OXFORD SCIENCE PUBLICATIONS

Tropical Mycorrhiza Research

Edited by P. Mikola

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PEITSA MIKOLA

CLARENDON PRESS OXFORD 1980

Oxford University Press, Walton Street, Oxford OX2 6DP

OXFORD LONDON GLASGOW
NEW YORK TORONTO MELBOURNE WELLINGTON
KUALA LUMPUR SINGAPORE JAKARTA HONG KONG TOKYO
DELHI BOMBAY CALCUTTA MADRAS KARACHI
NAIROBI DAR ES SALAAM CAPE TOWN

Published in United States by Oxford University Press,
New York

British Library Cataloguing in Publication Data

Tropical mycorrhiza research.
1. Mycorhiza
2. Tropical plants
I. Mikola, Peitsa
589'.2'04524 QK604 79-42778
ISBN 0-19-854553-3

Set by Hope Services, Abingdon
Printed by J. W. Arrowsmith Ltd., Bristol

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Foreword

In 1973 the International Foundation for Science (IFS) instituted a programme of grants for research in developing countries. The five subject-areas, in support of agriculture in the broadest sense, included research on mycorrhiza which was considered to be highly relevant. By 1978 the Foundation had approved only twenty grants for mycorrhiza research, a modest proportion (8 per cent) of the total grants.

The relatively few institutions receiving grants are widely separated in south-east Asia, Africa, and Latin America. For this reason they find it difficult or impossible to confer among themselves and with other experts in the field. Perceiving this, the IFS decided to arrange an international workshop in Kumasi, Ghana, in September 1978, to bring together all the grantees with several internationally recognized experts and specialists in the subject of mycorrhiza. The material presented at that workshop, edited and reorganized, forms the content of this book. The main part of the book consists of five extensive reviews by international experts. Also included are summaries, of varying length, contributed by recipients of IFS grants.

The various types of mycorrhiza and host plants involved in symbiotic associations are well represented here. Most space is devoted to the ectomycorrhiza of pines, both indigenous and exotic species as well as those of indigenous species of conifers other than pines. Special attention is accorded the practical applications of mycorrhiza in forest nurseries where widespread use is most likely to be found in future.

As happens in the whole field of mycorrhiza research, endomycorrhiza takes second place to ectomycorrhiza. Only two IFS grants are awarded for endomycorrhiza relations in agricultural crop plants; a few others are concerned with endomycorrhiza and natural vegetation of tropical regions. This is an area where more research is needed and future IFS support for the subject should be encouraged. It is hoped that this account will provide an overview of much of the knowledge about mycorrhiza in tropical countries as well as indicating the needs for research and the application of the research findings.

The Foundation wishes to express its thanks to the advisers in the mycorrhiza programme, Professor Peitsa Mikola of the University of Helsinki, and Dr Göran Lundeberg of the Royal College of Forestry in Stockholm. Their efforts over the years in defining the programme, giving individual assistance to those receiving grants, and planning the workshop in Kumasi have been invaluable. This is also the place to record the Foundation's gratitude to the late Professor Erik

Björkman of the Royal College of Forestry, who gave the first impulse to the mycorrhiza programme.

The Foundation is deeply indebted to authorities and persons in Ghana for the arrangements at Kumasi. Particular thanks go to Dr Albert Ofosu-Asiedu for his untiring efforts in the workshop preparations. The Salén Foundation of Stockholm shared the expenses with IFS, and a further contribution from UNESCO is gratefully acknowledged. Special thanks go to Professor Peitsa Mikola for editing the present book. Its acceptance for publication by the Oxford University Press is greatly appreciated by all the contributing authors.

Sven Brohult
President of IFS

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PART I

Introduction

1 Mycorrhizae across the frontiers

P. Mikola

Mycorrhiza, the symbiotic association of fungi and roots of vascular plants, has been known for about one hundred years. After several decades of sporadic studies and occasional heated controversy over the symbiotic or parasitic nature of the association, a great advance in mycorrhiza research was made in the 1920s, primarily through the pioneering work of the Swedish scientist Elias Melin. Melin (1923, 1925, 1936) definitely proved the symbiotic character of the ectotrophic mycorrhiza of forest trees, which, in turn, gave a strong impetus to increasing activity and even international co-operation in mycorrhiza research.

At about the same time, in the early decades of the current century, the role of mycorrhizal symbiosis was bitterly experienced in the emerging silviculture of many tropical countries. Practically oriented forest research usually began with planting trials of exotic species, and these, particularly the efforts of introducing exotic pines, very often failed. The reason for the failure was suspected, and later on proved, to be the absence of suitable symbiotic fungi which, again, could be corrected by intentionally or accidentally introducing mycorrhizal infection.

