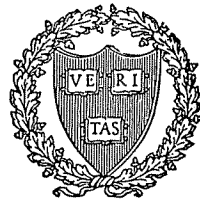


IMPORTANCE OF ANTS
TO BROWN PODZOLIC SOIL GENESIS
IN NEW ENGLAND

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Abstract

Return of subsoil material to the forest floor in small litter-concealed mounds by ants is an important process in the development of the Brown Podzolic soils of New England and probably in other kinds of soils elsewhere. Material brought back to the surface may built up to a thickness of an inch within 250 years. In fact, the entire A horizon of some, if not most, virgin Brown Podzolic soils in New England consists of material returned by ants to the surface from the B horizon over a period of many years. Conceivably a thickness of as much as 10 to 18 inches of soil material could be returned to the surface in a period of 3-4000 years.

Introduction

In studies of the genesis of podzolic soils major emphasis generally is placed on downward movement of materials from the upper few inches of the soil with subsequent accumulation in the lower part. Aside from the well known effect of earthworms first publicized by Darwin there has been very little work on processes leading to upward movement in podzolic soils. This paper calls attention to the role which ants play in the development of the Brown Podzolic soils of New England and attempts to evaluate the rate and importance of return of subsoil material to the surface in small litter-concealed mounds by ants in forested stony gravelly Gloucester soils at the Harvard Forest. The process here is of the same kind and magnitude as that seen by the writer in many other parts of eastern North America in the past 25 years but is more noticeable than in some places because the non-gravelly ant mound material contrasts

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sharply with the stony gravelly soil material where the ant tunnels and galleries are built. Ants are just as active in silty soils but the material returned to the surface is not of contrasting texture. This, and the tendency of soil scientists to attribute all silty material on the surface to wind action or weathering, may be the reason the importance of the action of small mound-building ants to soil genesis has been overlooked previously in areas outside the tropics.

Grateful acknowledgment is made to J.G. Cady, E.L. Stone, and the writer's colleagues at the Harvard Forest for helpful discussion. Especially thanks go to E.O. Wilson for identification of the ant species. Funds for this publication have been supplied from generous gifts by the Friends of the Harvard Forest.

Review of Literature

The activity of ants and termites in making conspicuous mounds is well known, especially in tropical regions (Nye, 1955) but their importance to soil genesis in the United States has been studied very little. Many years ago, Shaler (1891) called attention to the deposition of at least one-fifth inch of material yearly by ants on the surface of a field near Cambridge, Mass. Bryson (1933) measured the amount of soil returned to the surface by insects, including ants, in Kansas. Jacot (1936) stated that ants were the most active soil animals and every square yard of vegetated mesic soil contains at least one colony. Talbot (1948), Headley (1949, 1952), and others studied the nest building of ants but were not concerned with their effect on soil formation. Thorp (1949), MacAloney and Hosley (1934), and others described the rather conspicuous ant mounds that are a foot or more in height. No one has evaluated the importance of the ants that build small mounds to soil genesis.

Vegetation and Soils

This study was made in 30-60 year old hardwood stands in Compartments I and VIII, Prospect Hill Tract, Harvard Forest, Petersham, Massachusetts, on gently rolling areas of Gloucester stony gravelly sandy loam. Red oak (Quercus rubra)² and red maple (Acer rubrum) are the predominant trees. The areas were cleared and pastured in the late 1700's but never plowed. Nearly pure white pine (Pinus Strobus) stands grew on the areas after abandonment in the mid-1800's. These were cut about 1900 and followed by the present hardwood stands, (Fig. 1). Vegetation on a typical study area is as follows:

