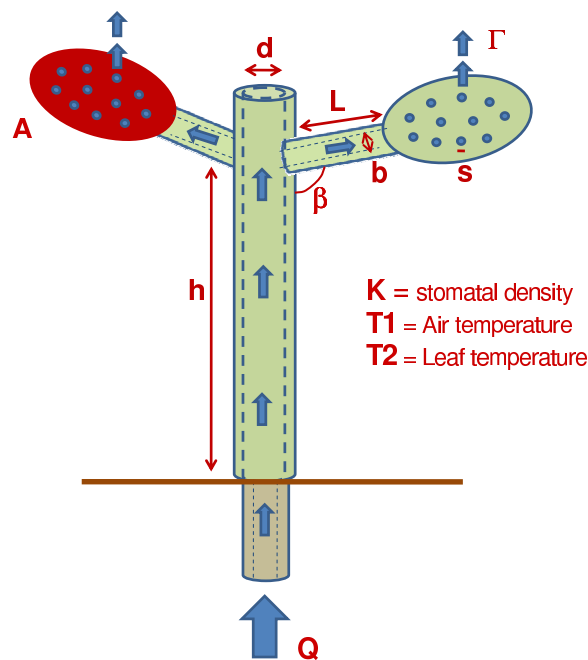


Figure 3.1: Model of water flow and leaf cooling.

The formulation of such a comprehensive model (such as the one shown in Fig. 3.1) and the development of appropriate solution techniques is an extremely complex biophysics problem which surpasses the scope of this four-day study group. We therefore have sought to identify the key components of the system which may highlight the significance of architectural adaptations.

It was assumed that leaf cooling was driven by evaporation at the stomata. A hypothesis was proposed which suggested that increased axes elongation at elevated temperatures separates boundary layers of saturated water vapour between leaves which would otherwise limit (and eventually prevent) evaporative cooling (Figure 3.2). Increased plant

height was similarly predicted to enhance leaf cooling by raising the underside of leaves (where the majority of the stomata are situated) away from saturated water vapour at the soil surface. A model to examine the effect of leaf separation on evaporative cooling was therefore developed.

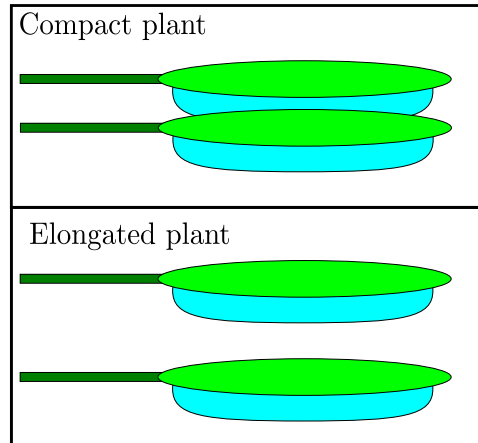


Figure 3.2: Evaporative boundary layers. In plants where the leaves are close to each other (top) the evaporation rate is limited by the boundary layer which fills the inter-leaf gap. Plants with larger inter-leaf gaps (bottom) provide a larger region for water vapour diffusion and should allow a higher evaporation rate.

4 Models of evaporative cooling

To study the effects of leaf separation on evaporative cooling at high temperatures, we developed a model of heat and mass transfer from “leaves” surrounded by air, with evaporation of liquid water at the stomata on the leaf surface.

4.1 Model assumptions

A number of assumptions and simplifications were made.

- Leaves are treated as continuously supplied reservoirs of liquid water, suspended in air.
- For the initial two-dimensional (2D) model, each leaf is taken to be rectangular.
- Heat and mass transfer are governed by heat diffusion in the leaf (liquid water) and heat and water vapour diffusion in the air.
- Evaporation occurs at the underside of a leaf only.
- Evaporation rate is proportional to both the stomatal density and the difference between the water vapour concentration and the saturation concentration.

4.2 Model formulation

We begin by formulating a model for each leaf surrounded by air. In Figure 4.1, we show the governing equations and boundary conditions for temperature T inside a single leaf (water), and temperature T and water vapour concentration C in the surrounding air.

