THE FEEDING POWER OF PLANTS

WALTER THOMAS

A. Introductory

1. VARIABLE COMPOSITION OF IDENTICAL SPECIES

The publication of Wolff’s monumental work on “Aschen-analysen” in 1871 (210), although compiled principally for the purpose of supplying information on the composition of plants used in feeding farm animals, nevertheless, served to crystallize the large amount of experimental data of English, French and German investigators that had accumulated even in those early days of agricultural science. Wolff’s data showed very clearly that plants even of the same species differed considerably both in the absolute and percentage amounts of the various elements absorbed, depending upon the composition and nature of the substrate (soil or nutrient solution). Indeed, Wolff himself (209) was the first to give definite proof that the composition of the ash of any plant could be changed by varying the proportion of salts in the nutrient culture medium.

2. SELECTIVE POWER OF DIFFERENT SPECIES

Numerous investigations, those of Newton (129) being the most recent, have since shown, moreover, that different species growing in media of identical composition possess selective powers with respect to any specific ion or ions. This marked difference in the assimilatory powers of different plants is very clearly exhibited in their different responses to such “insoluble” mineral fertilizers like rock phosphate, basalt, gneiss, etc.

3. ARE DIFFERENCES IN RESPONSE A SPECIES CHARACTERISTIC

But as the environmental conditions even in the water and sand culture experiments cited by Wolff were never identical, the question as to the

* Publication authorized by the Director of the Pennsylvania Agricultural Experiment Station as technical paper no. 502.
nature of the factors operative was still left open. Nor was it decided whether the differences in responses exhibited were characteristic of the species or the result of environmental or other unknown factors. And, although Newton (126) believes that with the exception of phosphorus (129) there is no characteristic difference in the type of absorption of certain species of plants (barley and peas, for example) in nutrient culture solutions, i.e., that there is no difference in percentage content with respect to any element in the plants examined that holds consistently in favor of one or the other throughout all stages of growth, it will be apparent as the subject is developed that the evidence is overwhelming that different plant species growing in media of identical composition not only exhibit differences in composition that can only be interpreted to indicate marked differences in what has been frequently designated in the literature by the expression feeding power or ability to utilize insoluble soil constituents to different degrees, which are characteristic of the species. The following data from König's experiments (82)—which are among the earliest—are typical as exemplifying this point:

<table>
<thead>
<tr>
<th>TABLE I</th>
<th>PER CENT. OF K₂O IN OATS AND PEAS GROWN UNDER SIMILAR CONDITIONS</th>
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<tbody>
<tr>
<td></td>
<td>SANDY</td>
</tr>
<tr>
<td>Oats</td>
<td>0.396</td>
</tr>
<tr>
<td>Peas</td>
<td>0.554</td>
</tr>
</tbody>
</table>

4. THE TERM "FEEDING POWER" DEFINED

The term "absorbing power" or "feeding power" as it is known in technical agronomy may connote several ideas (67). Many have objected to the use of the term feeding power. Shull (172) suggests that some plant physiologists prefer not to use the term on the basis that it has too much psychological implication and others (67) because of the many different interpretations given to it. But, as Crocker (27) points out, although the expression has undesirable implications, it is better to continue its use than to invent some new phrase that might, perhaps, be freer from these implications, because other terms suggested, like "absorbing power of crop plants" or even "specific absorbing power," do not imply quite enough. The term "feeding power" implies both power to absorb the soil nutrients and also the power of making use of many of the salts absorbed. This expression will be used in the present paper as a concise means of indicating
the difference exhibited by different types of plants in the absorption and utilization of difficultly available minerals, either native to the soil or added as soil amendments, as determined by the differences in the amount of nutrient elements absorbed from the minerals in question, the utilization of which is generally exhibited in different growth responses.

5. Theories advanced to account for different responses

From the numerous advanced experiments conducted to determine the cause of the characteristic differences in absorbing power by different species, a number of explanations have been advanced. The differences have been attributed to (1) the differences in the chemical nature (and possibly amount also) of other products of root exudations (acids, carbohydrates, etc.); (2) the differences in (a) the absolute amounts of carbon dioxide evolved, or (b) the amounts evolved per gram of dry weight of the roots (respiration energy); (3) the operation of the law of mass action between the carbon dioxide (carbonic acid) from the roots and the "insoluble material" in the soil; (4) unlike potential differences between the soil and plant; (5) differences in the permeability of the root membranes producing "selectivity" in absorption of roots; (6) the existence of a Donnan membrane equilibrium, and to a combination of one or more of the above factors (67).