Primary species	Secondary species
Trees - <i>Quercus rubra</i> <i>Acer rubrum</i>	Trees - <i>Pinus Strobus</i> <i>Betula lenta</i> <i>Betula lutea</i> <i>Fagus grandifolia</i> <i>Quercus alba</i>
Shrubs - <i>Gaultheria procumbens</i> <i>Vaccinium angustifolium</i>	Shrubs - <i>Kalmia angustifolia</i> <i>Vaccinium corymbosum</i> <i>Viburnum acerifolium</i> <i>Viburnum cassinoides</i>
Herbs - <i>Lycopodium complanatum</i> var. <i>flabelliforme</i> <i>Lycopodium obscurum</i> var. <i>dendroideum</i> <i>Dennstaedtia punctilobula</i> <i>Pteridium aquilinum</i> var. <i>latiusculum</i> <i>Maianthemum canadense</i> <i>Trientalis borealis</i>	Herbs - <i>Polygonatum biflorum</i> <i>Cypripedium acaule</i> <i>Crataegus</i> sp. <i>Rubus hispidus</i> <i>Aralia nudicaulis</i> <i>Pyrola rotundifolia</i> var. <i>americana</i> <i>Melampyrum lineare</i> <i>Mitchella repens</i> <i>Aster umbellatus</i> <i>Prenanthes altissima</i>
Regeneration - (tree species) <i>Betula lenta</i> <i>Castanea dentata</i> (sprouts) <i>Quercus alba</i> <i>Quercus rubra</i> <i>Acer rubrum</i>	

Mosses are rare and occur only on stones, tree-throw mounds, stumps, and tree trunks.

2- Scientific nomenclature follows that of Gray's Manual of Botany (8th Edition).



FIGURE 1

A hardwood stand on the Harvard Forest where small litter-concealed ant mounds are numerous. The large trees are red oak.

Gloucester soils are well or somewhat excessively drained Brown Podzolic soils developed from bouldery stony gravelly sandy glacial till of Wisconsin Age derived from granite and mica schist. Brown Podzolic soils have thin forest floors of the moder type, thin A₁ horizons, and B horizons in which 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 in Brown Podzolic soils. Details of the genesis and morphology of these soils can be obtained from recent publications (Northeast Soil Research Committee, 1954; Prince and Raney, 1961).

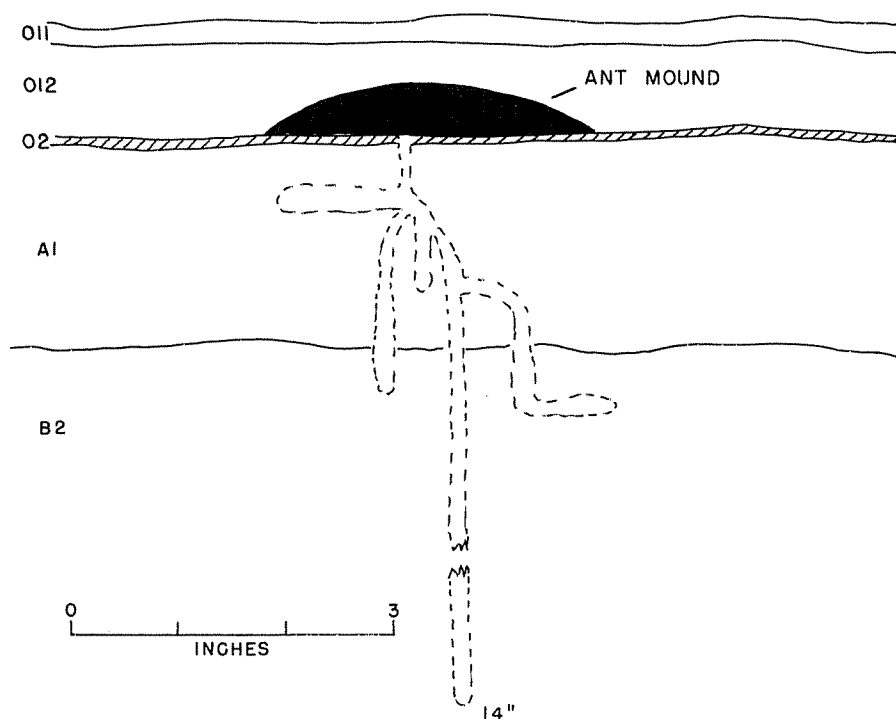


FIGURE 2

Schematic diagram of a litter-concealed small ant-mound showing typical position of the mound within the forest floor, overlying the O2 horizon.

