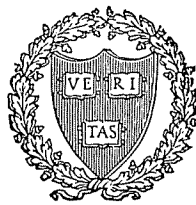


FUNGAL HYPHAE AND THE
MORPHOLOGY OF B HORIZONS
OF NEW ENGLAND SOILS

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ABSTRACT

Fungal hyphae are numerous in the B horizons of sandy and loamy Brown Podzolic (Orthod) soils of New England and are attached to, or enmesh soil particles. They probably account in large part for the massive condition of the undisturbed moist soil material and, to some degree at least, for the weak very fine granular structure of disturbed soil.

INTRODUCTION

Need for the identification of microscopically small features, such as clay films, in the classification of soils has led to increased use of the hand lens and low-power microscopes by field soil scientists. Over a period of about 15 years repeated microscopic examination by the writer of small fragments from the B horizon of sandy and loamy Brown Podzolic (Orthod) soils in New England invariably has revealed a network of fungal mycelium and it seems probable that enmeshment of soil particles by fungal vegetative tissue accounts in large part for the characteristic massiveness and very friable consistence of these soils and perhaps accounts for similar properties in other soils as well.

This paper is written primarily to call the attention of soil scientists, especially those interested in soil morphology, to the importance of fungal mycelium as a morphologic agent and to describe a simple means of demonstrating the presence of fungal hyphae in small soil fragments.

REVIEW OF LITERATURE

The binding effect of bacteria and fungi on silt and clay particles is well known as a result of numerous experimental studies dealing with the formation of aggregates in the soil. But generally these studies have been concerned with the improvement of structure in the plow layer and emphasis has been placed on the influence of the microbial decomposition products rather than the organisms themselves.

Since about 1950 increased attention has been paid to the fungal vegetative growth in soil, especially in Great Britain (Parkinson and Waid 1960, Garrett 1963). Burges and Nicholas (1961) indicated that hyphae in a sandy Podzol in July had lengths of about 6 meters of hyphae per milliliter of soil volume in the H horizon, 4 meters in the A1 and A2 horizons, 1 meter in the B1 and 0.4 meters in the B2 horizons. Barratt (1962) showed the en-

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meshing effect of hyphae around sand particles in sand dunes. Burges (1963) described the relationship between hyphae and soil particles in a sandy Podzol in considerable detail and pointed out the tendency for hyphae to be closely attached to some grains. Williams (1963), separated discrete soil particles to which hyphae were attached and showed that some species of fungi decreased in frequency with depth whereas others had a maximum in the lower horizons.

Two recent studies are especially valuable from the standpoint of soil morphology. Bond and Harris (1964) in Australia noted that hyphae are persistent within aggregates of fine-textured well-structured soils and also pointed out that an intense proliferation of mycelium always occurs in the massive horizons of sandy soils. Schramm (1966) in Pennsylvania made detailed studies of mycorrhizae and associated fungal vegetative tissue. His photographs of hyphae with adhering mineral particles are excellent.

MATERIAL AND METHODS

Characteristics of the B horizon of typical Brown Podzolic Soils.

Brown Podzolic soils of New England have thin forest floors of the moder type, thin A1 horizons, and B horizons in which the color is strongest in the upper part gradually paling with depth. The major cause of the color of the B horizon is the accumulation of highly colored sesquioxide-humus substances on or between the mineral particles. There is essentially no silicate clay eluviation.

Consistence of the soil material in the upper B horizons of sandy or loamy Brown Podzolic, such as the Gloucester soils, is loose to very friable when moist¹ and very little pressure is required to crush the material. When dry the soil material crushes to a powder condition with even less pressure. Careful examination shows that the moist soil material is massive in place and exhibits a complete lack of structure. No natural ped faces can be observed in undisturbed soil but when the soil is disturbed slightly, it easily fractures into angular clods (Figure 1). The location of the faces of the angular clods is dependent on the magnitude and direction of the fracturing force rather than on zones of natural weakness. For example, a large moist clod dropped on a hard surface breaks up into many sizes of clods, most of which are 5 cm or less in diameter and none of which show any natural faces. If the soil fragment is broken in the hands almost any shape of clod can be made by exerting gentle pressure; there are no zones of weakness along which the soil fractures preferentially. When examined under the microscope the faces of the clods formed by dropping do not appear different from surfaces made by fracturing the clod in the hands. The surface consists of a succession of protruding sand grains and adjacent cavities much like that of coarse sandpaper and there are no smooth, dense, silty or clayey films such as those on the outside of the natural subangular blocky peds that characterize the B horizons of many Alfisols (Gray Brown Podzolic Soils).