We shall discuss the evidence for the operation for these various factors separately.

B. The chemical nature of the root exudations

1. THE CARBON DIOXIDE FACTOR

The problem of determining the nature of root secretion is of importance not only from the standpoint of scientific inquiry, involving the fundamental question of the mechanism of absorption of nutrients and the reaction of protoplasm, but is of importance also from the practical aspect with respect to the economic utilization of minerals occurring naturally in the soil, and applied also as soil amendments.

a. Considerations of some of the experimental difficulties involved.—It must be granted that even if proof were forthcoming that carbon dioxide is the only factor involved, as indeed Hall (55) points out, the problem of isolating the factors that contribute to the sum total of the soil carbon dioxide is not a simple one. In the first place, the carbon dioxide is not all in the gaseous phase, a large part (163) (and, indeed, under some conditions nearly all) is present in solution (93); and in the second place, the soil respiration is the total of all the soil processes that give rise to the production of CO₂, viz., oxidation (83, 169, 213), the metabolic processes of the microorganisms (110, 181, 182, 183, 213), and the
respiration of roots and of the bacteria that inhabit them (58, 63, 110, 178, 181, 208). It follows that the concentration of carbon dioxide, as measured in most experiments conducted with soils, is a function of the absolute CO$_2$ produced by the soil particles together with the roots, and also of the diffusion velocity (102, 103).

Since the distribution of the CO$_2$ between the gaseous and liquid phases will depend upon a number of variables (water and calcium principally), the net effect of any one factor at any time is necessarily difficult to determine. Russell (162) believes that the CO$_2$ evolved from plant roots cannot be distinguished from that given off by microorganisms and this is also the conclusion drawn by Starkey (177, 178); but the work of Stoklasa (182), Headden (60), Turpin (198), Barakov (3) and Neller (124) indicates that approximate relative differentiation is possible.

b. THE VIEWS OF THE SEVERAL SCHOOLS.—Plant physiologists and soil scientists have been and still are divided into several schools. One group (10, 155, 162) maintains that plants do not dissolve significant quantities of minerals that would otherwise remain undissolved; another school emphasizes the important rôle that the root exudations exercise in this connection. The latter school is divided into two groups: One (26, 38, 39, 49, 77, 89, 96, 141, 145) subscribing to the view that "insoluble" substances are rendered soluble by the exudation from the roots of plants of substances (e.g., organic acids, acid salts, etc.) other than carbon dioxide; and the other school (1, 52, 55, 60, 117, 121, 182) that only CO$_2$ is exuded from the roots and that the influence of plants on the solubility of soil minerals is to be attributed solely to this factor. The rôle played by microorganisms in the soil and especially the action of microorganisms of the rhizosphere, isolated by Stoklasa (181) is recognized by all schools.

c. CHARACTERIZATION OF OBJECT OF EXPERIMENTS IN THIS FIELD.—Consequently, in the examination of the available evidence for the purpose of evaluating the contribution of the carbon dioxide evolved from plant roots as a factor in dissolving the "insoluble" soil materials, we must distinguish between (1) those experiments (3, 31, 59, 60, 84, 85, 86, 92, 102, 103, 163, 182, 198, 211, 212) that have for their purpose the determination of the relative contribution of carbon dioxide by root and microorganisms of the soil, and (2) those (28, 38, 49, 77, 89, 117, 121, 145) which, although accepting the important rôle of the carbon dioxide evolved from the roots, were carried out for the purpose of determining if acids and other substances than CO$_2$ are exuded by roots, and (3) those (37, 139, 140, 181, 191) that are concerned with the effect of CO$_2$ from whatever source derived.

d. OBSERVATIONS OF THE EARLIER INVESTIGATORS.—The older "corrosion" experiments of Sachs (165), Knop (80), Liebig (97), Kny (81),
Czapek (28, 29) and Molisch (122) and observations of the natural etchings frequently found upon calcareous stones lying in the soil were regarded as furnishing *prima facie* evidence that the roots of plants participate in dissolving "insoluble" nutrients of the soil. And more recently Fred and Haas (44) found that this action of roots on marble is increased when a sterilized soil was inoculated with pure cultures of various bacteria.

