FORESTRY COMMISSION

Bulletin No. 13

# STUDIES ON TREE ROOTS

LONDON: HIS MAJESTY'S STATIONERY OFFICE
1932
PRICE 3s. 6d. NET

## FORESTRY COMMISSION PUBLICATIONS

A list of Bulletins, Leaflets, Reports and publications currently available may be obtained on application to:

The Secretary:
H.M. Forestry Commission,
25 Savile Row,
London, W.1

FORESTRY COMMISSION BULLETIN No. 13

# STUDIES ON TREE ROOTS

LONDON: HIS MAJESTY'S STATIONERY OFFICE
1932
(Reprinted 1947)

## FOREWORD.

This bulletin contains an account of investigations on the roots of young trees carried out over a series of years for the Forestry Commission by Dr. E. V. Laing of the Department of Forestry, Aberdeen University. Special attention has been paid to the association of fungi (mycorrhiza) with roots and to the development and action of roots in peat soils. Both these questions are of great importance in afforestation operations in Great Britain.

It is obvious from general considerations that there must be a very close correlation between the development of the shoot (the part above ground) and the root of a tree from the seedling stage until the tree is felled ; but, while a great deal of investigation has been done into the visible parts, relatively little account has been taken of what is happening below ground. This is due no doubt in part to the intrinsic difficulty of observing root developments without seriously disturbing the conditions of growth, and partly to the long periods of time which are involved in the growth of forest trees.

R. L. ROBINSON,
*Chairman.*

FORESTRY COMMISSION,
25, Savile Row,
London, W.1.

*August,* 1932.

## BULLETIN No. 13

# STUDIES ON TREE ROOTS.

## CONTENTS.

# STUDIES ON TREE ROOTS.

## INTRODUCTION.

### The Root System of a Conifer.

As the studies of which this bulletin is composed deal so largely with tree roots and their functions, some elementary account of the structure of a typical coniferous root may not be out of place.

The first organ of the plant to emerge from the seed on germination is the primary root or radicle. This primary root may persist, in which case it is called the tap root of the tree. Sometimes, however, owing to bad soil conditions or to transplanting, the tap root disappears. Some species such as Norway spruce lose their tap roots very readily, whilst in other species such as European larch and Scots pine, the tap root is more persistent. Accordingly some species are described as being tap-rooted trees and others as non-taprooted trees.

At an early stage in the life of the plant, the tap root gives rise to other roots. These are the lateral or secondary roots, the first of which appear on the upper part of the primary root, and therefore, near the surface of the ground. The secondary roots in turn give off tertiary roots, and generally this is the furthest stage of root branching in the case of most species, during the first season. There are some exceptions to this general rule, as roots of a fourth order may frequently be seen on vigorously growing Scots pine, whilst tertiary roots may not be developed on Sitka spruce and such species as *Thuya plicata*. In the second year, in addition to general growth in length of most of the roots produced in the previous year, roots arise from the new growth of the current year and this growth in length and branching is repeated in all subsequent years. Many factors however interfere with the regularity in succession of roots and it often happens that new roots are produced out of their normal sequence or position on older parts of the root system or even at the base of the stem in which case they are termed adventitious roots.

A microscopical examination of a cross section of any young root of a conifer shows the following main features: an outer envelope consisting of thin walled roundish living cells, which is called the cortex; then a well marked ring of cells, the endodermis, and within this ring definite groups of cells which are the vascular strands or conducting tissue. A closer examination of the cortex shows that the thin walled cells have numerous, sometimes large, spaces between them—the intercellular spaces. The outer few layers of cortical cells are smaller than those towards the inside. In any one species the size of the cortical cell varies, as does also the number of cell layers.

Two types of cortical cells are found in coniferous tree roots and seem to be typical of certain genera. In one case there is thickening of the cortical cell walls and in the other case there is no thickening. Thickening, where present, occurs at the point of contact of neighbouring cells (Plate V, fig. 2 and text Fig. 2, p. 13). The thickenings appear in section as girders, often two such girders per cell being visible in one field of view. They are present in roots of *Taxus*, *Thuya*, *Cupressus*, *Sequoia*, and *Sciadopitys*, but are absent from all roots of the *Abietineae* such as *Pinus*, *Larix* and *Picea*.

The innermost layer of the cortex is differentiated and is called the endodermis. It appears normally as an unbroken regular band of thin walled cells of larger size than the cells of the cortex. At the point of union of adjacent cells of the endodermis, in certain genera such as *Taxus*, *Cupressus* and *Thuya*, pronounced thickening occurs. These thickenings are named the casparian bands or strips of the endodermis.

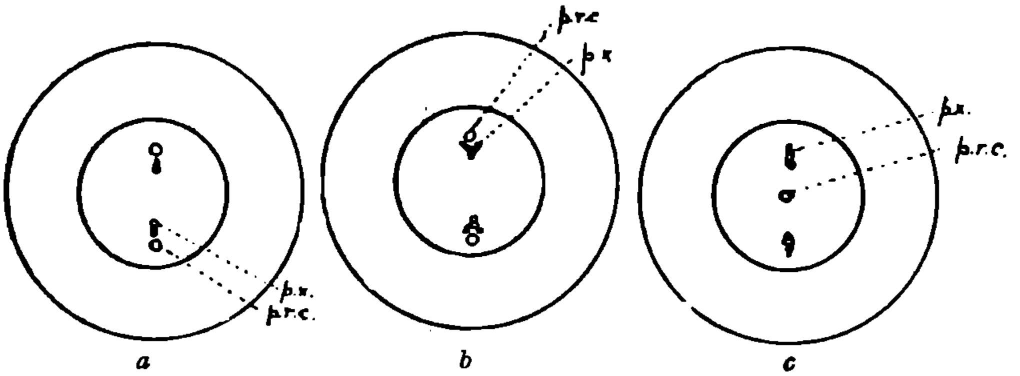


FIG. 1.

Diagrammatic representation of relative position of primary resin canal and primary wood in (*a*) *Picea*, (*b*) *Pinus*, (*c*) *Abies*.

The endodermis separates the cortex from the inner matrix of cells in which lie groups of cells arranged in a broken ring. The more conspicuous of these patches constitute the first formed or primary water-conducting or vascular tissue, which is called the primary xylem. The number of groups of primary xylem varies in different genera, and even within the same species; there being, for instance, in some cases only two such groups as in *Larix* and *Pseudotsuga*, two or three as in *Pinus sylvestris* and *Picea*, four or five as in *Cupressus* and *Thuya*.

In close proximity to the primary xylem of certain genera primary resin canals occur. These occupy a definite position in different groups of species: (1) subtending the primary wood as in *Pinus*, *Picea*, *Pseudotsuga*, *Larix* (Fig. 1*a*, *b*); (2) central or axile, i.e., situated in the centre of the root between the primary xylem groups as in *Abies*, *Tsuga* and *Cedrus* (Fig. 1*c*).

In *Pinus* the resin canal is situated in the angle of the Y shape which the primary xylem forms in this genus (Fig. 1*b*).

New roots arise from the older root in a definite order which depends on the number of groups of primary xylem. They generally arise opposite a group of primary conducting tissue. Where there are two primary xylem groups the new roots appear in two opposite rows: where there are three primary xylem groups there are three rows of developing roots and where five, there are five rows. During subsequent development of the root system this definite orientation may not be obvious due to twisting and deflection of the roots from various causes.

Some investigators regard the number of protoxylem groups as of importance in determining the number of rootlets which can be produced. Liese ($^{27}$) for instance points out that in any particular species (e.g., *Pinus sylvestris*) the greater the number of primary xylem bundles, the greater will be the abundance of rootlets and therefore the greater the potential absorptive surface of the root system of the tree.

The root tips in the *Coniferae* are of two types. One type possesses a root cap. The root cap protects the growing apex from damage while the root is boring through the soil. In the other type, the root cap is absent. This latter type occurs when the apical portion of the root becomes enveloped with fungus hyphae, the formation of which is called a " fungus root " or mycorrhiza. The root cap has a definite structure. Its outside covering consists of thin walled oblong cells with their long axis parallel to the axis of the root. At certain seasons many of these outer cells become loosened and detached from the cap. The central core or medulla of the root cap, consists of square cells. The outer cells of the root cap and frequently also the cells of the central core, contain starch grains, the presence of which led Haberlandt ($^{17}$) to formulate the Statolith theory explaining the geotropism of roots.

The root tips of conifers which possess root caps are often very thick and fleshy, those of Scots pine and spruce being frequently as much as one-tenth of an inch in diameter. The thickest root tips are to be found in the raw humus layer of the forest, the thinnest in clayey soils. The younger portion of the root of the current year is at first thicker than the portion behind from which it has arisen, and continues so for several inches until suberisation, or cork formation occurs. Frequently the root tip of certain species such as *Larix* and *Thuya plicata* is of a brilliant red colour. This coloration has been induced by the writer in non-coloured roots by subjecting them to ammonia fumes. It has also been observed that the presence of a red pigment in the root tip is associated with health and vigour.

At a very short distance behind the tip of the root are to be found the root hairs. These are outgrowths from an outer ring of cortical cells. In some cases the root hairs are large enough to be easily visible to the naked eye or with the aid of an ordinary pocket lens. These root hairs, although they become functionless in course of time, are not always thrown off as the root becomes older. This is the case, for instance, with Douglas fir, where very frequently on the older roots the root hairs persist and appear as a brown tomentum covering the roots.

Many of the older writers were under the mistaken impression that conifers do not possess root hairs. It is true that conifer roots are sometimes found without root hairs; Melin (32) recently has shown for instance that they may be present or absent, depending on the form in which the nitrogen occurs in the soil; further, root hairs are suppressed when fungus roots are formed. Fungus roots are of much more frequent occurrence in the *Coniferae* than roots with root hairs.

# THE MYCORRHIZA OF CONIFERS.

## 1. Structure.

Mycorrhiza may be defined as the association of a fungus and a root. Two main forms of mycorrhiza are recognised. The fungus may form a mat of hyphae which is external to the cortex of the root, and completely envelops the root tip, or the fungus hyphae may be inside the cortical cells of the root. The former is called ectotrophic mycorrhiza, the latter endotrophic mycorrhiza. Both forms occur in the *Coniferae*.

### (*a*) RESUMÉ OF THE LITERATURE ON THE STRUCTURE OF MYCORRHIZA.

The intimate union of tree roots and fungi was first recorded by Hartig in 1846. Gasparini in 1856 noted certain points regarding fungus roots such as the absence of root hairs, and about the same time Jaczewstei described the dichotomous branching of the mycorrhiza in pine. It was left to Kamienski, however, to give the first detailed description of the mycorrhiza of the conifers. The terms " ectotrophic " and " endotrophic " as applied to mycorrhiza were coined and first used by Frank. (12) Von Tubeuf (48) drew attention to the endotrophic form of mycorrhiza in certain conifers. In America McDougall (31) has described the mycorrhiza of many tree species and from his investigations into the anatomy of the fungus roots and their absence or presence at well-defined seasons of the year, he draws certain very important conclusions as to the relation of fungus and tree. The writer (22) in a paper published in 1923, described the ectotrophic and endotrophic mycorrhiza of our coniferous trees, whilst Melin (32) has given descriptions of fungus roots as found on the forest trees of Sweden. From time to time various investigators in different parts of the world have described the mycorrhiza as found by them on the trees which were under their observation.

### (*b*) DESCRIPTION OF MYCORRHIZA ON VARIOUS GENERA.

*Pinus.*

Both forms of mycorrhiza are found in the root system of the pine. The form which is more obvious, in that it causes pronounced modification of the rootlets, and which is more widespread and frequent in its occurrence, is the ectotrophic form.

The formation of mycorrhiza in pine, as in all ectotrophic forms, begins with the appearance of a weft of hyphae on the small lateral rootlets. The fungus hyphae increase in amount and gradually extend over the whole surface of the root tip. By their action they exert a retarding influence on the growth in length of the rootlet. When an infected rootlet continues to grow it branches dichotomously, i.e., the rootlet forks equally. Each branch in turn divides dichotomously and this branching may be repeated indefinitely.

That infection of a Scots pine seedling has taken place is generally visible to the naked eye in the autumn of the first year of growth. During August, it may be noticed that the fine tertiary rootlets have branched dichotomously. Only one forking of the root takes place during the first year.

According to the degree of the restraining influence of the fungus on the growth of the root, two main types of ectotrophic pine mycorrhiza may be distinguished, namely the " coralloid " mycorrhiza (Plate I, figs. 2, 3) and the " ball " mycorrhiza (Plate I, fig. 1). In the former inhibiting action on growth may be seen at its minimum for pine, each branch of the branch system being clearly visible. In the latter, the growth in length of each branch is extremely small, the branching is profuse, and the final result is a compact ball, composed of rootlets bound together by the wefted hyphae. The ball type varies greatly in size, ranging from the size of a pin-head up to nodules half an inch or more in diameter, as may sometimes be found on the roots of *Pinus montana* growing in peat. The coralloid type occurs in two forms, one where the individual branches are thick and fleshy; the other where the individual branches are thin and wiry.

In the course of the development of pine mycorrhiza the root cap disappears and no root hairs are formed.

It is very seldom that hyphae of the fungus roots can be seen with the unaided eye. The hyphae are closely adpressed to the root and usually can only be seen with the aid of a microscope. The white woolly secretion of an aphis on the root system of a pine may be mistaken however for the fungus hyphae of mycorrhiza (Plate III, fig. 1). The aphis (*Pachypappella piceae*, Hartig), the secretions of which are shown in the figure, is of common occurrence on pine and also spruce roots of trees growing in the nursery and in the plantation. The life history and ecological status of this aphis have not been fully investigated; the presence of the insect on the roots must be important, however, especially in relation to fungus infection.

The mycorrhiza varies in colour with that of the hyphae of the fungus which has entered into union with the roots. The colour of the mycorrhiza may be white, grey, yellow or pink.

A typical section of a fungus root shows on the outside of the cortex a layer of fungus mycelium, with hyphae which pass inwards between the cells of the cortex. These hyphae usually penetrate to within a distance of one cell layer from the endodermis, and in their penetration cause the separation of the cells of the cortex one from another. In the ball type of mycorrhiza a section shows numerous roots lying in a mass of mycelium, the hyphae of one root being fused to the hyphae of its neighbours (Plate IV, fig. 3*a*).

The fungus hyphae occur in two main forms; (*a*) regular septate hyphae with clamp connections; and (*b*) irregular vesicular hyphae. The former occurs on the exterior and the latter in the interior of the fungus mat and also between the cells of the cortex. These two forms of hyphae belong to the same fungus, since an individual fungus thread can be traced from the regular form to the irregular vesicular swollen form. The presence of clamp connections indicates that the fungus is one of the *Hymenomycetes.*

A point of very great importance and one which is often visible in a cross section is that the fungus gradually destroys the rootlet. The outer cells of the root are encircled by the fungus and disappear. The outline of the root section is not regular and in places cells are missing. In the dense fungus mat cortical cells of the root are found isolated from their companions, having for some reason escaped destruction. The fungus thus acts as a root pruner. This occurrence of root destruction will be more fully dealt with later.

Other points which may be noted in the cross section of a fungus root, are: (1) that the number of cortical cells is less and the cells are much larger than those of other roots of the same plant which have no fungus covering; (2) there are no resin canals subtending the primary xylem; (3) the primary xylem is small in amount as compared with other roots of the same age; (4) cork formation does not take place where the fungus is present.

Although ectotrophic mycorrhiza is the typical form found in pine, it must be noted that an endotrophic form also occurs. The tap root and the main strong growing lateral roots may show near their growing points a well-defined zone of fungus containing cells next to or a cell layer distant from the endodermis. The hyphae within these cells form into coils and from these coils hyphae proceed in a radial direction intracellularly towards the outside of the root.

*Picea.*

In this genus no ball or coralloid growths are formed as in the genus *Pinus.* A macroscopic inspection, therefore, owing to the absence of any very well-defined modification of root structure such as occurs in pine, may fail to indicate whether or not fungus roots are present. Typically, however, when the fungus is present a slight thickening and shortening of the rootlets may be noted. Systems of short compact rootlets occur (Plate II, fig. 1) and these are completely enveloped with hyphae (Plate IV, fig. 1). Sometimes these systems are coloured yellow or pink due to the colour of the fungus hyphae. As noted in the case of pine the woolly secretion by an aphis is often present on the roots and resembles fungus mycelium.

Although typically the fungus is only found on the finer roots, it may not be confined to them solely but may also occur on the older parts of the root system. New rootlets which arise from these older parts of the root system, carry the fungus web with them, so that the rootlet is never without a fungus covering. Cases are sometimes met with, as for example in peaty soils, where the greater proportion of the root system is fungus clad.

A cross section of a spruce fungus root is very similar to that of pine, but variations occur in spruce as regards the thickness of the fungus mat and the degree or depth of penetration by the hyphae among the cortical cells. The fungus hyphae may form a compact interwoven mass on the outside of the root, which may sometimes be as broad as the cortex, or there may be only a few scattered fungus threads on the outside which show no actual penetration between the root cells. In the latter instance, root hairs are not suppressed. In species of spruce there occur all gradations from no root hair suppression, to a combination of root hairs and fungus and finally total root hair suppression.

Destruction of the roots by the fungus, such as has been described in pine, also takes place in spruce. In spruce, however, it is much more complete than in pine (Plate IV, fig. 1*c*). Cases are not uncommon, for instance, in peat, where the destruction has proceeded so far that all tissues to the outside of the endodermis have been destroyed.

*Larix.*

The members of the genus *Larix* cultivated as forest trees in Britain develop mycorrhiza freely in most soils. Although the ectotrophic form is the one which is most frequent and most evident from a superficial examination of plants, there also occurs an endotrophic form, and in addition, a form which has been called by the writer (22) semi-endotrophic.

The ectotrophic mycorrhiza of a larch tree resembles very closely that of a spruce, although in general the root tip is more swollen and fewer side rootlets are produced (Plate II, fig. 2).

The endotrophic form is very obvious in a section of a larch root. The hyphae which occur inside the cortical cells, are short jointed or numerously septate, and the individual cells show only a slight tendency to become irregular and swollen. In certain cells of the cortex the hyphae are in various stages of disintegration, and there is evidence which indicates that the fungus is ultinately killed and digested by the cells of the root. Doubt may exist, however, as to whether this is true mycorrhiza or not.

Closely associated with the intracellular hyphae, i.e., the hyphae which occur inside the cortical cells, is a strong growth of intercellular filaments, i.e., hyphae which occur between the cortical cells, which completely envelops each cortical cell. The intercellular hyphae freely penetrate the walls of the cortical cells and produce in their interior the endotrophic form of mycorrhiza already mentioned.

*Abies.*

The ectotrophic form of mycorrhiza (Plate III, fig. 2) is typical of the silver firs and is similar to that of spruce. Here also the hyphae often completely envelop the lateral roots. As the young rootlets emerge through the cortex they carry with them the fungal mat, so that there is no time at which a new rootlet may be without its fungal covering.

*Pseudotsuga.*

In *Pseudotsuga,* where fungus roots are produced, in most cases the rootlets simply become enveloped with hyphae and appear to the eye rather thicker and more fleshy than in their normal condition. In rarer instances a tendency towards the development of short branched mycorrhizal clusters may take place. In the simple, i.e., unbranched, fungus roots, disintegration of the cortex occurs; in the branched cluster system, such disintegration has been found to be rare.

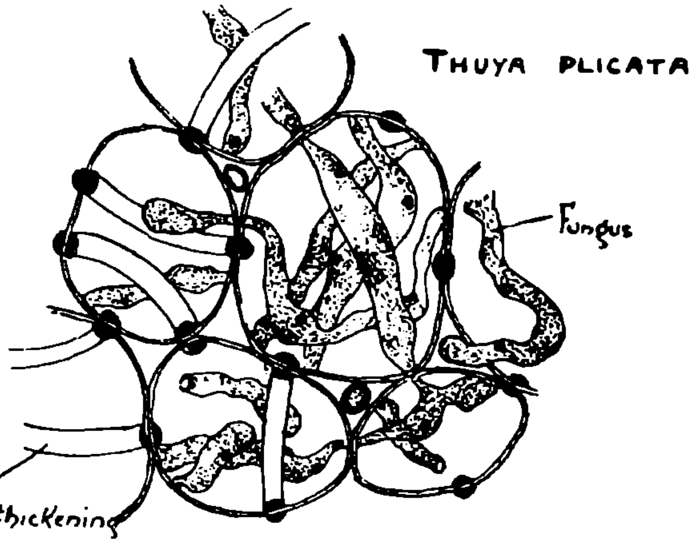


FIG. 2.

Only one definite disease of fungus roots has so far been observed, namely on Douglas fir. The disease is due to an eel-worm. In this particular case eel-worms were found in large numbers associated with the mycorrhiza and had bored into the fungal mat and destroyed the hyphae. Large depressions and holes in the fungal web had been made by the nematodes.

*Tsuga.*

The mycorrhiza in this genus is similar in every respect to spruce. It sometimes happens, however, that there is no fungus layer to the outside of the root, the fungus hyphae being intercellular, and resembling the semi-endotrophic form of larch.

*Thuya, Cupressus, Taxodium, Taxus.*

In these genera, so far as evidence shows, endotrophic mycorrhiza only is produced. The fungus is widely distributed throughout the cortex, appearing in coils (Fig. 2) within the cortical cells and also in the intercellular spaces. Cross walls are absent or of rare occurrence in the hyphae which are thick and swollen. A constriction always is formed where a hypha penetrates the cell wall. No indication of digestion of the fungus by the root has been observed.

The growth in length of the roots in these genera is unlimited (Plate II, fig. 3). The whole root system has a reddish hue more particularly at the root tip, and is fresh in appearance. There is a marked absence of suberisation of the cell walls of the root when the fungus is present.

*Sciadopitys.*

In this genus, although it has been found that the endotrophic form is the one usually produced, one or two instances have been noted where ectotrophic mycorrhiza is formed. The endotrophic form is the same in every respect to that of *Thuya* and the ectotrophic form to that of *Picea.*

### *Summary.*

The following points emerge from an analysis of the preceding descriptions of the mycorrhiza of the various genera of the conifers:—

1. The forms of mycorrhiza which occur in the *Coniferae* are—
    (*a*) Ectotrophic: *Pinus, Picea, Abies, Pseudotsuga, Larix, Tsuga, Sciadopitys.*
    (*b*) Endotrophic: *Pinus, Thuya, Cupressus, Taxus, Larix, Sciadopitys.*
    (*c*) Semi-endotrophic: *Larix, Tsuga.*

2. Ectotrophic mycorrhiza involves modification of the roots:—in respect of fleshiness, growth in length, method of branching, and root hair development.

3. The greatest modification of the roots takes place in pine, where the presence of the fungus leads to the repeated dichotomous branching of the rootlets, and the formation of balls or coralloid bodies. In other genera the branching is simple.

4. In both ectotrophic and endotrophic mycorrhiza suberisation is delayed.

5. Both forms, ectotrophic and endotrophic, may occur on the same tree.

6. Frequently the fungus envelops the older parts of the root system and the new rootlet on bursting through the cortical cells carries the fungal web with it so that at no time is it devoid of a fungal covering.

7. An eel-worm disease of mycorrhiza has been observed on Douglas fir.

## 2. The Fungi which form Mycorrhiza.

One of the main essentials in an investigation on mycorrhiza is to learn, if possible, the identity of the fungi which are responsible for the formation of mycorrhiza. Three methods have so far been available :—

(1) To grow in pure culture hyphae isolated from a mycorrhiza, until the fruiting bodies by which the fungus can be identified, develop.
(2) To grow pure cultures of hyphae from the spores of fruiting bodies of fungi found near the roots of a certain tree, and then to test by inoculation of the same or other tree roots if the hyphae so obtained can induce mycorrhiza formation.
(3) To trace connection between tree roots and the fruiting bodies of fungi in their neighbourhood.

