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## SOME SOIL FACTORS AFFECTING TREE GROWTH<sup>1</sup>

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It is just one hundred years since Liebig, in his famous report to the British Association upon the state of organic chemistry, delivered with vitriolic invective the death sentence to the theory held by contemporary plant physiologists that plants obtain their carbon from the soil. He did it in these words, "All explanations of chemists must remain without fruit, and useless, because, even to the great leaders of physiology, carbonic acid, ammonia, acids and bases are sounds without meaning, words without sense, terms of an unknown language, which awaken no thoughts

<sup>1</sup> Address of the retiring vice-president and chairman of the Section on Agriculture, American Association for the Advancement of Science, Columbus, Ohio, December 30, 1939.

and no associations." How different is the state of affairs to-day, how ramshackle have become the once hallowed walls dividing the natural sciences, must be apparent when an agronomist deigns to rise before a group of horticulturists and foresters and speak on a program dealing with the physiological aspects of tree growth. Fortunately it appears now well established that both fruit and forest trees send their roots into the soil, that natural medium which until recent times was peculiarly the domain of the agronomist. Fortunately, also, the interactions of the soil and tree appear not to differ materially from the interactions of the soil and agronomic crops. In fact, except in the degree of surface manipulation involved and in the

proportion of extracted soil constituents and residues returned, there exist no major differentials in the plant-soil relationships of trees and field crops. Accordingly, it may not be inappropriate for one who thinks chiefly in terms of the latter to discuss soil factors affecting tree growth.

This is obviously not the place to attempt a résumé of the extensive literature dealing with soil-tree relationships. Instead, therefore, I have chosen to present a rather generalized picture of certain root-soil relationships, especially those affecting the availability of water, oxygen and soil nutrients, as visualized in the light of recent researches in soil physics and soil chemistry. Acting within the prerogatives of this kind of a talk, this will be done with high disregard of the usual necessity for giving credit to individuals. Mention of some names will be inescapable.

#### PHYSICAL MAKE-UP OF THE SOIL

Let us picture first the soil as a physical body. It has a frame-work of rock particles, composed of primary minerals and ranging in size from small stones to particles of colloidal dimensions. However, few primary minerals occur in sizes below 0.002 mm diameter, which represents approximately the upper size limit of a second important group, the secondary clay minerals, the chief colloidal components of mineral soils. The latter are mainly hydrated aluminosilicates with varying admixture of hydrated oxides of iron and aluminum. These clay particles usually have a plate-like crystalline structure. Two fundamental types are recognized. One, the so-called montmorillonite type, characteristic of weathering in temperate climates, possesses an expansion joint in its crystal lattice which expands and shrinks with varying hydration and contributes enormously to the amount of reactive surface exposed. These clays exhibit in marked degree such colloidal properties as swelling and shrinking, cohesion and plasticity. Moreover, they are active chemically, being able to hold on their surfaces, through electrostatic forces, not only water molecules but considerable amounts of cations, and to a lesser extent anions, especially the phosphate anion. The second type, the so-called halloysite type, characteristic of tropical weathering, possesses no expansion joint in its crystal lattice, and, presumably because of lower specific surface, exhibits the previously mentioned colloidal properties in much lower degree. However, since such clays often carry much hydrated iron and aluminum, they frequently show high phosphate fixing power. Included in the solid body of the soil, but largely concentrated in the upper horizons in the case of mineral soils, is the soil organic matter or humus. Although comprising materials in all stages of chemical and physical degradation, the most important fraction from the standpoint of soil properties is the colloidal humus. The

latter represents an advanced stage of biochemical degradation, is mainly composed of lignin combined with microbial protein, contains carbon and nitrogen in nearly constant ratio, usually between 8 and 12, is fairly resistant to further biological attack, and exhibits in exaggerated degree most of the colloidal properties shown by montmorillonitic clays.

#### SOIL STRUCTURE

Except in coarse-textured soils low in colloidal components, the arrangement of the solid soil particles is seldom haphazard. The finer particles tend to occupy interstices between the larger, and the very fine colloidal clay and humus particles frequently occur as coatings on the larger particles, where, owing to their hydrated character, they serve to bind the particles together into various types of structural units. In the surface horizons where alternate wetting and drying or freezing and thawing occur, and which contain the major part of the soil humus, and of the plant roots and micro-organisms, the structural units formed are mostly irregular rounded granules, whose stability varies widely, but usually increases with increasing humus content and especially with increasing activity of plant roots and micro-organisms. In the lower soil horizons within the zone of weathering, structural units also develop, usually blocks which may be cubical, columnar or prismatic in shape, bounded by cleavage planes or cracks.