The growth fusion ideas (26, 176) and etching experiments of Sachs (165) and of Czapek (29) are of interest here. The former observed that only the smooth surfaces of the minerals that were soluble in carbonic acid showed "corrosion figures"; silicates did not. Czapek (29) sought further information on the problem by substituting plaster of Paris slabs which were incorporated with various carbonates and phosphates. He argued (28, 29) that since—in addition to the carbonates—the phosphates of calcium, magnesium and iron, but not of aluminum phosphate, were corroded by roots, the acids exuded from the roots must be limited to carbonic, acetic, propionic and butyric. Finally, all but carbonic acid were eliminated by means of qualitative results with Congo red. Czapek's deduction from these experiments, however, is not valid, for the evidence from the experiments of Cameron and Hurst (20), Prianishnikov (151, 153, 155) and Marias (107) is conclusive that aluminum phosphate is available to plants through hydrolytic processes. The use, therefore, of AIPO₄ is not justifiable in experiments to decide the nature of root exudations.

Moreover, all these "corrosion" experiments may be criticized on the basis that no mineral phosphates exist that are unavailable to plants when all factors that hinder the dissolving power of the roots are removed. The experiments of Butkewitsch (16), which will be discussed later in this paper, exemplify this very clearly.

e. **The use of seedlings in determining the nature of root exudations.**—The approach to the problem by the use of seedling plants, moreover, is not sound (1, 28, 29, 52). The mineral requirements of such young plants are too small to justify the suitability of such experiments to answer the question of root exudations, by whatever method and however carefully carried out. The conclusions from such experiments must be of doubtful value. For this reason we shall consider only those experiments in which mature plants were used.

f. **The problem of interpretation.**—The results of field plot experiments (59, 60, 92, 102, 103, 163, 211) are contradictory, but pot and lysimeter experiments (3, 92, 128, 182, 198), with certain exceptions (86) where the technique adopted may be open to criticism (55), agree in attributing to the roots a considerable and, indeed, preponderant contribution to the carbon dioxide of the soil.
(1) The work of the Rothamsted group.—Notwithstanding the fact that on the Broadbalk field and Hoos plots Russell and Appleyard (163, 164) found, in agreement with other investigators (3, 9, 59, 60, 92, 198), that at certain seasons of the year, especially at the time of active growth and ripening, cropped soils contain a higher content of CO₂ than uncropped soils, their interpretation of the results differ. Russell and Appleyard (163) attribute the conflicting results of the older workers (40, 41, 123, 211), even when comparison was made between cropped and fallow portions of the same plot, to failure to recognize the marked influence of differences in the physical and chemical structure on the carbon dioxide content of the soils in question. The Rothamsted investigators conclude that in their own experiments the difference in the physical structure and composition of the cropped (or grass) and uncropped (fallow land) soils makes comparison difficult. These authorities observed that the smaller the soil differences become, the smaller is the effect of the crop on the production of CO₂ and they postulate that, if it were possible to obtain absolute identity of conditions, the effect of the crop would vanish. But that the factor assigned by these authorities for the observed differences cannot be the only one is shown by the work of Headden (60), who found a marked depression of soil carbon dioxide after each cutting of alfalfa. There is, moreover, such a marked difference in the amount of CO₂ evolved from an uncropped and a cropped plot in some of the more recent field experiments (59) that it is difficult to conceive how such marked divergence could be due to physical differences in the soil of the plots. For example, Hasse and Kirchmeyer's (59) results indicate that four-fifths of the total CO₂ was due to root respiration.

(2) Are lysimeter results applicable to field conditions?—Moreover, if Russell and Appleyard's (163) conclusions are generally applicable, the question may be raised whether pot and lysimeter experiments of the type conducted by Barakov (3), Turpin (198) and others (9, 37) are applicable to field conditions. That the deductions drawn from some of these experiments may not be applicable to field conditions, on account of the conditions being too artificial, is possible. This criticism would apply to the conclusions of Kossowitsch (84, 85, 86) in which CO₂ was determined in percolates of the nutrient solution in quartz sand cultures, but for the fact that Dustman (37) has shown that, although the absolute respiration of plants grown in quartz and soil cultures is greater in the former, the relative differences between different plants are the same in both.

In Turpin's lysimeter experiments (198) the difference between the amount of carbon dioxide in the cropped soil and that in the uncropped
soil at the period of most active crop growth, divided by the amount of water transpired by the crop, gave a constant which varied with the season. Moreover, as there was no indication that the increased CO₂ in the cropped soil arose from the decomposition of root particles, TURPIN logically concludes from these experiments that the plant often produces at the period of its most active growth many times as much CO₂ as is produced by soil organisms.