Tulasne and Boudier about the years 1874 and 1876 observed a possible connection between the fungus *Elaphomyces* (the false truffle) and pine roots, an observation which was confirmed by Reess in 1880. Boudier, however, it must be noted described the false truffle as having yellow mycelium which was connected with the fungus roots of the pine, whereas in reality the yellow mycelium belongs to a species of *Cordyceps* which is parasitic on the false truffle (Plate XI, fig. 1). Noack (36) later reported that he had been successful in connecting *Geaster fimbricatus*, *Geaster fornicatus* and *Cortinarius callisteus* with pine mycorrhiza and *Tricholoma terreus* with spruce. Kauffmann (20) in 1906 stated that *Cortinarius* was a mycorrhiza producing fungus. In 1915-16 Boyer (2) succeeded in tracing the delicate mycelial filaments of species of *Amanita* and *Boletus* for a distance of an inch or so towards the mycorrhiza of forest trees. He further states that many truffles and similar fungi have mycelium which is scarcely apparent, and yet they possess hyphae which extend into the earth, and in many cases connect with the mycorrhiza of trees in the neighbourhood. Peyronnel (37), by following the same method as Boyer found a connection between various common woodland mushrooms and the fungus roots of trees. Peyronnel gives the following list :—

| | |
|---|---|
| *Larix europaea* | *Amanita muscaria, Russula laricina, Hygrophorus* sp., *Scleroderma vulgare.* |
| *Corylus avellana* | *Lactarius coryli, Boletus chrysenteron, Strobilomyces strobilaceus, Hypochnus cyanescens.* |
| *Fagus sylvatica* | *Cortinarius proteus, Boletus cyanescens, Boletus chrysenteron, Hypochnus cyanescens, Scleroderma vulgare.* |
| *Betula alba* | *Amanita muscaria, Lactarius necator, Boletus scaber, Scleroderma vulgare.* |

Melin's(32) results are probably more satisfactory than the previous in that he succeeded in inoculating tree seedlings grown in pure culture, with hyphae obtained from spores of numerous common woodland fungi, and in obtaining mycorrhiza formation from his inoculations. His results show that in all probability most of the common mushrooms and toadstools of humus soils will be found to be mycorrhiza-builders. Melin gives the following fungi as being capable for forming mycorrhiza :—

| | |
|---|---|
| *Pinus sylvestris* | *Boletus badius, Boletus granulatus, Boletus luteus, Boletus variegatus, Amanita muscaria, Cortinarius mucosus, Lactarius deliciosus, Russula fragilis.* |
| *Pinus montana* | *Boletus granulatus, Boletus variegatus, Cortinarius mucosus, Lactarius deliciosus, Russula fragilis, Tricholoma virgatum.* |
| *Picea excelsa* | *Boletus luteus, Amanita muscaria, Cortinarius balteatus, Lactarius deliciosus.* |
| *Larix europaea* | *Boletus elegans, Boletus luteus, Boletus variegatus, Amanita muscaria, Cortinarius camphoratus, Tricholoma psammopus.* |
| *Larix occidentalis* | *Boletus elegans, Boletus luteus.* |
| *Betula alba* | *Boletus edulis, Boletus rufus, Boletus scaber, Tricholoma flavobrunneum.* |

Some of these fungi are highly specialised, such as *Boletus elegans* which is confined to larch ; others are less specialised such as *Amanita muscaria* which may be found on spruce, pine and birch. A species such as *Boletus luteus* is capable of forming mycorrhiza only on conifers. Masui (30) working in Japan, and McDougall in America have also been able to trace connections between mushrooms and the fungus roots of trees.

Melin(32) succeeded in isolating various fungi from pine and spruce mycorrhiza, which were capable of forming mycorrhiza on sterile plants growing in sterile media. The fungi which he isolated, however, produced no fruiting bodies by which they could be identified, and were named accordingly *Mycelium radicis* α, β, and γ (from pine) and *M.r. abietis* (from spruce). *M.r. sylvestris* β though isolated from pine could form mycorrhiza on larch and spruce.

The writer, although numerous isolations have been made, has been unsuccessful so far in obtaining any fruiting bodies by which the fungi could be named. The procedure, however, of tracing the hyphae of various members of the *Hymenomycetes* to tree roots has been more successful. The work has been done in plantations formed on peat, in the nursery, and in woodlands growing on soils other than peat. In peat soils the results have been negative. The procedure is difficult in peat, fructifications have so far been found to be rare, and those which do occur, such as *Naucoria* species, were found to have no connection with the mycorrhiza of the trees growing in the peat. In the plantations on other soil than peat, however, *Lactarius deliciosus* could be traced quite easily to pine and spruce and *Amanita muscaria* (fly agaric) to Scots pine mycorrhiza. *Boletus elegans* was found to be constantly associated with European larch—an association which was demonstrated by Melin and who proved it to be a mycorrhiza fungus of larch. *Russula emetica* and other species of *Russula, Lactarius* sp. and also *Boletus* sp. were found connected with conifer mycorrhiza. In certain pine woods, e.g., in mineral soil where there is little raw humus formation, the fruiting bodies of *Elaphomyces granulatus* (false truffle) which are subterranean are to be found in direct contact with the tree roots (Plate XI, fig. 2). Microscopical examination shows that the hyphae of the mycorrhiza pass directly into the fruiting bodies. Species of *Tricholoma, Paxillus* and *Cortinarius* were found connected with *Pinus, Picea and Larix. Paxillus* sp. though rare, was in every instance connected with the type of pine mycorrhiza found in raw humus, namely, the ball type. Many of these fungi are apparently facultative, i.e., capable of entering into partnership with living roots or of existing as saprophytes on old cones, dead twigs or needles.

In the nursery, fructifications of *Cortinarius* were generally found to be in connection with the roots of *Pinus sylvestris, Pinus montana, Pinus contorta* and *Larix,* whilst fructifications of *Boletus badius* and *Russula fragilis* showed traceable connection with the mycorrhiza of pine and western hemlock respectively.

## 3. Soil Conditions influencing the Occurrence and Distribution of Mycorrhiza.

### (*a*) SOURCE OF INFECTION BY FUNGI TO FORM MYCORRHIZA.

Among coniferous forest trees, the genus in which mycorrhiza is most extensively developed is *Pinus.* In most soils ranging from sand on the one hand to peat on the other, the greater proportion of the rootlets of pine of all ages and types show mycorrhiza development. In the genus *Picea* fungus roots, if present at all on one or two year old seedlings, are never very numerous except in soils in which the humus content is high, although transplants, even when grown in the same soil as the seedlings, may produce mycorrhiza abundantly. Fungus roots are found more frequently in *Picea* growing in soils rich in organic matter—except certain kinds of peat—and in the raw humus layer of the forest floor. Members of the genus *Larix* rarely fail to produce mycorrhiza of one form or another in all soils. *Pseudotsuga Douglasii* on the other hand, in so far as has been observed by the writer, produces very few fungus roots, except in the raw humus layer of the forest. Species of *Tsuga* and *Abies* generally form fungus roots readily, particularly as transplants. Seedlings of species of *Cupressus* and *Thuya* may fail to produce mycorrhiza, but in transplants mycorrhiza usually becomes well developed. The examination of trees which usually form endotrophic mycorrhiza requires, however, to be very carefully made. The writer has found that, as in orchids, mycorrhiza may or may not be present according to the season of the year.

There is no evidence, such as Rayner, (39) has provided for *Calluna vulgaris,* to show that a fungus which can form mycorrhiza on the roots of conifers is not carried through the seed. Lewis (26) records that in certain conifers hyphae extend continuously from the root tip to the bud scales, and states, although his evidence is incomplete, that these hyphae are the same as those of the tree mycorrhiza. This statement is not borne out by the evidence obtained by the writer, who has failed to find any trace of fungus in the seed of pine, but has always found that the hyphae of mycorrhiza grow from the soil on to the roots of trees.

One of the conditions essential for the formation of mycorrhiza by first year seedlings of Scots pine is that the ground in which the seed is sown has recently been under some kind of tree crop. This may be seen, for example, when a new nursery is formed on ground which has previously been used for agricultural purposes. Foresters and nurserymen are familiar with certain features of a first year's crop of Scots pine in such a nursery. The needles of the plants frequently become reddish brown in colour in the autumn and they are much shorter than those of plants growing in old nursery ground. The length of the shoot is also generally much less. A further difference however may be noted if the plants are lifted in the late autumn, for, with rare exceptions, mycorrhiza is then absent (Plate XII, fig. 2).

Similar observations have been made in the case of European larch seedlings on nursery ground which has not recently borne tree crops. Like pine they are poor in growth, and this poor growth is accompanied by the absence of mycorrhiza.

Both in the case of pine and larch it must be noted that, in the beds of first year seedlings growing in ground which has never had a tree crop before, certain isolated cases do occur in which the seedlings have fungus roots and these seedlings are always of much larger size than the others.

The isolated occurrence of mycorrhiza on certain seedlings only indicates that the mycorrhiza forming fungus may be present in the soil. There is evidence to show that something more is necessary than the presence of the fungus and the tree root before a partnership between them can be formed. In places where mycorrhiza are either of rare occurrence or absent altogether, such as in new nursery ground, treatment of the soil with certain manures encourages the development of abundant mycorrhiza. The application of humus was found to encourage mycorrhiza formation on European larch equal to that which occurs in old nursery ground. In another experiment on the effect of various mineral salts on the growth of Scots pine seedlings, when grown in soil which had not previously grown a tree crop, it was noted that when calcium phosphate was mixed with the soil, the seedlings in the autumn of the first year developed very abundant mycorrhiza. Ammonium sulphate also was found to encourage the formation of fungus roots, but ammonium chloride was not so successful, only a few fungus roots being formed. In a similar experiment with Norway spruce seedlings, treatment with any manures did not improve mycorrhiza formation. Ammonium chloride, however, encouraged the general growth in length of the shoot and of the root system and root hair formation.

A class of soils in which mycorrhiza may or may not be produced is peat. Trees, when planted in the better kinds of peat, do produce mycorrhiza freely as has been recorded by Transeau (46) and Melin,(32) but in many of the poorer kinds of peat, particularly where trees have not previously been grown, mycorrhiza formation may be inhibited. As in certain mineral soils, it is not uncommon to find among trees growing in peat, under apparently similar conditions, some with normal roots and root hairs, whilst others have mycorrhiza. In every instance it is found that when only normal roots are formed in peat the needles of the trees are abnormal in colour and growth is poorer than when fungus roots are developed.

When transplants which have mycorrhiza are used in planting new areas, it is possible that the fungus thus brought into the peat with the tree is capable of carrying on the development of fungus roots.

An experiment with both seedlings and transplants of *Picea excelsa* and *Picea sitchensis* provided a certain amount of information on this aspect of mycorrhiza distribution. One year, two year, and three year old seedlings and 2 yr. + 2 yr. transplants of each species were planted with the semicircular spade on upturned turfs on *Calluna-Eriophorum-Erica* peat type. The data regarding mycorrhiza distribution are summarised in the following table, the depth of penetration of the root system being included.

*Picea excelsa.*

| Age when planted. | Type of rootlet when planted. | Type of rootlet two years after planting. | Depth of penetration of root system. |
|---|---|---|---|
| | | | Cm. |
| 1 year .. .. | Root hair-bearing .. | Root hair-bearing only | 9 |
| 2 years .. .. | With root hairs .. | Root hair-bearing .. | 15 |
| 3 years .. .. | Mycorrhiza .. .. | Only most recent rootlets in form of mycorrhiza | 17·5 |
| 2 year + 2 year .. | Mycorrhiza .. .. | Mycorrhiza .. .. | 17·5 |

*Picea sitchensis.*

| Age when planted. | Type of rootlet when planted. | Type of rootlet two years after planting. | Depth of penetration of root system. |
|---|---|---|---|
| | | | Cm. |
| 1 year .. | Root hair-bearing .. | Root hair-bearing type | 12·5 |
| 2 years .. .. | Root hair type .. | Root hair-bearing type | 18 |
| 3 years .. .. | Mycorrhiza .. .. | Mycorrhiza .. .. | 17·5 |
| 2 year + 2 year .. | Mycorrhiza .. .. | Mycorrhiza .. .. | 15 |

Thus plants which were devoid of mycorrhiza when planted were still without it two years later, and plants which had mycorrhiza when planted still had it two years later. In peat of the *Calluna-Eriophorum-Erica* type unless the fungus was brought in already in association with tree roots, mycorrhiza formation did not take place.

Lange ([25]), in his studies on the agarics of Denmark, says in reference to the birch mycorrhiza fungus, *Cortinarius hemitrichus*, that " it follows the birch tree as the dolphin follows the ship," but he further points out that certain wood-loving *Cortinarii* grow profusely in open pastures in northern countries such as Iceland, where there are no woods, but where the atmosphere is more humid than on the European continent, and that given suitable conditions it is possible for certain wood-loving fungi to live apart from the tree. My experiments on peat areas have shown that although mycorrhiza forming fungi are present they may be incapable of associating with tree roots to form mycorrhiza, unless certain conditions which are still somewhat obscure are created. The following experiment throws some light on the question.

The experiment was designed primarily to test the effect of different chemicals on the growth of *Picea excelsa* and *Picea sitchensis*, and was carried out on a deep peat with an *Eriophorum-Erica-Calluna* vegetation. Turf blocks were cut from the peat and reversed, and various chemicals were then thoroughly mixed with the peat in the upper core of each turf block. Three weeks old Sitka spruce and Norway spruce seedlings were planted in the turfs. Of the various chemical manures used, such as lime, potash, magnesium carbonate, phosphate, and nitrogen in the form of nitrates, magnesium carbonate alone was effective at the end of two years in promoting the formation of mycorrhiza. The development of the stems and the root systems of the seedlings was also better where magnesium carbonate had been applied to the peat (Plate X, figs. 2, 3). It would appear, therefore, that this particular peat did contain hyphæ capable of forming mycorrhiza, but that under ordinary conditions mycorrhiza did not form. When the untreated peat was examined microscopically it was found that hyphæ were present.

An experiment was carried out at a later date with *Pinus contorta*. Magnesium carbonate was again carefully mixed with the peat, which was in this instance not planted but sown with the seed of *P. contorta*; other untreated controls were also sown. At the end of the second year there was a striking difference in growth between the seedlings in the treated and the untreated peat (Plate X, fig. 1). An outstanding feature again was that the treated plants were mycorrhiza-bearing, whereas the control plants had roots with root hairs.

Frequently on the roots of trees which are of poor growth there are wefts of hyphæ which, however, do not form mycorrhiza. These very frequently occur on the roots of trees growing in peat when *Calluna vulgaris* is the dominant plant of the vegetation. The hyphæ are not closely applied to the root, but occur in masses or as scattered threads on the finer roots. They are black and would appear to be identical with the *Mycelium radicis atro-virens* of Melin, ([32]) which he believed to be harmful. It has not been possible as yet to grow this fungus artificially, nor to obtain any definite information regarding its relation to the tree, but it has been observed that the fungus disappears when basic slag is added to the peat and that then normal mycorrhiza develop and better tree growth results.

It has been found that in the same peat, mycorrhiza develops on *Pinus montana* and is absent in *Pinus sylvestris*, whether both are at the outset planted in the peat with or without mycorrhiza on their roots. It has to be noted that *P. montana* when growing in peat develops a root system which is much more vigorous than that of *P. sylvestris*.

### *Summary.*

The main conclusions to be drawn from the preceding discussion concerning the occurrence of mycorrhiza in different soils are as follows :—

1. In peat as in mineral soils, mycorrhiza-forming fungi, although present, do not necessarily produce mycorrhiza on the roots of trees, under all conditions.
2. Mycorrhiza development is more luxuriant in soils which have previously borne crops of trees.
3. The formation of mycorrhiza can in many cases be promoted by the addition of manures.
4. Mycorrhiza formation is greater generally on the more vigorous growing trees.
5. Inoculation of the soil can be effected by the mycorrhiza fungus of mycorrhiza-bearing transplants.

### (*b*) FACTORS CONTROLLING THE FORMATION OF MYCORRHIZA IN PEAT.

The most obvious essential for the formation of mycorrhiza is the presence of the fungus in the soil. As has been shown in the preceding section, fungi are often present in the soil, but fungus roots except in isolated cases are not formed. This implies that the fungus is not in a state suitable for combination with the rootlets, or the roots of the trees concerned are not in a condition which will allow the fungus to come into an association with them ; or both possibilities may exist. Present evidence indicates that the formation of mycorrhiza is dependent in some way on the condition of the plant. Fungus roots are always produced on the more vigorous plants in all soils. The question arises, is the better development of the tree with mycorrhiza due to the presence of mycorrhiza, or are the seedlings from the beginning stronger and conditions within the plant more favourable to mycorrhiza formation ? That mycorrhiza formation is in some way connected with the metabolism of the tree is indicated for instance by the occurrence of mycorrhiza on transplanted spruce and its non-occurrence on seedling spruce in one and the same soil. The presence of hyphæ in the soil of a new nursery, however, during the first year, when new fungus roots are formed and the abundant formation of fungus roots on Scots pine in the second year, might support the idea that the trees themselves create conditions suitable for the further development of the fungus, and make it more able to infect the root tips of the seedlings ; that is presuming that the fungus already present in the soil is the same fungus which produces the abundant formation of mycorrhiza in the second year. The problem presents a wide field of study.

When trees are transplanted into the forest which is being formed on ground which has not borne a crop of trees already, it has been shown that the trees can carry the fungus of the mycorrhiza with them. Frequently, however, as in certain peats, the trees fail to continue to form mycorrhiza. In the following notes factors which inhibit the formation of mycorrhiza, particularly in peat soils, are discussed.

#### (i) *Influence of the Amount of Water in Peat.*

Peat in its natural state contains a high percentage of water, which is often in a stagnant condition. Mycorrhiza is never formed on trees growing in water, and it has been observed that in very wet peats mycorrrhiza is not developed. The following table recording the data from eight different kinds of peat, shows that mycorrhiza develops on *Pinus montana* when the relative water capacity of the peat, i.e., the relation between the actual amount of water which the peat contains and the amount of water which it is capable of holding, is below a certain value.

| Sample. | Percentage of dry-weight. | Water-holding capacity of peat. | Relative water capacity. | Mycorrhiza. | Tree growth. |
|---|---|---|---|---|---|
| 1 | 614 | 808 | 0·76 | Absent. | Poor. |
| 2 | 700 | 940 | 0·74 | Absent. | Poor. |
| 3 | 344 | 571 | 0·60 | Rare. | Moderate. |
| 4 | 426 | 747 | 0·57 | Present. | Good. |
| 5 | 236 | 418 | 0·56 | Present. | Good. |
| 6 | 474 | 713 | 0·66 | Absent.* | Poor. |
| 7 | 379 | 491 | 0·75 | Absent. | Bad. |
| 8 | 308 | 533 | 0·57 | Present. | Moderate. |

* Some rootlets with scattered mycelium.

Thus, mycorrhiza was found to be more abundant and root development better the lower the relative humidity, which agrees with general observations made. It is interesting to note that Scots pine which was growing near the mountain pine in Sample No. 8 and under similar conditions had failed to develop mycorrhiza.

### (ii) *Aeration of Soil in Relation to Mycorrhiza Formation.*

When oxidation takes place in a soil it is an indication of better conditions for plant growth. The degree of oxidation which is proceeding in any soil can be determined by measuring the amount of oxygen absorption by the soil in the following way. The apparatus consists of a small wide-necked bottle of, say, a capacity of 60 c.c. with a perforated cork to allow a glass tube to pass through. The glass tube is bent into the form of a U and one end is within the bottle and the other dips into a small basin of mercury. A small bulb of caustic potash is introduced into the bottle to absorb $CO_2$. When the required amount of soil, say, 10 gms., has been placed in the bottle, it is sealed with paraffin wax and placed in an oven where the temperature can be kept constant. Batteries of such bottles can be set up, with a control for each battery, and a number of soils tested at one time. It was found that many peats tested direct from the field showed that little or no oxidation of the peat was taking place. There were no fungus roots present on the roots of any species of tree growing in such peats. In those peats in which oxidation was taking place more rapidly, "fungus roots" were formed. The data obtained from a test made in a number of peats in which *Pinus montana* was growing are given as an example in the following table :—

| Sample. | Quality of crop. | Mycorrhiza formation. | Rise in mercury. |
|---|---|---|---|
| | | | Cm. |
| 1 | Good .. .. | Present .. .. .. .. .. | 2·4 |
| 2 | Moderate .. | Present .. .. .. .. .. | 1·8 |
| 3 | Moderate .. | Present, but poorly developed .. | 1·6 |
| 4 | Poor .. .. | Absent .. .. .. .. .. | 0·95 |
| 5 | Poor .. .. | Absent .. .. .. .. .. | Nil. |
| 6 | Poor .. .. | Absent .. .. .. .. .. | Nil. |

There is naturally a direct correlation between the oxidation in the peat and the water content of the peat. Where the water content of the peat is high, oxidation processes are at a standstill. Wherever there is aeration of the peat, mycorrhiza will appear. For instance, in the hummocks formed by actively growing sphagnum, spruce and pine produce abundant mycorrhiza ; in the dead sphagnum remains, which are in the form of peat, mycorrhiza is absent. Aeration is present in the former, and absent in the latter.

### (iii) *Correlation of Mycorrhiza Formation with the Composition of the Soil Solution.*

Various authorities, as for example, Stahl and Frank, have stated that fungus roots are formed in soils in which mineral bases are absent or deficient in the soil solution. The substantiation or otherwise of this statement, except in a general way, is not easy, owing to the difficulties of determining the composition of the soil solution. The method used in this investigation was that described by Gola (15). By the use of alizarin red, he showed that it was possible to demonstrate which mineral base is in solution, since each mineral base gives a distinctive colour with alizarin red. In carrying out the tests in the present investigations, it was found that, when more than one base was present it was difficult or impossible to enumerate them individually, but the method was found to be useful in showing whether bases were in solution.

Samples taken from different depths up to 18 inches in the peat were tested. It was found that many peats, for instance those with a scirpus vegetation, showed no mineral bases in solution ; in others such as those which are generally described as molinia peats and rush peats, mineral bases were found in the peat solution at all depths. Very frequently a peat soil showed an entire lack of mineral bases in the top few inches of the soil, but an increasing amount with increase in depth. Generally the bases that could be detected with most certainty were iron and manganese, and their presence could be confirmed easily by general chemical tests. It was found possible to divide peats into those which contained iron and manganese and those which did not. Generally the iron in peat is in the ferrous state, although the ferric does occur, but usually associated with the ferrous state. The amount of iron which occurs in the ferric form depends on the degree of aeration.

It was found that there was no direct correlation between the absence or presence of mineral bases in the peat solution and the formation of mycorrhiza. Mycorrhiza may be formed on the tree roots which occupy the top layer of peat and which shows no bases in solution. Fungus roots may be absent from the peat which lies at greater depths, and which also does not show bases in solution. In all cases, however, when mineral bases are present, fungus roots are developed freely, such as in molinia and rush peats. The form of the mycorrhiza, however, differs in the two cases. When mycorrhiza occurs in the absence of mineral bases the fungus has a very retarding effect on the growth of the root in both pine and spruce ; when mycorrhiza occurs in the presence of mineral bases the " coralloid " type produces on pine and in spruce the form which shows least inhibition to the growth of the rootlets.

### (iv) *Relation of Oxidising Substances in Peat to Mycorrhiza Formation.*

The oxidising power of different peat soils was tested by means of a 0·05 per cent. aloin solution. When oxidising substances are present, the aloin solution changes from a yellow to a red colour. A large number of peat soils were tested, and it was found that peat soils could be divided into two classes, according to whether they could oxidise an aloin solution. It can be shown that the oxidation of an aloin solution by peat is not due to micro-organisms entirely, as very frequently oxidation is as intense in sterilised as in non-sterilised peat soil. Investigation and a study of the literature reveal that chemicals such as magnesium carbonate, calcium carbonate, iron, salts of alumina and barium can oxidise an aloin solution. Any one of these, when present in the peat soil in a free state can oxidise an aloin solution, and it can in the same way bring about or help in the oxidation of organic and inorganic matter of a low oxygen content.