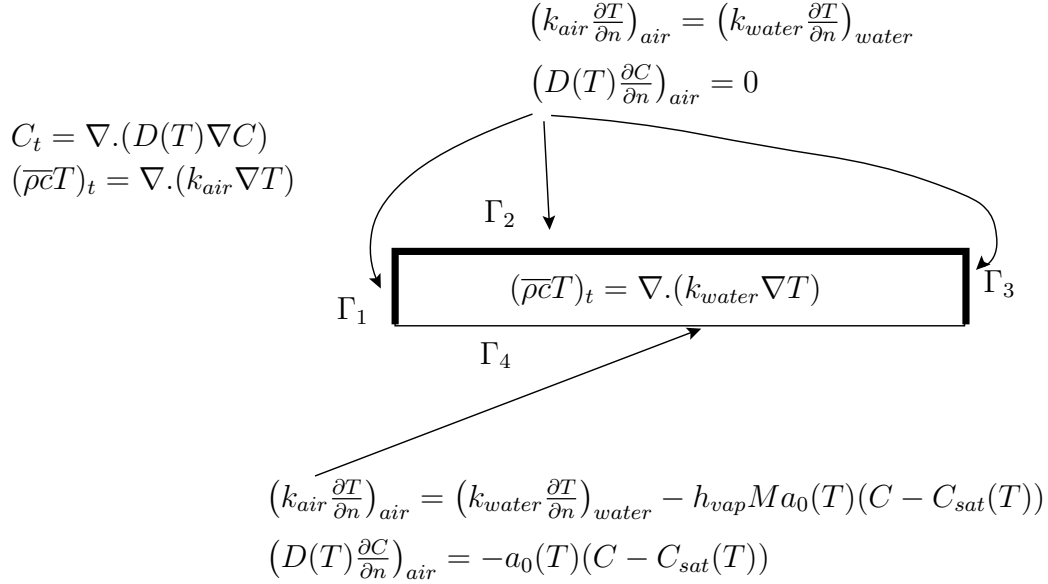


Figure 4.1: Model heat and mass transfer for a leaf suspended in air.

The diffusion coefficient D for water vapour in air is a function of temperature. The thermal conductivities are $k_{air,water}$, and $\bar{\rho}c$ is the product of density and heat capacity. The latent heat of vaporisation of water is h_{vap} , and $C_{sat}(T)$ is the saturation concentration of water vapour as a function of temperature (assuming the ideal gas law). The coefficient $a_0(T)$ is the leaf conductance which controls the evaporation rate. This conductance is a function of temperature, and will also depend on the stomatal density. M is the molar mass of water. The boundary conditions on the underside of the leaf Γ_4 represent heat and mass balances, including the effects of evaporation. On the other three leaf boundaries $\Gamma_{1,2,3}$, the energy and mass balance conditions do not include the evaporation term, and hence we have simple continuity of heat flux and zero mass flux. The direction n is the outward normal. At each of the four boundaries, the third condition is that temperature is continuous.

The model can, of course, be extended by adding in multiple leaves at various shapes, separations and orientations.

Typical parameter values are shown in Table 4.1. A challenge which still remained at the end of the study group was to find a sensible range of values and functional form for the leaf conductance $a_0(T)$.

Table 4.1: Typical parameter values and functional forms. Sources: www.engineeringtoolbox.com and [4].

Parameter	Value/function	Units
h_{vap}	3.4×10^6	J kg ⁻¹
k_{air}	0.026	W m ⁻¹ K ⁻¹
k_{water}	0.58	W m ⁻¹ K ⁻¹
$\bar{\rho}c_{water}$	4.2×10^6	J m ⁻³ K ⁻¹
$\bar{\rho}c_{air}$	1.0×10^3	J m ⁻³ K ⁻¹
$D(T)$	$21.2 \times 10^{-6}(1 + 0.0071T)$	m ² s ⁻¹
$p_{sat}(T)$	$190T - 1460$	Pa
$C_{sat}(T)$	$p_{sat}(T)/R(T + 273)$	mol m ⁻³
R	1.8×10^{-2}	kg mol ⁻¹
$a_0(T)$??	m s ⁻¹

4.3 Numerical results - 1D

Initial discussions centered around the solution of a one-dimensional reduction of the problem in order to validate the model. In this case, each leaf is reduced to an interval on the line (say the y -axis), and the upper and lower boundaries $\Gamma_{2,4}$ are reduced to points on the line. Water vapour emerging at the underside of each leaf can diffuse below that leaf.