The forest floor in the study area is representative of forested Brown Podzolic soils. It is described here because ant mounds occur within its confines, Figure 2. The 1/2-inch loose litter on the surface -- the O11³ (L) layer -- consists mostly of entire leaves or needles fallen during the past year and weakly, or not at all, tied together by fungus mycelium. Below the litter is an inch-thick layer of partially disintegrated leaves, needles, and twigs from the previous several years of litter-fall -- the O12 (F) layer -- representing an accumulation of 3 to 5 years. This is completely tied together by mycelium and rootlets. It shows increasing disintegration with depth and also an increasing intermixing with mineral particles. Abruptly underlying this is a 1/8-1/16 inch black layer -- the O2 (H) layer -- consisting of a mixture of finely divided organic matter and mineral particles. A few of the mineral particles

3- Symbols are those proposed in the May, 1962, supplement to the Soil Survey Manual, U.S.D.A. Handbook No. 18, 1951.

are shiny and completely clean but most have yellowish brown or black coatings. The finely divided organic matter seems to be coprogenic and to consist mostly of the excrement of litter-dwelling microscopic-sized arthropods such as mites and spring-tails, both of which are known to exist in forested soil in enormous numbers (Johnston, 1936; Kevan, 1962). Ant mounds generally are built over this O₂ layer and within, or on, the O₁₂ layer.

Procedure

Prevalence of small mounds on the surface of the soil was determined by raking away the litter and partially decomposed portion of the forest floor in square yard areas. The circular yellowish brown mounds are conspicuous on the black background of the O₂ horizon. Particle size distribution in individual ant mounds from forested areas and gravelled driveways was determined by sieving. Several ant nests were excavated to get an idea of their construction and the horizons from which soil material is removed.

There are many species of ants that live in the soils of New England (Creighton, 1950; Wheeler, 1916), and probably a number of species make mounds like those described. Most of the ants are 1 to 2 mm (1/25-1/12 inch) long and black, red or orange in color. In forested areas they are seldom seen on the surface of the litter; in fact, they are not often seen even when the litter is removed because they are active in the topmost part of the soil only at certain times of the day. To obtain some idea of the species which make the litter-concealed small mounds at the Harvard Forest, ants active at the entrance of eleven different mounds were collected in May and June and identified by E.O. Wilson. Aphaenogaster rudis Emery was at four mounds, Formica fusca Linné at one mound, Formica neogagates Emery at five mounds, and Lasius alienus Foerster at one mound.

Results

MODE OF ACTION

Ants move soil from the B horizon to the surface at intervals all during the growing season. Fresh mounds can be seen under the litter in forested areas at almost any time because a new mound can be built overnight. Mounds on the surface are the results of construction or repair of tunnels, chambers, and galleries. Pupae, larvae, and eggs are moved during the day or night from place to place in response to temperature and humidity requirements. At certain times of the day immature forms are at the surface, at other times in the bottom of the deepest tunnel.

Ants may occupy the same nest for many years. Collapse of tunnels probably occurs as a result of frost action in winter and of root growth and movement in summer necessitating cleaning out in the spring and more or less repair work all during the growing season. Chambers in some nests are filled with black forest floor materials, so there is a certain amount of movement of organic matter downward as well as of mineral particles upward.

Several ant nests excavated at the Harvard Forest (Fig. 2) penetrated to depths of 14 inches. In design the nests seem to be like those described by Talbot (1948) and Headley (1949).

SIZE AND SHAPE OF MOUNDS

Size and shape of the common small ant-mounds found in lawns and driveways on sandy soils is shown in Figure 3. The mounds are about 3 inches in diameter and about 1/2 inch in height. Those found in the forest floors are of about this same size but tend