#### SOIL PORE SPACE

That part of the total soil volume not occupied by solid particles, *i.e.*, the pore space, is obviously the direct complement, both in extent and geography, of the solid phase. The greater the volume of solid material within a given volume of soil, the smaller is the total pore space, hence the existence of a general inverse relation between pore space and volume weight. Corresponding to the multiplicity of shapes, sizes and arrangements of the solid particles is a similar multiplicity of shapes, sizes and arrangement of the individual pores. No simple concept such as that of a series of continuous capillary tubes of uniform cross-section can be applied to the soil-pore space, although such a picture does fit fairly well the larger pores formed by structural cleavage planes, and pores left by decaying plant roots, or formed by the burrowing of worms, insects, etc. The great bulk of the pore space is probably better pictured as angular-shaped cells connected in hit-or-miss fashion by small irregular openings. Although recent techniques for the direct microscopic study of soils, both en masse and in thin section, have added to our knowledge of soil structure and pore-space geography, no direct procedures are available for characterizing the latter. Hence, it has been necessary to resort to indirect meth-

ods, the most useful being the measurement of the amounts of water held by a soil at varying moisture tensions imposed by suction, centrifuging and in the drier ranges by reducing the vapor tension. Such measurements indicate that, depending chiefly on texture and structure, soils vary widely in the size distribution of their effective pore sizes, such variations being commonly much greater than variations in the total volume of pore space. Moreover, there often occur wide differences in pore-size distribution among the different horizons making up a given soil profile. These differences, both between soils and soil horizons, are of greatest significance in determining the availability of both air and water to plant roots.

#### SOIL MOISTURE

Under natural conditions the retention and movement of water in soils is controlled by several different forces, including molecular attraction at the solid surfaces, surface tension at the liquid-air interfaces, gravity and hydrostatic forces. Much attention recently has been given to measuring the energy with which water is held by soils at different moisture contents. By proper choice of method, it is possible to relate moisture content and energy potential throughout the complete moisture range from dryness to saturation. For example, vapor pressure, freezing point, centrifuge and tensiometer methods find adaptation in the order named as one passes from the region of high potentials and low-moisture contents to the region of low potentials and high-moisture contents. The results obtained have contributed greatly to our knowledge of the use of water by plants, of soil moisture movement and of the way water is held in the soil. The curves relating potential and moisture content are hyperbolic in type with no apparent discontinuities, the latter fact indicating that the older classification of soil water into hygroscopic, capillary and gravitational is largely arbitrary. A variation in the method of plotting potential against moisture content introduced by Schofield<sup>2</sup> consisted in plotting the common logarithm of the moisture-tension, expressed as cm of water and designated as pF, against the moisture percentage. This method permits increased refinement of interpretation in the lower potential range corresponding to moisture contents from saturation to the wilting point and including the full moisture range in which movement of water in the liquid phase normally occurs.

In a saturated soil with the normal pore space, the moisture tension approximates zero ( $pF = -\infty$ ), little or no force being required to extract the first increment of water from it. If such a soil is permitted to drain under gravity, the moisture tension increases as the moisture content decreases down to a certain point at

which water ceases to be lost, the so-called "field capacity" of the soil, or point of "zero capillary permeability." At this point according to Richards<sup>3</sup> the water is no longer present in a continuous liquid film and any water translocation must take place in the vapor phase. This point is ordinarily considered to be about pF 3 and approximately coincident with the moisture equivalent. However, recent work by Moore<sup>4</sup> indicates that it is nearer pF 2.0 and tends to vary with texture, being highest with fine textured soils. Moisture held at "field capacity" is readily utilized by plants. It represents the upper limit of the available water range, except when water is actually moving down through the soil, as after a rain, or when the root zone extends to within a relatively short distance of a free water table. The content of moisture held against gravity, *i.e.*, the field capacity, tends to increase exponentially with decreasing particle size, hence tends to be many times higher in clay soils than in sandy soils, and also increases with the amount of humus present.