The history of the invasion of mycorrhizal infection across the frontiers is like a series of detective stories (for details, see Mikola 1970). Where pines or other ectomycorrhizal trees were first introduced as potted plants, the mycorrhizal fungi travelled in their roots and no other importation was needed. This has, apparently, been rather common, since early settlers from Europe often carried tree seedlings of their home countries and planted them around their new homes. This is probably the way in which the first pines or other ectomycorrhizal trees with their mycorrhizal symbionts arrived in South Africa, Australia, New Zealand, and South America. Mycorrhizal fungi have also been carried in tree roots for shorter distances when, on the establishment of a new nursery, transplants have been brought in from older nurseries.

Mycorrhizal infection may also spread as spores through the air or shorter distances in soil adherent to shoes of workers, tools, car tyres, etc. This may explain how mycorrhizae have often developed in new nurseries far from existing pine forests, without intentional inoculation.

There are numerous examples, however, where all efforts at growing pines consistently failed until mycorrhizal fungi were brought in and inoculated into nursery soil. Such cases have been recorded, for instance, from Puerto Rico (Briscoe 1959), Trinidad (Lamb 1956), Nigeria (Madu 1967), Malawi (Clements 1941), Kenya (Gibson 1963), and Zambia (Mikola 1970).

Because of incidental sources of mycorrhizal inoculation, the fungal population in different nurseries and planting areas may vary greatly. This was clearly demonstrated by an extensive study on the structure of pine mycorrhiza in tropical nurseries (Mikola 1978). Although great variation was noticed in the external appearance and anatomical structure of mycorrhizae, such as colour or thickness of the mantle, three main types could be distinguished.

1. The most common type was a brown ectotrophic mycorrhiza with a thin mantle and Hartig net (Fig. 1.1). The mantle could even be almost absent. This type approximately corresponds to the 'hazelnut brown form' of Rambelli (1967). It was the dominant type in East African nurseries, for instance.

2. Ectotrophic mycorrhiza with a thick (20–40 μm) and compact mantle and well-developed Hartig net occurred in Trinidad (Fig. 1.2), where the mycorrhizal inoculum originates from the natural range of

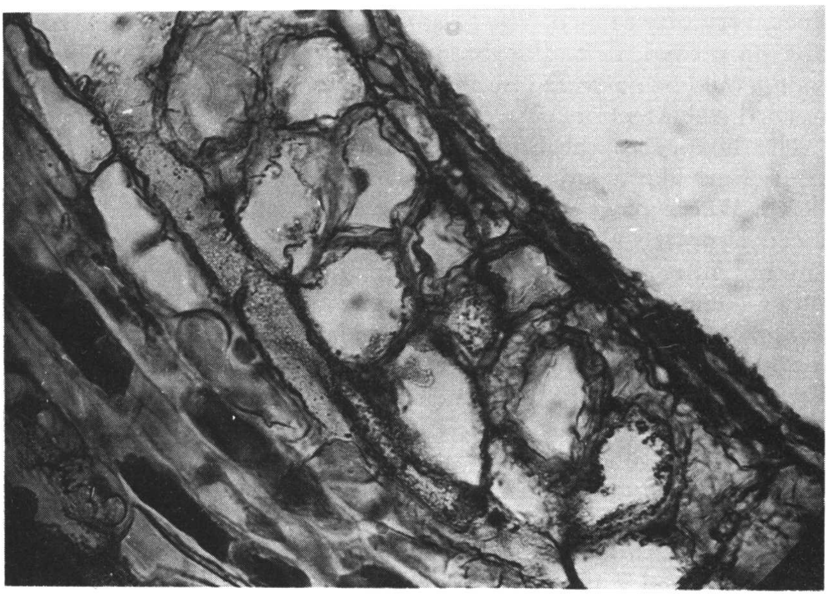

Fig. 1.1. Longitudinal section of an ectomycorrhiza of 3-month-old *Pinus patula*. The mantle is almost lacking but the Hartig net is well developed. Rwabaranda nursery, Uganda.

