

**THE PHYSIOLOGY
OF
FOREST TREES**

THE PHYSIOLOGY OF FOREST TREES

A Symposium Held at the
Harvard Forest
April, 1957

Under the auspices of the
Maria Moors Cabot Foundation

Edited by
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with the assistance of
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THE RONALD PRESS COMPANY · NEW YORK

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Library of Congress Catalog Card Number: 58-8810

PRINTED IN THE UNITED STATES OF AMERICA

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Preface

Few plant physiologists use trees for experimental material, and few professional foresters study plant physiology. The physiology of fruit-bearing trees, although not neglected to quite the same extent, has still received little fundamental study. It was these considerations that led The Cabot Foundation to the idea of organizing several days' discussion of forest tree physiology, with the aim of consolidating the small body of knowledge we already possess and stimulating the search for more. Thus the first International Symposium on Forest Tree Physiology took place, April 8-12, 1957, at the Harvard Forest. Although presented at the research level, the papers constitute something close to a textbook on the physiology of forest trees, and their broadly representative nature is the justification for publishing them in full in the present volume.

In planning the symposium, it became clear that participation should be limited to those men who are actively working on some aspect of tree physiology or on a closely related topic, and that the symposium papers should contribute to the broadest possible coverage of the main areas of the field. The limitation to actual research workers was dictated by the desire to hold the size of the meeting to one that would allow free and critical discussion, and in which each viewpoint could be adequately presented. The need for breadth of coverage stemmed not only from the lack of any similar international symposium in the past, but also from the desire to keep attention focused on the group of problems presented by the forest tree rather than on any specific branch of science.

Five of the participants came from Canada, three from Great Britain, one each from Norway, Germany, and New Zealand, and the rest from various parts of the United States. The topics of their papers, beginning with the perennial and classical problem of the ascent of sap, include other aspects of translocation in the tree such as the movement of organic food materials and the uptake of water by leaves. Photosynthesis, mineral nutrition, and the biochemistry of bark and wood are next covered. The last group of papers deals

with the growth of roots and of shoots, and the photoperiodic response of trees—topics which have recently come so much into prominence. In most of the papers the latest developments are presented against a background of our earlier state of knowledge, and a large part of the material has never been previously published.

An important part of the symposium was assigned to the discussions, and these proved even more stimulating and valuable than the sponsors had dared to anticipate. The records of these discussions, carefully revised by each participant and subjected to some editorial abridgment, are presented with the papers.

The authors are sincerely to be thanked for their promptness and thoroughness in reviewing their contributions. Thanks are also due Professor Hugh M. Raup, who acted as host, and to the many others who helped make the symposium a success. Drs. Martin H. Zimmermann and William B. Critchfield gave invaluable help in the recording and transcription of the long discussions.

The aims of the Cabot Foundation are to sponsor research on the production of fuel and other plant products and to make scientific knowledge about trees more generally available. The present publication is intended to further these aims.

KENNETH V. THIMANN

Cambridge, Massachusetts
March, 1958

Introduction

PAUL C. MANGELSDORF

The Maria Moors Cabot Foundation for Botanical Research shares with the Harvard Forest the honor of being host to this, the first international symposium on forest-tree physiology. It may be appropriate for me, as Chairman of the Administrative Committee of the Cabot Foundation, to describe the purposes of the Foundation and to explain the reasons for its interest and sponsorship of this symposium.

The Cabot Foundation was established by Dr. Godfrey Lowell Cabot, a remarkable Bostonian who recently celebrated his ninety-sixth birthday and who until a few months ago walked daily to his office. Mr. Cabot had many interests throughout his life, of which two, aviation and the utilization of solar energy, were predominant. He won his commission as Navy flier in World War I at the age of 57, and he has given a substantial part of his fortune to the endowment of research in aviation. His interest in solar energy grew out of his own world-wide experience and knowledge of the fossil fuel resources of the globe. He was convinced that these are exhaustible and must sooner or later be replaced by renewable sources of energy, and he believed further that the world's fuel problem would become acute before the food problem. In 1937 Mr. Cabot established and endowed two foundations concerned with the utilization of solar energy. One of these at Massachusetts Institute of Technology has, for its objective, research on the direct utilization of solar energy for heating and other purposes. The other, established at Harvard University, is concerned with the indirect utilization of solar energy. Its primary purpose, to use the founder's own words, is "by artificial selection and other methods, to increase the capacity of the Earth to produce fuel by the growth of trees and other plants."

Until recently, most of the resources of the Cabot Foundation have been devoted to research in forest-tree genetics and methods of

propagation of forest trees. More recently the members of the Committee which administers this Foundation have come to the conclusion that research on forest-tree physiology is also needed, for to be successful in improving trees we need to know much more about them as biological systems than we now do.