#### AVAILABILITY OF WATER TO PLANTS

It now seems fairly well established that plants can utilize water down to a tension of about pF 4.2, corresponding to an osmotic pressure of about 16 atmospheres, before complete wilting occurs, providing the soil is thoroughly permeated with roots and the rate of transpiration is low. This point has been designated as the "wilting point" or "wilting coefficient," and like the "field capacity" varies with soil texture and soil structure and apparently little or none with the kind of plant. On the other hand, there exist differences of opinion regarding the ease with which water above this point is utilized. Veihmeyer and Hendrickson,<sup>5, 6</sup> from studies with prune and peach trees, concluded that between field capacity and the wilting point there was no difference in the availability of soil water, that the wilting point is a critical soil moisture content, and that the trees either have readily available water or have not. There is considerable work opposed to this idea and indicating that entrance of water may become so restricted as to cause cessation of fruit growth—at least with pears, apples and citrus—and even incipient wilting of leaves at moisture contents considerably above the point of complete wilting. The idea of a "wilting range" has been suggested as better fitting the facts than a single "critical wilting point." A difficulty inherent in all this work is the inability to measure the moisture content of the soil immediately in contact with the root. If we accept the idea that there

<sup>3</sup> L. A. Richards, *Jour. Amer. Soc. Agron.*, 28: 297-306, 1936.

<sup>4</sup> R. E. Moore, *Hilgardia*, 12: 383-426, 1939.

<sup>5</sup> F. J. Veihmeyer, *Hilgardia*, 2: 125-284, 1927.

<sup>6</sup> A. H. Hendrickson and F. J. Veihmeyer, *Calif. Agr. Exp. Sta. Bul.*, 479: 1-56, 1929.

<sup>2</sup> R. K. Schofield, *Trans. Third Inter. Cong. Soil Sci.*, 2: 38-48, 1935.

is no appreciable movement of water by capillarity at moisture tensions below that at "field capacity," and this idea seems well founded, also the equally probable idea that movement of water in the vapor phase is too slight to be a factor (at 20° C., the relative humidity at pF 3.0 is 99.3 and at pF 4.2, 95.5), then it must follow that only as roots come directly in contact with hitherto untouched soil-moisture films can enough water be obtained to replace that lost in transpiration. The vital necessity for the rapid and continuous extension of root systems of transpiring plants has recently been pointed out by Kramer,<sup>7</sup> who states the belief that "when environmental conditions favor rapid transpiration, cessation of root-extension for only one or two days would result in death of many, and possibly most plants, from desiccation." He also calls attention to the work of Pavlychenko,<sup>8</sup> indicating that the number of growing root tips is extremely large and their extension must amount to many feet or, in the case of large plants, to hundreds of yards daily. Further, he states, "the roots of many plants are completely suberized when root extension ceases."

From the foregoing it is evident that the ability of trees to resist drouth will depend not only on the amount of available water held by the soil, *i.e.*, the spread between field capacity and wilting point, but, equally important, upon the volume of soil permeated by roots and the presence or absence of impediments, either mechanical or physiological, to rapid root extension. Obviously also, the frequency and ease of renewal of the available water in areas desiccated by root absorption through the processes of infiltration and percolation may be highly important.

The capacity of a soil to hold water within the available tension range is relatively insensitive to structural changes, although compaction tends to increase it somewhat, unfortunately, however, at the expense of permeability to air and water. Hence, although coarse-textured soils may benefit from compaction, medium-to fine-textured soils are more likely to be injured. The well-known effect of organic matter additions in increasing moisture held at field capacity appears, on the basis of recent studies, not to involve any similar effect on the amount of available water, since the wilting percentage is also increased in approximately equal degree.

#### PERMEABILITY OF SOILS TO WATER

The adequacy of soil moisture for growth and survival may depend as much upon frequency of renewal by rain or irrigation and upon the ability of the soil to absorb water—the infiltration capacity—as upon the capacity of the soil as a water reservoir. From a

study of the growth of apples in relation to soil moisture in ten New York orchards in 1936 and 1937, Boynton and Savage<sup>9</sup> infer that, although available water capacity is probably the most important soil factor determining the availability of water in the case of shallow soils, the infiltration capacity may be the most important factor with heavy soils. Moreover, the drainage of excess water from a soil is also dependent upon those properties which determine the rate at which water moves through a soil under the force of gravity. Hence permeability to water ranks high among soil factors determining the site quality for tree growth.