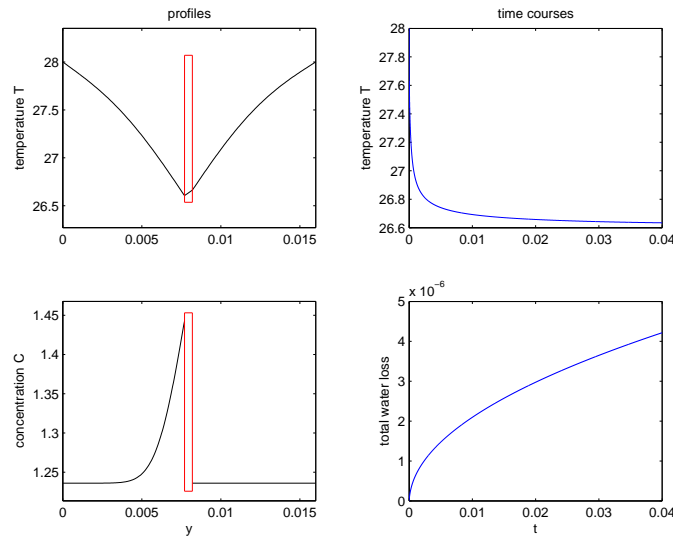


Figure 4.2: Temperature and concentration profiles at end time (left-hand column), and temperature and water loss time courses (right-hand column) for a single leaf.

In Figure 4.2, we show results of a finite difference simulation for a single leaf. The leaf

and surrounding air are initially at a temperature of 28C, and the water vapour concentration is initially uniform. In the left hand column, the temperature and concentration profiles at the end of the simulation are plotted, and shown with the leaf represented as a box. In the right-hand column, time courses are shown for average leaf temperature and total (cumulative) water loss. The growth cabinet boundary conditions are Dirichlet conditions for both concentration and temperature, which are held at their initial values. The leaf cools over time, and we see that the underside of the leaf (the left-hand side of the box) cools to a lower temperature than the upper leaf surface. There is an increase in water vapour concentration below the leaf as the liquid water evaporates and emerges into that region. The rate of cooling decreases as the water vapour concentration increases.

In Figure 4.3 we show results of a finite difference simulation with two leaves very close together. The leaf separation is half a leaf width. Both leaves cool, but we see that the upper leaf has a higher temperature. As the air between the two leaves becomes saturated with water vapour, the evaporation rate drops. After the initial transient during which the leaves cool rapidly, the leaf temperatures begin to increase. The water loss from the upper leaf reaches a maximum as the inter-leaf region becomes saturated.

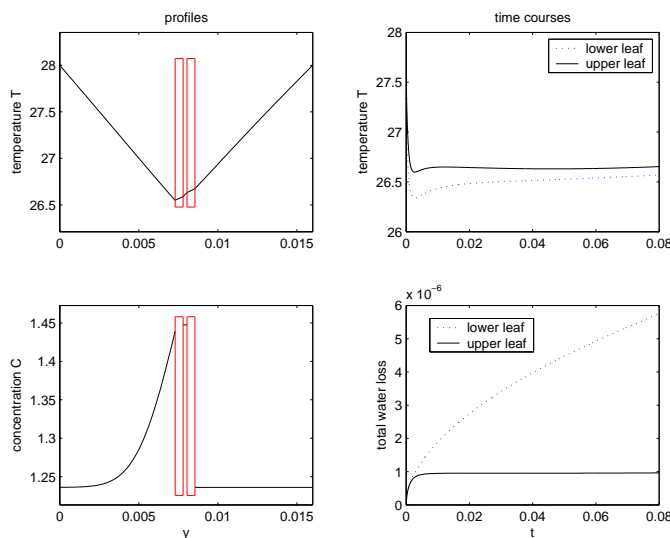


Figure 4.3: Temperature and concentration profiles at end time (left-hand column), and temperature and water loss time courses (right-hand column) for two leaves with small separation.

In Figure 4.4, we show results of a finite difference simulation with two leaves much further apart. In this case, the inter-leaf region does not become saturated so quickly with water vapour. The upper leaf still has a slightly higher temperature than the lower one, but the upper leaf cools and loses water at a higher rate than for the two leaves close together. The results appear as we would expect them to - rather like two isolated leaves which do not influence each other.