Trees are, after all, pretty important organisms. Approximately one-fourth of the land surface of the earth is occupied by forests whose trees furnish mankind with many useful and indispensable products, including fuel, wood, paper, rubber, resins, and medicinal drugs. Because of their economic importance and botanical interest, we should know much more than we now do about these plants which occupy so large a part of the earth's surface. It may be true, as one poet has said, that "only God can make a tree," but it should not be beyond the capabilities of man to learn how a tree is made and what it does. On the first point there already is a substantial store of knowledge. The anatomy of trees, which is concerned with their form, has been studied for many years, and an expert on wood anatomy can often identify a tree, living or fossil, from even a small fragment. But the physiology of trees, which is concerned with their function, is a neglected subject partly because plant physiologists usually prefer to work with smaller plants which are more easily manipulated. We know as a generality that trees are marvelously intricate and efficient biological systems, but their actual workings are still very much of a mystery to botanists and foresters alike. Their very size has been a deterrent to intensive studies of their functions.

The Administrative Committee of the Cabot Foundation, recognizing the need for basic research on the physiology of forest trees as an essential part of the purposes of the Foundation, in 1954 recommended the appointment of a forest-tree physiologist, Dr. Martin Zimmermann. Dr. Zimmermann and Dr. Thimann, in discussing the problems of forest-tree physiology, soon reached the conclusion that one of the most useful and stimulating things which the Cabot Foundation could do would be to sponsor a symposium in forest-tree physiology which would bring together all of the physiologists in the world who were actively engaged in research on forest trees. Their suggestion was enthusiastically endorsed by the Administrative Committee. In planning this symposium one objective from the beginning was to make it international in scope. It is gratifying to see so many different countries represented here: Canada, New Zealand, England, Germany, Norway, as well as the United States, all have their spokesmen. A second objective was to keep the symposium small, not for the sake of being exclusive in any snobbish

sense, but to confine it to those actually engaged in research in this field and to make it possible to hold the symposium at the Harvard Forest where living accommodations are limited.

In this sylvan atmosphere, remote from the distractions of a city, it should be possible for this small group to spend a concentrated week in discussing to mutual advantage the problems involved in forest-tree physiology. We know that the formal papers will be distinguished—we hope that the discussion will be spirited and lively and even more valuable than the papers and that when the symposium is over all will feel that it has been a success. And if it is a success, it will be because of the active participation of all those who have taken time out of their busy lives to come. We in the Cabot Foundation are indebted to all those who by their participation are sharing their own unique experiences with others in their field.

The Harvard Forest

HUGH M. RAUP

The Harvard Forest was established about fifty years ago as a field station to supplement the teaching of forestry at the University in Cambridge. As stated at the time, the Forest was to serve three purposes, in this order: it was to be a demonstration of practical sustained-yield forestry; second, it was to be a field laboratory for students; and third, it was to be a research station in forestry. Inherent in the statement of these purposes, and particularly in the order in which they were set forth, was a basic assumption that the methods for the management of our forests on a sustained-yield basis were at hand, and that they were practical.

During approximately the first twenty-five years of its history the Forest saw the establishment and maintenance of a rather elaborate set of demonstration experiments in the manipulation and regeneration of its stands. Gradually it became apparent that the methods which had been assumed to be effective were not sound. They were not practical when assessed critically either on biological grounds or on grounds of the existing or foreseeable economic situation. It is not surprising that restatements of purpose found in the Forest's records in the early 1930's moved research from the bottom of the list to the top of it. A searching analysis of the basic assumption upon which the initial purposes were laid down clearly demonstrated that this assumption was underlain by a cloud of other assumptions, none of which had been tested for application to the American scene.

Therefore the Harvard Forest has been drawn into research of an increasingly fundamental nature. Most of the old experiments in manipulation have been maintained, no longer as a demonstration of how to manage the woodlands, but rather as a source of materials and ideas with which to formulate problems in basic research. A large and highly significant segment of this research is in the eco-

conomic aspects of the production of wood on the land. Another large segment has to do with the vast network of interrelationships that exists between the trees and the sites on which they grow. The work in this field has led us into studies of the form and function of the trees themselves, into local climates among which there are large differences even within our small area of gently rolling topography, and into the history and development of our soils, particularly with regard to their water regimes. There is great danger in the pursuit of such research that we shall become so much concerned with minutiae that we may in time lose sight of our major problem, which is to become more intelligent in the making of investments in the forest resource. However, we live in the Forest, and it is immediately outside our doors, a fact which I consider to be of large significance for the maintenance of balance in the research program.

The Forest operates as part of Harvard University, not as a separate institution for professional training, but within the orbit of the Graduate School of Arts and Sciences. It regards this relationship as one of its most valuable assets, for thus it has ready access to the University's array of talents in many fields. We here know full well that we can personally deal with only a fraction of the research that needs to be done. When the Cabot Foundation was established about twenty years ago its people were immediately welcomed at the Harvard Forest, to use its facilities as best they could for research in tree nutrition, forest genetics, and a more extended program of tree physiology. We welcomed particularly a research program in tree physiology that would deal directly with maturing trees in the forest. The Harvard Forest now extends the same welcome to you who have come here to discuss this research and place it in a larger framework.

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