The results of Barakov’s lysimeter experiments (3), in which weekly determinations of CO₂ were made on different types of unsterilized soils, also indicate that the principal source of CO₂ is from the respiration of roots. The greatest absolute quantity of CO₂ was associated with the greatest development of the plant. He notes that each plant experimented with had its own specific respiration curve.

Starkey (177, 178), however, frequently found little effect on the CO₂ content of the soil or abundance of organisms, especially in the early stages of growth. He also noted the occurrence of larger numbers of microorganisms about plant roots than at a distance from them. On the basis of these findings Starkey questions the conclusions of Turpin (198) and Barakov (3). There is no reason to doubt that at certain periods a part of the carbon dioxide evolved in the respiration of roots is contributed by the bacteria that inhabit the root surface, i.e., the rhizosphere (58, 110, 180); but the weight of evidence (3, 60, 198) indicates that the total contribution to the soil CO₂ by such means is relatively insignificant compared with the amount evolved during the growing season by the respiratory activity of the roots. It is also apparent on physico-chemical grounds that determinations of carbon dioxide on samples of soil taken under such conditions as those described by Starkey (177) afford no basis for drawing conclusions concerning the quantitative relations relative to the carbon dioxide of the soil atmosphere in situ. This same disadvantage applies also to Metzger’s (111, 112) attempt to measure the concentration of bicarbonates in soil samples immediately around the roots with those taken away from the roots, for these methods obviously destroy the CO₂ equilibrium conditions actually existing in the soil. A review of methods used for the determination of carbon dioxide of the soil atmosphere will be found in a paper by Potter and Snyder (150).

Hutchinson (72) concludes that there exists a parallelism between bacterial numbers and CO₂ content of the soil. This report (72) is frequently cited in the literature; but it is sketchy and lacking in details. If the exact parallelism between soil CO₂ and bacterial numbers occurs throughout the growing season, this fact would tend to show that the root contribution would be small; but when such correlations are attempted
there are well defined periods when the bacterial numbers fall as the CO₂ increases. If, then, as WOLNY and others \((144, 198, 213)\) suggest, relatively large increases of CO₂ depress bacterial activity, no correlation would be expected, which may, as PLUMMER \((149)\) suggests, be due to the limitation of the oxygen supply. It should be noted, however, that STOKLAS \((180)\) finds that root respiration and the number of bacteria in the rhizosphere paralleled one another.

We must, therefore, conclude that either RUSSELL and APPLEYARD’s \((163)\) results were due to conditions not readily duplicated and that the conclusions drawn by them are not of general application, or that deductions from experiments of this type carried out in pots and lysimeters are not applicable to conditions in the field. The assimilation and utilization of nutrients in pot experiments is considerably greater than in field experiments. In the former the roots penetrate the soil more intensively than in the open field. As a result of this better utilization of nutrients, the yields in pot experiments are frequently six to ten times higher than those in the field. Recent suggestions \((32)\) to eliminate these differences include mixing the soil with equal parts by volume of quartz sand. Finally, it is to be noted that there is no evidence that the discrepancies in the experiments discussed above can be attributed to the relative predominance of root respiratory activities as a result of the relatively low rate of oxidation of organic matter or vice versa.

g. Intensity of CO₂ production by roots of different species.—Since the atomic groupings and reciprocal linkages of the roots of different plants are not similar, it could be postulated that the respiration activity of the root systems of plants would be different. The complexity of the problem is appreciated when specific data for the respiratory energy of the roots of different plants are considered. The causes of the wide variations reported by different investigators for identical types of plants must be sought in the different conditions of experimental technique, especially with respect to the difficulty in making a comparison of the influence of the various factors that influence respiration, such as concentration of oxygen, temperature, concentration of carbon dioxide, and nature and concentration of nutrients.

