Responses of Stomata to Environmental Factors – Experiments with Isolated Epidermal Strips of *Polypodium vulgare*

II. Leaf Bulk Water Potential, Air Humidity, and Temperature

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Summary. Stomatal apertures of isolated and suitably conditioned epidermal strips of *Polypodium vulgare* are described as the stomata respond to the influences of temperature, air humidity, and water potential at the epidermal inner walls. Water stress as a result of reduced water potential in the substomatal airspace leads to narrower stomatal pores when water potential falls below -8 bar. Water potentials above this threshold value show minor influence. Stomatal responses to such water stress strongly interact with the responses to humidity changes in ambient air and to temperature. The linear dependence of stomatal apertures on the vapor saturation deficit of the air (closing) is shifted to lower values (more closed) by lower leaf bulk water potentials.

Stomatal behavior depending on the temperature factor seems to be reversed by higher water stress. Without water stress, rising temperatures between 20 and 28°C are accompanied by further opening of the pores, whereas an increase of temperature within this range leads to narrowing of the stomata under the influence of lower water potentials within the substomatal airspace. It can be demonstrated that stomatal aperture values of *Polypodium vulgare* depending on temperature always describe optimum curves. With no water stress, closing does not occur before rather high temperatures are reached and above a broad range of maximal opening. Water stress, on the other hand, results in more pronounced narrowing of stomatal pores and shifts the onset to considerably lower temperatures.

Introduction

The water balance of the guard cells plays a decisive role for stomatal apertures. It is influenced indirectly by changes in the solute content of the stomatal apparatus and directly by the water gain and loss of the guard cells. This water turnover depends on the water supply from the rest of the leaf and on the evaporation demand due to the vapor saturation deficit (WD) between
leaf and atmosphere. In many cases guard cell water balance is linked very closely to the water relations of the conducting tissues and the mesophyll, thus representing a hydraulic unit that may even oscillate in phase within all parts of the plant (Sheriff and Sinclair, 1973; Sheriff, 1974). There are, on the other hand, plant species in which the epidermal water turnover seems to be more separated from that of the mesophyll. The reason for this may be a hypodermal cell layer separating mesophyll and epidermis as in conifer needles, or poor contact points between the spongy parenchyma and the epidermal cells (Sheriff and Meidner, 1974; Meidner and Willmer, 1975). In these plants with a reduced hydraulic link between the stomatal apparatus and the rest of the leaf, the water content of the guard cells is affected by the atmospheric evaporation demand in a very direct manner without extensive involvement of the water relations of the mesophyll. Due to peristomatal transpiration (Seybold, 1961/62; Maercker, 1965) or – more generally – a local shortage of water in the epidermis (Sheriff, 1977b; 1978) the stomata can therefore act as sensors for ambient humidity (Ziegler, 1967; Lange, 1969, 1972). The efficiency of this sensing ability has been demonstrated in several investigations (Lange et al., 1971; Schulze et al., 1972, 1975; Kaufmann, 1976; Aston, 1976; Lösch, 1977). Sheriff (1978) and Lösch (1979b) have listed the plants at present known to show such direct humidity responses.

Of course, even the guard cell water relations of leaves with an epidermis that is more or less isolated from the mesophyll are affected by the water supply of the rest of the leaf. The transpiration stream may occur mainly along the inner walls of the epidermis according to the proposal of Meidner (1975) or, as the classical view postulates, from the mesophyll via the vaporphase of the water-saturated substomatal cavity. Both concepts agree in that the transition between liquid water and vapor occurs at the inner walls of the guard cells, the direction depending on the sink of the water potential (see also Sheriff, 1977a).

Ambient humidity and plant internal water relations can thus influence the behavior of stomata as two separate factors. In order to analyze their simultaneous effects, experiments were performed with epidermal strips with both surfaces exposed to air of different vapor concentrations within the physiological range of values. Also the effect of temperature on stomata and its interrelationships with both of the other factors, external humidity and simulated leaf bulk water potential, have been investigated and are discussed. The results extend the data reported by Lösch (1977).

Material and Methods

For the experiments epidermal strips were used from *Polypodium vulgare* plants cultivated in the greenhouse at 15°C/70% relative humidity. As described in detail by Lösch (1977) they were observed in a conditioned observation chamber under the microscope. The metal chamber had an upper and a lower compartment. The only connection between the two compartments was a hole of 2 mm diameter that was covered by the epidermis. The chamber, and by heat transfer the epidermis, were temperature-controlled by Peltier elements. CO₂-free air of defined humidity was blown over the epidermis through the upper part of the chamber. The metal chamber was closed to the outside air by a cover-glass.