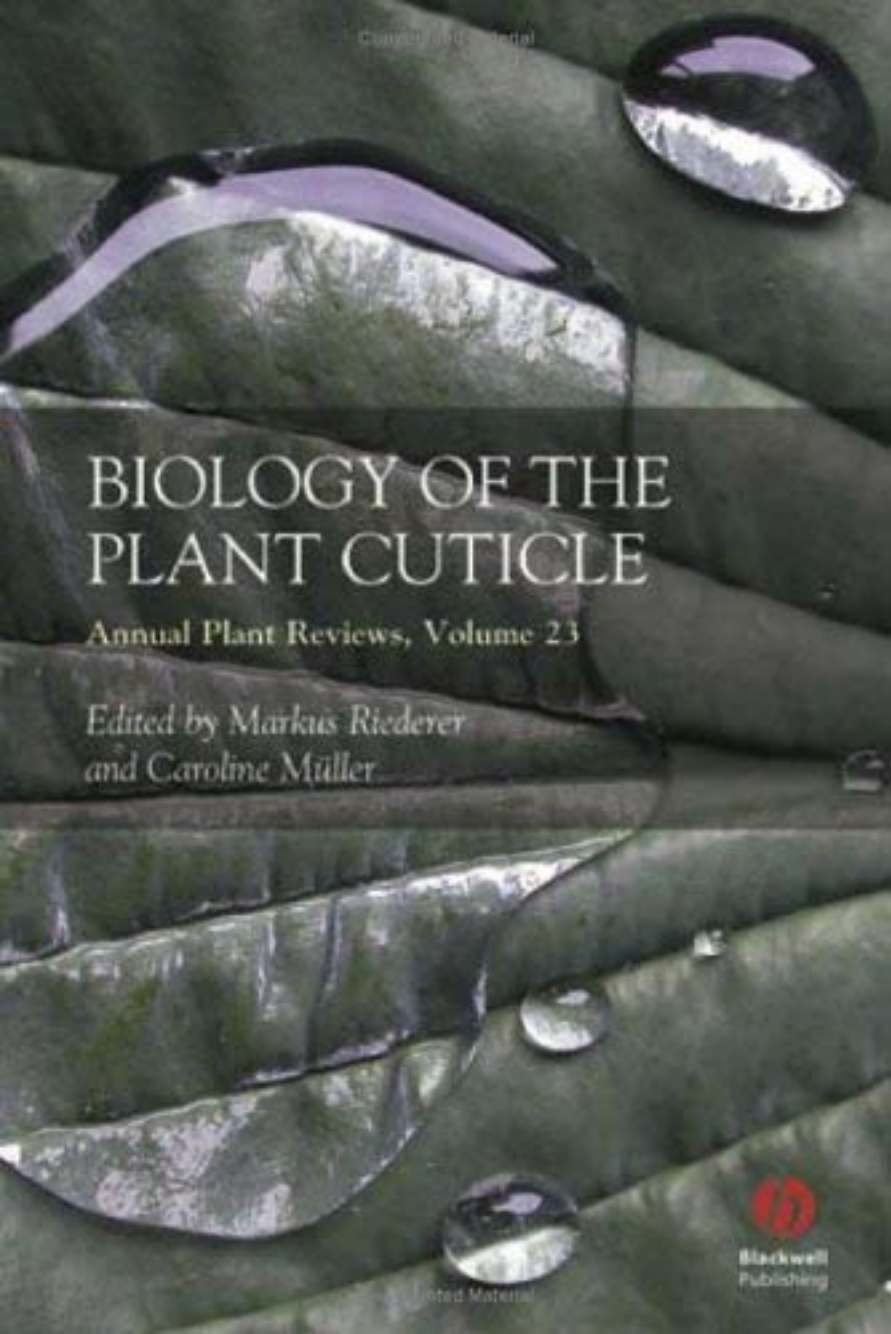
BIOLOGY OF THE PLANT CUTICLE
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Biology of the Plant Cuticle

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Biology of the Plant Cuticle

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Preface

During recent years the science of plant surfaces, and the cuticle in particular, has advanced at a fast pace, encompassing new fields of study along the way. Considerable progress has been made possible by the application of new concepts and techniques for investigating the biosynthesis, composition, structure and functional complexity of the plant cuticle.