Mycorrhiza was developed in all peat soils which had an oxidising action on an aloin solution, and the type of ectotrophic mycorrhiza in most cases was that in which the fungus shows the least retarding influence on the growth in length of the rootlets.

Organic and inorganic substances which have a low oxygen content are harmful to tree growth. When they are oxidised their toxicity is removed and tree growth becomes better and the fungus enters into association with the roots.

The beneficial effect of magnesium carbonate (which can oxidise an aloin solution) in causing the formation of fungus roots has been already dealt with (p. 20). Calcium carbonate which was also used in the experiment was not successful, but since the experiment was carried out it has been found that calcium carbonate is very variable in its oxidising qualities. What is described as "precipitated" calcium carbonate is non-oxidising. The mixture of manganese and iron with the peat soil did not result in mycorrhiza formation, although it may be noted that manganese dioxide when placed on the surface of the peat acted beneficially as regards the germination of tree seeds, but not as regards the growth of the seedlings. When mixed with the peat soil and out of direct touch with the air, both manganese and iron may intensify the process of reduction carried out by the organic matter.

In addition to certain mineral bases, certain plant roots are also able to bring about oxidation through the secretion of oxidising enzymes. It is noticeable, for instance, that mycorrhiza are more abundant on tree roots which are in the neighbourhood of molinia roots. *Molinia coerulea* produces oxidising enzymes abundantly.

### *Summary.*

1. The whole question of mycorrhiza formation in peat soils is connected with aeration, mycorrhiza being formed only in those peats in which there is aeration ; sometimes the aeration may be confined to the top few inches of the peat or the peat may be aerated to greater depths. Aeration can be helped by oxidising substances such as magnesium carbonate.
2. The type of pine ectotrophic mycorrhiza depends on the presence of mineral bases in the peat soil solution. Where there is aeration without mineral bases being present, the "ball" type of ectotrophic mycorrhiza occurs ; where there is both aeration and mineral bases the "coralloid" type occurs abundantly.
3. The addition of certain oxidising substances may result in mycorrhiza formation.

## 4. Relation of Mycorrhiza to the Tree.

### (*a*) RESUMÉ OF THE LITERATURE.

There are two schools of opinion regarding the relation of mycorrhiza to the tree. Some investigators believe that the presence of the fungus is markedly beneficial to the tree ; there are others who regard the fungus as decidedly harmful. One of the earliest investigators, Boudier, considered that the fungus did not injuriously affect the activity of the root, but tended, if anything, to increase its vitality and power of water absorption. Gibelli (14) thought that the fungus, so long as the tree was healthy, did no harm. He held the view that certain fungi could live on or in a tree without doing harm, but, given suitable conditions, could become parasitic. Frank (12) later developed the idea of symbiosis, and believed that fungus and tree root lived together for their common good, the tree giving carbohydrates to the fungus in return for the nitrogen, nutrient salts, and water which the fungus provided. His theory was substantiated by a certain amount of experimental work in that he obtained much better tree seedling growth in non-sterilised humus soil in which mycorrhiza were produced than in sterilised humus soil in which fungus roots were not formed. Sarauw (44) and Möller (33), however, emphatically denied as the result of their investigations that the fungus conferred any benefit to the tree. Unfortunately, the results of these investigators are vitiated in that no proper controls were used. Möller's results, for instance, were based on the comparison of seedling roots grown in sand with those grown in humus, while Frank contrasted root development in sterilised and non-sterilised humus, two media which are totally different physically. Möller, however, brought out definitely that pine seedlings could thrive in humus without fungus roots. Many investigators, although in certain respects they differ from Frank, have supported him as regards his general statement. These include Stahl (45), Elenken (7), von Tubeuf (48), Müller (34), Falck (11), and Melin (32). Stahl regarded the fungus as important, in that it passes mineral substances to the tree, and by its presence water absorption is intensified. Von Tubeuf ascribed to the fungus the power of converting nitrogen compounds into an available form for the tree. P. E. Müller thought that the beneficial effect of the presence of mountain pine on neighbouring spruce was due to the capability of the pine mycorrhiza to fix the free nitrogen of the air and so increase the nitrogen content of the soil. This observation was discounted by Möller, who noted that mycorrhiza was poorly developed on plants when grown in nitrogen free media, whereas it was plentiful when the plants were supplied with nitrogen in the form of sodium nitrate.

A group of investigators including Mangin (29), and McDougall (31), were totally opposed to the beneficial theory. It is interesting to note than Mangin connected disease of tree roots with mycorrhiza while McDougall described the destruction and loss of fungus roots at a time when these were required to the greatest extent by the tree, namely, at the beginning of growth in the spring time.

Interesting information on the rôle of mycorrhiza was supplied by Rexhausen (40) and Falck (11), the former finding an accumulation of potash and phosphorus in mycorrhiza of pine and spruce, the latter proving experimentally that the fungus presents carbon to the plant, and is therefore beneficial in raw humus where decomposition is slow.

The writer (22) has shown that mycorrhiza secrete oxidising enzymes, and may, therefore, be of the very greatest benefit to tree growth where aeration is poor, and where many substances of low oxygen content are present, substances which may be toxic to the plant unless oxidised. Against the beneficial functions of mycorrhiza, however, it has to be noted that destruction of rootlets by the fungus is of common occurrence.

Melin, from his critical investigations, has contributed much to our knowledge of this union of tree root and fungus. Briefly, his findings may be stated as follows. (1) The fungus or fungi do not fix atmospheric nitrogen. (2) Mycorrhiza develop to the highest degree where ammonium salts provide the source of nitrogen. For some fungi nitrates are favourable, for others unfavourable. (3) Mycorrhiza can utilise complicated nitrogen compounds more successfully than ordinary roots. (4) The best growth of mycorrhiza takes place in a medium with a *p*H value of about 5, but mycorrhiza tends to reduce acidity. (5) No evidence of parasitism is found in nature, but in pure culture if the plants are weak the fungus may become parasitic.

From a review of the literature it would appear that there is a certain amount of evidence that the fungus is distinctly beneficial and there is also evidence that the fungus may be harmful. It is difficult as yet to obtain a proper balance of evidence.

### (*b*) CORRELATION OF FORM OF MYCORRHIZA WITH TYPE OF CORTEX AND ENDODERMIS, AND DISTRIBUTION OF STARCH IN THE ROOT.

In one and the same soil, ectotrophic mycorrhiza may be formed on such trees as *Pinus*, *Picea* and *Larix*, whilst endotrophic mycorrhiza is formed on *Cupressus*, *Thuya* and *Taxus*. The question arises, as to whether the fungi present in the soil can form either ectotrophic or endotrophic mycorrhiza, or whether some fungi are specialised formers of ectotrophic, and others of endotrophic mycorrhiza. The question is important, but in the present state of our knowledge cannot be answered. The condition of the cortex and the nature of its cell contents, however, determines in some measure the conditions necessary for the development of either form.

The roots of conifiers, as has been already noted (p. 6) can be divided into two classes according to the type of cortex and endodermis. Each of these two classes has its own particular form of mycorrhiza. With certain exceptions the ectotrophic form is found in those roots where no thickening of the cortical cell walls has taken place, while the endotrophic form occurs in those roots where cortical and endodermal cell walls have become thickened.

Further, no starch is deposited in the cortex of that class of tree root in which the cortical cell walls remain thin. On the other hand in that class of root where the cortical cell walls become thickened, deposits of starch are found inside the cells of the cortex.

In all genera of the *Coniferae*, starch deposits may also occur in the root tip, where the starch grains appear in the medulla and the outer cells of the root cap. There are exceptions to this rule, in that, for instance, starch may be absent at all seasons from the root cap of seedling spruce trees.

Thus, where starch is not present in the cortex of the root but occurs only in the root tip, the ectotrophic form of mycorrhiza occurs, e.g., in all members of the *Abietineae*. When starch is present in the cortex the mycorrhiza assumes the endotrophic form.

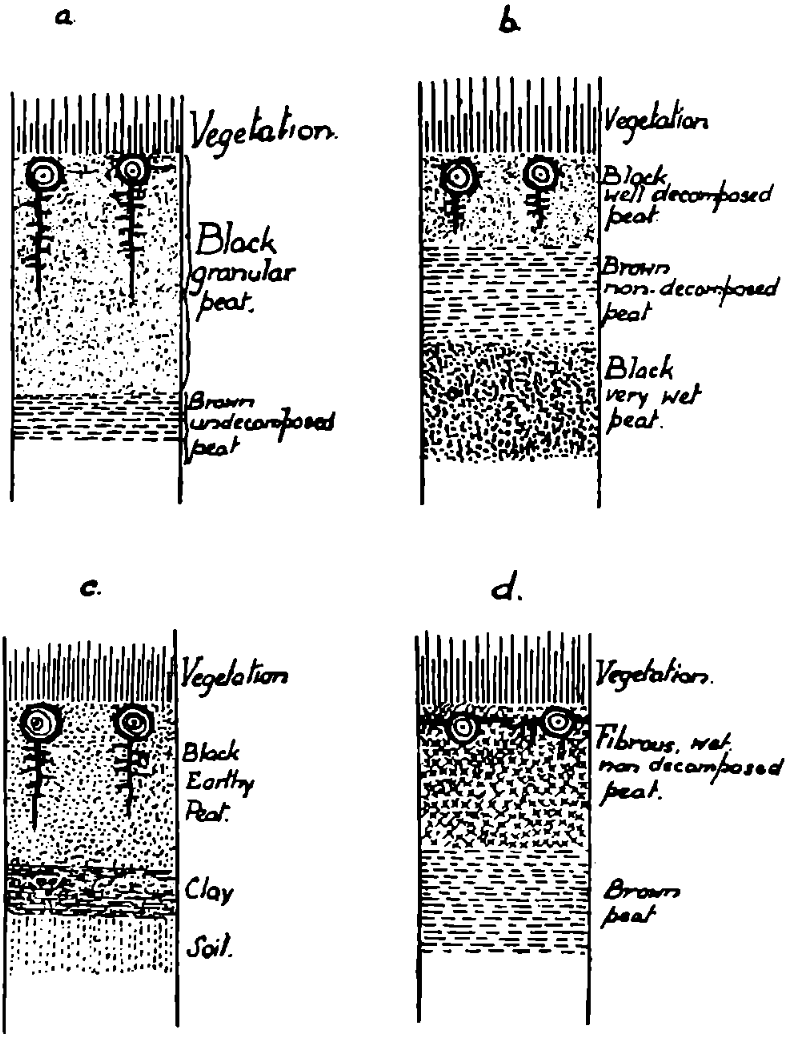
It would appear that the fungus, in the first instance at any rate, goes to the part of the root in which the greatest and most accessible reserves of starch are present. In the *Abietineae* it has to remain on the outside ; in the *Thuya* or *Taxus* root it concentrates on the greater accumulations of starch within the cortical cells. Also in such cases as in the *Thuya* root there is in addition to the stores of food material the protection which the fungus secures from its position inside the root cells. The fungus thus, to begin with at least, is a parasite.

### (*c*) RELATION OF MYCORRHIZA FORMATION TO THE GROWTH IN LENGTH OF TREE ROOTS IN PEAT.

It has been already noted in a previous section that mycorrhiza may or may not be developed on tree roots growing in peat soils. Its relative abundance on tree roots varies in different peat soils. In some cases every root, except the main growing roots, is enveloped with hyphae, whilst, at the other extreme, mycorrhiza may be totally absent. The poorest tree growth occurs in these two extreme cases, although the colour of the needle and the general vigour of the tree is always better where fungus roots are present than when they are absent. The best growth takes place where the proportion of mycorrhiza to ordinary roots is about equal. This occurs in molinia and rush peats.

The root system of trees when planted in peat soils develops near, or actually on, the surface of the peat. When those roots of *Picea excelsa* or *Picea sitchensis* which arise from the main surface roots are enveloped with hyphae their growth in length is very much arrested and they do not descend into the deeper layers of the peat. This occurs in peat with an *Eriophorum-Calluna-Scirpus* vegetation. Here the whole root system which is functioning lies in a horizontal plane (Fig. 3*d*). On the other hand, in soils with a *Molinia* vegetation (Fig. 3*a*) or in rush peat (Fig. 3 *c*) or *Molinia-Eriophorum* peat (Fig. 3*b*)—peats which may be called non-fibrous—many of the lateral roots are free from hyphae and descend into the well disintegrated peat layer for six or seven inches. On the rootlets which arise from these, mycorrhiza is usually formed. The same applies to *Pinus sylvestris* and *Pinus montana*. In *Eriophorum-Scirpus* peat or in growing *Sphagnum*, all the lateral roots of pine are " ball " mycorrhiza, while in peats like *Molinia* peats only certain roots are mycorrhiza and these are of the coralloid form.

In the " ball " type of mycorrhiza of pine and in the mycorrhiza of spruce where growth of the rootlets is very much restricted by the fungus, the root tissues are destroyed. In the more open types where there is less restriction on the growth of the rootlets, the fungus does not destroy the root tissues. In the one type the fungus overcomes its associate whilst in the other the balance of power between the fungus and root is maintained. Further, at the end of the growing season and throughout the winter the " ball " mycorrhiza of pine are usually very numerous, while in the spring and during the summer months they are less numerous. The fungus helps in great measure to bring about this loss, but other factors may contribute. Mycorrhiza of pine, particularly the " ball " type, and the compact type of spruce are very easily broken off from the root and root movement produced by the swaying of the tree in the wind would be sufficient to cause their separation from the root system of the tree. Thus the tree may lose many of its mycorrhiza at a time when they would be of a very great value to it. It has been noted that the destruction of mycorrhiza is much greater in *Picea excelsa* than in *Picea sitchensis*.



*Scale:* 1 inch = 1 foot.

FIG. 3.

Hyphae are found in varying amounts in the cortical cells of young roots of all speciesgrowing in peat. The cortical cells may be penetrated in all directions by fine hyphae. The endodermis may be pierced and the hyphae may penetrate to and destroy the vascular tissues. Hyphae similar to those of the mycorrhiza are frequently present throughout the tissues of the older parts of the root. The hyphae have been observed to enter by the root hairs, and when they pass through certain cells of the cortex they become irregular, swollen, and may develop vesicles. They thus resemble the hyphae of mycorrhiza. Any attempts which have been made to isolate the fungus and experiment with it in pure culture, have so far been unsuccessful. The resemblance of the hyphae to those of fungus roots and the definitely parasitic nature of the fungus suggest some relation between destructive root fungi and mycorrhiza. The hyphae are particularly abundant in the roots of trees growing in peat when *Myrica gale* or *Vaccinium* is present.

Hyphae of the mycorrhiza may also pierce the cortical cells in all directions. In one case, namely, in the fungus roots of *Abies grandis*, the hyphae formed coils within the cells of the cortex. Slight traces of disorganisation of the vascular tissue could be observed.

In an experiment carried out under green-house conditions on the effect of bog water on tree growth, the roots of seedlings of *Picea excelsa* and *Larix europaea* when grown in loamy soil and watered with bog water became shrivelled and black in colour. The roots of the seedlings in the control pots watered with tap water remained healthy. Further, whereas in the control, mycorrhiza formation was normal, when the plants were watered with bog water the fungus cap disappeared, hyphae pierced the tissues of the root in all directions, and there was marked disintegration of the vascular elements (Plate XII, fig. 1). It is possible that this is what happens when a tree with mycorrhiza is planted in bad kinds of peat. The tree is weakened by the adverse soil conditions and the fungus invades the tissues of the root.

### *Summary.*

1. The most successful tree growth in peat soils takes place when there is an equal proportion of " fungus " roots and ordinary roots.
2. The fungus in certain peat soils has a very powerful retarding influence on the growth in length of the sub-lateral roots and helps to keep them from penetrating into the deeper layers of the peat.
3. The mycorrhiza fungus is often parasitic in peat soils. The fungus roots are destroyed and the tree loses many of them during the spring and summer.

### (*d*) MYCORRHIZA AND THE LIBERATION OF MINERAL BASES FROM PEAT.

As mycorrhiza is very often formed on trees when grown in soils which are deficient or lacking in mineral bases in solution, experiments were devised to show whether mycorrhiza had any effect in increasing the quantity of mineral bases in solution and thereby help the tree. It was found that it was quite easy to show that seedlings bearing mycorrhiza did increase the quantity of mineral bases in solution in some peat soils, but whether the increase was due to the fungus roots or the ordinary roots or both was at first not evident. In the first experiment which was carried out, one year old seedlings of *Pinus montana* with very abundant mycorrhiza were used. The roots of the seedlings were thoroughly washed in distilled water to remove soil particles until, when placed in an alizarin red solution, they brought about no colour change. A seedling was then placed in a glass jar which contained a mixture of 4 gm. of peat and 5 c.c. of an alizarin red solution (0·05 per cent.) for each 100 cc. of distilled water. Different peat soils were used and each tested in duplicate. The results are summarised in the following table :—

| Sample. | Reaction without seedling. | Reaction with seedling. | Time. | Remarks. |
|---|---|---|---|---|
| | | | Hrs. | |
| 1 | Negative .. | Negative .. | 48 | — |
| 2 | Weak positive .. | Stronger positive | 48 | Positive deep blood red. |
| 3 | Negative .. | Positive .. | 48 | Positive brick red. |
| 4 | Weak positive .. | Strong positive.. | 48 | Positive violet red. |
| 5 | Negative .. | Negative .. | 48 | — |
| 6 | Negative .. | Very weak positive | 48 | Positive light red. |
| 7 | Negative .. | Very weak positive | 48 | Positive light red. |
| 8 | Negative .. | Positive .. | 48 | Positive light red. |
| 9 | Slight positive .. | Positive .. | 48 | Brick red. |

This experiment was repeated with mycorrhiza—bearing one year old seedlings of *Larix europaea* and *Pinus contorta*. The results were similar to those obtained with *Pinus montana*.

In order to find whether the change in colour took place as the result of the action of all roots irrespective of whether they were " fungus " roots or not, the experiment was repeated with *Pinus montana* seedlings and carefully watched. It was clear that the change in the colour of the solution took place in the neighbourhood of the " fungus " roots, and gradually the colour diffused throughout the solution. Further, when the " fungus " roots of *P montana* were crushed in water and added to a mixture of peat, distilled water and alizarin red, the colour of the solution gradually changed and became deeper than any colour developed in a control without peat. When the roots without fungus were crushed and added to a similar mixture no difference in the colour of the solution as compared with a control without peat could be observed.

The liberation of mineral bases by mycorrhiza was greatest where the peat already contained bases in solution as shown by alizarin red. Frequently the colour obtained with the seedling was different from that obtained with the peat alone, which indicates that the fungus roots may not only increase the quantity of a mineral base already in solution, but set free a new base.

### *Summary.*

Mycorrhiza can increase the quantity of mineral bases in solution in certain peat soils.

# TREE STUDIES ON PEAT.

## 1. Form and Development of Tree Roots in Peat.

Many peat soils possess properties which make them, if left undisturbed, unsuitable as a medium for the growth of timber trees. They have a high water content, a high water level, deficient aeration, and a soil solution in which plant nutrients are deficient or absent. In such a medium, tree roots tend to develop a more or less constant and definite form. In the following notes it is proposed to describe certain points connected with tree root development in peat soils. The species mainly investigated were *Picea excelsa* and *Picea sitchensis*, but observations were also made on other coniferous species, such as *Pinus sylvestris*, *Pinus montana* and *Larix leptolepis*, as material became available. The observations have been made over a wide range of peat soils, which are referred to individually by the characteristic higher plants of the vegetational complex existing on the peat, such as *Calluna*, *Scirpus*, *Molinia*, *Eriophorum*.

When a tree is planted in the ordinary way in peat, if the conditions are exceptionally bad, the root system may be immediately killed and the plant dies. Frequently, however, even in peat soils of poor quality, although a certain percentage of the plants succumb, many survive but make extremely little growth year by year. They may remain in this condition of retarded or checked growth for an indefinite number of years. In the better kinds of peat the period of check may vary from three to five years, but in the poorer kinds the check may be prolonged indefinitely. It is with the behaviour of the root system during the period of check and before the closing of the canopy that the following notes deal.

There are two main possibilities as regards tree root development in peat soon after planting.

1. Growth may continue for some time from the roots formed previous to planting without the formation of an adventitious root system from the collar or stem of the plant.

2. Extension of the root system which existed previous to planting may soon cease, and a new root system arise from the collar of the stem, near the surface of the peat.

The former condition is accompanied by checked growth of the shoot ; the latter condition may or may not be accompanied by better growth of the shoot and the removal of check.

The development of the root system in different kinds of peat soils was studied in the case of *Picea excelsa* and *P. sitchensis*.

In certain kinds of peat where the plant remains are not decomposed and conditions for tree growth are bad, such as an *Erica-Eriophorum-Scirpus-Calluna* type, the root system which ultimately develops and maintains the growth of the tree is an adventitious one. It arises from the base of the stem, and lies on or near the surface of the peat. This adventitious root system may not be formed until some years after planting, and until this new system is formed, absorption has to be provided for by the original nursery root system. An examination of a Sitka spruce tree from this kind of peat showed that the functioning roots belonged to an adventitious surface system, which consisted of a whorl of two to five roots ranging in age from two to seven years. The tree itself as shown by a count of the number of stem growth-rings was thirteen years of age, and assuming that it was four years old when planted, two years had elapsed before the first adventitious root had developed; that is, for two years the plant had been nourished by the original nursery root system.

The surface roots, which have been variously called "pioneer," "seeker" and "searcher" roots, reach a very great length in proportion to the height of the stem. The mean annual growth in length is about 1½ to 2 feet. The lateral roots of the "pioneer" roots do not grow down into the peat, but remain in a flat plane on the surface (Fig. 3*d*). Certain features may be noted in connection with this adventitious root system. (*a*) Although the roots spread on the surface they may arise a few inches down in the peat, below the collar of the tree. (*b*) Owing to their position in the soil, they lead a precarious existence. (*c*) A large proportion of the main growing tips are withered.

Where *Molinia coerulea* is dominant, the peat soil is black and crumbly as the result of better aeration and mineral bases, and tree growth is better. The dead leaves of molinia decompose very rapidly and the line of demarcation between vegetation and peat is very sharp. The surface roots lie in this line of separation and are therefore in a region of good aeration and in contact with a rich soil. The surface roots give off roots which penetrate into this rich peat soil for 7–8 inches (Fig. 3*a*). Further, the root system which the tree had in the nursery remains fresh and healthy although it does not extend. Examination of plants from molinia peat shows that the surface roots may develop in the season of planting. Their mean annual growth is about 18 inches.

The root form which develops in rush (*Juncus*) peat is similar in most respects to that formed in molinia peat. This peat occurs where conditions are much better, that is, where the water is in movement and is charged with a certain amount of mineral bases. The root system lies near the surface, but is in finely decomposed peat. The side roots of the main roots penetrate for a few inches down into the peat.

In peat soils where *Eriophorum vaginatum* is dominant, the root system in its main features is also similar to Nos. 2 and 3, but the depth of penetration of the lateral roots is usually less (Fig. 3*b*).

Where sphagnum is an important constituent of the vegetation, however, or indeed where peat is accumulating rapidly, as for example, where *Scirpus caespitosus* is dominant or co-dominant, another feature in tree root development appears. Sphagnum is one of the most active peat forming plants. By its growth it will in a short time completely bury a tree checked in growth or, as often happens, the tree just succeeds in keeping its growing point above the sphagnum. An examination of a plant from peat which is forming rapidly (Plate XIV, fig. *a*) shows that the original nursery root system dies completely off and adventitious roots are developed in succeeding whorls one above the other. Each new adventitious whorl of roots as it becomes more deeply embedded in the growing peat is succeeded by another whorl. Relatively, the plant is making little or no growth. The roots so formed are usually bare and straggling although they produce side rootlets which, however, are soon destroyed. For instance on several roots an average of twenty-four traces of rootlets per inch were counted on a two-year-old root (Fig. 4).