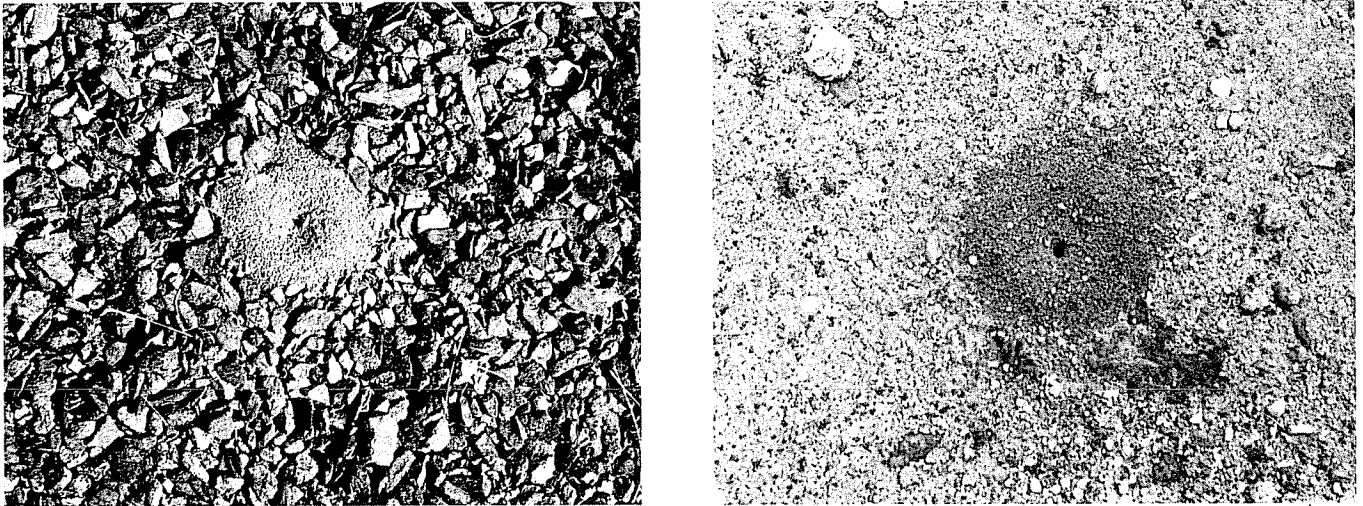


FIGURE 3

Ant mounds about 3 inches in diameter built overnight on a crushed stone surface and gravelled driveway. This illustrates the process whereby fine soil material is placed over coarser material.

to be somewhat less symmetrical (Fig.4), perhaps because different ant species are involved but more likely because the freshly excavated material characteristically is placed just under loose leaves or needles of the last leaf fall, and the shape of the mound is influenced by the space available. Most of the soil is placed in more or less symmetrical mounds like the one shown in Fig.3, but some is placed in thin 4-6 inch wide bands between leaves.

Average weight of mounds in forested areas of Gloucester sandy loam at the Harvard Forest is about 25 grams, with a range of from 10 to 50 grams. The bulk density of the mounds themselves is about 1.0, but the overall bulk density of the horizon in which the mounds are placed is less than this because the mound material is surrounded by much lighter forest floor material. Bulk density of the A1 horizon as a whole in forested areas is about 0.5.

OCCURRENCE

Pattern of occurrence of mounds easily exposed by raking is shown in Figure 5. Based on counts from 22 square-yard samples, there is an average of about 5 ant mounds per square yard overlying the thin black finely divided material of the forest floor, or a total of about 25,000 per acre. This is comparable with Headley's (1952)

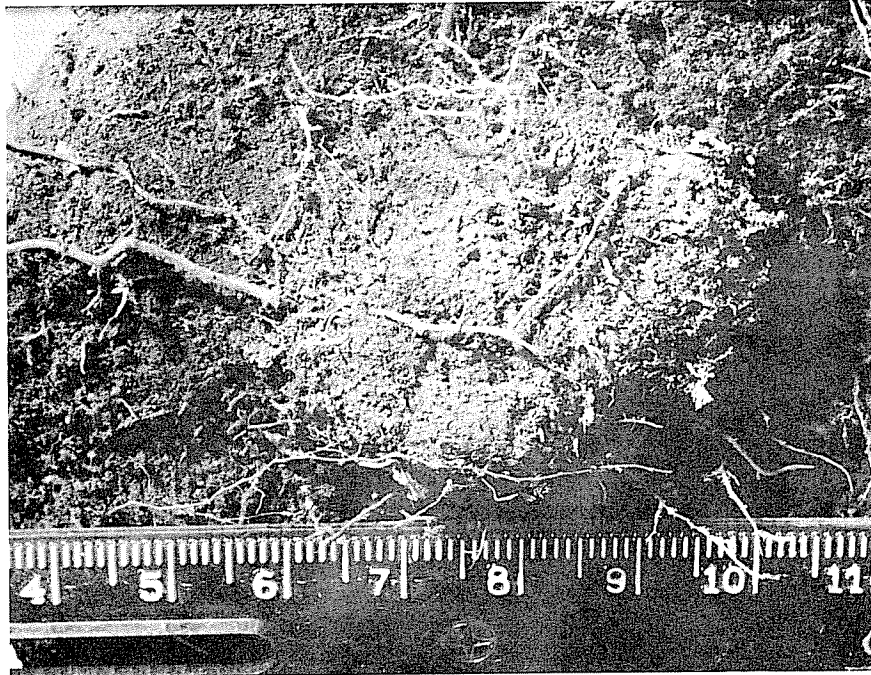


FIGURE 4

Ant mounds in the forest floor. The upper part of the forest floor has been removed in these photographs. Scale is in centimeters.