Permeability to water depends both upon the amount and size distribution of the pore space in a soil. Assuming an idealized cylindrical pore in a saturated soil with no impediment to drainage, the amount of water transmitted by gravity under constant head should be a direct function of its cross-section and an inverse function of its surface, which retards flow through frictional stress. Since the amount of surface per unit cross-section varies inversely with pore diameter, it follows that the amount of water transmitted per unit of total pore volume will be larger with large than with small pores. A useful concept originally introduced by Schumacher in 1864,<sup>10</sup> divides the pore space in a soil into two categories. In modern terminology these may be characterized as (1) pores still completely filled with water at "field capacity," designated as "capillary pores" and (2) pores containing varying amounts of air under the same conditions, designated as "non-capillary pores." Capillary pore space is considered the chief reservoir for water held against gravity, whereas movement of water through a soil takes place chiefly through the non-capillary pore space. Although two soils having the same total non-capillary pore space will not necessarily transmit water with equal facility, owing to variations in the size distribution of the non-capillary pores, recent studies by Bayer<sup>11</sup> upon a widely diverse group of soils indicate that the amount of non-capillary pore space of a soil is in general a fairly good criterion of its permeability. Moreover, the relation of permeability to non-capillary porosity appears to be exponential, the former tending to increase somewhat faster than the square of the latter. Thus a soil with 10 per cent. of non-capillary porosity will have a permeability more than four times as great as one with 5 per cent. and more than 25 times as great as one with 2 per cent. of non-capillary porosity. Another important fact shown in Bayer's work is that compaction of a soil tends to reduce the non-capillary porosity relatively much more than the

<sup>7</sup> P. J. Kramer, "Transactions American Geophysical Union, 1937." Part II, p. 313. National Research Council, Washington, D. C., July, 1937.

<sup>8</sup> T. K. Pavlychenko, *Ecol.*, 18: 62-79, 1937.

<sup>9</sup> D. Boynton and E. F. Savage, *Cornell Univ. Agr. Exp. Sta. Bul.*, 706: 1-36, 1938.

<sup>10</sup> Schumacher, "Die Physik," Weygandt, Berlin, 1864.

<sup>11</sup> L. D. Bayer, *Proc. Soil Sci. Soc. Amer.*, 2: 52-56, 1938.

total pore space. For example, compaction of a Cecil clay to a point where it had lost about 10 per cent. of its original total pore space, reduced its non-capillary porosity 60 per cent.

In contrast to the "capillary porosity" and "field capacity" of a soil, non-capillary porosity is enormously influenced by variations in soil structure. The effect of compaction has already been noted. Granulation is highly effective in increasing the non-capillary porosity of fine-textured soils, likewise the addition of organic matter. In lysimeter studies at Clarinda, Iowa, Musgrave and Norton<sup>12</sup> showed that the amount of water percolating through Marshall silt loam was increased 54 per cent. and through Shelby silt loam 135 per cent. by the incorporation of 16 tons of manure per acre. Continuous pores left in the soil by the decay of plant roots or by the burrowing of small animals may contribute greatly to the permeability of soils, especially under forest conditions, but often to an important extent in pasture and field soils. The abnormally high rates often found in infiltration studies on forest soils are thus explained. Deterioration in site quality for trees of land once in forest after utilization for cropping or pasture for a period of years is probably due in part to the disappearance of these biotic channels, although loss of humus and bases and decreased granulation may also be involved. Another factor affecting non-capillary porosity is the tendency of soil colloids, both clay and humus, to swell when wetted, the effect being to transform a part of the non-capillary porosity into capillary porosity. A lesser tendency to hydrate and swell probably explains the relatively high permeability of certain tropical clay soils compared to humid temperate soils of equally fine texture. Although the colloids in the soil profile are usually fully hydrated, except in the upper few inches of surface soil the swelling of the colloids in this layer after a rain may decrease materially the non-capillary porosity of a fine-textured soil or one high in organic matter.

The old adage that "a chain is no stronger than its weakest link" applies to the movement of water through the soil profile. In other words, the transmission characteristics of the profile are determined by the permeability of the least permeable horizon. The presence of even a thin horizon of impermeable soil may block rather completely the drainage of a soil which otherwise would be well drained. Thus it is necessary to recognize that soils possess a "permeability profile" corresponding to their textural and structural profiles. This is especially important in the temperate humid region where it is normal to find a heavy layer in the upper subsoil, notably in poorly drained light-colored soils, the so-called "clay pan

soils." A very important factor in decreasing the infiltration of rainwater on soil unprotected by vegetative cover is the decrease in non-capillary porosity of the soil at the immediate surface, resulting chiefly from the mechanical impact of raindrops destroying granulation, an effect facilitated by the accompanying removal of electrolytes and hydration of the colloids. This effect is almost completely prevented by dense growing vegetative cover or by a layer of surface litter.