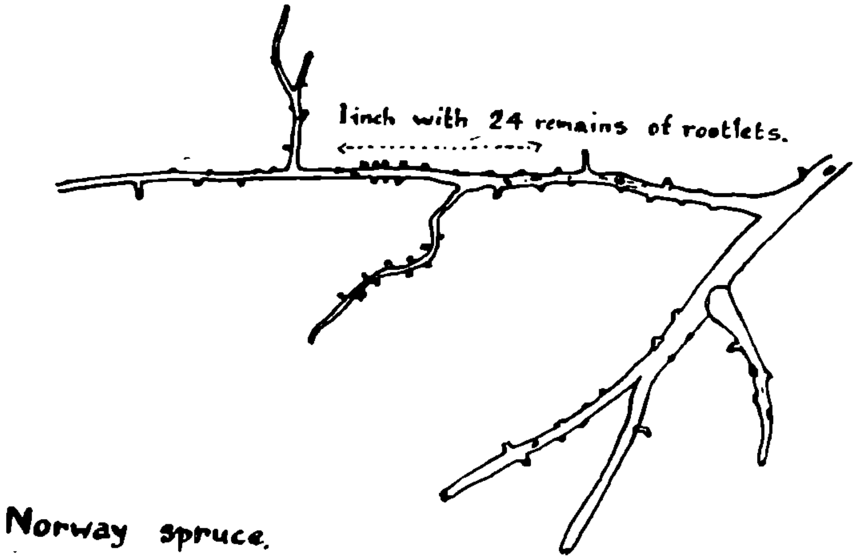


FIG. 4.

In order to give the tree a more favourable medium for growth by promoting aeration and drainage on all peat soils it is now a common practice to plant the tree on a mound or turf. A block of peat 12–15 inches square and 6–9 inches thick is cut from the peat and inverted on the surface adjoining the hole from which the turf has been cut. As regards root development, even when turf planting is employed, dissection of the root systems shows that in all kinds of peat, after a short interval, the roots grow from the turf into the surrounding peat. They grow to great length, and remain always near the surface of the peat. There is little tendency for the roots to remain in the turf except where manure has been applied to it. Although the root system developed in the nursery tends to persist, roots arise from this root system or from the stem, and proceed horizontally through the turf, dip down when the edge of the turf is reached, and again take up a horizontal direction when contact is established with the natural peat surface. Ultimately the root system is similar to that which develops without turfing. The roots which grow from the original root system, however, being in a better aerated medium (viz., in the turf) produce new rootlets in greater numbers than where planting is done on the natural surface and this fact may account for the more successful growth generally.

More rarely, in kinds of peat where *Calluna* is the dominant plant, growth is found to be continued from the nursery root system. The roots descend into the peat; they are thin and wiry; the finer rootlets are scarce or absent, and when present are blackened and shrivelled. Evidence is by no means lacking that the spruces make an effort to form a surface root system, particularly where there is moss beneath the *Calluna*, but the roots die back or wither away after some time.

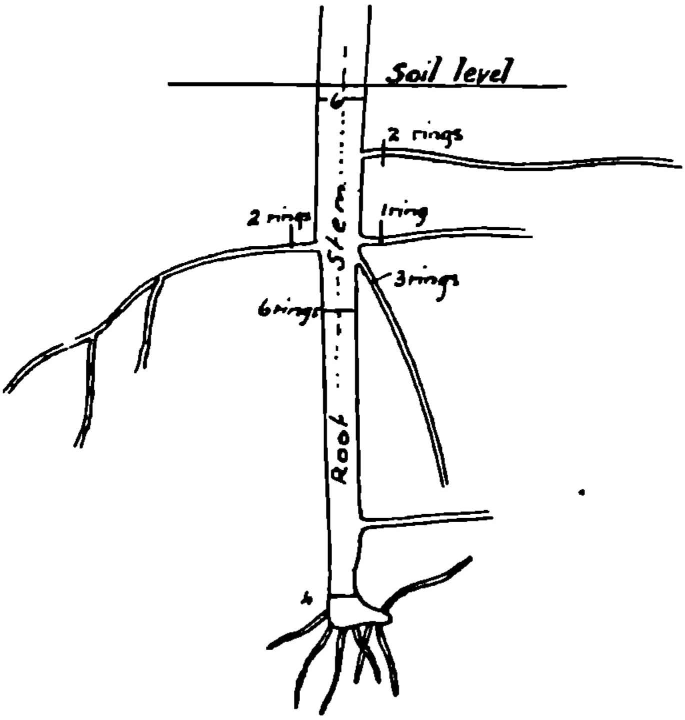


FIG. 5.—Diagrammatic representation of root system of Japanese larch from peat.

The root system therefore which is developed typically on spruces planted on peat soils is a surface one and is adventitious in origin. The formation of this adventitious system may be commenced during the season of planting, or it may be delayed for an indefinite number of years. It may develop with subsequent death of the previously existing root system—only a dead " stump " remaining—or the older roots may persist and remain fresh giving rise to new roots, although there may be, until after the closing of the canopy at any rate, no extension of the root system from that point. The surface development of roots, although it has been described for *Picea excelsa* and *Picea sitchensis*, occurs in other coniferous species when planted in peat, including *Pinus sylvestris*, *Pinus montana*, *Abies grandis*, and *Larix leptolepis* (Fig. 5). It may be noted that the adventitious root system described above is not a form of root system peculiar to peat, as it occurs in sand (Plate XI, fig. 1).

In the development of this surface root system in all kinds of peat soils, it very often happens that a single root first appears. This root grows in a more or less constant direction for any given site, namely, against the prevailing wind (Plates VI, VII). Proximity to a drain may cause a change in direction of such single roots. If a drain is near the tree, the root grows in a line which approximately bisects the angle made by the prevailing wind direction and the shortest distance to the drain.

It has been found that *Picea sitchensis* produces fewer surface roots than *Picea excelsa*. The number of surface roots in the case of *P. sitchensis* is usually about half that of *P. excelsa* growing on the same kind of peat soil.

In order to investigate root development of seedlings raised from seed sown on peat, seeds of *Picea excelsa* and *Picea sitchensis* were sown on the natural surface, screefed patches, on turfs reversed and on prepared patches where burning of the herbage had been done. The peat on which the experiment was made had an *Eriophorum–Erica–Calluna* vegetation of an open nature, which permitted sowing on the natural surface. The peat was deep and fibrous with little mineral matter. On the natural surface, although good germination was obtained in both species, many of the seedlings failed to push their radicles into the peat. Those individuals which did succeed in penetrating the surface failed to push their roots in deeply, the maximum depth of penetration of Norway spruce being 1½ cm. and of Sitka spruce 1 cm. The root system, however, was very compact (Plate XV, fig. *a*), many of the Norway spruce developing tertiaries in the first year. In the screefed unburned patches the root systems were deeper and more extensive (Plate XV, fig. *c*), being even more so in the screefed burned patches (Plate XV, fig. *e*), but the greatest depth of penetration took place on the turfs (Plate XV, fig. *d*). In peat soils Norway spruce has a more extensive lateral growth than Sitka spruce, just as it has in other soils. The greater depth of penetration on the turfs may be attributed to the drier, better aerated medium.

The sowing of spruce seed on the natural surface of peat or indeed on turfs, in so far as tests have up to the present provided data, is not successful. Better results are obtainable by pricking out seedlings 1—3 weeks old from seed sown in ordinary soil. Growth of the roots and the stem is about twice to three times that of seedlings of the same age reared from seed sown in the peat.

### (*a*) FACTORS CAUSING OR CONTRIBUTING TO THE FORMATION OF AN ADVENTITIOUS ROOT SYSTEM IN PEAT.

Several factors may contribute to bring about the formation of an extensive adventitious root system near the surface of peat soils, namely the height of the water table, deficient aeration, toxicity or reducing properties of peat, the point of origin of the roots, destruction of lateral roots, the form in which the nitrogen occurs, the concentration of the soil solution, absence of iron, and death of older roots.

### (i) *Height of the Water Table.*

Emerson (8) has shown that some plants are capable of sending their roots down below the water level, whilst other plants have roots which when they reach the water level take up a horizontal position above it. An examination of the plants of our peat soils shows that we have plants like *Myrica gale* and even *Calluna vulgaris* whose main underground parts may be horizontal (Plate XI, fig. 2). Other plants again, such as *Scirpus caespitosus*, have deep-going vertical roots, encased within the undecomposed leaves and giving off, as the peat forms, succeeding whorls of roots (Plate XVI). There is a parallel condition to this in such trees as *Picea* when they are introduced into peat soils. When the growth of the peat is inappreciable the number of root whorls in *Picea excelsa* and *Picea sitchensis* is limited to one, but where the growth of the peat is relatively more rapid the number of successive root whorls developed may be considerable (Plate XIV, figs. *a*, *b*). Such plants as *Picea*, therefore, are able to adapt themselves to peat soils, though the height growth of the plant is not such as to produce large-sized trees.

### (ii) *Aeration, Toxicity and Reducing Properties of Peat.*

There has been considerable controversy among investigators as to the importance of aeration and the toxicity of peat water as factors which inhibit tree growth in peat soils. The two factors are necessarily inter-related. Dachnowski, (6) although he denied that lack of aeration directly caused the inhibition of tree growth in peat, found that aeration considerably lessened the toxic properties of bog water, whilst Rigg (41) considered that from the evidence available aeration may be a contributing factor indirectly. On the other hand, Rigg (41) and Transeau (46) have produced experimental evidence to show that there are decidedly toxic substances in peat. The toxic substances are in a soluble form, due to the acid nature of the peat. Acidity *per se* is not considered by most authorities, such as Truog, (47) to cause pathological symptoms in roots. He concludes that the acidity of the soil solution never becomes high enough to be directly toxic or destructive to plant roots. Negative results were obtained by Livingstone (28) and Dachnowski (6) in their experiments on the effect of acidity.

Bog water has been shown by the writer to have certain properties which influence the point of origin of the roots. *Picea excelsa* seedlings were grown in water cultures of the following description: tap water, diluted bog water, equal volumes of bog water and tap water, bog water, concentrated bog water. In tap water the existing root system gave rise to new rootlets without any roots arising from the stem. The length of the roots varied from 30–34 cm. In diluted bog water the root system remained comparatively fresh, and gave rise to all the new rootlets with the exception of one or two roots on each plant which grew from the stem, near the surface of the water. The average length of the roots was 16–18 cm. In undiluted bog water, however, the original root system became unhealthy, and most of the new roots developed from the collar of the plant, or from the oldest parts of the existing roots near the surface of the water. These roots grew to 14–15 cm. in length. In concentrated bog water this condition was slightly more pronounced, and the average length of the roots was only 8–10 cm.

Thus, as the concentration of the bog water increased, the original root system tended to die off and new roots to arise from the collar region. It is doubtful if this phenomenon is due to absence of oxygen *per se* as air was bubbled through the solutions repeatedly. The result points rather to toxic substances or to the strongly harmful reducing properties of the peat water. Roots are produced in the most aerated region and where there are more stabilised conditions as regards the oxygen content of the water. The water solution in immediate contact with the air absorbs oxygen and the decomposition products are oxidised, permitting of the development of roots near the surface.

Further, in another experiment already mentioned (p. 31) seedlings grown in loam and watered with bog water produced rootlets which, however, soon became shrivelled and black in colour, particularly at the tip and in the root hair region.

The toxicity of *Calluna* leaves to seedlings of *Picea excelsa* was established in water culture. When decaying heather leaves were added to water cultures which contained all the elements necessary for plant growth, the root system of the seedlings quickly began to develop an unhealthy appearance, and the rootlets shrivelled and died. Decaying molinia leaves, on the other hand, were found not to cause any harmful effect on the root system of the seedlings.

The conclusion arrived at is, therefore, that in peat there are water-soluble substances which are harmful and cause the destruction of the rootlets. New rootlets arise where these toxic substances are in contact with a continuous supply of air, that is, near the surface of the peat.

### (iii) *Point of Origin of Roots.*

The development of the new root system in a horizontal plane may be due to the point of origin of the roots. For instance, the long surface rooting habit is common in trees growing in sand, and it may even develop in the nursery if the roots arise from the stem, as they frequently do when the trees are planted too deeply. Surface roots which have arisen from the stems of *Picea excelsa* transplants (2 yr. + 3 yr.) have been found to measure 4 to 5 feet in length.

Four points observed in the field are suggestive as supporting the hypothesis that the point of origin affects the direction in the soil taken by the roots :—

(1) Roots which arise from a side branch descend perpendicularly into the peat or other soil.

(2) When a horizontal stem root is broken the lateral roots which take on the growth are positively geotropic.

(3) In peat those side roots which arise from the long surface roots and which have not their tips enveloped by hyphae and thus are capable of elongating considerably, are positively geotropic.

(4) Trees in close canopy in other classes of soil where conditions for root growth are good, and which have roots penetrating the deeper layers of the soil, frequently show roots which arise from the stem and maintain their growth near the surface of the ground, unless broken. Surface roots which arise from the stems of pine and larch, for example, have been measured up to 20 feet in length, while side roots of these are positively geotropic.

Roots which arise from the stem, therefore, tend to grow horizontally unless broken; roots from branches are positively geotropic; roots arising from the long horizontal roots unless this growth is inhibited are positively geotropic; that is, the order in which a part of a plant organ is laid down determines in great measure its behaviour. Each plant has its own specific symmetry. Each branch of the primary stem, each side root, arises at a definite angle. The primary stem and root are vertical; branches from these are set at right angles or at a definite angle, and tertiary members are again set at right angles to the secondary or parallel to the primary. The surface roots in peat, therefore, since they arise from the primary axis, will be at right angles or at some definite angle depending on the symmetry of the plant.

### (iv) *Destruction of the Lateral Roots.*

The destruction of the mycorrhiza of the surface roots has already been discussed in a preceding section. This destruction of the lateral roots or even their reduction in vitality is comparable to the removal of lateral buds in the case of the leader of the tree. The effect of side root removal on the growth of the main surface root may be assumed to be the same as the effect of side bud removal on the growth of the leader of the tree. There is a flow of food materials to all growing points. The supplies which would normally go to the side roots proceed in their absence to the main growing tip, which gains increased vitality and grows much longer than it would otherwise do.

### (v) *Nitrogen Supply.*

According to Melin (32) the length of the roots depends on the form in which the nitrogen is supplied to the plant. In pure culture he found that the roots were shortest when nitrogen was supplied in the form of nitrate, ammonium chloride, and asparagin, and longest when nucleic acid or peptone, for instance, were used. In nitrogen-free media the roots measured three times the length of those where ammonium chloride had been added as the source of nitrogen.

The nitrogen in peat is, according to Dachnowski(6) bound up as organic compounds which are unavailable for plants, whilst Robinson (43) found that the nitrogen in peat occurs in numerous unknown forms. Jodidi (19) states that all the nitrogen in peat is of an organic nature and available nitrogen increases only with the weathering of the peat. The absence of available nitrogen in peat, may, therefore, in the light of Melin's researches help to account for the length of the roots.

### (vi) *Concentration of the Soil Solution.*

The weaker or less concentrated the nutrient medium in which the plant is growing the longer generally are the individual roots. One of the characters of peat is that the peat solution has an abnormally low concentration, mineral bases being infinitesmal in amount or altogether absent. As already noted, Golas's(16) alizarin red method for the detection of mineral bases in a solution often fails indeed to show bases dissolved in peat water particularly from that layer near the surface in which the roots have to lie by by force of other factors. That layer in the great majority of cases is the poorest nutrient layer, richer layers often occuring at greater depths, but depths which in ordinary planting in the natural surface are not tapped by the tree roots. This may, along with improved aeration, account for the somewhat better growth on upturned turfs.

### (vii) *Iron Deficiency.*

*Picea excelsa* and *Picea sitchensis* seedlings grown in iron free media develop very few roots (loc. cit. p. 55) but these are long and lacking in side rootlets; that is, there is not the wealth of roots developed, such as is found in other cultures. As many peats do not give a reaction for iron the point is suggestive.

### (viii) *Inhibition to Growth of Older Roots.*

Where the original main root system is destroyed or weakened by fungi, bad soil conditions, deep planting or any other cause, the downward flow of manufactured material is arrested and accumulation occurs near the collar of the plant and new roots arise at this point.

Even with seedlings the removal of the tip of the radicle makes a significant difference to the degree of extension of the side roots. In an experiment to test the effect of removing the root tip of the primary root, it was found that the length of the lateral roots was half as long again as compared with the control, at the end of the first year, in both *Picea excelsa* and *Picea sitchensis*. From the measurement of a large number of seedlings so treated and averaging the results, the following data regarding the extension of lateral roots were obtained.

| Species. | Root tip not removed. | Root tip removed. |
|---|---|---|
| | Cm. | Cm. |
| *Picea excelsa* .. .. .. | 4 | 6·5 |
| *Picea sitchensis* .. .. | 3·5 | 6 |

The direction of growth instead of being vertical was lateral. It is interesting to note in this connection, however, that although the tip of the tap root had been removed or damaged it was found at the end of the period that the trees in many instances had tap roots which were indistinguishable from the original tap roots, since a root had developed which took on the function and appearance of a tap root.

### (*b*) WITHERING OR DIE-BACK OF ROOT TIPS.

Withering or die back of the root tips is a common feature in those peats in which there is little or no decomposition of the plant remains. A similar withering of the root tips occurs in spruce or pine forest where the superficial roots of the tree live in the accumulated undecayed needles. In the latter instance the die back occurs during a dry period when the raw humus layer dries out. and the same cause, namely drought, is likely to be a causal factor in peat. It has been prevented in peat where *Calluna* is dominant, by spreading sacking or any cover over the heather. In peat frost may play an important role in destroying lateral roots by heaving and splitting apart by ice. Further the action of the wind in causing the stem to sway, may contribute in no small measure to loss of rootlets and the bruising of the main growing tips of the roots. There is no trace of fungus in the tissues and the cause appears to be purely physical.

The roots most affected are those which are sometimes referred to as " seeker," " searcher " or " pioneer " roots.

### (*c*) AERENCHYMA.

The formation of aerenchyma is a common feature on woody plants when grown in soil which contains a large amount of water (Plate XIII, fig. 2). It develops on tree roots also, which are growing in water cultures, and it may form on young roots, older roots, and on any part of the stem which is under ground or under water. It may develop to a very small extent, or as frequently happens it may be very abundant on the lower part of the stem or on the root system, giving the plant the appearance of being in a diseased condition. Superficially it appears as erumpent masses of cells, white to reddish in tint.

Aerenchyma is a common phenomenon on tree roots in peat, where it may be produced to an extraordinary degree on the part of the stem below ground and on the older roots, although it is generally rarer on the superficial long roots.

The aerenchymatous tissue is in every respect similar to the lenticel in its structure except that the cell mass is protruding. (Plate XIII, fig. 3.) The main function of the tissue has been regarded, as the name implies, as aerating; that is, it absorbs oxygen and passes it to the inner tissues, and it occurs in soils or under conditions where oxygen is not supplied through the proper channels. Recent opinion tends to regard the production of this tissue, however, as a means of getting rid of excess water—a rôle also of the lenticel—and to regard its function as an oxygen absorbing mechanism, as a subsidiary one. Supporters of this view regard aerenchyma as being produced on plants which are absorbing more water than can be passed off by the shoots and roots. It has been shown* that the aerenchyma produced by conifers in various kinds of soil is the result of excessive moisture and is a method used by the plant to get rid of water it is unable to get rid of through the needles. In conifer roots there is no indication of aerating tissues within the root such as are found in some bog plants. Aerenchyma is thus in the nature of a safety valve.

## SUMMARY.

1. The surface rooting habit is characteristic of conifers planted in all kinds of peat soils. Pending the development of an adventitious surface root system, the tree is checked in growth. The development of a surface root system does not necessarily remove check. The check is prolonged in those peats where the surface layers are undecomposed, and is shortest where the surface layer of the peat is well disintegrated, and the peat is in a crumbly state such as where *Molinia caerulea* is a dominant plant. In the peats where the top layer is well decomposed and crumbly, the depth of penetration of the side roots from the main surface roots can be correlated with the depth of the layer itself. Where the peat is undecomposed the rootlets rest on or near the surface. Before the closing of the canopy, only the surface six inches of peat are used by the tree roots even in the better quality peats, and it is upon the quality of this surface layer that the growth of the tree depends.

---

* Journal of Agricultural Research, 1920, No. 20.

2. In certain instances the development of a surface adventitious root system is prevented, due to the repeated " die back " of roots arising from the stem. The die back is probably due to drought, and occurs typically where *Calluna* is dominant. In other cases adventitious root systems do arise, but they are of a temporary nature, and are succeeded by a new adventitious root system arising higher up the stem. This occurs in peats which are actively growing. The habit adopted by trees resembles the habit of the natural peat vegetation, such as *Calluna, Scirpus, Myrica gale.*

3. The factors which cause the surface spread of roots and their abnormal elongation are discussed. The factors include water level, aeration, toxicity, reducing properties of peat, the point of origin of the roots, mycorrhiza, concentration of the soil solution, nitrogen supply, iron starvation, weakening of the nursery root system.

## 2. Notes on Leaf and Stem Structure of Coniferous Trees checked in their Growth.

The following brief descriptions of the transverse sections of a leaf and a stem of a conifer are given for the purpose of helping readers to an understanding of the points described in the succeeding sections.

All conifer leaves when sectioned and examined with the microscope show the following main structures in order of succession, from the outside inwards. The leaf is covered by a distinct outer layer of cells, the epidermis, the external walls of which are strongly thickened. The outermost layer of this thickened wall is termed the cuticle. The hypodermis, which is in close contact with the epidermis, is composed of one or more layers of thick-walled cells. The mesophyll consists of large cells, which contain the chlorophyll, and intercellular spaces. One or more resin canals may be present in the mesophyll. A ring of large colourless cells, the endodermis, separates the mesophyll from the matrix of cells which contains the vascular bundles. The vascular bundle is made up of xylem above and phloem below.

A transverse section of a stem of a conifer, e.g., a 4-years-old stem of *Pinus sylvestris*, shows the following main structures. On the outside there is the bark, the cells of which are dead. To the inside of the bark is the primary cortex, and adjacent to this is a zone of small thin-walled regularly arranged cells, the phloem. The cambium is an inconspicuous ring of cells which gives rise to the phlœm to the outside and the xylem to the inside. In the xylem are concentric zones which are the growth rings. Each ring is composed of spring and autumn wood. On the inside of the xylem is a ring of primary xylem bundles. The medulla or pith occupies the centre of the stem and consists of large thin-walled cells. The fine lines which radiate from the medulla to the phlœm are the medullary rays.

Trees planted on peat soils which are checked in growth develop certain abnormalities in their leaf and stem structure which indicate the factors which cause or contribute to their poor development. For instance, the stem of *Picea sitchensis* may develop a sabre-like bend, the leaves are shorter than the normal, and are frequently yellow or greenish yellow in colour, whilst there is an accumulation of starch in the tissues, frost rings and marks are of frequent occurrence in the xylem, and the phlœm often contains an abnormal amount of calcium oxalate. The pith of *Picea sitchensis* may have transverse plates, whilst resin cells may be formed in the neighbourhood of the primary xylem of the stem of all species of coniferous trees.

### (*a*) LEAF.

The needles of *Picea*, *Pseudotsuga*, *Tsuga* and *Pinus* when the trees are in a checked condition in peat soils may be yellow in colour. The yellow colour may remain throughout the whole year or the leaves may become slightly greener in October, but regain the yellow colour in February. If a yellow needle is sectioned and treated with an aqueous solution of potassium iodide and iodine the reaction for starch is obtained in practically every cell of the leaf. The mesophyll cells particularly are filled with starch.

The yellow coloration and the accumulation of starch may be due to one or more of the following factors : too high light intensity, low temperature, absence of iron and magnesium, deficiency of lime, potash and phosphorus. The yellow coloration of the needles has been attributed by some foresters to fungi, but no trace of hyphae has ever been found in the yellow needles of conifers growing in peat soils.

