THE FORMATION OF WOOD IN FOREST TREES

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The Second Symposium Held under the Auspices of the Maria Moors Cabot Foundation for Botanical Research, Harvard Forest, April, 1963

Edited by

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PREFACE

This volume is a record of the proceedings of the second Cabot Foundation Symposium, held at the Harvard Forest, in Petersham, Massachusetts, on April 15–19, 1963. The aims of the Cabot Foundation, originally more directly oriented toward improving the growth of trees, have gradually turned toward fundamental problems of tree growth, because it was realized that, before we can effectively improve the growth of trees, we have to learn a great deal more about how they grow.

Many symposia have been held during recent years on various aspects of tree growth, such as the chemistry and submicroscopic morphology of wood, the effects of the environment on growth, etc. Superficially seen, an additional conference might look superfluous. However, there was, and is, a serious need for bringing small groups of investigators of these different fields together in a quiet place, remote from distraction and the burden of administration. A few days of unhurried contact between representatives of these very different and yet so closely related fields proved to be a most stimulating experience.

Early in the planning stage it was agreed that the results of the symposium should be made available to everyone interested. The discussions were all recorded on magnetic tape. They were transcribed after the conference, edited, mimeographed, and sent to all participants for correction. Thus cleared and reduced to essentials, they were prepared for the printer.

I would like to thank all those who have made this volume possible: first of all the authors for their excellent contributions and for their cooperation and efforts to meet the various deadlines, Dr. Brayton F. Wilson for the transcription of the discussions from tape, Miss Margaret F. Stieg for her invaluable help in preparing the material for the publisher, and Professor Kenneth V. Thimann for his ever-available counsel and help in all editorial matters.

May 1963 MARTIN H. ZIMMERMANN

CHAIRMAN'S INTRODUCTION

It is my pleasant duty as chairman of the Maria Moors Cabot Foundation to welcome you all. We are very happy that everyone who was invited was able to come to the Symposium, with the single exception of Bruno Huber, whose health did not permit him to attend. Professor Huber was one of the most active and expert contributors to the previous Symposium, and we shall greatly miss him at this one.

I had hoped to have a message for you from Godfrey Lowell Cabot, who set up this Foundation just 25 years ago with the aim "to increase the capacity of the Earth to produce fuel by the growth of trees and other plants." Unhappily, however, Mr. Cabot died last year, some time after celebrating his 100th birthday amid a host of laughing children, grandchildren, and great grandchildren. Surely few men had a fuller and more satisfying life, for he lived to see the business which he founded and ran for many years become a great success, then turned his attention to his two hobbies, aviation and the utilization of solar energy. He became a Navy flier at the age of 57, and at the age of 75 endowed this Foundation. Mr. Cabot was disturbed at the rate at which man is exhausting the stocks of fossil fuel from the world, and foresaw the day when we should be forced to return to the use of the renewable fuels such as wood and water power. Fortunately, the coming of atomic power, which has appeared within about one generation of the time when many people foresee the beginning of the end of our oil supplies, is just in the nick of time and perhaps enables us to take a more detached view of the aims of our Foundation.

Because relatively little really scientific work is done on forest trees, we decided to devote our first Symposium, six years ago, to the Physiology of Forest Trees, and many of the topics discussed there were taken up further at the Tree Physiology session held during the International Botanical Congress at Montreal in 1959. For the present Symposium we thought it better to take somewhat less broad a field and decided that a good topic, with enough interrelations to interest workers in many areas, yet delimited enough to serve to crystallize our thoughts, was the formation of wood. This subject comprises, of course, the function and growth of cambium, the chemistry and physics of secondary wall formation and of specific polymers, the conditions, both internal and external, which govern these processes, and the role of wood formation in the world's economy.

We decided to hold the Symposium here at the Harvard Forest, partly because our previous one here was a success, partly because we are remote and undisturbed here, but partly because the size of the building automatically imposes a limitation on the size of the gathering, which we really need in order to keep our discussion within bounds. May I take this opportunity of thanking the Director of the Forest, Professor Hugh M. Raup, for his cooperation and hospitality.

Recently in England a competition was held for the composition of a chemist's prayer. I think one of the most appealing entries which I read was the following:

O Lord, I beg upon my knees
That all my various syntheses
May not turn out to be inferior
To those conducted by bacteria.

I can only hope that we, in our turn, may find that the syntheses of knowledge we shall hope to achieve during this week will not be too greatly inferior to those possessed by the living cells of the tree.

April, 1963 KENNETH V. THIMANN

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PART I

THE CAMBIUM AND ITS DERIVATIVES

Evolution of Cambium in Geologic Time

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If major evolutionary events in the geologic history of plant life are considered in their broadest terms, irrespective of phylogenetic implications, certain fundamental advances in the course of evolution might be recognized as follows:

1. Origin of a stabilized genetic system for the replication of form from generation to generation.
2. Development of autotropic photosynthetic metabolism.
3. Emergence from an aquatic or free moisture dependent environment and adaption to withstand conditions of the terrestrial environment.
4. Development of an internal system of vascular tissues and the incorporation into it (and other tissues) of lignin as a chemical entity of the plant body.
5. Origin and development of cambium and the capacity for theoretically unlimited secondary growth and increase in size of the plant body.