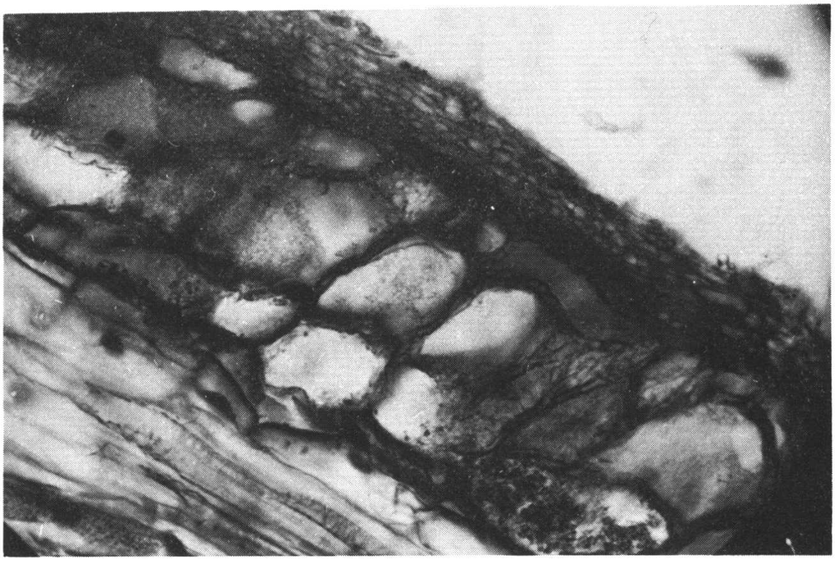

Fig. 1.2. Longitudinal section of an ectomycorrhiza of 6-month-old *Pinus caribaea*. The thick mantle and Hartig net are clearly visible. Cumuto nursery, Trinidad.

Pinus caribaea in British Honduras (Lamb 1956). The colour was light-brown. A somewhat similar mycorrhiza with a thinner (15-20 μm) mantle and very thin hyphae in the Hartig net was dominant in one nursery in Swaziland. Ectotrophic mycorrhizae with a loose, white mantle and rich external mycelia were also sometimes met although they were uncommon.

3. A typical ectendotrophic mycorrhiza with very coarse hyphae and Hartig net and heavy intracellular penetration, and almost without a mantle (Fig. 1.3), dominated some nurseries and was lacking in others. This type closely resembles the description of the 'chestnut-brown form' of Rambelli (1967). It was also very similar to the ectendotrophic mycorrhiza which is common on pine in Finnish forest nurseries (Mikola 1965), as well as elsewhere (Laiho 1965), and is probably caused by the same fungus. The degree of the intracellular penetration can vary considerably, whereas the very coarse Hartig net is the most characteristic anatomical feature. The ectendotrophic type is found, for instance, in Tanzania, Zambia, and Swaziland, and also in several comparative samples outside the tropics, e.g. in Australia, New Zealand, the Mediterranean countries, and Central Europe. The presence of the ectendotrophic infection in some nurseries and its absence in others was most conspicuous in this study.

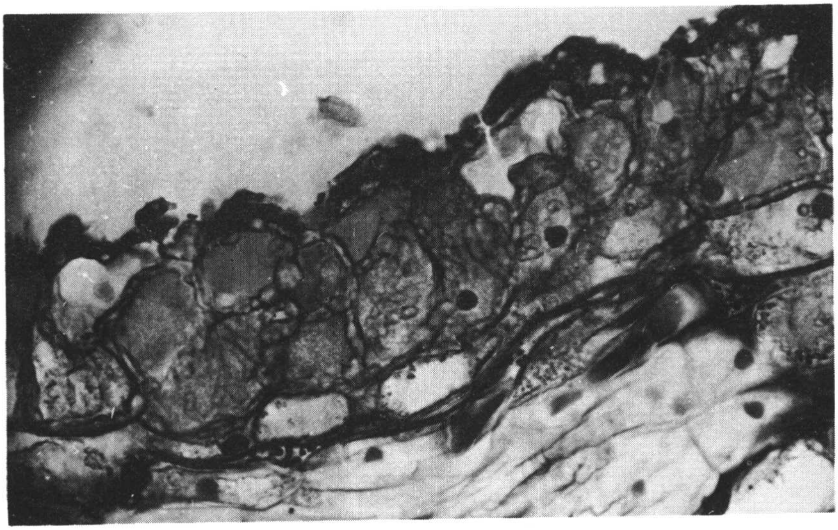

Fig. 1.3. Longitudinal section of an ectendomycorrhiza of 1-year-old *Pinus kesiya*. The very coarse Hartig net is most conspicuous. Chati nursery, Zambia.

Transportation of mycorrhizal infection from one country to another is technically easy in soil or roots of living seedlings. However, as quarantine regulations usually prohibit import of living plants and unsterilized soil, there have often been bureaucratic difficulties and, in fact, mycorrhizal inoculum has been smuggled illegally to some countries. Such cases, of course, have not been well documented.

The transport of soil or living seedlings for mycorrhizal inoculation is not at all a satisfactory method. Although the technique itself is easy, there are several drawbacks. Soil can be bulky for long-distance transport, and disadvantageous selection of the fungal population may take place during prolonged storage and transport. Furthermore, the fungal population of such a mixed inoculum is unknown; the fungi present may be less suitable for the prevailing conditions of the new site. The greatest danger, however, is the risk of introducing pests and diseases with the mycorrhizal infection.

To overcome the above drawbacks, inoculation with fungal spores or pure cultures has repeatedly been suggested (e.g. Bakshi 1967). Pure cultures have been commonly used in scientific experiments, but practical application has not been so successful. Besides technical difficulties in isolating, culturing, and inoculating mycorrhizal fungi, there are still several fundamental questions to be answered; for instance, which fungal species would be the best symbionts for