#### (i) *Light Intensity*.

It is known that injury may result from continuous and prolonged exposure of the leaves to too intense light, if nutritional and other factors upon which the growth of the tree depends are upset. For instance, strong light inhibits the action of various enzymes. Diastase, which changes starch into sugar, may be destroyed, and the starch which has accumulated cannot be transported to other parts of the plant. Too intense light combined with extended periods of low temperature may bring about the permanent destruction of the chlorophyll. The leaves of certain species of trees such as *Pinus montana* and *Picea sitchensis* when first planted in peat soils may be observed to develop a reddish pigment, called anthocyanin. Some plant physiologists believe that this pigment acts as a screen which protects the underlying tissues against too intense illumination. Under better growth conditions the pigment may reappear in the following years, until the tree becomes vigorous enough to carry on without it. Where growth conditions are bad, however, the pigment may never be formed and the chlorophyll or some constituent of the chlorophyll may become permanently destroyed.

Needles of young conifers which are protected by the neighbouring vegetation, such as *Calluna vulgaris*, maintain their normal green colour. Experiments by the writer on the effect of shading *Picea excelsa*, *P. sitchensis* and *Pinus montana* when growing on peat soils have been successful in showing that the green colour (if the needles have not been too long exposed) can be restored. Further the shading had a decidedly beneficial effect on shoot growth and length of needle. Shaded *Picea excelsa* 2yr. + 2yr. transplants had a shoot growth of two inches as compared with one half inch of shoot growth where the plants were unshaded.

(ii) *Low Temperature.*

The effect of high light intensity is increased by low temperature. Neger(35) found that by placing plants with yellow leaves in a cool room, the starch was removed gradually. The starch first disappeared from the mesophyll cells, next from the epidermis and remained longest in the endodermis. He found that the highest degree of starch accumulation took place at the end of October when the temperature had sunk very low. At this time and during the first half of November, the starch moved from the leaves towards the stem, until, at the end of November only certain cells of the leaf contained starch. His conclusion was that the starch accumulation in October was due to the sudden fall in temperature. On peat soils low temperatures are present for a very extended period. There is only a short time during the summer when cold is not an important factor on these soils. Frost has been reported by Cox (4) in a peat bog even during July. The evidence generally would indicate that throughout the year lower temperatures prevail over peat soil than over mineral soils and contribute to the accumulation of starch in the leaf.

(iii) *Iron Deficiency.*

It has already been recorded (p. 24) that peat soil solutions can be divided into two classes according to whether iron is present or absent. The needles of the trees which grow in those peat soils where it can be shown that iron is absent from the soil solution are always yellow in colour and contain an accumulation of starch. When *Picea excelsa* and *P. sitchensis* seedlings are grown in water culture free from iron (p. 55) their needles are yellow in colour, and all cells of the leaf contain an abundance of starch. The absence of iron does not result in typical chlorosis.

It has been established experimentally by Haag and McCall (16) that even if iron is present in the soil solution, if the reaction for iron cannot be obtained by chemical means the iron is unavailable to the plant (in this case wheat plants). The availability of the iron depends on the *p*H value or acidity of the soil or culture solution. They found that in their culture solutions only those with a *p*H value between 3.06 and 3.56 produced normal green plants; and these solutions alone gave a reaction for iron, although iron had been added to all the other solutions. The reaction of the soil solution may render the iron insoluable and make it unavailable to the plant or it may have a direct effect on the plant by rendering immobile such iron as may actually be in the plant already.

### (iv) *Magnesium Deficiency.*

Magnesium is an essential constituent of chlorophyll and in its absence the needles will lose their green colour. When magnesium is left out of the water culture (loc. cit. p. 55) the needles of *Picea excelsa* and *Picea sitchensis* become yellow and starch accumulates in the cells, similar to what happens in many peat soils. There is one important difference, however, namely that whereas in the water culture where magnesium is absent there is a withering of the needles from the tip backwards, this symptom of magnesium starvation is absent from checked plants in peat soils. Magnesium, however, applied to peat soils has a marked effect on the maintenance of the colour of the needles of *P. excelsa* and *P. sitchensis* and on the rate of growth of both shoot and root (loc. cit. p. 20).

### (v) *Potash, Lime and Phosphorus Deficiency.*

In certain soils the light yellow colour of the needles of *P. excelsa* has been found to be due to deficiency of potash. Experiments on the effect of different mineral fertilisers on the growth of *P. excelsa* in the nursery have shown repeatedly that potash manure causes a deep healthy green colour to appear where the needles are otherwise yellow. On peat soils, however, potash has not been found to be particularly beneficial as regards restoring or maintaining the green colour of the needles.

Potassium has an important effect on the production and action of the enzyme, diastase. The literature on the subject of the relation of potassium salts to carbohydrate metabolism in plants however is somewhat conflicting. It appears that much depends in the first place on the concentration of the potassium salts, and in the second place on the soil to which it is added. Englis and Lunt (10) for instance, show that in the leaves of the nasturtium when grown in sand, the activity of diastase decreases with increase of potassium, whereas in peat soils a medium application of potassium gives the highest diastase activity and the smaller amount the least activity. The amount of potash added to the peat soil would therefore appear to be important. The application of wrong quantities to peat soils may have been the cause of negative results being obtained in the past.

Basic slag on the other hand in very many cases (23) has been eminently successful in restoring a healthy colour to the needles of *P. excelsa* and *P. sitchensis* planted in peat soils, and finally bringing about better growth.

In connection with potassium deficiency it may be noted that frequently the terminal bud of *Picea* growing in peat fails to develop. It is recorded on p. 55 that absence of potassium brings this about in water culture. Lack of potassium may, therefore, in certain cases be an important factor in inhibiting the growth of coniferous trees in some peat soils.

### (*b*) STEM.

#### (i) *Accumulation of Calcium Oxalate in the Phloem.*

Calcium oxalate crystals frequently occur in the tissues of conifers. The calcium oxalate, which is in the form of monohydrated calcium oxalate crystals, is found typically in the phloem. Oxalic acid is a common by-product of plant metabolism in general, and of protein synthesis in particular. The free acid has a decidedly poisonous effect on protoplasm, but it is rendered innocuous when combined with calcium to form almost insoluable calcium oxalate.

Calcium oxalate is frequently formed as the result of fungus infection. In plants in check on peat soils, however, there is no evidence that the calcium oxalate crystals are formed as the result of the presence of a fungus.

The crystals occur in the thin walled cells of the phloem in a single layer which may in places become double. The crystals are more abundant in trees from some kinds of peat than others—notably those peats which bear *Calluna* and *Scirpus* as the dominant plants, i.e., in peats where calcium is deficient. The relative production of calcium oxalate in different peat soils is shown in the following table.

| Dominant plants in the peat vegetation. | Calcium oxalate in trees out of " check " or showing better growth. | Calcium oxalate in trees " checked." |
|---|---|---|
| *Calluna* | Nil | Very abundant. |
| *Erica-Eriophorum-Scirpus* | Small in amount | Moderate. |
| *Scirpus* | * | Moderate to abundant. |
| *Sphagnum* | * | Abundant. |
| *Calluna-Molinia* | Nil | Moderate. |
| *Molinia* | Nil | Weak. |

* Data not available (due to absence of material).

When the plants leave the check condition, the deposition of calcium oxalate ceases or becomes very much reduced in amount, and the stores of crystals are dissolved and reabsorbed into the metabolic cycle. This phenomenon has been observed by De Vries, and Schimper. In plants grown on peat soils the oxalate crystals are found to disappear when growth improves, as, for instance, when basic slag has been added to the peat soil. It is possible that the plant in check is utilising all available calcium to neutralise the oxalic acid produced, and is suffering from lime deficiency. Lime is considered, for instance, to play an important part in the conversion of starch to sugar. If the lime already within the plant or available from the peat soil is used up in removing poisonous oxalic acid, the conversion of starch to sugar will be prevented. This leads to starch accumulation in the tissues—a feature which has been already described for certain forest trees growing in peat soils. The amount of lime already within the tree when planted on the peat soil, and the amount of available lime in the peat soil itself may indeed be limiting factors to tree growth on certain kinds of peat. The statement of Ingle (18), that calcium oxalate is soluble in sugar suggests that once the factor which inhibits the translocation of carbohydrates is removed the calcium oxalate will be dissolved and the calcium made available for other purposes.

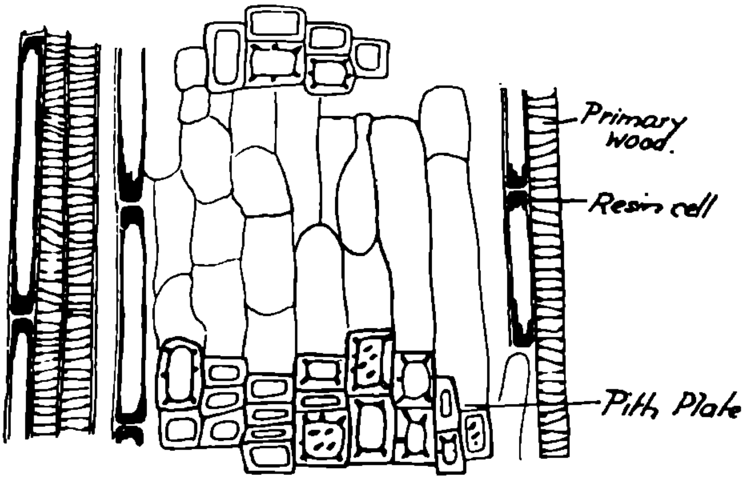


FIG. 6.

(ii) *Resin Cells.*

In all species of coniferous trees growing in peat soils of poor quality the cells associated with the primary xylem which normally contain starch, are converted into resin cells. The resin is massive in form (Fig. 6) and tends to be aggregated at the terminal walls of the cell. In this instance, the conversion of the cell contents to resin is probably due to cold. Hartig has said that the pith of trees and the cells in the immediate neighbourhood of the pith are the first to be affected by frost. In cold the starch of conifers is converted into oils and fatty substances.

### (iii) *Pith.*

In many cases the pith of trees on peat moors is found to be browned and dead. The death of the pith, however, is only local, and is frequently connected with frost damage. For instance, it may be browned near the base of the tree, fresh at a higher level, and slightly browned at a still higher level, the browning coinciding with the presence of frost rings.

In *Picea sitchensis*, which is checked in growth, the pith may show transverse plates at regular intervals (Fig. 6). The plates are 2–4 cells in thickness, and alternate with wider zones of normal thin-walled cells. The individual cells of these transverse plates are thick-walled, and oblong in longitudinal section, whilst in transverse section they are rounded, and they are pitted on all walls. At the points where the plates occur there are bulges in the medullary sheath, the elements of the primary xylem having a wavy outline.

The significance of these plates is not known.

### (iv) *Frost Marks or Rings.*

Trees when grown on peat soils are particularly liable to frost damage. An examination of trees in the checked condition may show frost rings and marks in a large percentage of the total number of growth rings ; for instance, trees from *Erica-Eriophorum-Molinia* peat, Corrour, planted in 1918 have been found to show rings due to frost as follows :—1919—nil ; 1920—trace of a ring in the spring wood ; 1921—frost rings in both spring and autumn wood ; 1922—nil ; 1923—frost rings in both spring and sutumn wood. The longitudinal fissures on the stems of young *Picea sitchensis* and *Pseudotsuga Douglasii* and the other external signs of frost damage which have been described by Professor Borthwick (¹) are absent from the checked trees on peat moors. The absence of the cracks in the bark is probably due to the slow growth of the trees.

The frost ring may appear when the stem or branch is cut across, as a brown circle. When examined with the microscope there is found to be much contortion and swelling of the medullary rays, and the production of thin-walled parenchyma cells in place of the thick-walled cells of the normal wood (Plate XVII). The frost ring usually completely encircles the main stem of the tree growing in peat. In the case of the side branches, particularly of *Pinus*, the frost marks occur only on the under side of the branch. A feature of the frost ring or frost mark of trees, in peat soils at any-rate, is that the cells of the ring or mark become filled with starch and fats. The frost ring or mark is a storehouse of reserve food material.

### (v) *Tree Habit and its Relation to. Frost.*

Certain trees, especially *Picea sitchensis*, often develop a peculiar form on peat moors. The leading shoot is killed by frost or some other cause, and its place is taken by a lateral shoot. The shoot retains the characters of a branch, with the lower needles in pectinate arrangement and the upper needles pointing slightly forward, instead of the definite radial arrangement of the needles as is found on a true leading shoot. Frost rings are present in most of those cases. The tree does not assume a definitely vertical position, but is curved or sabre like. Such shoots are extremely slow in growth and tend to develop most characteristically on *Erica-Calluna-Scirpus* peat types.

## SUMMARY.

An analysis of the points which emerge from an examination of the anatomy and habit of coniferous trees checked in their growth in peat soils would indicate :—

(1) The climate on a peat moor, particularly low temperature, plays a very important part in causing inhibition to growth. Starch accumulation in the leaves and frost rings, resin cell formation, the sabre-like habit, indicate adverse temperature conditions.

(2) Intense light, when the nutrition of the plant is impaired, has a destructive effect on the chlorophyll. This has been shown to be possible of remedy by shading *Picea excelsa, P. sitchensis* and *Pinus montana.*

(3) Metabolism is imperfect, and poisonous substances tend to be produced, e.g. oxalic acid. This is neutralised by the calcium already existing in the plant, or which the plant derives from the peat soil, to form calcium oxalate. The addition of calcium in the form of basic slag helps to remove check, the plant thus probably suffering from calcium deficiency which leads to the non-conversion of starch to sugar.

(4) Magnesium is of value in accelerating growth.

# MINERAL REQUIREMENTS OF CONIFER SEEDLINGS WITH SPECIAL REFERENCE TO ROOT DEVELOPMENT.

Comparatively little information is available regarding the mineral requirements of conifer seedlings. Möller (33) carried out certain studies with pine seedlings, using washed sand as the medium to which the various plant nutrients were added, and obtained certain interesting results on pine seedling development as the result of omitting any one mineral base. Melin (32) in connection with his mycorrhiza investigation has provided valuable information on the relation of different forms of nitrogen to seedling growth.

In the present investigation, water cultures were used to determine the effect of the common inorganic elements on the growth of seedling *Picea excelsa* and *Picea sitchensis.* Crone's culture medium was used as the control, the composition of which is as follows :—

| | |
|---|---|
| Potassium nitrate .. .. .. | 1·00 grams. |
| Iron phosphate .. .. .. .. | 0·50 ,, |
| Calcium sulphate .. .. .. .. | 0·25 ,, |
| Magnesium sulphate .. .. .. | 0·25 ,, |
| Distilled water .. .. .. .. | 2·0 litres. |

In the potassium free culture solution, sodium nitrate was used to replace the potassium ; in the iron free culture solution, potassium phosphate replaced iron phosphate ; and in the phosphate-free culture solution, iron chloride replaced iron phosphate.

The seeds were germinated in sawdust and the seedlings transferred to the culture jars. The experiment was carried out in duplicate, ten seedlings of *P. sitchensis* and five seedlings of *P. excelsa* were placed in each jar. The jars were aerated daily by bubbling air through the water, whilst the solution was changed every fortnight. The experiment was carried out in a green-house until the seedlings had completed two years' growth. The height growth of the stem is given in the following tables :—

*Picea excelsa.*

| — | End of first year. | | End of second year. | |
|---|---|---|---|---|
| | Height. | Remarks. | Height. | Remarks. |
| | Cm. | | Cm. | |
| 1. Control .. | 3·3 | Needles dark green .. | 5·3 | Needles dark green. |
| 2. Minus potassium | 2·33 | Needles light green .. | 2·5 | Needles light green. Non - development of terminal buds. |
| 3. Minus nitrogen | 1·32 | Needles dark green, buds large | 2·3 | Needles greenish yellow. |

| — | End of first year. | | End of second year. | |
|---|---|---|---|---|
| | Height | Remarks. | Height | Remarks. |
| | Cm. | | Cm. | |
| 4. Minus iron | 2·11 | Cotyledons green, otherwise chlorotic. Roots long, few, and devoid of laterals | 2·7 | Chlorotic. Roots long, without side roots. |
| 5. Minus phosphorus | 1·73 | Needles light green | 1·9 | Sickly. |
| 6. Minus calcium | 2·2 | Needles dark green | 2·7 | Bushy plants. |
| 7. Minus magnesium | 2·3 | Needles being shed, greenish yellow | 2·7 | Needles withering at tips and being shed. |
| 8. Half concentration | 2·8 | Needles dark green | 4·9 | Needles dark green. |
| 9. Double concentration | 2·1 | Needles dark green | 3·7 | Needles dark green. |

*Picea sitchensis.*

| — | End of first year. | | End of second year. | |
|---|---|---|---|---|
| | Height | Remarks. | Height | Remarks. |
| | Cm. | | Cm. | |
| 1. Control | 3·2 | Needles dark green | 9·2 | Needles dark green. |
| 2. Minus potassium | 2·7 | Bluish-green needles | 8·1 | Non-development of terminal buds. |
| 3. Minus nitrogen | 0·8 | Needles light green | 1·2 | Dying. |
| 4. Minus iron | 1·4 | Cotyledons green, otherwise chlorotic | 1·6 | Chlorotic. Roots long and devoid of laterals. |
| 5. Minus phosphorus | 1·14 | Dark green | 2·2 | Sickly. |
| 6. Minus calcium | 2·2 | Dark green | 7·9 | Green. |
| 7. Minus magnesium | 2·76 | Light green | 3·8 | Needles falling or yellowish and dying back from tips. |
| 8. Half concentration | 3·05 | Light green | 6·25 | Light green. |
| 9. Double concentration | 2·6 | Light green | 3·45 | Light green. |

The absence of any one element had a marked retarding effect on the growth of *P. excelsa*, the poorest growth being in the absence of phosphorus. The results with *P. sitchensis* did not compare in every respect with those for *P. excelsa*. The absence of lime and potassium, for instance, had not the adverse effect on growth that might have been expected—a result which corresponds with that obtained in manuring tests in certain nurseries, where it was found that *P. excelsa* reacted to an application of potash manure under conditions where *P. sitchensis* failed to react. In the water culture the sodium which was substituted for the potassium was able to replace the potassium in the case of *P. sitchensis*, but not in the case of *P. excelsa*. Where potassium was omitted, a feature in the second year of growth in both species was the non-flushing of the terminal buds, growth being continued by lateral buds—a feature which was observed by Möller. Abnormal colour of the needles occurred most markedly in the absence of magnesium, nitrogen and iron. During the second year, die back of the needles occurred in the magnesium-free medium. In the lime-free culture the *P. excelsa* plants became very bushy.

The root systems of both spruces were normal in development for water culture, and called for no comment except in the case of plants in the iron-free media. Here in both species the roots were few in number without or with only few tertiary roots, whilst the tips of the roots were swollen.

At the end of the second year, when the experiment became inconvenient to handle, the plants were removed, the shoots were detached from the roots and weighed separatively to give the comparative weights, and the relation of shoot to root, in the different culture solutions. The plants were also used to obtain information on the effect of different elements on the formation and distribution of starch and fats.

*Average Weight of Shoot and Root and Proportion of Shoot to Root.*

| — | *Picea excelsa.* | | | *Picea sitchensis.* | | |
|---|---|---|---|---|---|---|
| | Shoot. | Root. | Ratio of shoot to root. | Shoot. | Root. | Ratio of shoot to root. |
| | Gm. | Gm. | | Gm. | Gm. | |
| 1. Control .. | 0·242 | 0·143 | 1·68 | 0·272 | 0·122 | 2·23 |
| 2. Minus potassium | 0·088 | 0·044 | 2·01 | 0·252 | 0·086 | 2·93 |
| 3. Minus phosphorus | 0·047 | 0·042 | 1·13 | 0·029 | 0·021 | 1·38 |
| 4. Minus magnesium | 0·078 | 0·062 | 1·27 | 0·078 | 0·084 | 0·92 |
| 5. Minus calcium.. | 0·065 | 0·067 | 0·97 | 0·133 | 0·085 | 1·56 |
| 6. Half concentration | 0·170 | 0·178 | 0·95 | 0·241 | 0·108 | 2·23 |
| 7. Double concentration | 0·132 | 0·140 | 0·93 | 0·180 | 0·071 | 2·53 |

The plants grown without iron or nitrogen were not weighed.

The results obtained by shoot weighings agree with those obtained by measurement of length of shoot. Absence of phosphorus next to nitrogen and iron, had the greatest effect on root weight of *P. sitchensis*. In *P. excelsa*, phosphorus and potassium starvation lead to poor root growth. In both species the weight of the roots was the same in both the calcium and magnesium-free media.

Two further points would appear to emerge from the investigation, namely :—

(1) That the two species differ greatly in their mineral requirements, and in their reaction to different minerals. For instance, the strongly retarding effect on the growth of *P. excelsa* of absence of potassium may be contrasted with the small effect which the absence of potassium produces on the height growth and weight of the shoot of *P. sitchensis*.

(2) The absence of any element tends to react in greater measure on shoot growth than on root development. With *P. sitchensis*, for instance, potassium, calcium, and magnesium all produce the same result, the weight of the roots being the same in each case, although their influence on shoot development is different.

A comparison was made between the weight of plants from the control solution which contained all nutrient elements considered essential for plant growth, and plants of the same age from the nursery.

| Species. | From Control Solution. | | | | From Nursery Soil. | | | |
|---|---|---|---|---|---|---|---|---|
| | Shoot. | Root. | Total. | Ratio of shoot to root. | Shoot. | Root. | Total. | Ratio of shoot to root. |
| | Gm. | Gm. | Gm. | | Gm. | Gm. | Gm. | |
| *Picea excelsa* .. | 0·24 | 0·14 | 0·38 | 1·71 | 0·44 | 0·21 | 0·65 | 2·09 |
| *Picea sitchensis* .. | 0·27 | 0·12 | 0·39 | 2·25 | 0·47 | 0·17 | 0·64 | 2·77 |

In the water culture, the shoot and root and total plant weight are smaller than in the nursery plants, probably due to absence of silica in the culture solutions.

In the plants grown in water culture as well as in the plants from the nursery, *P. sitchensis* has a smaller root in proportion to shoot than *P. excelsa*. The root system of *P. sitchensis* would appear to be more efficient than that of P. *excelsa,* less root being necessary to produce a greater bulk of stem and branches.

The distribution of starch as the result of the absence of any one element varies in the case of both P. *excelsa* and P. *sitchensis*. In both species the absence of iron resulted in an accumulation of starch in all the tissues. This result is interesting in connection with the observations made on trees grown in peat. Although root development in water culture may be abnormal, and observations made thereon cannot be applied to soil, it has been shown that in many peats the soil solution fails to give a reaction for iron, and in such peats the tree shows a similar accumulation of starch in all tissues (*loc. cit.*, p. 46). Similarly the roots tend to be long, straggling, and devoid of side roots. Absence of calcium in both species led to the non-deposition of starch in the roots, and while magnesium deficiency in P. *excelsa* brought about an accumulation of starch in all plant organs, its absence in the case of P. *sitchensis* had no effect in this direction.

In both species under all treatments fats were found in the leaf, except where potassium was omitted from the water culture. A stronger reaction for fats was obtained, however, in the root system of plants grown in potassium-free culture than in other species. Fats were absent from the root tissues of P. *excelsa* when phosphorus was not present.

## PERIODICITY OF ROOT AND SHOOT GROWTH AND RELATION OF WEIGHT OF ROOT TO WEIGHT OF SHOOT.

The name most intimately associated with studies on the periodicity of the root growth of forest trees is that of Arnold Engler (9). Engler carried out researches with a wide variety of trees including silver fir, Scots pine, beech, oak and birch. He found that the root growth of conifers took place between the months of April and October, and was entirely suspended between November and April, whereas in deciduous trees a certain amount of growth took place during the winter months.

The primary object of the present investigation was to determine the periodicity of root growth of conifers in the nursery under our climatic conditions, but data were also obtained regarding periodicity in shoot growth and regarding the seasonal variations in the proportion of shoot to root. The main method of investigation was to weigh large numbers of plants at short intervals of time. This method was supplemented by measurement of growth in length of root and shoot, by field observations on the time of root growth in length, and studies on starch deposition in the various plant tissues.