There is always some variation among soil scientists in clasifying the grade of structures in the upper B horizon of the sandy Brown Podzolic soils of New England, even though

¹ Terminology follows that of the Soil Survey Manual U.S. Dept. Agri. Handbook 18, 1951, and Soil Classification: A Comprehensive system 7th Approximation: Soil Survey Staff, Soil Conservation Service, U.S. Dept. of Agri. August 1960.

all use standardized descriptive terms. Most agree that the smaller units of the crushed soil material are very fine granules even though they are irregular, angular, very porous and only a millimeter or so in diameter. These granules are thought to qualify as peds rather than clods because they exist as discrete units in the undisturbed soil and because the faces are natural. There has been somewhat less agreement about the structure of the soil in place. Many think the soil has very weak medium or coarse subangular structure; others think the soil is massive and lacks any kind of structure.

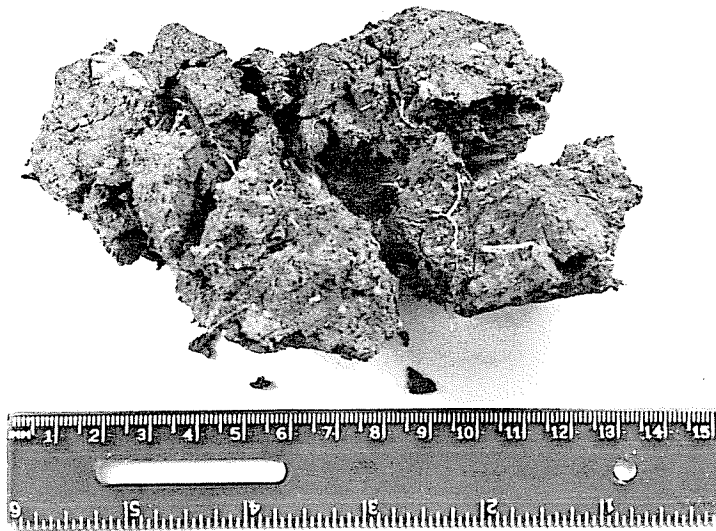


Figure 1 Characteristic fracture into angular clods of massive material from the B horizon of the Gloucester soil series.

In large measure the disagreement about structure probably occurs because the soil is not repeatedly examined in the same place to see how it changes in appearance from season to season.

The true situation was revealed to the writer following a detailed study of moist soils made during the late fall of 1955 on an 8 acre tract of the Tom Swamp I tract of the Harvard Forest, at Petersham, Massachusetts. (Lyford, Goodlett & Coates 1963). Detailed descriptions were made of Paxton and Woodbridge soils in about 50 pits and particular attention was given the structure of the upper B horizon. This was described as weak medium subangular blocky structure because at that time the faces of the soil fragments were thought to be natural, truly represented natural planes of weakness, and year after year would always part along the same planes of weakness. Disillusionment came when these same soils were re-examined in place the next year following a period of low rainfall.

Then the upper B horizon material was almost powder-like and no vestige of subangular blocky structure remained. This effectively demonstrated the lack of natural planes of weakness in these soils and led to the hypothesis that the lack of structure and weak consistence results in large part from the influence of fungal hyphae. These hyphae had been observed repeatedly during microscopic examination of the B horizons of Brown Podzolic soils during the previous three or four years.

Enmeshment of sand particles by fungal hyphae

The manner by which fungal hyphae enmesh sand particles in the B horizon of Scituate fine sandy loam, a moderately well-drained soil at the Harvard Forest, is shown in Figure 2. Enmeshment of almost every sand particle in the B horizon occurs. In fact, as Buller (1933) points out, fusion of one hypha with another is common and so the network of fungal mycelium in the soil is probably three dimensional. Thus each particle is held physically in place as though in a basket.