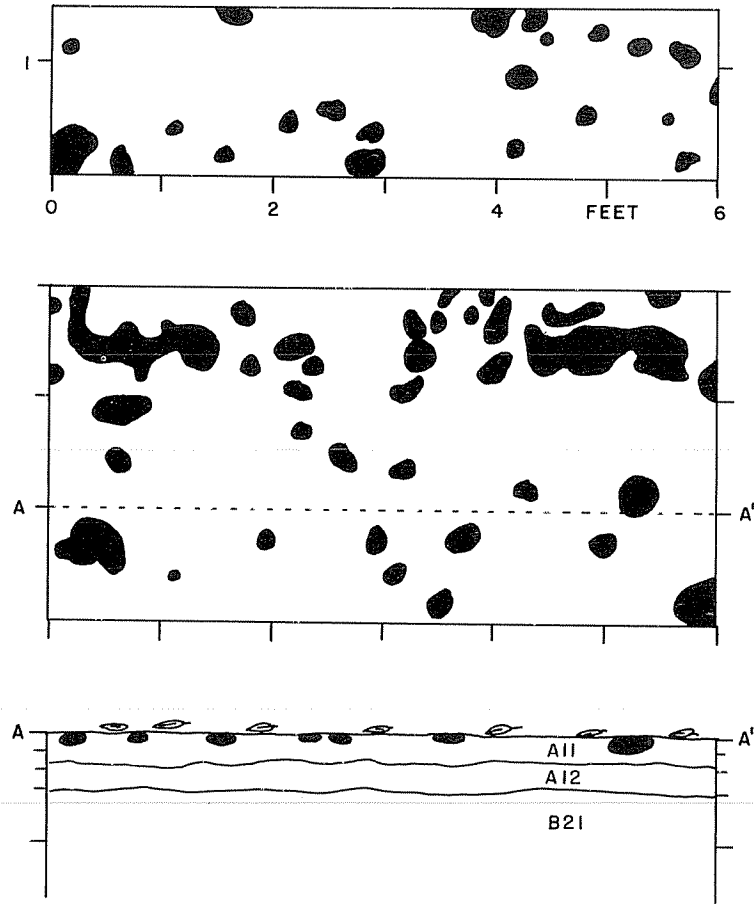


FIGURE 5

- Upper diagrams --- Two locations showing ant mounds on the surface after exposure by raking away the upper part of the forest floor.
- Lower diagram --- Soil profile along line A - A' of the middle diagram showing mounds not exposed by raking.

11 colonies per square meter in a locust woods and 2 per square meter in a beech-maple stand.

Some mounds are made each year. Studies in June showed an average of one and a half mounds per square yard where ants actually were observed carrying out fresh B horizon material. Ant activity continues throughout the growing season, so a figure of 2 new mounds per square yard per year is a conservative estimate.

In addition to the mounds easily exposed by raking and lying completely within the forest floor there are many older mounds that are now in the A1 horizon and covered

by the O2 layer. Some idea of the number of ant mounds that may be missed by raking is shown in Figure 5. The lower diagram is a scale drawing of a vertical section along a straight line (A-A') of the central diagram where there is only one ant mound in the forest floor. Six additional mounds occur within the A1 horizon along this straight line.

Ant mounds are so common in forested areas of Brown Podzolic soils in New England that with very few exceptions fairly recent mounds consisting of the characteristic strong yellowish brown B horizon material can be found just beneath the litter within any square foot area. Mounds in the upper part of the forest floor on partially disintegrated leaves cannot be over a year or two in age. Those overlying the O2 layer may be 5-10 years of age, while those in the A1 may be older still. As yet no certain method has been found for dating the mounds other than by actually seeing the ants at work or by noting that the material is placed over recently fallen leaves or needles.

RANGE IN SIZE OF MINERAL PARTICLES IN ANT MOUNDS

Ants are justly famous for the large particles they can move. Material in the litter-concealed small ant mounds is much coarser than one would expect considering the 1-2 mm. length of the ants involved. Mounds in the gravelly Gloucester soils commonly have about 5 percent of the particles in the 1/4 inch - 2 mm. size class (Table 1) but not many particles larger than 1/4 inch.