#### MINERAL UPTAKE

It has already been pointed out that continued intake of water by the plant necessitates the continuous extension of the absorbing roots to provide fresh contacts with unexhausted moisture films. Recent studies have suggested that root-soil contact may be equally important to the intake of mineral elements. It is now generally recognized that, although the weathering of primary minerals is necessary to the maintenance of adequate available supplies of such mineral elements as potassium, calcium, magnesium, etc., the process is generally too slow to take care of the requirements of rapidly growing vegetation. Instead, the immediate reservoir of available mineral elements appears to be the ions held by electro-static forces on the surfaces of the soil colloids. A small proportion of the ions so held (Mattson<sup>13</sup> estimates of the order of 0.2 per cent.) enter the film water bathing the colloid from which they may be taken in by the plant root. The distribution of any given ion between the soil solution and the colloid being in the nature of a highly mobile equilibrium, continuous renewal of any ions taken up is to be expected. There is no reason to doubt but that the mechanism just described does contribute to the mineral nutrition of the plant. On the other hand, it has recently been suggested by Jenny and Overstreet<sup>14</sup> that it may not be the sole mechanism nor necessarily the most important one. Aside from the fact that the concentration of most nutrient ions, as judged from displaced soil solution studies, is so low even in fertile soils as to require a very large number of complete replacements to account for the total intake by plants during the growing season, the concentrations of certain ions (*viz.*, the  $\text{PO}_4$  ion) are frequently considerably below the concentrations found in flowing solution culture studies to be necessary for satisfactory growth. Parker<sup>15</sup> found practically no phosphorus in the displaced solution from a soil which normally produced a fairly satisfactory yield of corn without phosphate fertilization. By exposing the roots of plants to suspensions of mineral colloids saturated either with hydrogen or basic cations, Jenny and Over-

<sup>13</sup> Sante Mattson, *Jour. Agr. Res.*, 33: 553-567, 1926.

<sup>14</sup> H. Jenny and R. Overstreet, *Soil Sci.*, 47: 257-273, 1939.

<sup>15</sup> F. W. Parker, *Soil Sci.*, 24: 129-146, 1927.

<sup>12</sup> G. W. Musgrave and R. A. Norton, United States Department of Agriculture, *Tech. Bul.*, 558: 1-182, 1937.

street have succeeded in demonstrating what they consider to be a direct surface exchange of ions between the root and the colloid. Employing the hydrogen saturated colloid, hydrogen ions are apparently absorbed by the root and equivalent amount of K, Ca, Mg, etc., released by the root to the colloid. When a potassium saturated colloid is employed, potassium seems to be absorbed by the root in exchange for hydrogen ions. Translating these observations to soil conditions, it is suggested that the carbon dioxide produced by respiration within the root cell combines with the water forming carbonic acid which diffuses through the cell wall, on the outer surface of which a certain number of  $H^+$  and  $HCO_3^-$  ions produced by dissociation are held electrostatically. Whenever the root surface lies sufficiently close to a colloidal clay surface that the "oscillation space" of an  $H^+$  ion on the root overlaps with the "oscillation space" of a cation held on the clay, a direct interchange may take place. The same type of exchange may take place between an  $HCO_3^-$  ion on the root and an anion held on the clay. Should this idea of direct contact nutrition be substantiated by further work, the desirability of extensive root soil contact may be found as necessary for mineral nutrition as for water absorption.

#### SOIL FACTORS AFFECTING ROOT GROWTH

The apparent importance of expanding root-soil contact to the intake of water and probably also of mineral nutrients, emphasizes the significance of factors that either favor or impede the direction and extent of root development. It must be admitted that present knowledge is wholly inadequate for a full understanding of the effect of individual factors or of their interactions. There is evidence for believing, however, that under conditions of limiting moisture supply roots will develop toward a positive moisture gradient. Similarly, under conditions of poor aeration, growth will take place toward a negative  $CO_2$  gradient or a positive  $O_2$  gradient. The foregoing relations probably explain the deep rooting of certain field crops in Nebraska as observed by Weaver<sup>16</sup> and the comparatively shallow rooting of the same crops as observed by Farris<sup>17</sup> in New Jersey, also similar differences between fruit trees in Utah, as observed by Ballantyne,<sup>18</sup> and in New York, as observed by Oskamp and Batjer.<sup>19</sup> There is also evidence that roots may develop in response to a favorable nutrient gradient. For example, Bushnell<sup>20</sup> caused potatoes to

