Proceedings of the Iowa Academy of Science

Volume 65 | Annual Issue Article 21

1958

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Growth and Differentiation of the Epidermal Wall*

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Waxy coatings on leaves and other plant surfaces have been studied since DeBary's (1) early work. Surface wax has assumed additional importance with the advent of systemic and herbicidal sprays. The retention and absorption of these sprays depend upon the waxy coatings and other properties of the epidermis. Earlier publications (3, 4) have pictured the first development of the cuticle and the extrusion of surface wax through it. None of our observations have demonstrated any channels associated with wax extrusion, and we conclude that it permeates the cellulose matrix of the primary epidermal wall in a softened form, which then hardens on the surface of the leaf.

Surface wax is, in general, extruded only in young, growing leaves, and the pattern remains unchanged during a leaf expansion of hundreds of times. If the expansion of the surface wall of epidermal cells is uniform throughout, this retention of the original pattern and distribution of wax is difficult to explain. A study of surface replicas of growing leaves has shown the general presence of anomalous areas above the lateral walls of the cells, suggesting that the surface wall enlarges at the margins rather than throughout. When surface wax was wiped from rapidly growing leaves of corn seedlings, the wax was not replaced in the center of the cells but normal waxy coatings developed at the margins of the cells. These observations are evidence for marginal growth, with wax being extruded only through the newly formed wall at the margin of the cell. Such growth accounts for the uniform wax pattern and for the intact cuticular layer under the surface wax. Deposition of surface wax appears to be stopped by the development of the cuticle.

Surface wax normally forms an open pattern (Fig. 1) that would affect retention of watery sprays but would not be a decisive factor in either cuticular transpiration or chemical penetration, provided a suitable wetting agent were used with the chemical spray. Our work has shown, however, that the permeability of the cuticle to both water and 2,4-dichlorophenoxyacetic acid decreases with age of the leaf

*Journal Paper No. 3396 of the Iowa Agricultural Experiment Station, Ames, Iowa. Projects 944 and 1139.

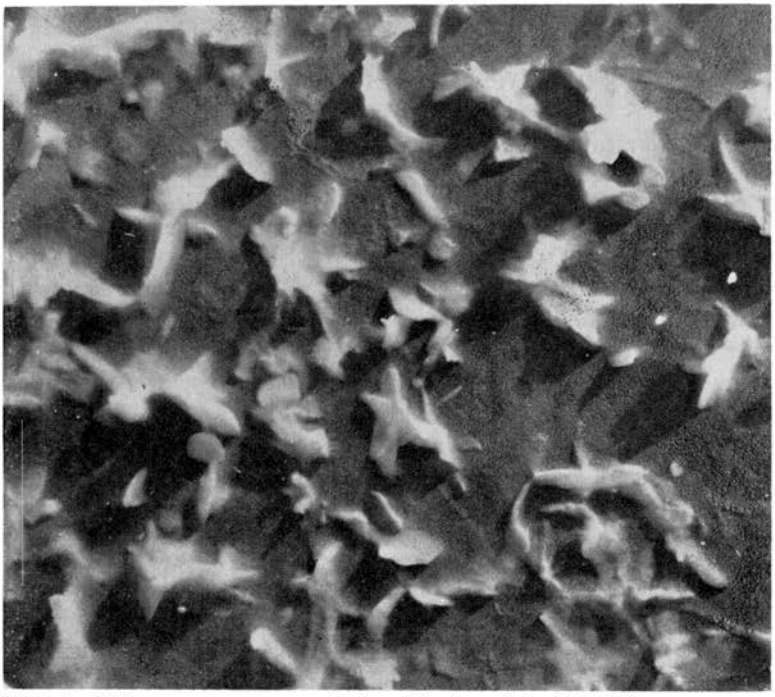

Figure 1. Surface wax on sugar cane leaf; cuticle shows dark (X12,000).

and in the absence of any changes in surface morphology. Analyses show that subsurface wax tends to increase with age of the leaf, but that surface wax remains unchanged or decreases with weathering.

From these data we draw the following picture of the development of the outer epidermal wall. In the embryonic stage the wall consists of cellulose microfibrils embedded in pectin, with a surface layer of pectin (2). About the time that the wall is first exposed to the air, or possibly before, fatty substances, analogous to drying oils, permeate the wall, harden on the surface and form the first cuticular layer. Apparently wax is extruded through this layer until such movement is stopped by the thickening and hardening of the cuticle. The end of this stage constitutes what we call the primary cuticle—*B* in figure 2. The cuticle can now be removed by pectinase in the form of a continuous sheet. In the growing stage it is removed as cell-sized flakes, indicating again the presence of marginal growth. Further developments are subcuticular and involve the deposition of wax, possibly cutin also, within the epidermal wall—*C* and *D* in figure 2. It is now no longer possible to remove the cuticle with pectinase. If a cell in stage *D* is treated with a pectinase-cellulase mixture, the entire upper wall separates as an intact layer, indicating complete impregnation with wax.

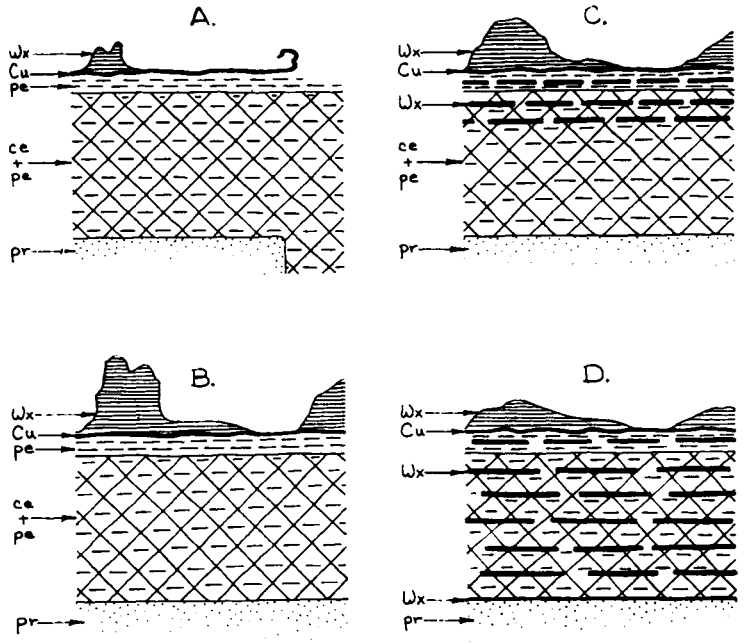

Figure 2. Diagrams of cuticular development: A—cell margin of growing leaf; B—primary cuticle; C and D impregnation of epidermal wall of mature leaf.

Summary

The outer walls of leaf epidermal cells appear to grow from the margin. A cuticular layer is formed rapidly, but this is weak enough at first that wax may be extruded through it. About half of the plant species observed show such extrusion, which is apparently halted by further thickening of the cuticle. A more effective protective layer is formed in older leaves by intrusion of wax, and possibly cutin, into the matrix of the epidermal wall.

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