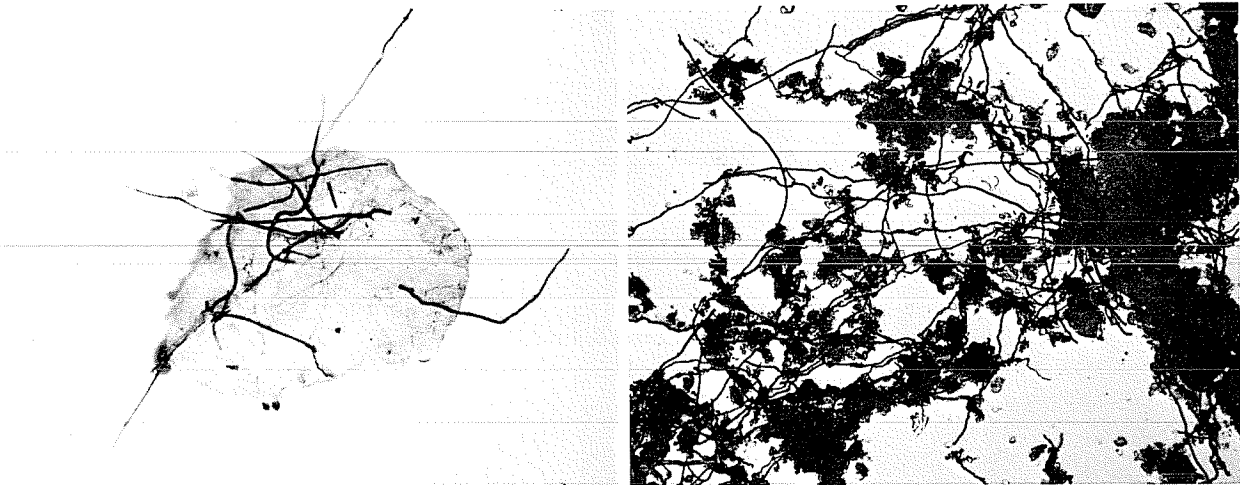


Figure 2. Photomicrograph showing (left) hyphae 2-5 μ in diameter attached to and enmeshing a sand particle from the B horizon of the Gloucester soil series, and (right) an interwoven mass of hyphae and bits of humus remaining after the sand particles have been washed out.

Methods of demonstrating presence of fungal hyphae.

Although masses of fungal vegetative growth in the form of mycelium, strands, wefts or rhizomorphs are readily visible to the unaided eye in most B horizons of sandy and loamy well-drained soils in New England an individual hypha is too small to be seen. Hyphae are only 1-5 microns in diameter (the diameter of a fine silt particle) and even when examined under 60 power magnification are not readily visible in the soil unless heavily pigmented, suspended across a cavity, or artificially stained by means of a dye such as 1 per cent aqueous crystal violet.

But although not readily visible the presence of fungal hyphae or mycelium in the soil can be demonstrated easily by taking advantage of the effects resulting from the enmesh-

ment of the soil particles. A satisfactory and quick method mentioned by both Hubbell and Chapman (1946) and Bond and Harris (1964) is to place a fragment of freshly collected moist B horizon about 5 mm in diameter in water in a shallow container such as a petri dish or saucer. When the fragment is crushed with the tip of the finger and the resulting crushed mass gently washed back and forth the larger sand grains are gradually freed from the fungal network by the wave action and sink to the bottom of the dish where they remain stationary. The remaining mass is now buoyed up slightly by the hyphae and continued wave action causes still further disentanglement of the larger sand grains. Finally there remains a tangled mass consisting of hyphae, bits of other organic matter, a few medium and coarse sand particles, and a considerable amount of fine sand and silt, (Figure 2). This mass is now buoyed sufficiently so that it rolls along the bottom of the dish by the continued wave action. The buoyed masses gradually become entangled with one another and roll up in long, narrow cylindrical masses in parallel rows (Figure 3) appearing somewhat like tangled masses of fine cotton fibers. Hyphae still are not visible to the unaided eye but their presence is strongly indicated by the manner in which the rolled-up masses can be pulled through the water by a needle. Examination of a stained portion of the mass at 60 power or greater magnification reveals the hyphae and effectively counteracts the idea that only electrostatic forces are involved. The presence of a single hypha also can be demonstrated without staining even though it cannot be seen by the unaided eye. For example, a silt-size particle attached to a stationary sand particle by a single hyaline hypha is conspicuous in the gently agitated water by its flag-like "waving" back and forth. Also in a dry soil fine sand particles suspended like beads along an individual hypha (the festoons of Bond and Harris, 1964) can be seen dangling from the edge of a soil fragment if the soil mass is slightly disturbed.