We now have an increased understanding of the microscopic and submicroscopic fine structure of the cuticular membrane as a whole, as well as of the cutin matrix and the associated wax deposits. By employing mutants and applying molecular biological techniques and advanced analytical tools, a much clearer image can now be drawn of the composition of cuticular waxes and the biosynthetic pathways leading to them. Intriguing variations can be found in the cuticular chemistry, morphology and function between and within plant species. Studies assessing the impact of UV radiation on plant life have emphasised the role of the cuticle and the underlying epidermis as optical filters for solar radiation. The field concerned with the diffusive transport of lipophilic organic non-electrolytes across the plant cuticle has reached a state of maturity, which makes it possible to quantitatively analyse and predict permeabilities based on physico-chemical predictors and to manipulate them *in vivo*. Recently, a new paradigm has been proposed for the diffusion of polar compounds and water across the cuticle. Within the context of plant ecophysiology, cuticular transpiration can now be considered in the perspective of whole-leaf water relations. New and unexpected roles have been assigned to the cuticle in plant development and in pollen–stigma interactions. Finally, much progress has been made in understanding the cuticle as a specific and extraordinary substrate for the interactions of the plant with microorganisms, fungi and insects.

Since the early 1970s, three books on the plant cuticle have been published. Only the first addressed all aspects of the subject; the other two were multiauthor volumes arising from scientific meetings. Considering the progress made in this field, a book which deals comprehensively with plant surface characteristics and functions is overdue. The title, *Biology of the Plant Cuticle,* is intended to express the multidisciplinary and integrative approach to the subject. As functions are interconnected and rely heavily on the (bio)chemistry and properties of the cuticle, it is hoped that bringing together thus far disparate views of the subject will substantially advance the field of plant surface science. The book is also intended to provide a comprehensive overview and critical discussion of the current state of knowledge, paying close attention to the applied aspects of the field wherever appropriate.

Biology of the Plant Cuticle is aimed at a broad audience, ranging from biologists working on the molecular and whole-organism level to industrial agrochemists.

It is hoped that it will be of interest to phytochemists, plant (eco)physiologists, ecologists and environmental scientists, as well as to scientists and practitioners from the agricultural and horticultural sciences. In comparison with its predecessors, this book extensively considers the biological interactions occurring on plant surfaces and, therefore, is hoped to be of special appeal to scientists who, in the past, did not consider the plant surface *a priori* as a subject of prime importance. Thus, this volume is furthermore directed at phytopathologists, environmental microbiologists, entomologists and chemical ecologists.

The editors are indebted to the chapter authors for an enjoyable collaboration on this project and for timely delivery of carefully prepared manuscripts. In addition, the editors gratefully acknowledge the encouragement, advice and support continuously provided by Graeme MacKintosh and David McDade of Blackwell Publishing.

Markus Riederer
Caroline Müller

Biology of the Plant Cuticle
Edited by Markus Riederer, Caroline Müller

1 Introduction: biology of the plant cuticle

Markus Riederer

'Does it make sense, and is it fun at all, to spend so much time with the outermost micrometer of a plant?' This was the question a member of a search committee asked when the author applied for a job at a German university. As all scientists in this field know and deeply feel, it is fun indeed to study the plant cuticle and the plethora of processes related to it. The authors of this book hope that the reader will come to the conclusion that it is worthwhile to invest time, brains and funds into this endeavour.