Thus, the average amount of CO₂ evolved in 24 hours from barley grown to maturity was found by STOKLASA and ERNEST \((182, 183)\) to be 70 mg. per gm. dry weight of roots, whereas NEWTON \((127)\), in plants 35 days old, found only 3.5 mg. of CO₂ per gm. dry weight of roots evolved in 26 hours. Both of the above investigators used sand as the substrate. STOKLASA used sterilized sand and KNOP’s nutrient solution. NEWTON used HOAGLAND’s culture solution. NEWTON has thought that possibly his method
of simple diffusion may not have measured all the CO$_2$ evolved (130). But the agreement between Dustman's (37) results and Newton's shows that this is not the reason and, theoretically, no great difference would be expected to result between systems depending on diffusion and air currents, respectively, since the measurements must necessarily have been made when each system was in a state of equilibrium between output and removal of CO$_2$ (104); nor is there any evidence that these large differences in Stoklasa's and Newton's values can be attributed to any great difference in the age of the plants used. Values obtained by the writer (186) for sweet clover in sand cultures by a similar method to that used by Pfeiffer and Blanck (145) ranged from 8–9 mg. per gram. of dry weight of roots evolved in 24 hours, compared with values of 4.5 mg. obtained by Newton. Dustman's (37) results are in relative agreement with Newton's. That Stoklasa and Ernest's (182) values are far higher than is usual under field conditions will be evident from a consideration of the following facts: Stoklasa concludes that the microorganisms in an acre of soil to a depth of 1.5 feet may produce between 65 and 70 pounds of CO$_2$ a day for 200 days in the year, and that during the growing period the roots of oats or wheat would give off nearly as much to an acre. This would mean a loss from decomposition of organic matter of 13,500 pounds of CO$_2$ per acre per year, or $0.471 \times 13,500 = 6,358$ pounds of organic matter. This value is abnormally high. As Newton (130) points out, a loss of one-half to one ton of organic matter per acre per year is closer to the average loss from normal soils.

It must be admitted (87) that calculation of the carbon dioxide production per gram of dry weight of material is not a very refined method of measurement, owing to the variation in the percentage amount of protoplasm in the various plants and parts of plants, the respiratory gas exchange of which depends entirely upon the activity of the living substance. Some tissues, such as wood and cork, consisting for the most part of dead cells, do not respire at all. But, owing to the impracticability of the alternative methods proposed (87), the simple method of calculation on the basis of total weight must be used.

Studied from a relative standpoint, however, Stoklasa and Ernest's results are decidedly valuable. Thus, the specific respiration energies (amount of CO$_2$ evolved per gram of dry weight) of roots found by them were barley 68, wheat 90, oats 127, rye 118, buckwheat 227. In sterilized sand culture experiments they found that the above values were in the same relative order as the utilization of P$_2$O$_5$ and K$_2$O from basalt and gneiss. As already pointed out, Barakov (3), too, in experiments with lupin, oats, barley and rye, found that the capacity to absorb Ca from rock
phosphate paralleled their values for the specific respiration energy. Stoklasa and Ernest, whose results are in substantial accord with those of Barakov's (3), point out that the values found by them for the respiration energies do not, however, afford any indication of the relative yields under conditions where readily assimilable nutrients are supplied. Thus, in Knop's nutrient solution the yield of barley was found to be far greater than that of wheat, rye or oats. This might be attributed to the compensating factor of extensive root development in the case of barley, as Hesse's measurements (62) of the root hairs of barley, oats, rye and wheat indicate and which are in harmony with the measurements of Nobbe (131).

### TABLE II

<table>
<thead>
<tr>
<th>Size of root hairs on cereal crop plants</th>
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<tbody>
<tr>
<td>Length (mm)</td>
</tr>
<tr>
<td>Barley</td>
</tr>
<tr>
<td>Oats</td>
</tr>
<tr>
<td>Rye</td>
</tr>
<tr>
<td>Wheat</td>
</tr>
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If Stoklasa and Ernest's results can be corroborated we could postulate: (1) That when the rate of supply of N, P and K are sufficiently rapid, as in the case of access to an ample supply of easily soluble nutrients, the yield will be proportional to the extent of root system. (2) But if one of these elements, such as phosphorus, is present only in a difficultly soluble form, the yield will be proportional to the respiration energies.

If these conclusions of Stoklasa and Ernest (182) and of the other investigators cited (p. 446) can be proved to be of general applicability to our economic plants, we should be forced to accept the views of the school that regards the rôle played by carbon dioxide as the greatest factor determining their feeding power. The need, therefore, for more exact information on the respiration coefficients of the various types of economic plants is apparent.