The species used in the investigation were *Picea excelsa, Picea sitchensis* and *Larix europaea* seedlings in their second year. All the plants used in the investigation were taken from the one nursery, namely Seaton Nursery, near Aberdeen, and lifted from the same seed-bed throughout.

The plants were lifted as carefully as possible, the roots separated from the shoots at fixed points, and the roots washed in water to remove the adherent soil particles. The shoots and roots were then placed separately in weighed glass containers, and dried in an over at 100° C. until a constant weight was reached.

It is realised that the method of determining accretion in plants by weight is unsatisfactory in many respects, and that only indications of weight accretion can be hoped for. The degree of accuracy or the value of the results increases with the frequency of the weighings and the number of plants weighed at any one time. In the first year when the determinations were made it was found that the greatest source of error lay in the preponderance of any one grade of plants; for example, small plants over large plants or vice versa in a bundle. In the second year of the investigation the plants were therefore graded into large and small, and separate determinations were made for each grade. The results are given in the following tables the value in grammes representing the average weight of each plant. The percentage increases in dry weight are also given.

(*a*) *Picea excelsa—2nd year Seedling.*

| Date of collection of samples. | Shoot. | | | | Root. | | | |
|---|---|---|---|---|---|---|---|---|
| | Large grade. | | Small grade. | | Large grade. | | Small grade. | |
| | Average weight. | Increase. | Average weight. | Increase. | Average weight. | Increase. | Average weight. | Increase. |
| | Gm. | Per cent. | Gm. | Per cent. | Gm. | Per cent. | Gm. | Per cent. |
| March 31st | 0·13 | — | 0·11 | — | 0·06 | — | 0·05 | — |
| April 14th | 0·14 | — | 0·10 | — | 0·06 | — | 0·04 | — |
| „ 27th | 0·13 | — | 0·10 | — | 0·06 | — | 0·05 | — |
| May 13th | 0·14 | — | 0·11 | — | 0·06 | — | 0·05 | — |
| „ 30th | 0·14 | — | 0·10 | — | 0·05 | — | 0·04 | — |
| June 14th | 0·18 | 30 | 0·15 | 50 | 0·06 | — | 0·05 | — |
| „ 30th | 0·31 | 121 | 0·18 | 80 | 0·13 | 116 | 0·08 | 60 |
| July 15th | 0·33 | 136 | 0·26 | 160 | 0·13 | 116 | 0·09 | 80 |
| „ 29th | 0·36 | 157 | 0·25 | 150 | 0·14 | 133 | 0·10 | 100 |
| August | — | — | — | — | — | — | — | — |
| Sept. 14th | 0·43 | 207 | 0·29 | 190 | 0·17 | 183 | 0·16 | 220 |
| „ 28th | 0·42 | 200 | 0·30 | 200 | 0·18 | 200 | 0·16 | 220 |
| Oct. 14th | 0·51 | 264 | 0·32 | 220 | 0·23 | 283 | 0·17 | 240 |
| „ 28th | 0·56 | 371 | 0·32 | 220 | 0·26 | 333 | 0·16 | 220 |
| January | 0·54 | — | 0·30 | — | 0·24 | — | 0·16 | — |

(*b*) *Picea sitchensis—2nd year Seedling.*

| Date of collection of samples. | Shoot. | | | | Root. | | | |
|---|---|---|---|---|---|---|---|---|
| | Large grade. | | Small grade. | | Large grade. | | Small grade. | |
| | Average weight. | Increase. | Average weight. | Increase | Average weight. | Increase. | Average weight. | Increase. |
| | Gm. | Per cent. | Gm. | Per cent. | Gm. | Per cent. | Gm. | Per cent. |
| March 31st | 0·07 | — | 0·05 | — | 0·03 | — | 0·025 | — |
| April 14th | 0·08 | — | 0·05 | — | 0·04 | — | 0·025 | — |
| 27th | 0·08 | — | 0·05 | — | 0·03 | — | 0·025 | — |
| May 13th | 0·10 | 25 | 0·04 | — | 0·04 | — | 0·02 | — |
| „ 30th | 0·11 | 37 | 0·08 | 60 | 0·04 | — | 0·04 | — |
| June 14th | 0·15 | 87 | 0·09 | 80 | 0·04 | — | 0·03 | — |
| „ 30th | 0·16 | 100 | 0·11 | 120 | 0·06 | 50 | 0·03 | 20 |
| July 15th | 0·18 | 125 | 0·11 | 120 | 0·06 | 50 | 0·04 | 60 |
| „ 29th | 0·26 | 225 | 0·21 | 320 | 0·08 | 100 | 0·06 | 140 |
| August | — | — | — | — | — | — | — | — |
| Sept. 14th | 0·37 | 362 | 0·24 | 380 | 0·12 | 200 | 0·08 | 220 |
| „ 28th | 0·42 | 425 | 0·26 | 420 | 0·12 | 200 | 0·08 | 220 |
| Oct. 14th | 0·51 | 537 | 0·36 | 620 | 0·18 | 350 | 0·12 | 380 |
| „ 28th | 0·56 | 600 | 0·38 | 660 | 0·20 | 400 | 0·13 | 420 |
| Nov. | 0·52 | — | 0·35 | — | 0·18 | — | 0·12 | — |
| Feb. | 0·55 | — | 0·35 | — | 0·19 | — | 0·13 | — |

### (c) *Larix europaea—2nd year Seedling.*

| Date of collection of samples. | Shoot. | | | | Root. | | | |
|---|---|---|---|---|---|---|---|---|
| | Large grade. | | Small grade. | | Large grade. | | Small grade. | |
| | Average weight. | Increase. | Average weight. | Increase. | Average weight. | Increase. | Average weight. | Increase. |
| | Gm. | Per cent. | Gm. | Per cent. | Gm. | Per cent. | Gm. | Per cent. |
| March 31st .. | 0·11 | — | 0·09 | — | 0·10 | — | 0·10 | — |
| April 14th .. | 0·16 | 46 | 0·13 | — | 0·14 | — | 0·11 | — |
| ,, 27th .. | 0·21 | 91 | — | — | 0·14 | — | — | — |
| May 13th .. | 0·25 | 128 | 0·14 | — | 0·13 | — | 0·11 | — |
| ,, 30th .. | 0·29 | 164 | 0·16 | 23 | 0·13 | — | 0·11 | — |
| June 14th .. | 0·32 | 191 | 0·29 | 123 | 0·15 | — | 0·10 | — |
| ,, 30th .. | 0·24 | 118 | 0·23 | — | 0·15 | — | 0·11 | — |
| July 15th .. | 0·20 | 82 | 0·17 | — | 0·16 | 23 | 0·14 | 27 |
| ,, 29th .. | 0·32 | 191 | 0·19 | — | 0·19 | 47 | 0·14 | 27 |
| August .. .. | — | — | — | — | — | — | — | — |
| Sept. 14th .. | 0·61 | 455 | 0·33 | 154 | 0·22 | 69 | 0·15 | 36 |
| ,, 28th .. | — | — | — | — | 0·23 | 77 | 0·16 | 45 |
| Oct. 14th .. | — | — | — | — | 0·23 | 77 | 0·15 | 36 |
| ,, 28th .. | — | — | — | — | 0·25 | 92 | 0·15 | 36 |

In Norway spruce the increase in the weight of the shoot was most rapid in the last fortnight of June ; thereafter it increased gradually until the end of October. The average was more or less constant during the winter months. The weight of the roots also increased during the last fortnight of June, and there was a constant increase until the end of October. Although the main increase in both shoot and root occurred during the last fortnight of June, it has to be noted that in the shoot there was a gradual increase preceding the main increase, whereas in the root the rise was abrupt and extended over a very short period. In the larger plants an increase took place from September to October in the case of both shoot and root.

In Sitka spruce a very pronounced increase in the weight of the shoot occurred during the last fortnight of July. The increase proceeded very rapidly throughout August, slowed down during September, but again rose rapidly between the end of September and the beginning of October. The main increases in the root weights occurred during July and August and the first fortnight of October.

In European larch the weight increased gradually from April onwards, the greatest gain being between July and September. No optimum period of increase could be distinghished in respect of the roots, from the data available.

The increase in weight of the shoot began in all species in advance of the root. In general for the set of conditions under review, the increase in the weight of the shoot was gradual from the beginning of June in the case of Norway spruce, from the middle of May in Sitka spruce, and from April in larch. On the other hand, the weight of the roots was constant until the middle of June in Norway spruce, until the end of June in Sitka spruce and until the last fortnight of July in European larch.

In all species the period of root growth corresponded with the period of low soil moisture, and with low moisture content of the roots. (*See* graphs, Fig. 7).

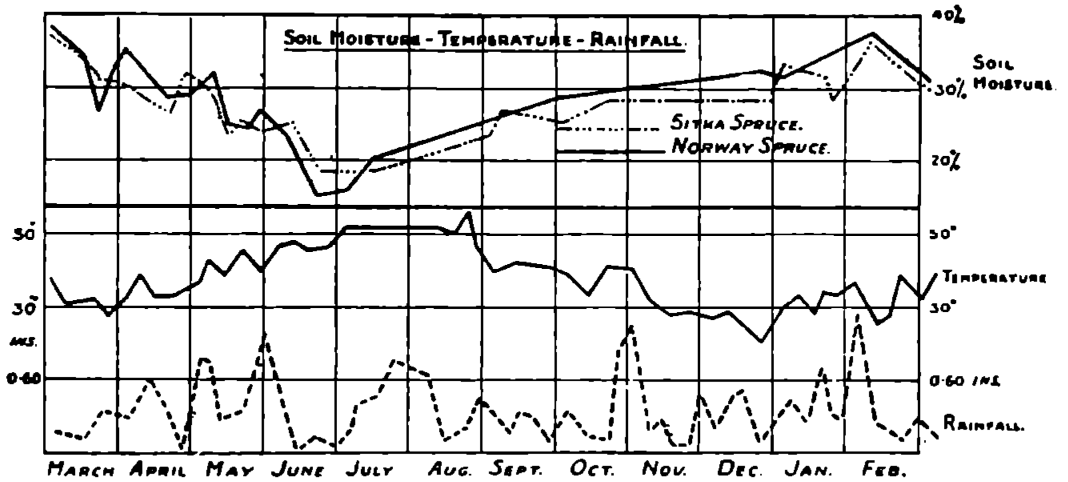


FIG. 7.

## 1. Field Observations on Growth in Length of Root and Shoot.

In the root, growth was first noted in both spruces on 18th June, but whereas there was little growth on this date in Sitka spruce, in Norway spruce growth was taking place rapidly. The greatest production of new rootlets in Sitka spruce appeared to be delayed until about 15th July. The next period when root growth was noted to be particularly strong was in October. The root system of larch was noted to be developing on 20th May, and to be particularly active about the beginning of June. Thereafter, there was a lull in extension until 15th July, when growth again commenced. New rootlets were again produced in abundance at the end of September.

The depth to which the roots penetrate the soil was found to be constant until July, viz., 15–17 cm. in Norway spruce, 12 cm. in Sitka spruce. In September the depth of penetration had increased in the case of Norway spruce to 22 cm. and in Sitka spruce to 23 cm. Until 18th June the average lateral extension of the root system of Norway spruce and Sitka spruce was 7½ cm. and 5 cm. respectively, while in September the lateral extension in Norway spruce and Sitka spruce was found to average 25 cm. and 10 cm. respectively.

As regards the shoot, periodic measurement showed that height growth in Norway spruce appeared to be most rapid in the first fortnight of June, when the plants increased in height from 6 cm. to 10 cm. In Sitka spruce height growth continued until the beginning of July. It gradually rose from 5 cm. in the middle of May to 10 cm. in July. Unlike Norway spruce, where further height growth was small, the height of Sitka spruce increased during the month of August and the first fortnight of September by 2 to 3 cm.

Thus in Norway spruce field measurements and observation showed that the greatest shoot growth during the first fortnight of June was followed by a period of intense root growth beginning on the 18th June and continuing throughout July and August. A slight further increase in height was followed in October by root growth. Shoot growth of Sitka spruce continued into July and then slowed down, but about 15th July root growth was particularly strong. Further shoot growth until 21st September was followed by a period of intense root growth.

The larch results were complicated on account of disease (*Meria laricis*) of the shoots, but the data available indicate that height growth proceeded rapidly until 11th May, after which date new root growth was observed. The period of root growth was again followed by shoot growth until the beginning of July, and this second period of height growth was observed to be succeeded by a second period of root growth beginning on 15th July.

Thus it would appear that shoot growth and root growth alternate.

## 2. Relation of Weight of Shoot to Weight of Root.

The dry weight ratio of shoot and root is given in the following table :—

| Date of collection. | *Picea excelsa.* | | *Picea sitchensis.* | | *Larix europaea.* | |
|---|---|---|---|---|---|---|
| | Large plants. | Small plants. | Large plants. | Small plants. | Large plants. | Small plants. |
| March 31st .. | 2·16 | 2·20 | 2·33 | 2·0 | 1·10 | — |
| April 14th .. | 2·33 | 2·5 | 2·0 | 2·0 | 1·14 | 1·18 |
| ,, 27th .. | 2·16 | 2·0 | 2·66 | 2·0 | 1·50 | 1·27 |
| May 13th .. | 2·33 | 2·20 | 2·5 | 2·0 | 1·92 | 1·45 |
| ,, 30th .. | 2·80 | 2·5 | 2·75 | 2·0 | 2·23 | 2·90 |
| June 14th .. | 3·00 | 2·0 | 3·75 | 3·0 | 2·13 | 2·09 |
| ,, 30th .. | 2·31 | 2·25 | 2·66 | 3·66 | — | — |
| July 15th .. | 2·54 | 2·66 | 3·0 | 2·75 | — | — |
| ,, 29th .. | 2·57 | 2·5 | 3·25 | 3·50 | 1·68 | — |
| August .. .. | — | — | — | — | — | — |
| Sept. 14th .. | 2·53 | 1·81 | 3·09 | 3·0 | 2·77 | 2·20 |
| ,, 28th .. | 2·38 | 1·88 | 3·50 | 3·25 | — | 2·50 |
| Oct. 14th .. | 2·22 | 1·88 | 2·83 | 3·0 | — | — |
| ,, 28th .. | 2·15 | 2·0 | 2·80 | 2·9 | — | — |
| Feb. .. .. | 2·25 | 1·88 | 2·89 | 2·68 | — | — |

The earliest growth of the shoot caused an increase in the proportion of shoot to root, but as the root began to grow the proportion was again reduced. The ratio of shoot to root, therefore, varies as the result of the interplay in growth. The highest proportion of shoot to root occurred in both Norway and Sitka spruce during the first fortnight in June, and again, particularly in Sitka spruce, at the end of July and in Sitka spruce again during September. During the latter part of June and beginning of July, and in October, subsequent in each case therefore to shoot growth, the ratio was reduced as the result of root growth.

In October the ratio between shoot and root had regained the March and April value in the case of the larger-grade Norway spruce plants. In the smaller-grade spruce plants the value was slightly lower. On the other hand, in Sitka spruce the ratio was higher in October than in the beginning of the year in the case of both larger and smaller-grade plants, the root not keeping pace with the shoots in weight accretion.

During April different types of nursery plants growing under similar conditions were collected; namely, 2-year seedlings, 3-year seedlings, 2 yr. + 1 yr. transplants, and 2 yr. + 2 yr. transplants, and the proportion $\frac{\text{weight of shoot}}{\text{weight of root}}$ was determined with the following results:—

| Species. | Second year. | Third year. | 2 year + 1 year. | 2 year + 2 year. |
|---|---|---|---|---|
| *Picea excelsa* . . | 2·2 | 2·2 | 1·4 | 1·4 |
| *Picea sitchensis* . . | 2·05 | 2·6 | 1·5 | 1·9 |
| *Larix europaea* . . | 2·3 | 2·2 | 2·2 | 2·1 |

The results indicate that while *P. sitchensis* is kept as a seedling the shoot increases at a greater rate than the root, but that after it is transplanted there is a more even balance of weight between shoot and root. In *P. excelsa* the seedling does not show an increase in the proportion of weight of shoot to that of the root with advance in age. After transplanting, however, there is an increase in the proportion of root weight to shoot weight. *L. europaea*, in so far as results are available—this species is found to be extremely variable and not dependable—maintains a more or less constant proportion between shoot and root in all descriptions of plant.

### *Summary.*

There is no appreciable root growth during the winter months in coniferous nursery plants, and there is thus agreement with Engler. Shoot growth commences first in the spring and is followed by root extension, and thereafter, throughout the season there is an interplay between shoot and root development. The root system which is laid down at the end of the year supplies the needs of the shoot at the commencement of its new growing season. In the latter part of the year, after shoot growth has ceased, the root growth is still active and preparing a larger absorptive surface for the growth of the shoot in the following spring. The shoot continues to grow until the root is no longer able to supply the greater transpiring surface created by the new leaves, and new root extension is required. This interplay between shoot and root growth is confirmed by weight determinations, variations in the ratio of shoot to root, actual field observations and measurement of root and shoot growth.

The proportion of shoot to root in *Picea excelsa* seedlings or *Larix europaea* seedlings does not vary with the age of the seedling ; that is, the balance between shoot and root is maintained throughout the life of the plant before transplanting. In *Picea sitchensis* the proportion of shoot to root increases in the third year of the plant as a seedling. The effect of transplanting, except in the case of *Larix europaea*, is to increase the proportion of root to shoot, although with *Picea sitchensis* there is an indication that in the second year after transplanting the ratio of shoot to root again increases.

## SEASONAL VARIATIONS IN THE STARCH STORES.

It is considered that weight determinations by themselves do not give data which necessarily indicate periods of root growth. For instance, a non-varying root weight from April to June does not necessarily mean that there is no root growth in bulk during that period. When growth commences in the spring, reserve stores of carbohydrates are used up for new growth, and the root system or any part of the root system may be depleted of reserve starch to build up the new tissue of the stem. Increase in root growth may, therefore, be compensated for as regards weight by movement of reserve food materials to other parts of the plant. Starch was the main reserve tested for in this instance.

Starch is found deposited throughout the plant in various places from the root cap to the epidermis of the leaf. There are, however, seasonal variations in the amount of starch in any one part of the plant.

If a needle of Norway spruce is sectioned during March, it will be found that most of its cells contain starch—epidermis, hypodermis, mesophyll, and certain cells of the vascular tissue. In April the reaction for starch is not visible except in the epidermis, hypodermis, and the cells in the neighbourhood of the vascular tissue. In May generally, only the hypodermis contains starch granules. There is, thus, throughout these months a gradual reduction in the amount of starch in the leaf, the cells farthest removed from the vascular tissues being the last to give up their stores. In June no starch grains are found in the leaf. The deposits reappear again in July and September, but disappear during October and the latter months of the year, to reappear again in March. The periodicity in starch accumulation in the leaf of Sitka spruce agrees with that of Norway spruce, except that, in addition, starch accumulation in the leaf is found in the month of October.

In so far as microscopic tests can determine, the amount of starch in the stem becomes reduced in amount from May to September, and again from December to January. In December only a few grains in the cortex could be detected. In the older parts of the root system, the only time when a reduction in starch reserves could be noted was during December, but in the younger roots a great reduction in the amount of starch occurred during June and July.

Thus during the period of shoot growth, the starch accumulation in the older leaves and in the stem disappeared, but during this period there was no appreciable reduction in the amount of starch in the roots, except in the younger parts of the root system, that is, the roots which continued growth or gave rise to new roots.

The movement of reserve materials such as starch is, therefore, not considered to prejudice to any extent the weight determinations.

From the above it would appear, as might be expected, that there was a correlation between starch accumulation and growth of shoot and root. When shoot growth is strong, starch deposits are absent from the shoots ; when root growth begins or is active starch grains appears again in the leaf. This apparent periodicity in starch accumulation, however, may be due to other causes than growth. The phenomenon of starch accumulation in the leaves of conifers has been investigated for example, by Neger, ([35]) who has shown that starch accumulation may be due to cold. Korstian, ([21]) again, could detect no starch in conifers in January and February, the starch being then converted into oil or fatty substances as the result of cold. In July and the summer months generally starch accumulation might be explained in such semi-shade bearing species as the Spruce, as resulting from too high light intensity.

## PERIODICITY IN THE GROWTH OF MYCORRHIZA.

Although periodicity in the growth and development of mycorrhiza can be shown to occur in *Picea*, it can best be demonstrated and is more evident in *Pinus*. In the coralloid type of pine mycorrhiza, or in that type in *Picea* where the growth of the rootlets is not inhibited to such a marked degree by the fungus, there are constrictions, each constriction representing a check to growth in length.

In the first year of growth, the pine seedling produces the primary root, secondaries and tertiaries. The tertiary root varies in length according to growth conditions. At the end of the first year, and even until June of the second year, the tertiary root may be a small protuberance, it may be lengthened, it may be infected with mycelium but not branched, or it may be infected with mycelium and bifurcate—the bifurcation being the first stage usually recognised in the formation of the typical mycorrhiza of the pine. The latter condition (i.e. elongated and bifurcated) usually occurs in pine seedlings growing in old nursery soil or ground which has previously borne conifers; the former (i.e. infected with mycelium but not branched), usually associated with root hairs, occurs in new nursery ground.

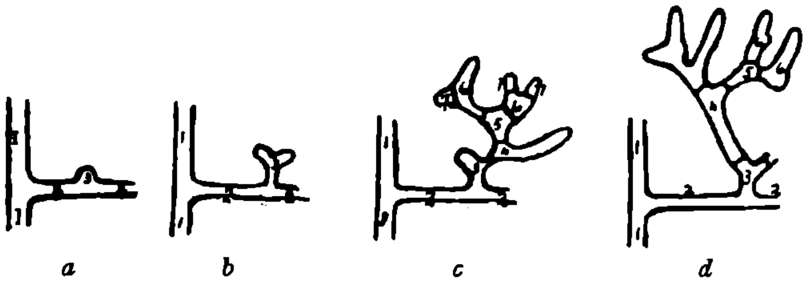


FIG. 8. Periodicity in growth of mycorrhiza of pine.

(*a*) Condition of tertiary root (3) during first winter without or with traces only of fungus infection.

(*b*) Condition of tertiary root during first winter where bifurcation has taken place.

(*c*), (*d*) Condition of (*a*) and (*b*) at the end of second winter.

Taking any of these conditions of the tertiary root, it is found that there is no further development until May or June; that is, until the beginning of the second year of growth. Subsequent to this there are three or four growth periods as represented by the constrictions on the mycorrhiza body (Fig. 8). The condition in Fig. 8*c* and 8*d* is found in the following spring.

These growth lines of marks can be made out quite clearly if the mycorrhiza body is stained with Cotton blue and mounted in glycerine jelly.

## SUMMARY AND CONCLUSIONS.

### Relation of the Research to Practical Forestry.

The problem of the checked growth of trees may be approached in two ways. First, by a study of the plant itself including the influence of the factors which determine its habit and form, as such a study is likely to yield information which would indicate the cause of " check " or failure. Second, by a study of the actual growth factors of the locality before planting. Ecological studies may be made to discover the natural sequence of vegetational types, and to indicate the essential factors which control this sequence. A scheme may then be mapped out to show the stage in the sequence at which tree growth would naturally take place. By a proper understanding of the factors which give rise to the sequence of types, a speeding up of the methods adopted by nature may be brought about artificially and plantations may be formed more quickly on sites at present unsatisfactory for tree growth.

The main subject dealt with in the preceding sections has been that of mycorrhiza or " fungus roots." Mycorrhiza have been shown to be of different forms and types which are correlated with soil conditions and the condition of the tree itself particularly of the root tip. Mycorrhiza are present on the roots of certain forest trees such as Scots pine when the trees are growing satisfactorily. Whether the better growth is due to the action of the mycorrhiza or whether the mycorrhiza are there because of the healthy condition of the tree is an open question. Evidence has been advanced in support of both views. On the one. hand, it has been shown, for instance, that the fungus may benefit the tree by means of its strong oxidising properties and its ability to liberate mineral bases from the soil. On the other hand, it has been shown that the fungus exerts a retarding influence on root growth and acts as a root pruner ; that is, the fungus is frequently distinctly parasitic. Whether as a partner or parasite the fungus has an influence on the root form.