develop deeper root systems by incorporating phosphorus and nitrogen fertilizers in the subsoil. It is also possible that roots may be prevented from occupying a zone of fine-textured densely packed soil by mere mechanical impedance. Braun-Blanquet<sup>21</sup> states that if soil grains are less than 0.02 mm in diameter, root hairs are no longer able to penetrate through the spaces between them if the soil has a single grain structure, also that "raw clay" with a grain diameter of less than 0.002 mm will stop the movement even of bacteria. Although little is known regarding the interaction of the factors affecting root growth, it may be postulated that most rapid extension will occur when all the gradients in a given direction are favorable, also that a favorable gradient in one direction may be offset by an opposing unfavorable one. Thus roots may be prevented from occupying a zone of favorable nutrient supply because of a limitation of oxygen. In some cases there appears to exist a mechanism for internal adjustment which neutralizes the effect of an unfavorable gradient if some portion of the root system is developing under more favorable conditions. Thus, the normally deep-rooted crop, alfalfa, will not send its roots through a lime-deficient acid subsoil in response to a favorable moisture gradient except as an abundance of lime is supplied to some part of the root system. In the light of Jenny and Overstreet's<sup>22</sup> work, it would be interesting to determine whether, under the latter condition, lime moves from the root into the adjacent layers of acid soil. It seems possible that a similar mechanism may explain the ability of certain plants to send their roots into soil zones having extremely low oxygen and correspondingly high carbon dioxide contents.

#### SOIL AERATION

Quantitative studies of the distribution within the soil profile of the roots of both fruit and forest trees in humid regions show a general tendency for the roots to be concentrated in the upper soil horizons, also for rooting to be sparse in dense horizons of fine textured soil, usually characterized by a gray or mottled color, associated with the presence of reduced iron. These facts suggest that aeration may be a highly important factor in determining root distribution in such regions. Obviously, its importance will be greatest in fine-textured soils with naturally poor drainage.

Respiration is a necessary activity of all living plant roots and soil micro-organisms. Hence removal of oxygen from the soil atmosphere and its replacement by carbon dioxide goes on continually at a rate depending upon the number of roots and micro-organisms present and the favorableness of growth condi-

<sup>16</sup> J. E. Weaver, "Root Development of Field Crops," McGraw-Hill, New York, 1926.

<sup>17</sup> N. F. Farris, *Soil Sci.*, 38: 87-111, 1934.

<sup>18</sup> A. B. Ballantyne, *Utah Agr. Exp. Sta. Bul.*, 143: 1-15, 1916.

<sup>19</sup> Jos. Oskamp and L. P. Batjer, *Cornell Univ. Agr. Exp. Sta. Bul.*, 550: 1-45, 1932.

<sup>20</sup> J. Bushnell, *Amer. Potato Jour.*, 14: 78-81, 1937.

<sup>21</sup> J. Braun-Blanquet, "Plant Sociology" (Trans. by G. D. Fuller and H. S. Conard). McGraw-Hill, New York, 1932.

<sup>22</sup> H. Jenny and R. Overstreet, *loc. cit.*

tions such as temperature, moisture and nutrients, including organic matter in the case of heterotrophic organisms as well as upon the partial pressure of oxygen. In the absence of free gaseous exchange between the soil and the atmosphere, there develops an increasing oxygen deficit and carbon dioxide excess in the soil air, readily reaching a point where root growth is inhibited or prevented. According to Lundegårdh<sup>23</sup> plants are more sensitive to the presence of carbon dioxide than to the absence of oxygen, although large differences exist among plants in their reactions to both factors. These facts are supported by the tabular summary of existing data on critical oxygen and carbon dioxide concentrations given by Romell.<sup>24</sup> Lundegårdh states that the growth of most mesophilous plants begins to fall off when the concentration of carbon dioxide reaches 1 per cent. This figure appears low in view of certain data in Romell's summary, *i.e.*, that restrictions of root growth of beans begins at 2-4 per cent., of vetch at 3 per cent. and of peas at 5 per cent. Little specific information appears to be available on the CO<sub>2</sub> tolerance of tree roots.