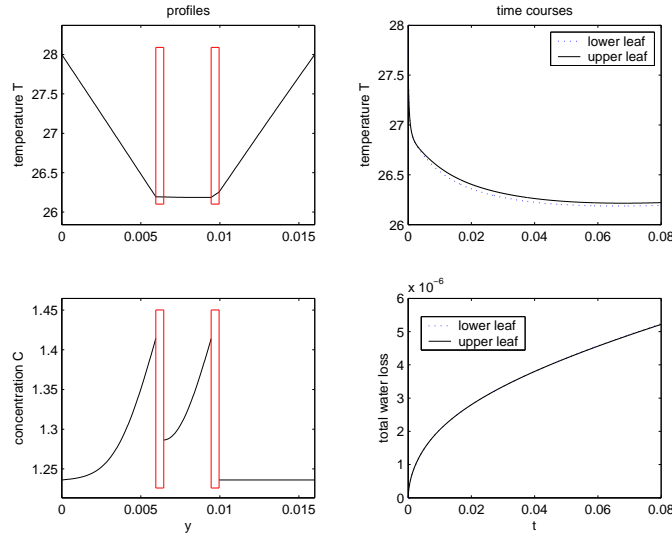


Figure 4.4: Temperature and concentration profiles at end time (left-hand column), and temperature and water loss time courses (right-hand column) for two leaves with large separation.

4.4 Numerical results - 2D

While the 1D simulation results capture the behaviour that we expect to see (increasing leaf separation indeed aids evaporative cooling) and thus validate our model, these results provide a somewhat limited picture. There is some question over the time scales involved as our chosen value for a_0 (now taken to be constant) is a pure guess. A detailed nondimensional analysis and scaling argument would be a useful addition to our work, as quantitative results as well as qualitative pictures are sought. Furthermore, restricting attention to one dimension limits the diffusion of the water vapour. As water vapour cannot diffuse through the leaf in our model, any diffusion of water vapour to the region above a leaf requires computational solution of the original 2D problem. As such, we developed a finite element solution framework for studying multiple leaves and different geometries in 2D. Again, these computations were performed using parameter values from Table 4.1, but with a view to later completing the parameter search and working with more realistic values.

In Figure 4.5, we show the temperature distribution around two leaves after several minutes, both for leaves close together and far apart. In both cases, we see the underside of the leaves at a lower temperature than the upper and side surfaces, from which there is no evaporation. The leaves with larger separation have cool to lower temperatures than those with smaller separation.

The effect of leaf separation on water vapour concentration is shown in Figures 4.6 and 4.7. As seen in the 1D case, the leaves with small inter-leaf gap have a much higher concentration of water vapour in the gap, which slows evaporation and cooling from the upper leaf. The 2D formulation allows for diffusion of water vapour around both leaves,

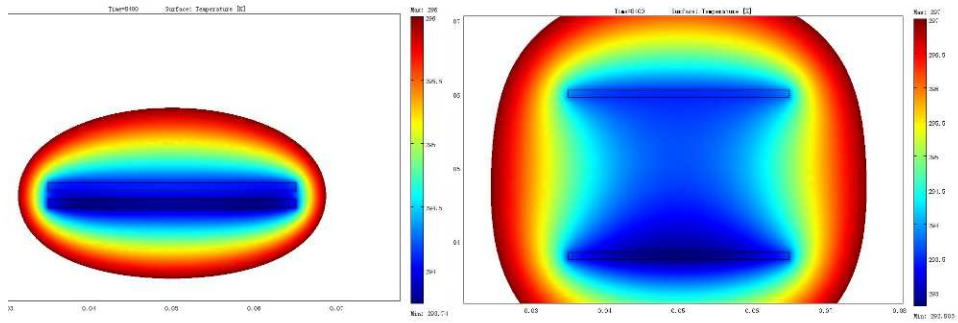


Figure 4.5: Temperature distribution around two leaves.

giving a concentration distribution above the upper leaf. As the leaves are moved further apart, a bigger region is available for water vapour diffusion and the inter-leaf gap is not saturated.