In those cases where fungus roots are not produced and where the trees remain in check, the question arises whether a fungus can be introduced which will unite with the tree roots and thus improve growth. In the foregoing pages it has been shown that fungus roots are developed normally on tree roots in most. soils if given the proper conditions for their development. When planted out from the nursery into the plantation most species of trees have fungus roots, and therefore the trees themselves should inoculate the new ground. It has been shown by field experiment that this happens. Where the development of fungus roots is stopped it must be due either to the conditions necessary for their formation not being present or to the fungus which is introduced with the tree not being a suitable one for that particular soil. It has been shown, however, that in poor types of peat where fungus roots are absent they can be formed if inorganic salts such as magnesium carbonate or fertilisers such as basic slag are mixed with the peat. A fungus capable of forming mycorrhiza must therefore be present in the soil, but the conditions necessary for its union with tree roots may be absent. This again indicates that mycorrhiza formation would take place if suitable soil conditions existed. The question of mycorrhiza formation and the parasitic or non-parasitic tendencies of the fungi concerned is largely one of soil improvement.

The critical problem of whether more efficient fungi can be introduced in place of existing fungi opens a wide and important field of research and experiment. The ecology of the fungi which enter into association with tree roots requires to be fully worked out, and experiments on soil inoculation with this end in view are now in progress. In order that the requirements of beneficial soil organisms may become better known and the conditions under which they grow and develop more fully understood continued experimental work in the field is necessary. Inoculation of soil or seed with definite micro-organisms is known to be a necessity on some soils if certain plants, as, for example, lupins, are to be grown successfully. Much work on forest soils and the requirements of trees is, however, still necessary before the same exact knowledge can be obtained as the agriculturist possesses regarding leguminous plants and the soil conditions suitable for their growth. The failure of inoculation experiments on peat soils has shown that the mere introduction of bacteria or fungi will be a waste of effort unless conditions are present or can be created which will allow these organisms to live and act.

The absence of mycorrhiza on tree roots in peat soils has been shown to be due partly to imperfect aeration. As a rule the only part of the peat which is aerated is the upper few inches. Mycorrhiza are formed only when the peat is aerated and therefore only occur in this layer. Aeration and oxidation of the peat can be obtained by effective drainage and also by the help of oxidising substances. It is a noteworthy feature that even the worst types of peat can be made to grow seedlings successfully in the laboratory when mineral bases are added to them. Spring water alone may suitably influence such peat as a medium for tree growth and mycorrhiza may be produced abundantly. How can a comparable effect be brought about in the field? The Belgian method of planting, which unites ordinary drainage of the peat with localised intensively drained and manured spots in the form of turfs, gives the most promising method of peat treatment yet devised. Its failure where failure does occur is due, in the writer's opinion, to two causes. First, the treatment of the peat soil is too localised. It has been shown that the roots when they leave the turf pass into the surrounding peat which, even when drained, may be unsuitable for proper root development. This is particularly the case in regions of high rainfall. Second, the food materials in the turf itself become exhausted. It would appear that on certain peat types as soon as the artificial manure applied to the turf is exhausted or beyond the reach of the more vigorous newly formed roots, the trees pass into check.

Thus the first conclusion which might be arrived at is that on the poorer peat types the top layer of peat must be brought into a more fertile state. Cultivation, drainage, the broadcasting of artificial fertilisers on the peat—all or individually—would be indicated as being necessary. The solution of the problem of how to secure the movement of water throughout the peat, how to obtain the percolation of water containing plant nutrients and oxygen and oxidising substances, would remove the difficulty of the production of forest crops in peat. This involves the carrying out of such operations as irrigation, flushing and drainage ; in the writer's opinion there are many peat areas which could be flushed with fresh water from mountain streams by the use of intakes and contour ditches.

It has been shown that forest trees such as spruce and pine possess a striking adaptability to peat conditions. The ecological adaptability of these trees which enables them to persist in the peat for an indefinite number of years in a condition of check conforms to that of plants which are natural to peat soils, such as *Scirpus caespitosus* and *Myrica gale.* Spruce, for instance, when planted in actively accumulating peat maintains its roots in the better aerated surface later by producing them in successive whorls. A parallel behaviour is found in *Scirpus caespitosus.*

The surface rooting habit is typical of trees planted in peat. The depth of root penetration which takes place depends on the quality of the peat. The better the peat the deeper do the lateral roots penetrate ; the poorer the quality of the peat the more likely is the root system as a whole to take up a position in a horizontal plane on the surface or even in the vegetation itself.

The fact that the roots of trees like spruce come ultimately to lie on the surface of the peat has suggested a method of planting whereby the roots are placed directly on the surface when the tree is planted. The method consists in slitting a shallow turf from the outside to the centre and passing the stem of the plant by the slit to the centre of the turf and spreading the root system beneath the turf. Some measure of success might be looked for by this method of planting in that (1) the nursery roots might be saved and the tree relieved from the necessity of producing a completely new root system ; (2) active feeding roots, where the surface peat is of better quality, are placed at the beginning in a position where food materials can be obtained. In the poorer peat soils, however, the root system will have as great difficulty in obtaining food material as in the ordinary planting method, and there is danger of the root system suffering from drought. Before the method can meet with general success the top layer of the poorer quality peats must be brought into a fit condition to nourish the tree roots, possibly by some such method as ploughing, broadcast manuring, or using peat improving plants.

Soil improving plants might be used to change the upper layer of peat into a more productive state for forest trees. Such plants may be trees, shrubs, grasses or herbs. *Pinus montana*, for instance, is a tree which at one time was considered hopeful in this respect. *Larix leptolepis* also presents possibilities as a peat improver. Probably, however, broadleaved species such as rowan *Sorbus aucuparia* and (*Pyrus aria intermedia* may be more successful on account of the better type of humus which their leaves help to form. Experiments with possible soil improving plants which are in progress indicate that this method is as likely as any to be a profitable one.

The research concerning tree growth in peat soil has demonstrated that check may not be due to adverse soil conditions alone, but that climatic factors may in many cases be important contributory causes. It is difficult to dissociate the climatic factors and the soil conditions which operate on peaty ground. For example, frost incidence is related to the type of vegetation and the amount of soil moisture. It has been shown that frost is inimical to trees growing in peat. The question arises as to how far the forester can improve the climate on a peat moor. In the first place, he may grow more hardy and less exacting plants to act as a shelter and protection for the less hardy but more valuable forest trees. Such hardy trees or shrubs would not only provide shelter, but would alter the soil conditions and help to create a forest soil which would permit the growth of other and more valuable tree species. In the second place the forester may by direct soil treatment improve the climate. It is well known, for instance, that frost damage can be removed or minimised by irrigation, as is done in the cultivation of cranberries in the bogs of North America.

Similarly where inhibition to growth is due to translocation of starch being prevented by too intense light, a nurse crop of some non-sensitive species is required.

Experiments on the mineral requirements of conifer seedlings have shown that the absence of certain bases such as iron and magnesium bring about the same physiological disturbances within the plant as have been shown to occur in trees growing on peat. The problem of removal of check as indicated by the imperfect metabolism of the tree depends on the artificial supply of food substances which are lacking in the soil.

The investigations dealing with the mineral requirements of trees and the periodicity of shoot and root growth were incidental to the main research. They have shown the effect on the growth of seedling trees, of the absence or deficiency of certain minerals and that the reaction varies according to species. They have also shown that nitrogen and phosphorus are the most important elements for conifer seedlings; and that the absence of those elements leads to almost complete arrest in growth. They have shown that certain abnormal features in the tree may be traced to a deficiency of a particular mineral base. Knowledge of this kind should assist endeavours to improve conditions for tree growth in nurseries and plantations.

The investigations concerning the seasonal growth of roots are of silvicultural importance not only in regard to transplanting and " wrenching " in the nursery but also in the operations of packing, transport, and " heeling in " of young plants. Further, such knowledge may be of assistance to the forester in connection with planting procedure in time and sequence according to the seasonal vegetative activity of the roots of the species he intends to plant.

Printed under the authority of HIS MAJESTY'S STATIONERY OFFICE
by Percy Lund, Humphries & Co. Ltd.
(20911) Wt. 4662/1525/Ps.85711. 1,250. 2/47. P.L.H. & Co. Ltd. G.943.

# PLATE I.

FIG. 1.
" Ball " mycorrhiza from Scots pine (*Pinus sylvestris*) raw humus.

FIG. 2.
" Coralloid " mycorrhiza from Scots pine growing on loamy soil.

FIG. 3.
" Ball " and " coralloid " mycorrhiza on the same root system as that shown in Fig. 2.

FIG. 4.
Mycorrhiza from transplant in the nursery showing different degrees of inhibition to growth of the rootlets as the result of the presence of the fungus.

PLATE II.

FIG. 1.
Mycorrhiza of Norway spruce (*Picea excelsa*). The mycorrhiza is simple.

FIG. 2.
Mycorrhiza of European larch (*Larix europaea*).

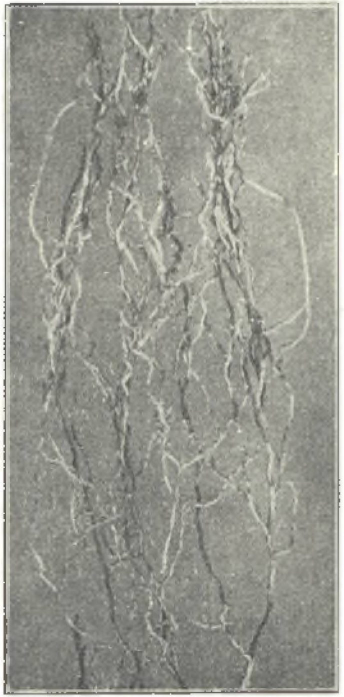


FIG. 3.
Roots of *Thuya plicata*.
Mycorrhiza is endotrophic.

FIG. 1.
Scots pine (*Pinus sylvestris*) roots infected with aphid (*Pachypappella piceae*, **Hartig**), the woolly secretion of which may be confused with the hyphae of mycorrhiza.

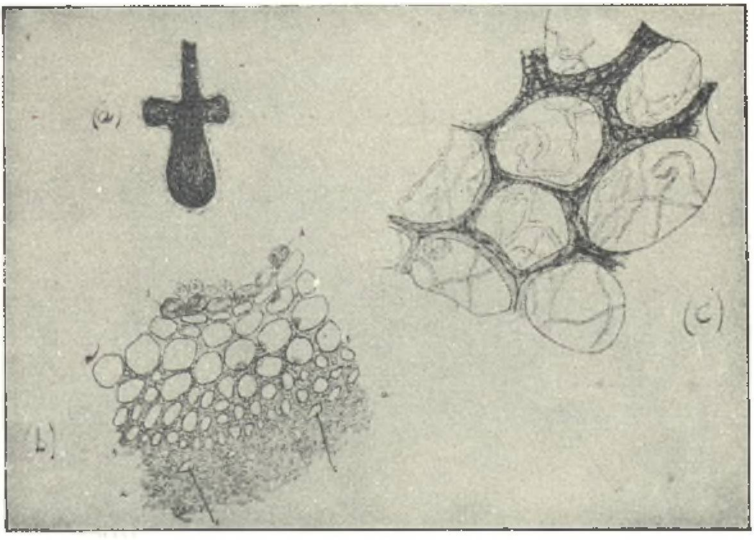


FIG. 2.
Mycorrhiza of silver fir (*Abies grandis*) : (*a*) general appearance of rootlet, (*b*) cross section of rootlet showing mat of hyphae to the outside penetrating between cells of cortex and destruction of cortical cells, certain cells being isolated within the mass of hyphae, (*c*) part of cortex enlarged showing masses of hyphae within the cells.

# PLATE IV.

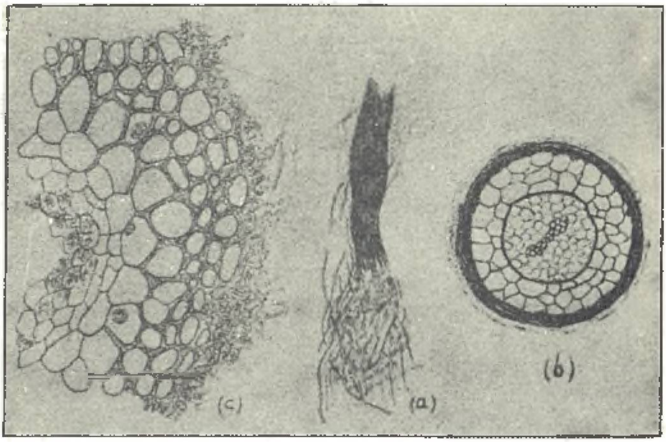


FIG. 1.
Mycorrhiza of Norway spruce (*Picea excelsa*) showing (*a*) rootlet covered with fungus hyphae, (*b*) cross section of rootlet with fungus mat to the outside, (*c*) part of cortex enlarged to show disintegration of the cells by the fungus.

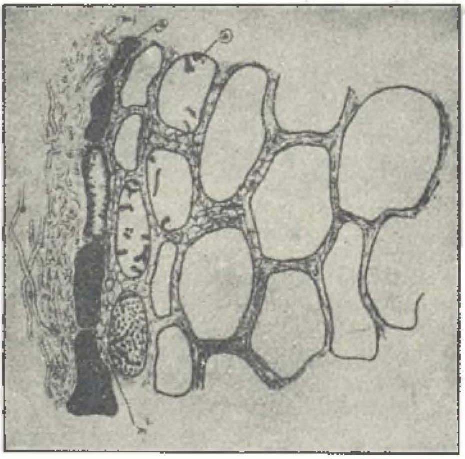
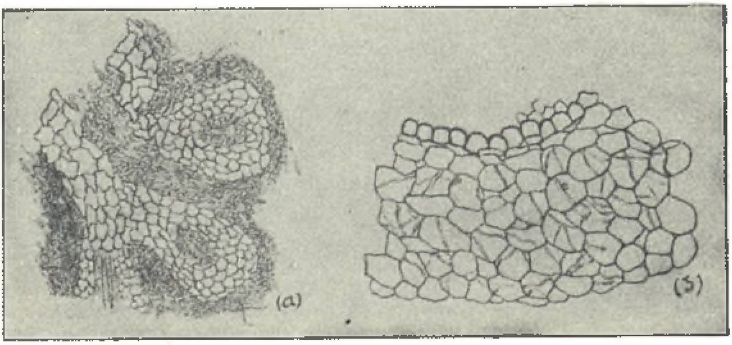


FIG. 2.
Cross section of root of mountain pine (*Pinus montana*) showing envelopment of the root and intercellular penetration of the cortex by the fungus. In the outer cells a large amount of tannin is produced (*a*).



Fi3. G.
Cross sections of " ball " mycorrhiza of mountain pine. The rootlets are embedded in a matrix of hyphae (*a*). A piece of cortex is enlarged to show the intracellular penetration by the fungus (*b*).

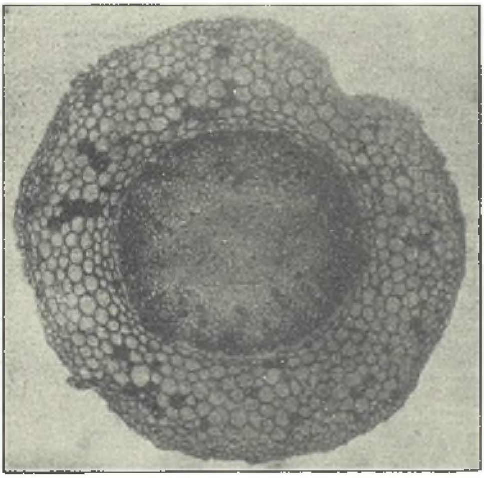


FIG. 1.

Cross section of young root of *Picea excelsa* showing cortex, endodermis, primary xylem, primary resin canals, phloem.

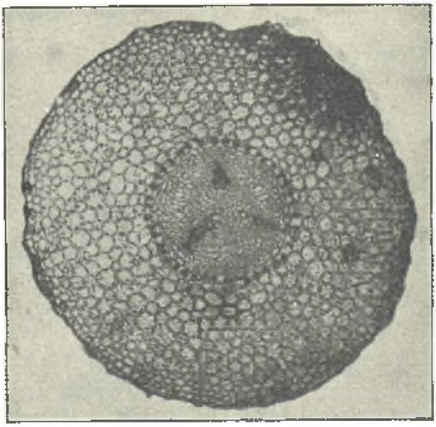


FIG. 2.

Cross section of young root of *Thuya plicata* showing cortex with thickened bands ; endodermis with pronounced casparian strip ; primary xylem ; primary phloem.

PLATE VI.

Fig. 1.

Sitka spruce (*Picea sitchensis*) from peat showing the remains of original root system and the single adventitious root.

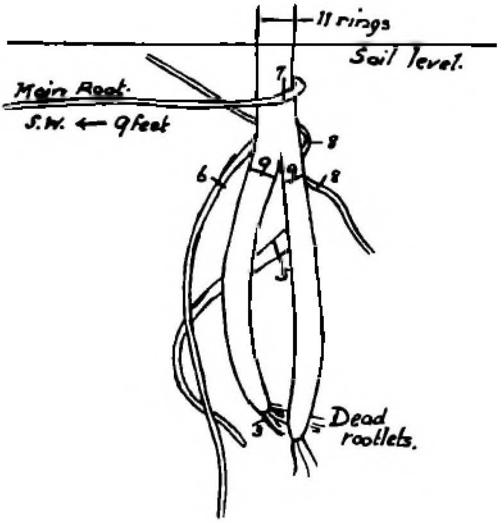


Fig. 2.

Diagrammatic representation of Fig. 1 after plant has been dissected.

## PLATE VII.

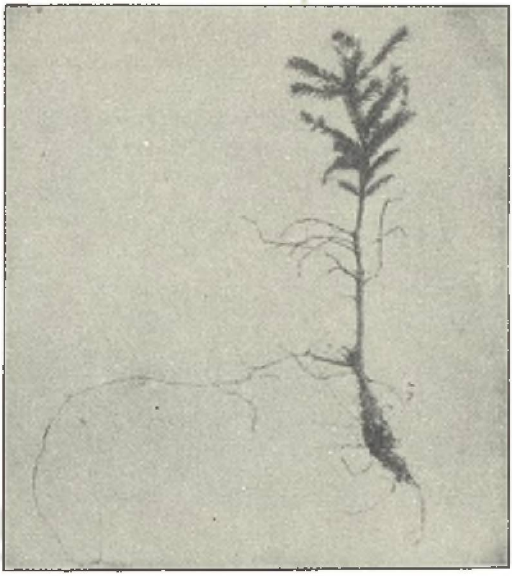


FIG. 1.
Sitka spruce (*Picea sitchensis*) from a peat soil.

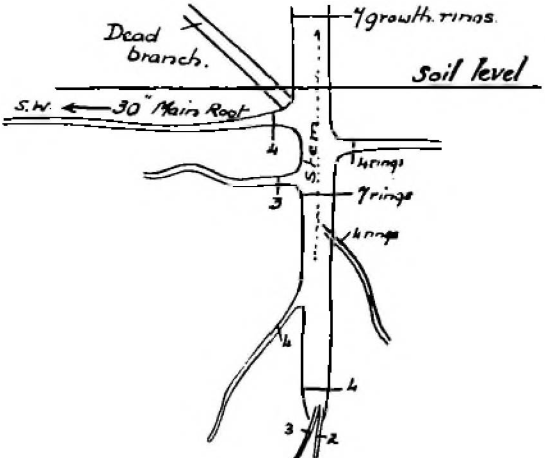


FIG. 2.
Diagrammatic representation of Fig. 1 after plant has been dissected.

PLATE VIII.

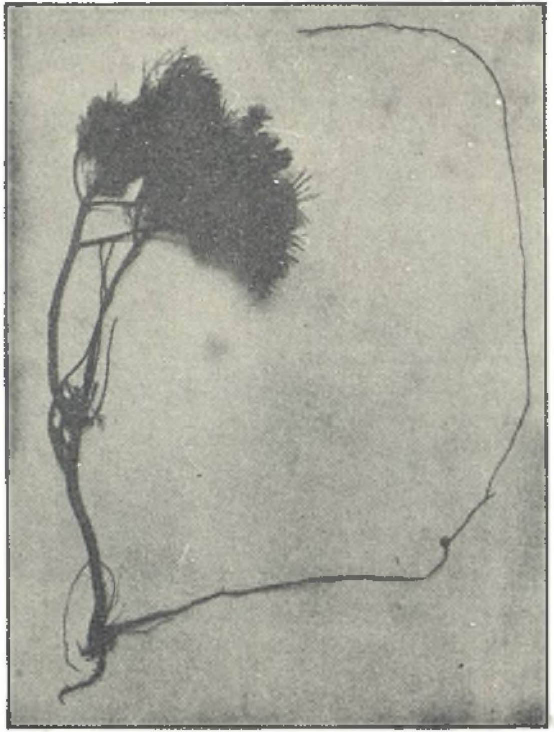


FIG. 1.
Mountain pine (*Pinus montana*) showing remains of nursery root system and single bare long adventitious root.

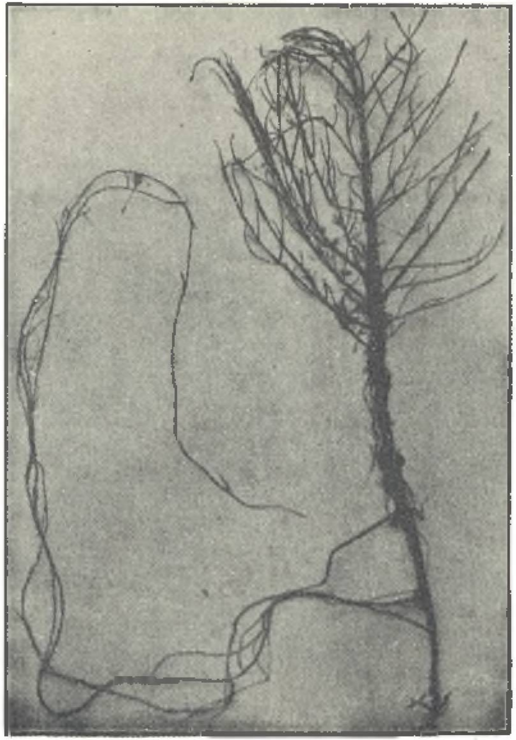


FIG. 2.
Norway spruce (*Picea excelsa*) showing adventitious roots. All the roots have arisen on one side, one above the other. The original root system is dead.

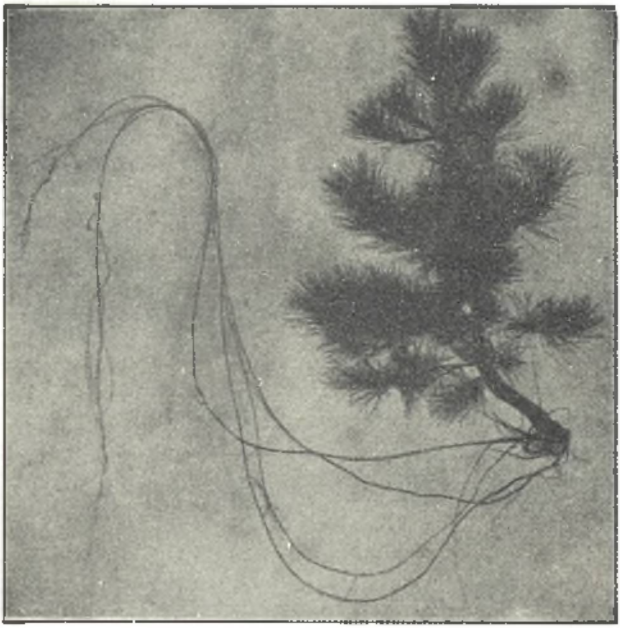


Fig. 1.

