II. The Leaf Epidermis: Its Ecophysiological Significance

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1. Introduction

The epidermis is the outer cell layer of the primary plant body. Concentrating on photosynthesis as obviously the main function of leaves has brought the usually chlorophyll-free epidermal cells of higher plants out of focus for many plant biologists. Nevertheless, a considerable number of publications provide information on the tissue-specific role of the epidermal cells and have deepened our insight into the various functions of the epidermis as a barrier interconnecting and separating leaves from the environment, and their importance in the response of plants to external stimuli. To a significant extent this progress was due to methods which were frequently employed to analyze leaves and not primarily to characterize the leaf epidermis. Instead, these approaches gave information on the epidermis more as a side product. This will be illustrated in the section on new methods. To put the subject of this review in concrete terms: stomatal functioning will not be treated here, since it has been concisely reviewed recently (Raschke et al. 1988; Tallman 1992). This review will also not deal with specialized epidermal cells or cell descendants such as idioblasts, hairs, glands, absorption scales, and papillae (Wagner 1991; Romberger et al. 1993). However, it can be hypothesized that the latter structures developed by advancing and optimizing functions which were already inherently associated with normal epidermal cells of cormophytes. This will be evident for ion compartmentation, synthesis of secondary plant compounds, or protection of shoot surfaces (Romberger et al. 1993). The scheme of Fig. 1 summarizes ecophysiologically important functions of the leaf epidermis either in the direct interaction with environmental factors or indirectly as part of the response of plants to changes in growth conditions such as salinity.

2. The Morphology of Epidermal Cells and Their Subcellular Organization

The epidermis consists of a dense layer of cells. In leaves, either the lower or the upper epidermal cell layer, or both, are interrupted by stomates as
Fig. 1. The epidermis of leaves is the tissue of first interaction with environmental factors such as pathogens and light. The epidermis is the compartment of permanent or transient deposition of specific ions and assimilates. It has a tissue-specific biochemistry and plays an important role in phytohormone homeostasis.

regulated pores which facilitate gas exchange between the intercellular gas phase and the atmosphere. Epidermal cells of monocotyledons are usually linearly extended. For example, in barley they reach longitudinal extensions of up to 5 mm. This contrasts with the more isodiametric shape in dicotyledons with sinuous anticlinal cell walls. The size of the epidermis has recently been investigated in detail for spinach and barley (Dietz et al. 1992a; Winter et al. 1993, 1994). In barley, 27–35% of the whole leaf water volume is bound to the cells of the upper and lower epidermis. On average in all epidermal cells, 99% of the intracellular space is filled with the extremely large vacuole. The cytoplasm and the nucleus occupy the residual 1% of the cell volume. In spinach leaves, the epidermis corresponds to only 4.4% of the leaf water space, 9/10 of which is filled with the vacuole. The other tangential cell wall is frequently thickened. A waxy lipophilic membrane of about 1 to 15 μm thickness consisting of the cuticle and epicuticular waxes represents the main outer barrier against solute and water loss, and against harmful compounds and organisms.

3. New Methods in the Investigation of Epidermal Functions

To study epidermal functions, two approaches are practical: on one hand, the epidermal cells may be isolated from other cells of the leaves. For this and in