TABLE 1

Size distribution of rock fragments in small ant-mounds

Source of Mounds	No. of Mounds	Percent by weight, less than 2 mm. oven dry basis		
		Greater than 1/4 inch	1/4 in. - 2mm.	2-1 mm.
Ant mounds in forested areas of Gloucester gravelly sandy loam	22	1	7	7
Ant mounds on gravelled driveways	17	1	4	10

Ant action in silty or clayey soils easily can be overlooked because all the particles are small enough to be returned to the surface and so there is no segregation by particle size. In such soils the amount of return must be judged principally by color of material or shape of mound. The material brought back to the surface in the soils at the Harvard Forest seems to be little or no higher in silt and clay content than that of the fine earth material in the horizons below, but so far this has not been studied in detail.

TABLE 2
Size distribution by horizons of rock fragments larger than 2 mm.
in a pit in Gloucester very stony gravelly sandy loam.

Horizon	Depth in inches	Percent by weight on less than 2 mm. oven dry basis Size classes of rock fragments		
		Greater than 1 inch ⁴	1-1/4 inches	1/4 in. - 2 mm.
Individually sampled ant mounds		0	0	5
A11	0-1	0	1	4
A12	1-3	21	2	5
B21	3-5	104	17	6
B22	5-8	91	19	7
B23	8-24	183	23	11
C1	24-33	386	25	14
C2	33-46	635	36	15
C3	46-57	695	25	10

⁴ - Some of these percentages are large because rock fragments occupy a much larger proportion of the soil in the lower horizons than the fine earth.

PARTICLE SIZE DISTRIBUTION IN SMALL ANT-MOUNDS IN COMPARISON WITH THAT IN SOIL HORIZONS BELOW

In connection with a study of coarse skeleton in the Gloucester soils at the Harvard Forest, all soil in a 2 by 6 by 5 foot section was weighed and sieved. At this location ant mounds were also collected, sieved and weighed. This provides data (Table 2) that can be used to estimate the amount of return to the surface by ants. Percent by weight in the 1/4 inch - 2 mm. size class in the upper 3 inches of the mineral soil is like that of the ant mounds in this same horizon and supports the

hypothesis that the upper 3 inches of mineral soil -- the entire A1 horizon -- is material brought to the surface by ants. There is no evidence that fauna other than ants have been active in this process of soil return at the sample spot. Earthworms, for example, seldom occur in forested Gloucester soils. An examination of the data for the 3-8 inch horizon leads to the hypothesis that a fairly high proportion of the finer-textured material in this horizon also is the result of movement to the surface at some previous time by ants. This is all the more plausible if one assumes that at least some of the pebbles larger than 1/4 inch in this horizon were once on the surface and have been covered by material brought to the surface by ants. Small stones, roots, or other objects once at or near the surface may be completely buried by ant activity. Larger stones which once projected through the soil surface to a height of only 2 or 3 inches now may be completely buried. This of course assumes that stones and boulders are not raised to the surface by frost action, root growth, or some similar process as rapidly as they are buried by material brought to the surface by ants.

Galleries, chambers, and tunnels with diameters up to 1/2 inch are constructed in the soil when the ants make their nests. When nests are abandoned, or, even under ordinary circumstances when the nests are continually occupied for a period of years, these tunnels and cavities collapse and there is a corresponding subsidence of approximately the same magnitude as the volume of material placed on the surface. There is no evidence that tunnel or root channels persist in the soil indefinitely thereby making it continually more labyrinthine. Consequently although material is continually brought to the surface there is no appreciable thickening of the solum and the surface of the soil relative to nearby stationary objects such as bedrock remains the same.

Discussion

RATE OF RETURN OF SOIL TO THE SURFACE

No accurate assessment has been made as yet of the rate at which ant mounds accumulate at the surface. The best estimate at the present time is based on the number of new mounds on the surface. If two new mounds per square yard are constructed each year (and this is a conservative estimate), an amount of about 50 grams per square yard each year is returned to the surface. Adjusting for bulk density this amounts to about an inch every 250 years. Considering the intense activity of the ants, this figure at first seems small. Yet the effects of plowing in this same soil type persist for at least 2-300 years, so the rate of an inch per 250 years may not be far off. Indeed, a good place to study rate might be in formerly plowed areas where date of last plowing is known.

