Effects of Light and Temperature on Leaf Anatomy and Photosynthesis in *Fragaria vesca*

Brian F. Chabot and Jean Fincher Chabot

Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853, USA

**Summary.** *Fragaria vesca*, the woodland strawberry, was grown under a series of controlled environments including variations in light intensity, average temperatures, and temperature amplitude around a constant mean. Observations on CO₂ exchange capacities, leaf anatomy, and cell ultrastructure were made for each treatment to determine relationships between these variables. With increasing light intensity, leaf thickness, leaf density, and mesophyll cell surface area and volume per leaf surface area increased. Net photosynthesis (NPS) per leaf weight decreased with increasing light pretreatment while NPS per area increased from low to medium intensity, then decreased at the highest intensity. Depression of photosynthesis at the highest light pretreatment may have been due to massive starch accumulation in the chloroplasts associated with the sodium vapor lamps used. Correlation of all anatomical variables was highly significant with dark respiration and NPS per dry weight but insignificant for NPS per leaf area. In the variable temperature treatments, photosynthetic acclimation occurred with a shift in optimum temperature for NPS in the direction of prevailing growth temperature. Absolute rates were highest at moderate pretreatment temperatures and were reduced by extreme growth temperatures. Thick leaves with low density mesophyll became thinner and more dense with increasing growth temperature corresponding to an increase in maximum net photosynthetic rates. Leaves became thicker and more dense at the highest temperatures, but with an increase in cell damage and indications of changes in metabolic pathways. Highest correlations for gas exchange rates were with specific leaf weight (weight per area). Correlation with other anatomical variables were scattered or insignificant. It was concluded that adaptation to a range of environmental conditions cannot be consistently attributed to changes in mesophyll cell volume or surface area.

**Introduction**

Several studies have pointed to important relationships between leaf anatomy and photosynthetic performance. In a heterogeneous group of species, (El-Sharkawy and Hesketh, 1965) net photosynthesis was negatively correlated with leaf
thickness and mesophyll cell diameter. Cunningham and Strain (1969) found an inverse relationship between specific leaf weight (SLW, weight per area) and the rate of net photosynthesis expressed on a dry weight basis. Charles-Edwards et al. (1974), using temperature and light pretreatments, determined that differences in photosynthetic performance (per unit area) were removed when differences in mesophyll cell volume per area were accounted for. Similar results were obtained by Nobel et al. (1975) for plants grown under different light regimes. In this latter case photosynthetic differences were related to mesophyll surface area per leaf area. For field grown soybeans, the carbon exchange rate was positively correlated with mesophyll volume (Dornhoff and Shibles, 1976).

The behavior of plants under different environmental regimes has been useful in exploring rate limiting factors in photosynthesis (Björkman, 1973). The effects of light are, perhaps, the best understood particularly at a biochemical level. Temperature, moisture and other factors have received less systematic attention and a coherent explanation of these environmental effects is not available. There are studies of anatomical and ultrastructural changes to environment (Haberlandt, 1914; Ballantine and Forde, 1970; Goodchild et al., 1973), but for the most part, correlation with function has been only qualitative. The success of the few attempts to quantify leaf structure holds the promise of relating whole plant physiology to biochemical and cellular changes.

The objective of this study was to investigate the interaction of anatomical structure and gas exchange in leaves grown under different temperature and light pretreatments. Using Fragaria vesca, we attempted to either confirm previous observations or to discover alternative patterns which may exist within the diversity of biological species. Additionally we sought to combine and compare in one study the several different anatomical measures used previously. Toward this end we utilized some of the advanced techniques of stereology which have had as yet little impact on such botanical studies.

Methods

Fragaria vesca, the woodland strawberry, was used in these studies because aspects of its growth and physiology had been previously characterized (Chabot, 1975). Plants were collected as vegetative material near Ithaca, New York. Cloned material was grown in 500 cm$^3$ plastic pots in peat-vermiculite (Jiffy-Mix). All plants were watered daily with distilled water and fertilized weekly (50 cc, Peters, 20-20-20).

The three series of experimental growing conditions used included variation in light intensity, average temperature and temperature amplitude around a mean. Light intensities used in the variable light experiments were 25, 150, and 650 $\mu$E·m$^{-2}·$s$^{-1}$ (400–700 nm) as measured at the height of the leaves and averaged for several positions in the chamber. Lower intensities were produced with fluorescent-incandescent lamps and wire screen filters. The highest intensity was obtained with a combination of incandescent, color improved mercury vapor and sodium vapor lamps. Photoperiod was 15 h. Thermoperiod was 12 h with day/night temperatures of 25/15°C. Anatomical samples also were taken from plants grown under natural lighting in a temperature controlled greenhouse.

In one temperature series, controlled environment growth chambers (Sherer) were programmed for 12 h thermoperiods with day/night temperatures (°C) of 10/2, 20/10, 30/20, and 40/30. Additionally, a series with varying amplitude around a mean of 25°C was established with day/night temperatures of 25/25, 30/20, and 35/15. For both temperature series photoperiod was 15 h using fluorescent-incandescent lamps with an intensity at pot height of 200 $\mu$E·m$^{-2}·$s$^{-1}$. 