Corsican pine from sand showing long bare surface roots. The nursery root system has died.

**Fig. 2.**

Heath (*Calluna vulgaris*) and bog myrtle (*Myrica gale*), showing surface rooting habit in certain peat soils. Note the bare single root of bog myrtle with nodules.

# PLATE X.

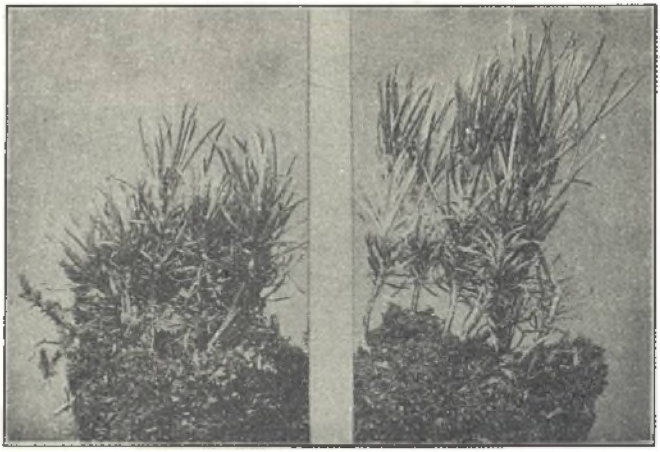


Fig. 1.
*Pinus contorta* raised from seed sown on peat turf. Control (left) and peat treated with magnesium carbonate (right).

Fig. 2.
*Picea excelsa* seedlings on peat; treated with magnesium carbonate (left), and control (right).

Fig. 3.
*Picea sitchensis* seedlings on peat; treated with magnesium carbonate (left) and control (right).

PLATE XI.

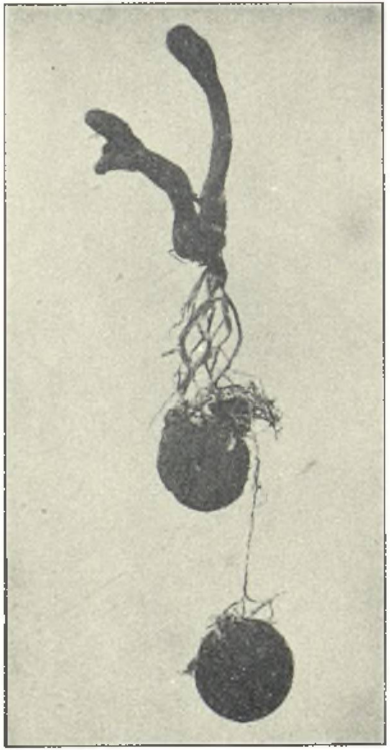


Fig. 1.
*Cordyceps* with yellow hyphae parasitic on false truffle (*Elaphomyces*).

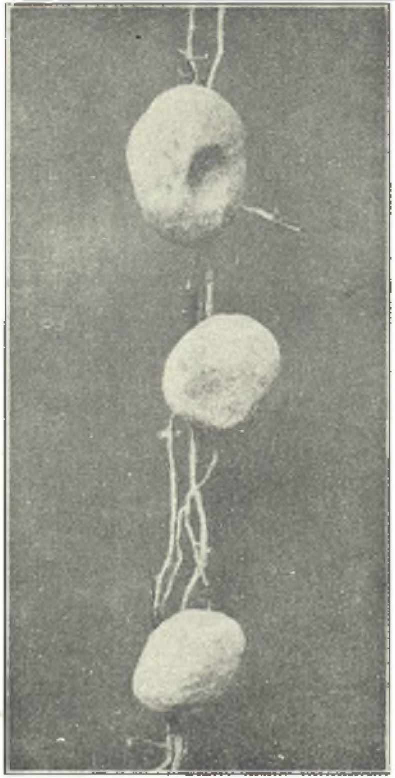
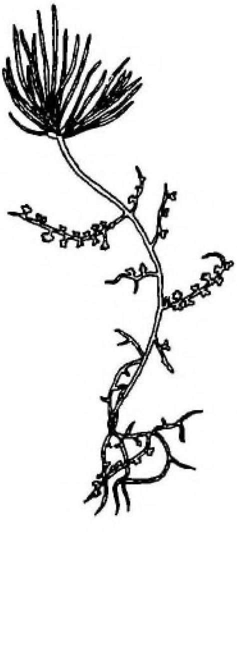


Fig. 2.
False truffle (*Elaphomyces*) on roots of *Pinus sylvestris* (dissected).

FIG. 1.

Section through triarch root of Sitka spruce from peat showing pathological condition, *e.g.*, disintegration of the bast by fungi.



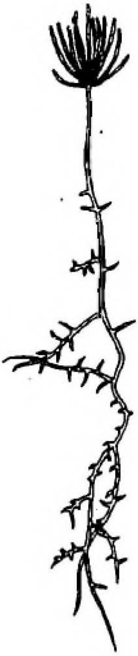


FIG. 2.

Scots pine seedlings from old (left) and new (right) nursery ground.

# PLATE XIII.

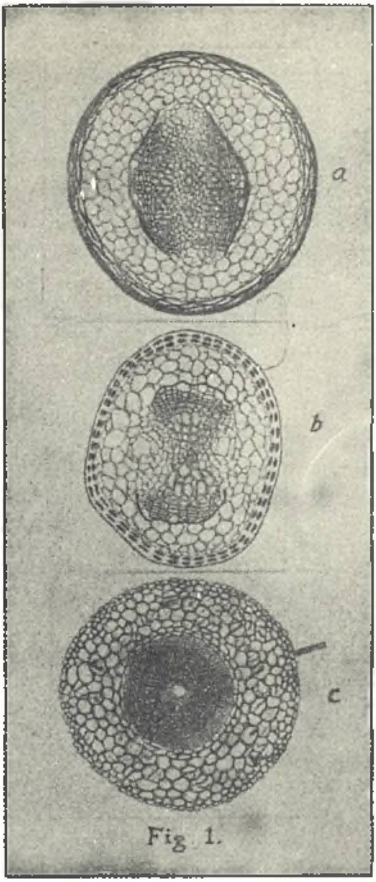


Fig. 1.

Sections of older roots of (*a*) spruce, (*b*) Scots pine, (*c*) silver fir, showing the relative positions of the primary resin canal.

Fig. 2

Aerenchyma on spruce.

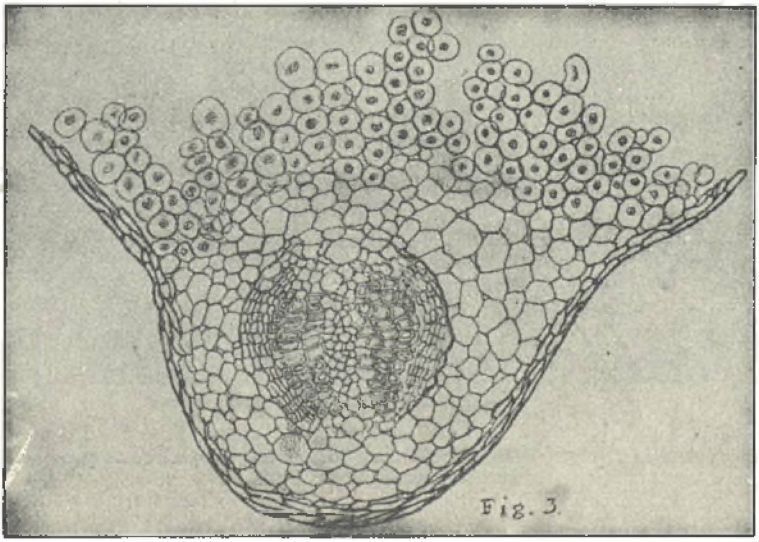
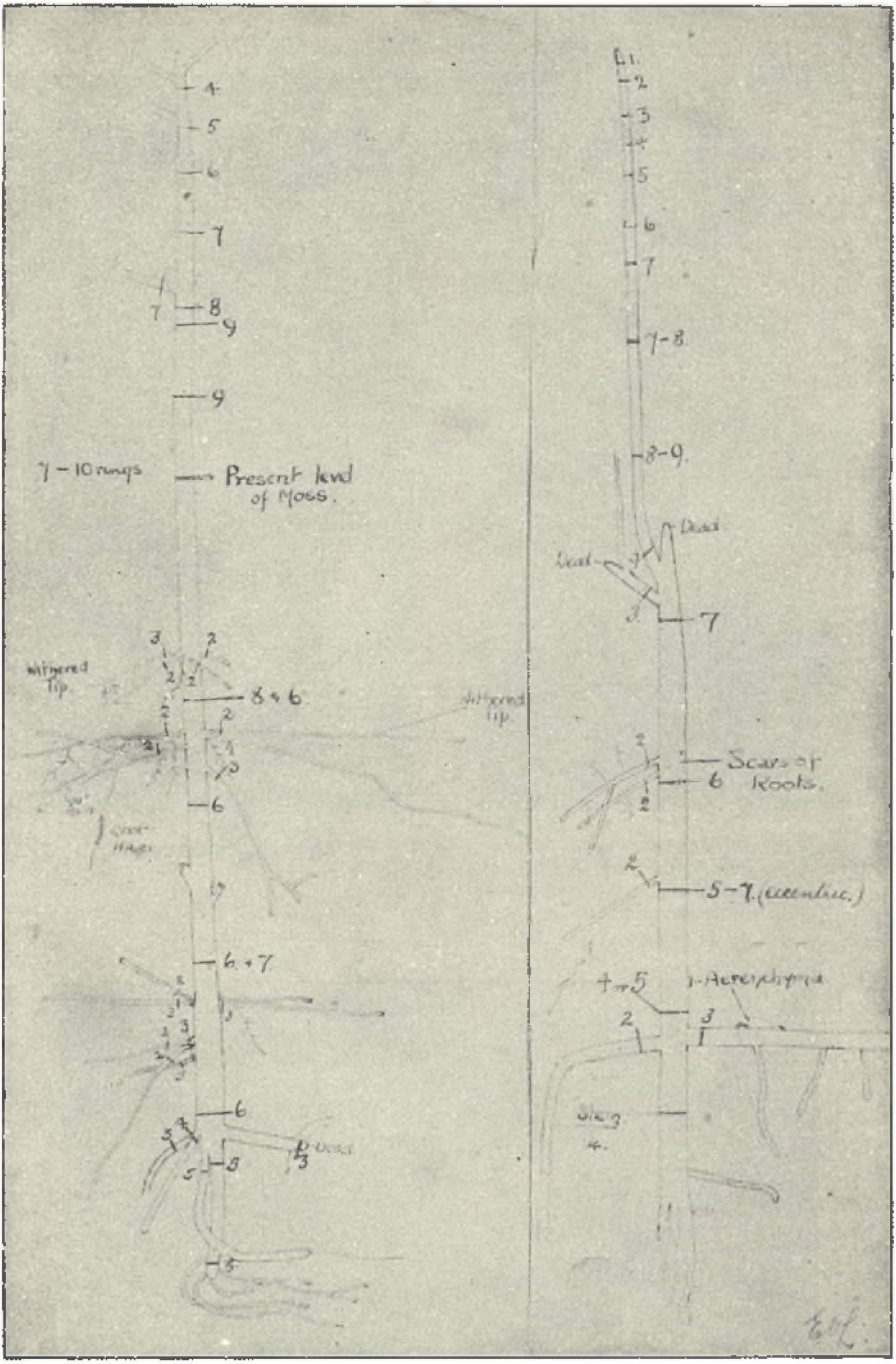


Fig. 3.

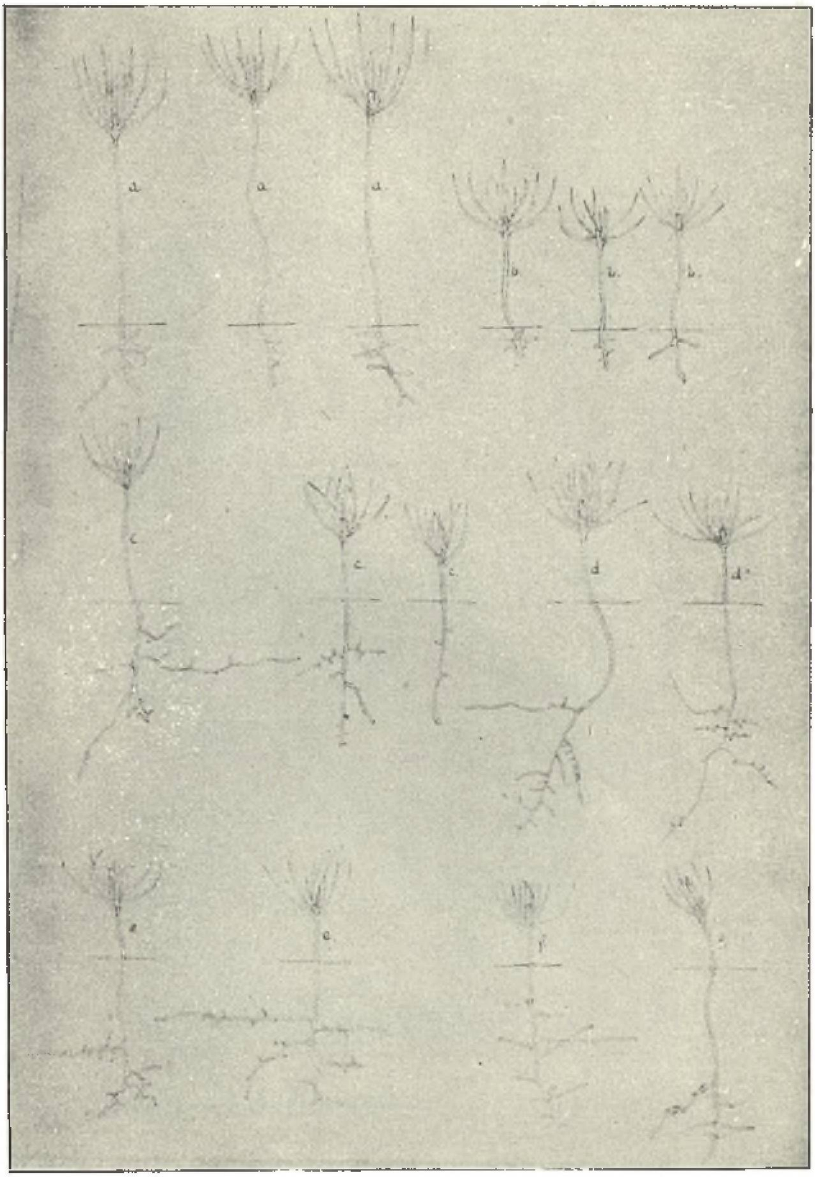
Cross section of aerenchyma pustule.

# PLATE XIV.



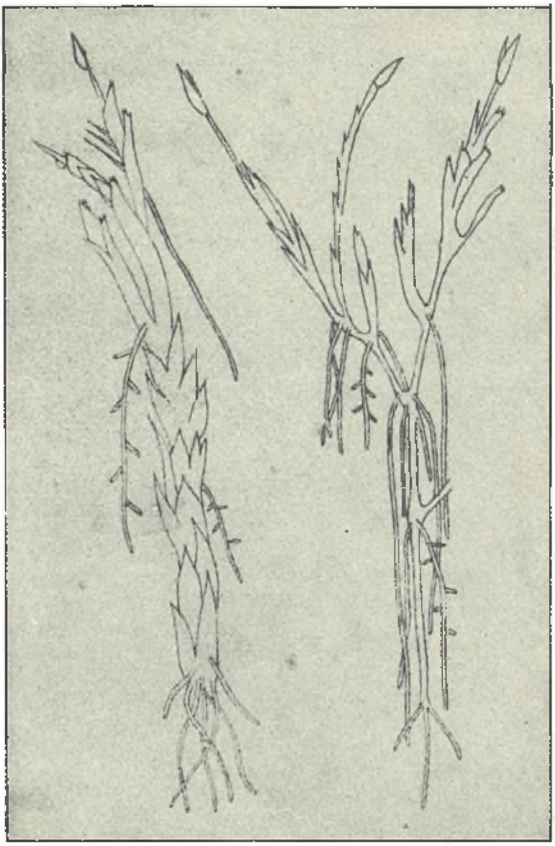
(*a*) (*b*)

Diagrammatic representation of Norway spruce from (*a*) *Calluna* peat, (*b*) *Erica-Scirpus-Calluna-Molinia* peat.



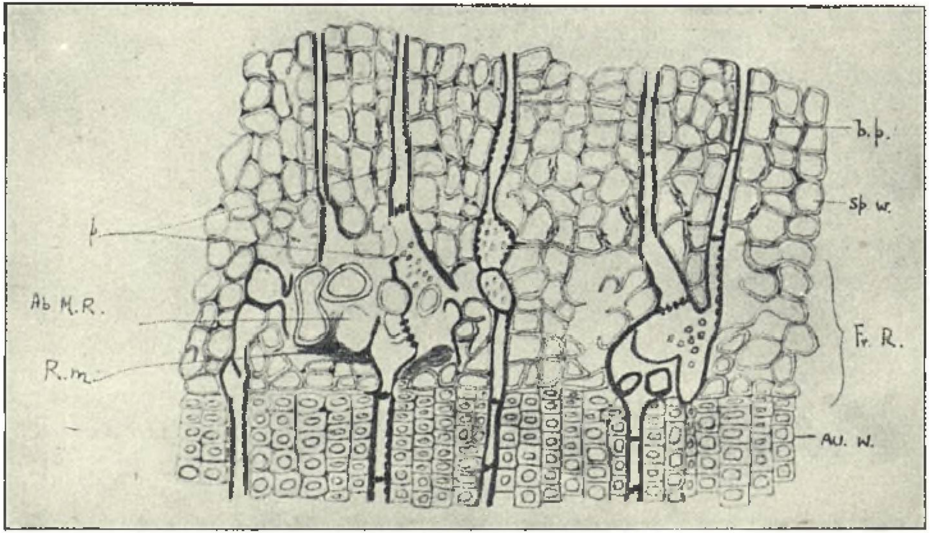
One year old seedlings from peat (slightly reduced).

(*a*) Norway spruce from natural surface.
(*b*) Sitka spruce from natural surface.
(*c*) Norway spruce from screefed patch.
(*d*) Norway spruce from upturned turfs.
(*e*) Norway spruce from screefed patches on burned area.
(*f*) Sitka spruce from screefed patches on burned area.



*Scirpus caespitosus* showing production of roots in whorls.

PLATE XVII.



Frost ring in Sitka spruce.

Fr. R.—Frost ring.
Ab. M.R.—Abnormal medullary ray.
b.p.—Border pit.
p.—Pits.
Sp.w.—Spring wood.
Au.w.—Autumn wood.
R.m.—Resinous material.

# BIBLIOGRAPHY

(1) Borthwick. *Scottish Forestry Journal*, Vol. 42, Pt. 2, 1928.

(2) Boyer, G. *Actes Soc. Linn.*, Bordeaux. *Proces verbaux*, 1915–16.

(3) Costantin. *Annales des Sciences Naturelles*, Tome IX, 1, 1927.

(4) Cox. *United States Dept. of Agric. Weather Bureau, Bull.* No. 1, 1910.

(5) Craib. Notes *R.B.G.* Edinburgh, Vol. XI, No. LI, Nov., 1918.

(6) Dachnowski. *Bot. Gazette*, 46.

(7) Elenkin A. A. *Jahrb. f. Pflanzenkrankh.*, 1, 1907.

(8) Emerson. *Bot. Gaz.*, 1921.

(9) Engler. *Mitt. d. Schweiz. Centralanst. f.d. forstl. Versuchw.*, VII, 1903.

(10) Englis and Lunt. *Soil Science*, Vol. XX, No. 6, 1925.

(11) Falck. *Mycol. Untersuch. u. Ber.*, 2. Cassel, 1923.

(12) Frank, A. B. *Ber. d. deutsh. Bot. Gessellsch.*, 3, 1885 ; 6, 1888; 10, 1892. *Lehrbuch der Botanik.*, Bd. 1, 1892. *Fortwiss. Centralblatt*, 16, 1894.

(13) Fuchs, J. *Bibl. Bot.*, 18, 1911.

(14) Gibelli, G. Bologna, 1883.

(15) Gola. Rev. by Cavers. *Jour. Ecol.*, Vol. 2, 1914.

(16) Haag and McCall. *Soil Science*, Vol. XII, No. 1, July, 1921.

(17) Haberlandt. *Physiological Plant Anatomy.*

(18) Ingle. *Manual of Agricultural Chemistry.*

(19) Jodidi. *Mech. Agric. Coll. Exp. Stat. Bull.* 4, 1909.

(20) Kauffmann. *Bot. Gazette*, 42, 1906.

(21) Khorstian. *Jour. Agric. Research*, Vol. XXVIII, No. 9, 1924.

(22) Laing. *Trans. Roy. Scot. Arbor. Soc.*, Vol. 37, Pt. 1, 1923.

(23) —— *Ibid.*, Vol. 40, 1926.

(24) —— *Scot. Journ. of Forestry*, Pts. 1 and 2, 1927.

(25) Lange. *Dans. Bot. Ark.*, 4, 1925.

(26) Lewis. *Proc. Linn. Soc.*, London, Dec., 1925.

(27) Liese. *Zeitschr. f. Forst-u. Jagdwesen*, 1926.

(28) Livingstone. *Bot. Gaz.*, 37, 1904 ; 39, 1905.

(29) Mangin. *Nouv. Arch. du Musee d'Hist. Nat.*, Paris, Ser. 5, 2, 1910.

(30) Masui. *Memoirs of the College of Science*, Kyoto Imperial Univ., Vol. 2, No. 1, 1926.

(31) McDougall, W. B. *Amer. Journ. Bot.*, i, 51, 1914 ; *Amer. Journ. For.*, XX, iii, 1922.

(32) Melin, E. Untersuchungen uber die Bedentung der Baummykorrhiza Gustav Fischer, 1925.

(33) Möller, A. *Zeitsch. f. Forst-u. Jagdwiss.*, 34, 1902 ; 35, 1903 ; 36, 1904.

(34) Muller, P. E. *Tidsker, f. Skovbr.*, 1903; *Medd. Forstl. Forsogsoesen*, 1905–08.

(35) Neger. *Naturwiss. Zeitsch. f. Forst-u. Landwerts.*, 1906.

(36) Noack, R. *Bot. Zeit.*, 47, 1889.

(37) Peyronnel. *Bul. Soc. Bot. Ital.*, 1922.

(38) Prat, H. *Annales des Sciences Naturelles*, Tome VIII, Nos. 1 and 2, 1926.

(39) Rayner. *Annals of Botany*, Vol. XXIX, No. CXIII, Jan., 1915.

(40) Rexhausen. *Beitr. z. Biol. d. Pflanz.*, 14, 1920.

(41) Rigg. *Bot. Gaz.*, 55 ; *Bot. Gaz.*, 61 ; *Amer. Jour. Bot.*, 3, 1916.

(42) Rigg and Thomson. *Bot. Gaz.*, 68, 1919.

(43) Robinson. *Mich. Agric. Coll. Exp. Stat. Tech. Bull.*, 7, 1911.

(44) Sarauw. *Rev. Mycol.*, 26, 1904.

(45) Stahl. *Jahrb. f. wiss. Bot.*, 34, 1900.

(46) Transeau. *Bot. Gaz.*, 40, 41.

(47) Truog. *Soil Science*, Vol. V, No. 3, 1918.

(48) Von Tubeuf. *Naturw. Zeitsch. f. Land- und Forstwertsch.*, 1, 1903.

LONDON
PUBLISHED BY HIS MAJESTY'S STATIONERY OFFICE
To be purchased directly from H.M. STATIONERY OFFICE at the following addresses:
York House, Kingsway, London, W.C.2; 13A Castle Street, Edinburgh 2;
39–41 King Street, Manchester 2; 1 St. Andrew's Crescent, Cardiff;
80 Chichester Street, Belfast;
or through any bookseller
1932
(Reprinted 1947)
Price 3*s*. 6*d*. net

S.O. Code No. 70–31–13