Events 1 and 2 above are lost in the geologic record of life and at present may only be surmised through theories or concepts of chemical and biochemical evolution (Clarke and Synge, 1959). It should be noted, however, that quite highly organized and presumable photosynthetic (as evidenced by stable carbon isotope ratios of the organic matter present) primitive organisms are now known from sediments whose age approaches one-half that of the currently accepted value for the age of the earth (Tyler and Barghoorn, 1954; Rutten, 1962). The time of emergence of photosynthetic, presumably algal or protovascular plants into subaerial or terrestrial environments is likewise imperfectly known. It is conceivable that the moister or more humid continental surfaces were occupied in Late Precambrian or Early Paleozoic time by a shallow superficial covering of algal growth whose collective organic activities and residues would have facilitated the formation of a primitive sort of soil. The character of presumably terrigenous sediments of these units of geologic time are not incompatible with this view. However, the subsequent events, viz., 4 and 5 above, are featured by a more perfectly known chronological and morphological documentation and it is to these that the present paper is directed.

The evolution of vascular plants possessing primitive adaptation, or structural modifications adequate to withstand the stress of terrestrial environments, was one of the broadest revolutionary advances in the plant kingdom (Bailey, 1953), enabling complete independence from the ambient aquatic or subaquatic environment. The play of natural selection operating on the primitive vascular plants in conjunction with the innumerable new ecological niches of the terrestrial environment allowed for rapid evolution of form and diversity, both of vegetative and reproductive structures. The rate of evolutionary change during the short segment of geologic time between the appearance of the earliest true land plants (i.e., vascular plants) of Silurian-Devonian time and the rich and varied flora of the Carboniferous is probably unique in the history of plant life. The only other segment of the geologic record which seems comparable is the rapid evolution and diversification of the flowering plants during Cenozoic time. In fact, it is even the more striking if we consider that all the major subphyla of the Trachophyta became highly diversified in the interval between the Middle Devonion and the later Carboniferous, an interval of approximately 75 million years (slightly longer than the duration of the entire Cenozoic era).

The question arises as to whether the seemingly explosive evolution of vascular plants after their establishment in terrestrial environments is an artifact of an incomplete fossil record, or of some other cause. It must always be recognized that a fossil assemblage is a mere fraction of its contemporary biota, yet the continuity of the fossil record, supported within the framework of absolute chronology lends confidence to our acceptance of the evolutionary sequences. Currently there is no tangible evidence that vascular plants existed prior to the Middle or Late Silurian and it is of interest to examine possible reasons for this fact, particularly in view of our recent knowledge of the existence of well-organized algal and related plants in sediments approximately 2000 million (2.0×10^9) years earlier.

It is my contention that one of the answers to this enigma is the "discovery," so to speak, of the chemical entity lignin. Lignin is one of the few chemical complexes which appears to be unique to the vascular plants as distinct from the nonvascular, i.e., algae, fungi, and their relatives. The physical properties imparted by lignin to the lignin-cellulose framework of tracheary tissues provides the essential physical characteristics of the plant body on which natural selection would operate in the adaptation of plants to the terrestrial environment. The increase in vertical dimensions of the plant body made possible by the rigidity of lignified cell walls places a survival value on the capacity to increase in height in competition for available light. It is entirely possible, particularly in view of the peculiar biochemical attributes of lignin (aromatic structure, physical dispersion, etc.), that all vascular plants are monophyletic. This would imply that the mutation providing the chemical pathways for lignin formation arose only once in the chemical evolution of plants and triggered the mechanism for evolution and selection of entirely new aspects of morphological expression and specialization. The fossil record, with its preponderance of small, simple, and poorly differentiated forms in the Early Devonian tends to support this concept. The recognition of the Psilophytales as a supposedly natural group of ancient and primitive land plants is an outgrowth of this monophyletic view.

Increase in height of a free-standing vascular plant which possesses no mechanism for increase in girth is obviously sharply limited by the rigidity of its primary vascular and associated tissues. Further increase in height, upon which natural selection operates in a positive direction as previously noted, necessitates increase in girth. Various mechanisms have evolved in relation to this biophysical necessity and it is of interest to examine these in some detail, particularly with respect to the expression of secondary vascular tissues. It should be kept in view, in this connection, that our survey of the evolution of cambium is based almost entirely on examining the products of secondary growth as expressed in the woody cylinder. Cytological and histological innovations in the cambium of plants which are known only as fossils may be inferred only by examination of the daughter cells or derivatives in the secondary xylem.

I. Psilophytales and Their Presumed Immediate Derivatives

Among Lower Devonian vascular plants there is little or no evidence of vascular cambium and this fact is correlated with their relatively small size. Unfortunately entire plants, unless of very small size, are seldom found as fossils. However, by piecing detached parts together in formulating a morphological entity it is sometimes possible to reconstruct a reasonable facsimile of an extinct plant as it grew in nature. It is quite possible that the ultimate height to which a plant possessing a simple protostele or actinostele and without excessive cortex of periderm could attain would be about 2 meters. This seems to have been attained in certain Lower Devonian forms in which some internal structure is recognizable (Höeg, 1942). The primary vascular tissues in the relatively few cases of three-dimensional preservation known among Early and Middle Devonian plants consist of simple or lobate strands