The cuticle has often been called the 'skin' of the primary parts of higher plants, and in fact, the Latin word from which this term is derived (*cuticula*) means 'thin skin'. The term cuticle has undergone a kind of evolution and profound changes in meaning during the last two centuries. At the beginning, the whole primary integument tissue or epidermis of a plant was called 'cuticle' stressing the convergence with animal skin, which is also cellular in nature. The modern usage of the word, meaning 'a superficial film formed of the cutinized outer layers of the superficial walls of the epidermal cells' (*Oxford English Dictionary Online*) of a plant, goes back to A.P. de Candolle. In 1827, he restricted the use of the French term 'cuticule' to the meaning in which it is used today (Wagenitz, 1996). Thus, the word cuticle is no longer used for a cellular layer but for a continuous extracellular membrane. In 1852, the word appeared in English for the first time in Henfrey's translation of H. von Mohl's 'Grundzüge der Anatomie und Physiologie der vegetabilischen Zelle' (OED Online). It is this term which will accompany us throughout this book.

1.1 The evolution of the plant cuticle

The cuticle as a structure has a very long history on the palaeobiological timescale. It is fortunate that the cuticle is a highly recalcitrant material which can easily resist decay for millions of years under favourable deposition conditions. It is fascinating that major chemical features like cutin composition are preserved over such prolonged periods of time (Ewbank *et al*., 1996; Edwards *et al*., 1997). Thus, essentially intact cuticles with clearly delineated epidermis cell silhouettes can be obtained from old sediments. The oldest remnants of plant cuticles date back to the boundary between the late Siluarian and the early Devonian (about 400 million years ago) periods. The earliest cuticles, in the modern sense of the term which is assigned to higher plants, were found dispersed in sediments and belong to sporangia of rhyniophytoids. These specimens lack the impression of stomata while beginning with the

basal Devonian period, preserved cuticles show imprints from guard and accessory cells that are comparable to the modern stomatal apparatus. For a recent review on this subject see Edwards *et al*. (1996).

The finding that cuticles and stomata appear concomitantly in early kormophytes has profound impact on modern concepts of the evolution of vascular land plants and also on the interpretation of the selection pressure which acted on the evolution of stomata (Raven, 1977, 2002). Palaeoecophysiology has interpreted the simultaneous appearance of cuticles and stomata as evidence for the physiological adaptations to the colonisation of the land and thus for the relatively dry atmosphere by basal precursors of modern higher plants. Cuticles and stomata form a syndrome together with extended root systems, supracellular transport in vascular structures and the development of intercellular air spaces (Raven, 1977, 2002). These features are interpreted as necessary adaptations for photosynthesising homoiohydric life forms in an atmosphere with low water activity. The early cuticle probably also had additional functions equivalent to those of modern cuticles with defence against parasites, protection against ultraviolet (UV) radiation and water repellence being the most important ones.

1.2 Major functions of the plant cuticle

The cuticle is a structure that incorporates numerous functions of essential importance for plant life (Kerstiens, 1996b). This book treats the major functions in detail and, in most cases, devotes separate chapters to each of them. Nevertheless, a short synopsis is included in this introduction because it appears necessary to make one point very clear: the cuticle is a non-living though highly multifunctional structure into which numerous functions have been integrated. As will be shown later, this integration is sometimes not ideal as some physiological demands are in conflict with each other.

1.2.1 Transpiration control

As mentioned earlier, one of the major exigencies of the terrestrial lifestyle of higher plants is to have control over water relations. In order to stay alive, which essentially means to be more or less turgescent, the plant has to maintain the equilibrium between transpirational water loss and root water uptake. Any pronounced disequilibrium will severely compromise the viability and thus the fitness of the plant.

The control of transpiration from leaves, primary stems, flowers and fruits has two components: the stomata and the cuticle. Depending on the primary focus of scientific interest, the importance of either the stomata or the cuticle will be stressed by different authors. However, an effective control of transpiration is feasible only if the stomata *and* the cuticle act together in an optimised way. The low permeability of the cuticle makes it possible to control water loss by adjusting stomatal aperture.