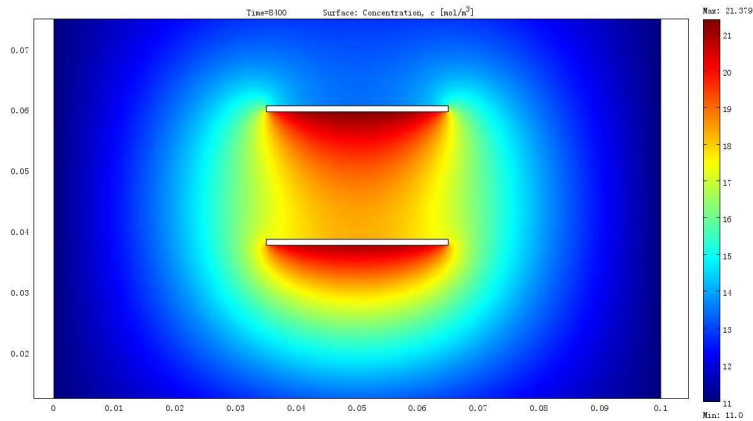


Figure 4.6: Water vapour concentration around two leaves far apart.

The water vapour concentration distribution around two skewed leaves is shown in Figure 4.8. The concentration is between the two leaves, limiting evaporation from the left-hand side of the upper leaf.

These preliminary 2D computations provide further validation of our model and give a clear picture of the effects of leaf separation on cooling. Further, implementing the finite element solution of our model using COMSOL gives us a framework on which to easily build study more complex geometries.

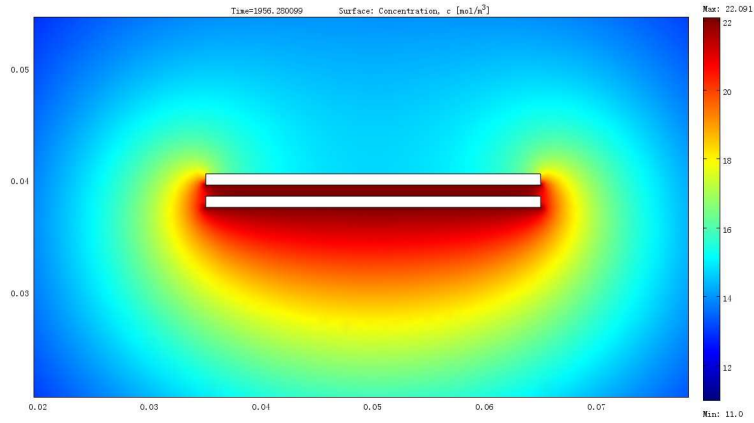


Figure 4.7: Water vapour concentration around two leaves close together.

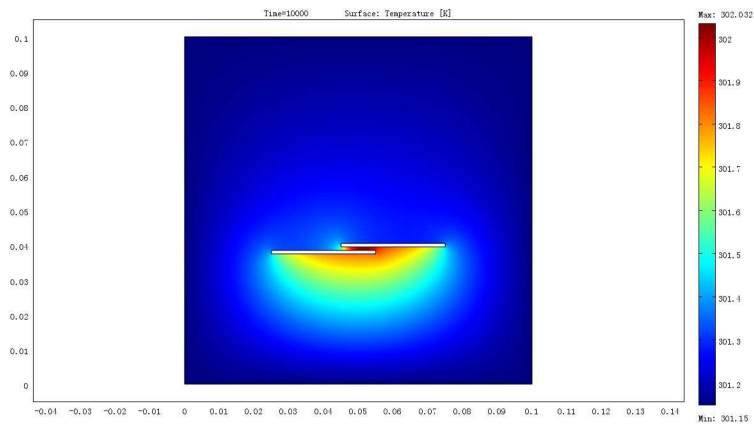


Figure 4.8: Temperature distribution around two leaves skewed leaves.

4.5 Boundary layer analysis

Convective boundary layers above vegetation have been studied (see, for example, [5]). Here, we are interested in the diffusive boundary layer. Some progress was made on calculations for the width of the evaporative boundary layer under each leaf.