It appears well established that gaseous diffusion accounts for practically all the exchange of CO<sub>2</sub> and O<sub>2</sub> between the soil and the atmosphere. Movement of air either into the soil or out of it resulting from pressure gradients produced by temperature differentials, changes in barometric pressure, air movement over the surface soil or even the tendency of water draining into a soil to replace the soil air contribute in very minor degree to the renewal of the soil atmosphere.

With a given gradient in CO<sub>2</sub> and O<sub>2</sub> concentration, the rate of diffusion is a function of the total volume of free pore space, *i.e.*, that not filled with water. In contrast to permeability to water the size distribution of the pore space appears to have no effect on the rate of gaseous diffusion. Hence, in soils having equal amounts of free pore space, differences in texture or structure exert no influence. Under natural conditions, however, pore-size distribution does affect aeration in a most important manner, *i.e.*, in determining what fraction of the total volume will be filled with water under given conditions of rainfall, drainage and use by plants. Since at those times of the year and in those regions of the soil where poor aeration is likely to limit root growth, the capillary pores usually will be filled with water, it follows that the non-capillary porosity will be most effective in contributing to soil aeration.

The excellent early work of Buckingham<sup>25</sup> led him to conclude that the rate of gaseous diffusion through

soils varies directly with the square of the free pore space. Although Romell<sup>26</sup> has questioned his interpretation of the data, and the constancy of the foregoing relation, in the absence of more precise data, it may at least serve as a basis for speculation. For example, assuming that diffusion varies as the square of the free pore space, one inch of soil with only 5 per cent. of free pore space will offer as much resistance to CO<sub>2</sub> and O<sub>2</sub> interchange as 25 inches of soil having a free pore space of 25 per cent. Employing Buckingham's method for calculating the CO<sub>2</sub> concentration gradient from the porosity and amount of CO<sub>2</sub> released to the atmosphere per unit area in unit time, and assuming that the latter value is equal to 0.4 gm CO<sub>2</sub> per sq. meter per hour (Romell<sup>27</sup> states that average values for forest soils lie between 0.2 and 0.7 gm), given a free pore space of 25 per cent., the contents of CO<sub>2</sub> in the soil air at 1', 2' and 4' at equilibrium will be 1.63 per cent., 3.26 per cent. and 6.52 per cent., respectively. If now we assume that the upper two inches of the same soil has been compacted or puddled so that its free pore space is only 5 per cent., then the concentration immediately below this layer will be 6.8 per cent., or slightly higher than that at the 4' depth in the uncompacted soil. Free pore space values of the order of 5 per cent. or even less are not uncommon in poorly granulated fine-textured soils or in the heavy layers which frequently underlie coarser-textured surface soils in the humid region. The example cited serves to show how very important even thin horizons of dense soil may be in reducing aeration and thereby limiting root growth. The effect of such a heavy layer will be influenced by its position with regard to the distribution of CO<sub>2</sub> production in the soil. Romell<sup>28</sup> points out that since most of the CO<sub>2</sub> is produced in the upper one or two feet of soil, an impervious layer at the immediate surface is likely to be most detrimental, since it tends to make the entire profile unfavorable to root growth.

Any consideration of root distribution of trees in relation to soil aeration is limited by the paucity of direct experimental information. Even such measurements as have been reported on the CO<sub>2</sub> content of soil air probably do not represent the composition of the air at the immediate disposal of the growing root tips where higher concentrations of CO<sub>2</sub> may be expected than in samples obtained by merely pushing a tube into a soil to the desired depth and withdrawing a certain volume of air, the usual technique. The existence of a "second atmosphere" in the soil was recognized by Russell and Appleyard,<sup>29</sup> who found that,

<sup>23</sup> Hendrik Lundegårdh, "Environment and Plant Development." Edward Arnold and Company, London, 1931.

<sup>24</sup> L. G. Romell, *Soil Sci.*, 34: 161-188, 1932.

<sup>25</sup> E. Buckingham, United States Department of Agriculture, Bureau Soils, *Bul.*, 25: 1-52, 1904.

<sup>26</sup> L. G. Romell, *Meddel. Statens Skogsförsöksanst* (Sweden), 19: 125-359 (Swedish with German summary).

<sup>27</sup> L. G. Romell, *Soil Sci.*, 34: 161-188, 1932.

