CHAPTER 4
HIGH TEMPERATURE STRESS
THOMAS D. SHARKEY AND STEPHEN M. SCHRADER

Department of Botany, University of Wisconsin-Madison,
430 Lincoln Dr., Madison, Wisconsin 53706, USA
(e-mail: tsharkey@wisc.edu)

Keywords: Energy balance, heat shock proteins, isoprenes, photosynthesis, pollen development, rubisco activase

1. INTRODUCTION

The global mean temperature increased by 0.6°C between 1990 to 2000, and is projected to increase by another 1.4 to over 5°C by 2100 (Houghton et al., 2001; McCarthy et al., 2001). Plants suffer the ups and downs of temperature of their environment, while animals often regulate their temperature, either by movement or metabolism. Therefore, global warming may affect plants more than animals and there are indications that plants experience substantial damage from high temperature stress. Estimates range up to a 17% decrease in crop yield for each degree Celsius increase in average growing season temperature (Lobell and Asner, 2003).

While the temperature of plants is strongly dependent on ambient air temperature, it is also dependent on radiant energy fluxes. Almost all crop plants, and most plants in nature experience the full intensity of sunlight for at least part of their lives. To fully understand heat stress effects on plants it is necessary to know what temperatures plants experience; this is analyzed by energy balance equations. At equilibrium, energy gain and loss is constant and heat gain by one process is balanced by heat loss by another. Three important routes of heat gain or loss are (1) sensible heat transfer, (2) radiant heat transfer, and (3) latent heat transfer (e.g., evaporative cooling). Typically, a photosynthesizing leaf is being heated by radiant heat gain and losing energy by sensible heat loss and latent heat loss, but each of these factors can be negative or positive.
1.1. Sensible Heat Transfer

Heat will flow to or from a plant depending on the difference in temperature between the plant and its environment. This heating or cooling is intuitive; whenever a plant is above air temperature it will lose heat to the air, if it is below air temperature it will gain heat. The rate of transfer will depend on the wind speed because of the boundary layer between the leaf and the well-mixed air. Small structures like stems and small leaves have low boundary layer resistances to heat flow, while large leaves can have large boundary layer resistances to sensible heat exchange with the air.

1.2. Radiant Heat

Radiant heat gain is responsible for most of the stressful high temperatures experienced by plants. Because plants photosynthesize, many plants are optimized to receive sunlight, which will also optimize radiant heat gain. Many leaves are very thin, optimizing the ability to intercept photosynthetically active radiation but also reducing the heat capacity of the leaf. This makes leaves susceptible to very rapid temperature changes. If all of the energy in sunlight were absorbed by a thin leaf (e.g., 0.4 mm² with 50% of the leaf being airspace and 50% being liquid phase) then the following equation applies:

\[
0.1367 \frac{J}{^\circ C \cdot g \cdot cm^3} = 1.1^\circ C \cdot sec^{-1}. \quad [1]
\]

In words, if a thin leaf had no mechanisms for losing heat, strong sunlight could cause that leaf to boil in less than 2 min. Obviously, heat loss by leaves is an important consideration.

The energy in sunlight is often divided into two parts: (1) ultraviolet, visible, and near infrared (wavelengths between approximately 280 nm to 4 \(\mu\)m) and (2) thermal wavelengths (greater than about 4 \(\mu\)m). Very hot objects like the sun emit nearly all of their radiant energy in the visible and near infrared regions of the electromagnetic spectrum, while objects with temperatures of plants and their surroundings emit radiant energy in thermal wavelengths (Nobel, 1999). Infrared radiation exchange of a leaf is estimated by the Stefan-Boltzman law:

\[
IR = a \cdot \sigma \cdot T^4 \quad [2]
\]

where \(a\) is the absorptivity (or emissivity for emission) for infrared energy, \(\sigma\) is the empirical Stefan-Boltzman constant \((5.67 \cdot 10^{-8} \, W \cdot m^{-2} \cdot K^{-4})\) and \(T\) is temperature in