We consider a steady state solution of the problem since this state is reached almost immediately as can be observed from the experimental evaporation rate which is constant in all studied cases, given that the water resources supplied into the soil are not limited. At equilibrium, water is continuously lost by evaporation through the stomata. The heat needed to evaporate this water is taken from the leaf leading to a cooling mechanism. The total water flux of water loss J can be computed from the experimental data available and can also be written as:

$$J = \frac{dm}{dt} = \rho S v \quad (4.1)$$

where m is the water mass evaporated, ρ is the water density, S is the area of the evaporation surface and v is the evaporation speed. At the steady state we can assume that advection and diffusion currents for both air and vapour are opposite and of equal magnitude. This equilibrium results in the formation of a usually very narrow region called the boundary layer. We can write:

$$v C_X = D C_{XX} \quad (4.2)$$

where v is the advection speed, C is the concentration of water vapour (a similar equation can be written for air; the equations are coupled by the constraint that the total concentration/ air pressure is constant and we can only use one of them for our estimates), D is the diffusion constant of water vapour into the air. By scaling arguments we deduce that:

$$v \frac{C}{\delta} \sim D \frac{C}{\delta^2} \quad (4.3)$$

where δ is the boundary layer thickness. Hence, we get our estimate as:

$$\delta \sim \frac{D}{v} \sim \frac{D \rho S}{J}. \quad (4.4)$$

With the above formula we estimated the boundary layer length near the leaf surface to be of the order (i) of up to one 1mm if we take for S the area of one stomata and the corresponding water loss rate and (ii) up to 0.5 cm if we considered the whole surface area of one leaf S and its corresponding water loss. These results might give an explanation of leaves getting separated to avoid ‘suffocation’, but still do not explain why the plant invests so many resources in elongation in order to do this.

To explain elongation we need to consider one more factor: the water evaporation from the soil. Indeed, computing the boundary layer near the soil surface we obtain quite an interesting result, approximately 3.5 cm! This is obviously a good reason for the plant to elongate in order to allow the plant to ‘breathe’ properly and avoid the already vapour saturated air near the soil surface. However, in our experiment, the soil was covered by

a plastic sheet in order to avoid the water evaporation. As observed, the reaction of the plant was still the elongation mechanism, although there were no vapours coming from the soil surface. In order to understand this behaviour, we need to take into account that the Arabidopsis plant adapts to high humidity soil locations and the elongation was the natural response for those environment conditions. The plastic cover experiment is from this point an artificial and unknown condition for the plant to adapt to, and the plant then basically applies its natural elongation survival mechanism as a response to the stimuli such as heat and plenty of water resources. It can also be noted that the geometry of the leaf stems naturally allow for leaves separation when elongation occurs.

The conclusion that can be drawn from these estimates is that the elongation of the Arabidopsis plant is an adaptation mechanism that allows the plant to effectively cool by perspiration. When the plant is in the vicinity of the soil, the cooling mechanism based on the evaporation of water from the stomata is severely impaired due to the fact that the air in the vicinity of the soil is already saturated with vapours coming from water evaporation at the soil surface.

5 Discussion and future work

In answer to the questions of the adaptive significance of plant architectural adaptations to elevated temperature, we have developed a mathematical model for heat and mass transfer with evaporation from multiple leaves to study the effect of leaf separation on leaf cooling. Preliminary numerical solutions to the model problem in 1D and 2D clearly show that increased leaf separation aids leaf cooling. While there is still some question over the time scales involved (an issue that will be addressed by performing a more thorough search for realistic parameter values), these solutions are useful in both showing qualitative behaviour in agreement with our intuition and providing a computational setup into which we can incorporate more realistic parameters and add further effects.

We suggest that the plant, when grown in hot and wet conditions, responds by adapting its shape in order to maximise evaporative cooling. The mechanism by which the plant does this is to elongate, separating the leaves from each other and from the soil, in order to prevent the air around the stomata becoming saturated. This adaptive mechanism only works while water is abundant, as in times of water stress the increased evaporation rate will hinder plant survival.

A boundary layer analysis has been performed which predicts the width of a layer next to a leaf surface from which water evaporates. Incorporating this with a nondimensional analysis of the full model is suggested as a future extension of this work towards better understanding effects over the time and length scales involved.

The use of COMSOL enables easy manipulation of the leaf geometries and this will be a valuable tool as we add further components to the model. Adding plant stem, leaf stems, soil and air effects to the model will eventually result in a full 3D model of a plant taking up water from the soil through its root and transporting water to the leaves.

6 Acknowledgements

The authors wish to thank the organisers of the Mathematics in the Plant Sciences Study Group held on December of 2009 in the University of Nottingham. We also wish to thank John King and John Ward for valuable discussions.

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