2. To what extent does CO₂ function as a solvent

a. The imbibitional water of the root hairs is not a saturated solution of carbon dioxide.—Aberson (1), on the basis of titration and hydrogen-ion concentration values obtained on seedling roots, concluded that the hydrogen-ion concentration of the water of imbibition of the mucilaginous "membranes" of the root hairs in close contact with the soil particles contains a saturated solution of carbon dioxide. Experimen-
tal evidence is cited to show that a saturated solution of CO₂ is able to bring into solution the insoluble soil minerals, especially phosphates.

But ABERSON’s view is not valid for the following reasons: (1) A saturated solution of carbon dioxide has a hydrogen-ion concentration of 1.2 \times 10^{-4}; this exceeds the hydrogen-ion concentration values of any of the root exudations found by ABERSON. (2) With any given content of carbon dioxide in the soil atmosphere it is possible to calculate the content of CO₂ and HCO₃⁻ ions in the water of imbibition in contact with it.

\[ \text{HA} = \text{H}^+ + \text{A}^- \quad (1) \]

\[ \frac{[\text{H}^+] \cdot [\text{A}^-]}{[\text{HA}]} = K_a \quad (2) \]

\[ \therefore [\text{H}^+]^2 = K_a \cdot [\text{HA}] \quad \text{or} \quad [\text{H}^+] = \sqrt{K_a \cdot [\text{HA}]} \quad (3) \]

and

\[ [\text{H}^+] = \sqrt{K_a \cdot (C - [\text{H}^+])} \quad (4) \]

where C is the concentration of the original acid.

Since \([\text{H}^+]\) is small, we have

\[ [\text{H}^+] = \frac{\sqrt{K_a \cdot C}}{1 + K_a} \quad (5) \]

or

\[ \text{pH} = -\frac{1}{2} \log K_a + \frac{1}{2} \log C \quad (6) \]

For polybasic acids the first ionization constant may be taken, since the second ionization constant is small compared with the first.

Since the Henry coefficient at N.T.P. is approximately 1:1 (199), the percentage by volume of carbonic acid of the soil solution and the percentage in the soil air are approximately identical. Hence, even if the soil air contained as high as 10 per cent. CO₂, the soil solution (if it consisted of pure water) would also contain 10 per cent. by volume of CO₂, since the Henry coefficient is 1:1. The pH of such a solution calculated from the above equation would be 4.10. Since, however, it is a solution of salts, and especially of bicarbonates, the dissociation of the carbon dioxide would be depressed even below the above value. Moreover, ABERSON has neglected to consider the influence of the salts present in the cell sap of the roots.

b. HOAGLAND’S VIEW.—The data of HOAGLAND et al. (68, 70, 170) would seem to afford evidence that CO₂ may not play an important rôle in all soils. These investigators found no measurable change in the reaction of soils of such markedly acid character of which the hydrogen-ion concentration is of the order of magnitude of the dissociation constant \((3.0 \times 10^{-7})\) of carbonic acid (200), when such soils are partially saturated with carbon dioxide. In soils having a lower hydrogen-ion concentration (higher pH), however, the change in reaction due to partial saturation with CO₂ was
quite significant. The decomposition of stall or green manures in acid soils of hydrogen-ion concentration of the above order of magnitude would, therefore, not be expected to increase the hydrogen-ion concentration of the soil to such an appreciable extent as to have any effect on the solution of "insoluble" materials. Inasmuch as there is an overwhelming amount of evidence from field and laboratory experiments that decomposing matter is a potent source of rendering the "insoluble" minerals of the soil available, the rate of decomposition varying with the age and nature of the material (108) and also nature of fertilization (206), we should—on the basis of Hoagland and Sharp's data—be forced to attribute the major favorable effect in the majority of soils not to carbonic acid but to the intermediate products of decomposition by the soil microorganisms, such as butyric, acetic and lactic acids—the dissociation constants of which are of the order $1.8 \times 10^{-4}$ to $1.7 \times 10^{-5}$—and possibly also to replacement effects in the exchange complex.

Hoagland (68) sums up the situation as follows: "It appears to me that some soils are so acid that CO$_2$ is of slight effect, and that in other soils the nature of the soil minerals is such that CO$_2$ may have very little influence in promoting the solution of PO$_4$ or K; but, nevertheless, that CO$_2$ is of great general significance because of the existence of a great number of soils—not inconceivably the majority of soils—where CO$_2$ does appreciably alter the culture medium of the plant. In all this, we presumably must constantly keep in mind the difficulty of knowing just what the chemical system, and influence of CO$_2$, is at root-soil particle interphases." Yet it is evident from more recent field experiments (166) that there are exceptions even to this generalization.