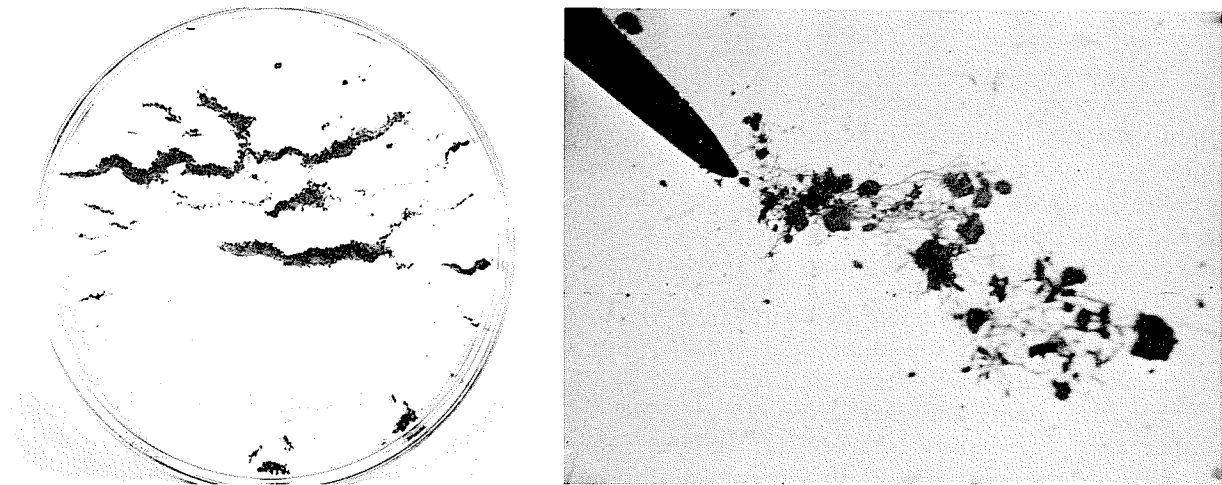


Figure 3 Masses of hyphae and humus roll up into parallel rows (left) when the water in the petri dish is moved gently back and forth. Portions of these rolled up masses can be pulled through the water with a needle (right). After staining, the hyphae can be seen readily under magnification.

In some soils the presence of the network of fungal hyphae can be demonstrated more readily if a chemical dispersant such as sodium hexametaphosphate (Calgon) is used. The fine material in suspension is removed by decantation leaving masses of fungal hyphae still enmeshing by sand particles. For such a demonstration chemicals that cause flocculation of the fine material should not be used because the "flocs" tend to form rolled-up masses even in the absence of filamentous vegetative growth. It is always desirable therefore to demonstrate the actual presence of hyphae by microscopic means.

DISCUSSION

A high proportion of sand grains in the B horizon of Brown Podzolic soils have hyphae firmly attached to their surfaces as well as being enmeshed in a mycelial network. Microscopic examination suggests that most of the hyphae are attached to the sesquioxide-humus coating rather than to the bare surface of the sand particles (Figure 2). Sand particles from the upper part of the B horizon are almost completely coated with yellowish-red sesquioxide-humus which is intermixed with silt, very fine sand and clay. A clean mineral surface on a sand particle in this portion of the horizon is rather hard to find. With depth the coatings become patchy and in the lower part of the B horizon sand particles have less than 25 per cent of their surface coated. Hyphae attached to medium and coarse sand particles in the upper B horizon apparently are attached to sesquioxide-humus coatings. Portions of some hyphae are completely buried in the coating and it seems likely that this is a result of penetration by hyphae as they grow. In fact some fungi may use the humus in the coatings as a source of energy. Burges (1963) suggested that certain long-lived basidiomycetes may gradually break down the dark colored humus material in the uppermost portion of the B horizons of some Podzols. The hyphae of some fungal species growing in the soil (Pramer, 1964; Schramm, 1966) are sticky and simple adhesion may account for a good deal of the effects of fungal vegetative growth on the character of the soil but this is thought to be less important than enmeshment and attachment as a cause of the massive nature of these soils.