<sup>28</sup> *Ibid.*, *Meddel. Statens Skogsförsöksanst* (Sweden) 19: 125-359.

when placed under vacuo, soils released considerable gas, consisting mainly of carbon dioxide with some nitrogen and almost devoid of oxygen. This gas was believed to be held by the soil "dissolved in the surface films of water and other substances." On the other hand, the first portion of gas thus removed contained in several instances nearly as much nitrogen as atmospheric air, hence it seems doubtful that it was present in dissolved form. Instead, it probably came from the smaller pores and more poorly ventilated portions of the soil. Thus, although "free air" samples taken at 6" depth on an area known as the "Broadbalk wilderness" contained generally less than 0.8 per cent.  $\text{CO}_2$  and more than 19.6 per cent.  $\text{O}_2$ , the first 30 cc of gas removed under vacuo from 400 grams of the same soil contained 19.3 per cent.  $\text{CO}_2$  and only 5.5 per cent.  $\text{O}_2$ , along with 75.2 per cent.  $\text{N}_2$ . It would appear that much more refined techniques, possibly of a "micro" character, will need to be developed before the actual conditions at the immediate surface of the growing roots will be known.

#### ROOT RESPIRATION AND MINERAL NUTRITION

The vital role of root respiration in the physiology of the plant is emphasized by recent work of Hoagland and Broyer,<sup>30</sup> who showed that salt intake by roots tends to vary directly with the intensity of root respiration. Previous work by other investigators had strongly indicated that such a relation between respiration and electrolyte accumulation applies generally to living plant cells. For example, Steward<sup>31</sup> found that it applied to potato tuber tissue and voiced the opinion that respiration "supplies the energy necessary for salt absorption against a concentration gradient as well as the maintenance of existing concentra-

tions of solutes in the vacuole much greater than in the surrounding medium," also that "other variables being adequately controlled, any treatment which either decreases or increases the total respiration . . . causes a corresponding decrease or increase in the total salt absorbed." Not only may respiration supply the energy required to move electrolytes from the normally low concentrations in the soil solution to the relatively high concentrations in the root cells, but also, considered from the viewpoint of Jenny and Overstreet's<sup>32</sup> theory of "contact nutrition," respiration also supplies the  $\text{H}^+$  and  $\text{HCO}_3^-$  ions which the root exchanges for cations and anions on the surface of soil colloids.

#### SUMMARY

(1) It becomes increasingly evident that continued root growth with the establishment of new root-soil contacts is necessary for the normal entrance of both water and mineral nutrients into the root. This concept emphasizes the ecological importance of factors tending either to impede or favor the spread and permeation of roots in the soil.

(2) The characteristics of soils with respect to (1) available water capacity, (2) permeability to water and (3) permeability to air are largely determined by the volume and size distribution of the soil pore space. The latter is conveniently characterized by measuring the water held by a soil at varying moisture tensions.

(3) In recognition of the foregoing, it may be concluded that a better understanding of root-soil relationships should result from more general application of interpretative studies of soil pore space conditions to root development, and from the development and application of micro-methods for studying the conditions, both physical and chemical, existing at the actual root soil interface.

## SCIENTIFIC EVENTS

### MATHEMATICAL SYMPOSIUM AT THE UNIVERSITY OF NOTRE DAME

A SYMPOSIUM on the Foundations of Topology was held at the University of Notre Dame on April 10 and 11.

In the classical topology, the concept of space was introduced as a set of points for which certain relations are defined which distinguish the space from an abstract set, *e.g.*, it was assumed that a limit concept has been defined in the space or that neighborhoods of points are given. A recent trend of topology seems to lead away from this set theoretical foundation, and points in the direction of a

foundation on relations between the subsets of the space rather than between the points. The points, in this new approach, are introduced only later as certain sequences or systems of subsets of the space.

At the first of the three meetings of the symposium, conducted by Professor S. Lefschetz, of Princeton University, Professor R. L. Moore, of the University of Texas, spoke on "Contiguous Points," a theory somewhat intermediate between the set theoretical foundation and a theory of lumps. Professor Karl Menger, of the University of Notre Dame, developed a theory in which points are defined as certain nested sequences of lumps, a procedure similar to that of physics.

At the morning meeting on Thursday, Professor

<sup>29</sup> E. J. Russell and A. Appleyard, *Jour. Agr. Sci.*, 7: 1-48, 1915.

<sup>30</sup> D. R. Hoagland and T. C. Broyer, *Plant Physiol.*, 11: 471-507, 1936.

<sup>31</sup> F. C. Steward, *Protoplasma*, 17: 436-453, 1932.

<sup>32</sup> H. Jenny and R. Overstreet, *Soil Sci.*, 47: 257-273, 1939.