The influence of nitrification processes must, however, not be underestimated (187). In soils rich in calcium, nitrification processes are generally accompanied by the destruction of bicarbonates, i.e., with a decrease in the buffer value and increased utilization (p. 466). In practice, then, the aim should be made to increase the decomposition of organic matter without greatly increasing the calcium concentration of the soil solution. One way of doing this would be to apply lime in small amounts.

c. Experiments on the Influence of Artificial Additions of Carbon Dioxide to the Soil.—It might be expected that the results of experiments in which definite quantities of carbon dioxide are introduced into the soil in which plants are growing would give results from which definite conclusions could be drawn; but this is far from being the case. Lundegårdh (103) has shown the beneficial effects of increasing the carbon dioxide concentration of the atmosphere surrounding the external assimilatory organs, and Breazeale and Burgess (11) noted increased absorption of
PO₄ by seedlings from "floats" when saturated with CO₂. The results obtained by Mitscherlich (118), Pfeiffer and Blanck (145), and also by Parker (140) are, however, decidedly negative with respect to its influence on the absorption of difficultly soluble materials; even distinct injury has resulted in some experiments (118, 145). These negative results, however, afford no proof that the carbon dioxide produced under field conditions does not play an important rôle in the assimilation of mineral nutrients. As Truong (50) suggests, the equilibrium conditions governing carbon dioxide evolution in the soil at the interface of the plasma membrane of the root hairs may not as yet have been duplicated in the laboratory.

It is unfortunate that all investigators have used either quartz sand or soils low in colloidal material in which the factor of ion replacement does not play the important rôle that it does in soils high in colloidal material. In view of the fact, moreover, that carbon dioxide is well known to have toxic effects when the CO₂/O₂ ratio is relatively high (21, 24, 56, 118, 145, 167), this possibility must also be considered in the experiments hitherto conducted on the effect of CO₂ additions. Pfeiffer and Blanck (145) observed distinct injuries, especially to oats, in their first series of wheat, lupine and oats cultures, when washed CO₂ gas was introduced at the bottom of the vessel for 10 minutes, 3 days a week at a pressure of 2.5 atmospheres. In their second series, when water saturated with CO₂ was used, no injury resulted; but even this procedure did not in Mitscherlich's experiments (118) prevent injury to the plants.

In none of the experiments on the effect of the artificial addition of CO₂ is the total concentration of carbon dioxide in the soil at any definite interval of time known. The possibility of toxic doses, therefore, is not eliminated. Thus, in Parker's experiments (140) the concentration of carbon dioxide was sufficient to increase markedly the absorption of silica. Evidence exists that different plants differ in sensitivity to CO₂ (45, 179), although in the culture solution experiments of Hall (56) wilting occurred when CO₂ was aspirated through all culture solutions. Stoklasa (182) and also Lundegårdh (102, 103) found that a concentration as low as 1 per cent. of CO₂ in the soil atmosphere 15 cm. below the soil surface retarded growth, and was even toxic to some plants.

It is of interest to note here that Pfeiffer and Blanck (145) argue from the negative results obtained by CO₂ additions in their "oder-sand" cultures in the presence of rock phosphate that the data afford proof that other acids are exuded by roots, because, although many of the plants with which they experimented were able to utilize rock phosphate quite well, the artificial addition of CO₂ gave in all cases decreased yields.
3. Root excretions other than CO₂

a. The divergent views.—The tendency of the European workers (1, 28, 55, 120, 183) and also of some of the American investigators (52, 67, 68) is to emphasize the importance of carbon dioxide exudation, and to regard the rôle of other acid exudations, relatively, of little significance, and, indeed, in some cases (52, 55, 183) to question their existence. Others (28, 120) have claimed to have found substances other than acids in the root exudations.

b. Distinction between excretions from living and dead cells.—Although the fact that acids may be excreted from dead cells was early recognized by Czapek (28), it may be questioned if, in planning some experiments (12), sufficient attention has been paid to the necessity for making conditions such that the excretions of living and dead cells could be differentiated. That this point is of importance is shown by the results of Johnson (75), who found marked differences in the quantities of Ca⁺ and Cl⁻ absorbed from a CaCl₂ solution, in the case of live and dead beet cells. The dead beet cells removed only 26.2 per cent. Cl from the roots whereas living beet cells removed 43.7 per cent.; but the proportion of Ca absorbed was nearly the same in both cases.