The massive condition of the upper portion of the B horizon of moist Brown Podzolic soils in New England is without doubt the result of a combination of several different forces among which are cohesive and adhesive forces caused primarily by moisture films around particles, bridging across particles by sesquioxide-humus substances, enmeshment and attachment of soil particles by fungal hyphae, gluing by mucilaginous microbial decomposition products, direct effects of bacteria either as individuals or as colonies, and probably many other agencies. Of these various agencies, however, the effect of the fungal hyphae is thought to be a major factor.

Although the strength of an individual hypha is slight the combined strength of all the hyphae in a small mass of soil is sufficient to account for the manner by which the soil material is held together. According to Burges (1963) there can be as much as a meter of fungal hyphae per milliliter of B horizon material in sandy Podzols and this probably holds true for sandy and loamy Brown Podzolic soils of New England as well. If the mycelium in the soil exists in a three-dimensional network as a result of numerous fungal fusions between adjacent hyphae (Buller 1933) the force is exerted more or less equally in all directions and counteracts any tendency to form planes of weakness.

When the B horizon of a sandy Brown Podzolic soil dries in place it tends to slake and become a loose powdery mass consisting mostly of irregular shaped fragments 1/2-1 mm

in diameter. Slaking to the powdery mass possibly takes place because the hyphae become brittle when dry (McLennon 1928) and are no longer strong enough to hold the soil material in a large mass yet are strong enough to hold a few grains of sand together. Many, if not most, of the individual tiny angular soil fragments (commonly described as weak very fine granules) consist of a porous mass of weakly adhering mineral particles held together by hyphae. Growth of hyphae is initiated when the dry powdery soil again becomes moist.

The presence of fungal mycelium probably accounts not only for the characteristic lack of structure but also the characteristic very friable consistence and low bulk density ("fluffiness") in the upper part of the B horizon of Brown Podzolic soils. Alexander (1961) believes that in well-aerated, cultivated soils fungi make up the largest part of the total microbial protoplasm and there may be from 10 to 100 meters of fungal filaments per gram of soil. Thomas et al. (1965) measured from 90-141 meters per gram in the soil they studied.

Apparently there is considerable variation in the length of life of the fungal filaments depending not only on the species but also the environment in which they grow. Some hyphae may live only a day or two before being destroyed by bacteria or eaten by mycophagous fauna such as mites. But some species are long-lived and produce a large mass of tissue. Under ideal laboratory conditions some hyphae may grow up to a centimeter in length per day. (Burgess 1960). Some idea of the magnitude and rapidity of some kinds of fungal tissue growth can be obtained by observation of the rapidity of growth of fleshy mushrooms. It is not at all unusual for the fruiting body of a fleshy mushroom weighing up to 500 grams to appear above the surface of the soil in forested areas within a period of 2 or 3 days. This mass of fungal tissue is all derived from mycelium growing in the soil.

Many species of fungi exist in the soil. Raymond (1954) found 50 or more species in three soil samples collected at the Harvard Forest; Williams (1963) listed about 40 kinds from a sandy Podzol in England and Warcup (1957) identified 210 species in an Australian pasture soil. This large number of species makes it unlikely that any portion of the soil lacks mycelium for more than a short period of time.

Mycelium is not limited to the solum. Its presence in freshly exposed deep strata of sand and gravel banks can be demonstrated by the presence of festoons if the dry soil surface is very gently disturbed.

Most hyphae have a diameter of about 1 to 5 μ and this is also the diameter of fine silt particles. Thus to the fingers a mass of moist hyphae has much the same feel as a mass of moist silt particles. This may be one reason why texture determined by feel is not always close to the texture determined by particle-size analysis in the laboratory.

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