EFFECTS ON SOIL GENESIS

Return of B horizon material to the forest floor is an important activity of the ants from a pedogenic standpoint. The B horizon material is placed in small mounds and is not intimately mixed with the surrounding organic matter, but nevertheless it is placed in an environment of decomposing organic matter where organic substances active in decomposition and solution are formed. This mound material consists of mineral particles covered by coatings of sesquioxide-humus substances and these coatings doubtless provide a ready source of rather soluble iron and aluminum compounds for reentry into the eluviation-illuviation podzolization cycle. This return to the surface is an anti-eluviation process and one which is generally overlooked by pedologists. All the mineral particles now in the A1 horizon of the Brown Podzolic

soils probably were once in the B horizon and coated with sesquioxide-humus. This is important information in any study of the genesis of the soil.

Activity by soil fauna in the upper part of the soil is probably a major reason why Brown Podzolic soils rather than weak Podzols occur in southern New England. Ants provide an important part of the activity by placing sesquioxide-humus covered B horizon material within the forest floor, separated by a layer of organic matter from the topmost mineral soil. The rate of return is greater than the rate of bleicherde and orterde formation. This return of material also is a reason for moder rather than mor forms of forest floor.

But ants are by no means the only fauna that are important. Small rodents such as moles, mice, and voles (Hatt, 1930) move enormous amounts of soil by tunneling within the surface 2 or 3 inches of mineral soil, but they mix rather than move the soil upwards. This action by small rodents cannot be overlooked in any study of the amount of material brought to the surface by ants because the small rodents mix the fine-textured ant-mound material with the coarser material just below. Tunnels of small rodents can be observed in almost every square foot of the forest floor, and the thickness and homogeneity of the A1 horizon in Brown Podzolic soils probably is due in large part to their tunneling, whereas the larger proportion of fine earth material in this same horizon is the result of ant activity.

Other fauna such as beetle larvae, solitary bees, and wasps also bring B horizon material to the surface but their effects are local.

Material brought back to the surface by ants is not modified appreciably in the process so far as is observable. It is not passed through the gut as in the case of earthworms but some sticky secretion may be used to moisten the soil when the latter is dry.

Ant nests at the Harvard Forest penetrate the soil to a depth of 14-16 inches. They penetrate to at least this depth in other kinds of soil in other places. Ant mounds consisting of reddish brown B horizon material occur in the strongly developed sandy Podzols of the Lakewood series in New Jersey and the Dukes series of Cape Cod. These soils have 14-16-inch-thick gray A2 horizons and reddish brown B horizons below, and so the reddish brown material can have come only from the B horizon. Similarly fine-textured B horizon material has been observed by the writer in ant mounds on the surface of a Red Yellow Podzolic soil in southern Ohio and its source was at a depth of 14-16 inches in the horizon of clay accumulation. This suggests that the action of ants may be important in the genesis of soils other than Brown Podzolic soils. For example, this might explain why the junction between eluviated and illuviated horizons in medium- and fine-textured soils with textural B horizons (Gray Brown Podzolic and Red Yellow Podzolic soils in the eastern United States) is so commonly at a 14-16 inch depth. It might also help explain the islands of B horizon material found within the A horizon zone in some soils, as well as other irregularities at or near this junction in many soils.

B horizon material brought to the surface in Podzols is decolorized rapidly enough so that continual return to the surface does not change the overall character of the soil appreciably. In Brown Podzolic soils the process of gray layer formation is less rapid and the B horizon material returned to the surface exerts a much larger influence.

EFFECTS HAVING PRACTICAL IMPLICATIONS

Fine material returned to the surface of coarse-textured soils provides increased cation exchange capacity and available moisture over that in the coarser-textured horizons below and may be important in burial of seeds, roots and charcoal. It also

promotes localization of fine materials in the B horizon because the fine materials on the surface when mixed into the B horizon by tree throw or frost action will be preserved, at least to some extent, as discontinuous strata, lenses, or as isolated small bodies of material. In any case, this is one more possible explanation for the inch-to-inch variability common in the B horizons of many soils.

There may be some archaeological as well as ecological importance. Studies made in 1960 at an archaeological site on Cape Cod first drew the writer's attention to the potential importance of ants because calculations showed they could have built up the 16 or so inches of material covering the site if they worked for 4,000 years at the same rate at which they are now working.

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