Osterhout (133) and also Rudolfs (160, 161) have also called attention to the effect of hydrolytic dissociation of neutral salts and to the effect of the differential rate of ionic absorption. These secondary effects, due to differences in the permeability of living and dead cells, will be discussed later in this paper.

c. Root sap acidity as a basis for chemical methods of determining nutrient requirements.—(1) The direct method of approach.—The assumption that acids were exuded from roots served as a basis for the attempts of Dyer (38) and his school to ascertain the fertilizer requirements of soils. Dyer argued that if acids are exuded, the total acidity of the sap should be an approximate measure of its solvent action. The sap acidity was obtained by averaging the results of determinations for total acidity of the water extracts of the roots from over a hundred different species of plants. This was found to be equal approximately to a 1 per cent. solution of citric acid. Lemmermann (96) also adopted a similar criterion and, as we shall see later, the greater assimilatory ability of the Leguminosae compared with the Gramineae was attributed by him to the greater total acidity of the root sap of the former.

Information on the nature of the root exudations was also sought by Czapek (28) and Kunze (89) by bringing intact seedling roots in contact with litmus paper and noting the change in color. It has been suggested by Haas (54) and others, however, that it is not possible to reach definite
conclusions from this type of experiment because different roots may differ in their capacity to absorb the blue dye of litmus. Differential absorption cannot account for all the facts, for KUNZE (89) showed by titration in parallel experiments that the acidity exhibited was far greater than that indicated by the turning point of litmus. And there is no evidence in KUNZE's experiments that the acids arise from injured or dead cells. It is clear, too, that KUNZE recognized the limitations of litmus paper as an indicator, for he states that in some plants the amount of acid lies below the sensitivity of litmus.

CZAPEK (28) attributed the red color obtained by pressing seedlings against blue litmus paper to the exudation of KH₂PO₄, and emphasized the fact that the exudation of this salt could not be explained by any injury to the cells of the root hairs because the same result was obtained in culture experiments where there could be no question of injury; but it is to be noted that CZAPEK did not find the drops of liquid—always to be observed on the roots of seedlings developed in a humid atmosphere—to be acid. PRIANISHNIKOV (153) also found traces of PO₄ in the root secretions of seedlings, but not from full grown normal plants.

The whole subject of the secretion of acids other than CO₂ was subjected to a critical investigation by STOKLASA and ERNEST (183) with Hordeum vulgare and Zea mays, using a different technique. The seedlings were allowed to develop for 15 days in distilled water and then transferred to experimental cylinders, through which 20 liters of sterilized air free from CO₂ were passed. In one series of experiments a mixture of O₂ and N₂ gas was used. Under these conditions CO₂ and a trace of H₂ was found, but no PO₄ nor SO₄. In view of the fact that a large number of investigators (8, 13, 79, 94, 101) had reported the presence of lactic, acetic and formic acids in the root exudations of plants, STOKLASA and ERNEST carried out a similar series of experiments from which they conclude that these acids were only exuded when the root system suffers from lack of oxygen and is the result of partial intramolecular respiration. When the supply of oxygen was sufficient only carbon dioxide was found. These experiments were carried out at a uniform temperature (20–22° C.) and observations were made for 10–20 days. Air containing α-radium emanations increased respiration considerably.

STOKLASA and also HALL (55) have argued, from an ecological standpoint, that it is improbable that such important nutrients as K and P₂O₅ would be exuded from the root system; but this position is untenable, for many experiments (15, 207) show very clearly that plants may return to the soil at some stage of their growth, usually at maturity, some of these important nutrient elements.
The indirect method of approach.—Some investigators (117, 145, 181, 192), on the other hand, have sought a solution of the problem of acid exudation of roots by determining the assimilatory power of different plants for difficultly soluble materials, like rock phosphate, and Hall (55) has sought a solution by taking out a balance sheet between the acid and bases contained within the completely developed plant.

(a) Mitscherlich’s view.—The conclusions from the indirect methods devised by Mitscherlich (119) and that adopted by Pfeiffer and Blanck (145) are contradictory. Mitscherlich (119) maintains that his “Wirkungsfaktor” values are a constant characteristic for each manure (fertilizer) on all crops and all soils. This “law” of Mitscherlich is expressed by the equation

\[
\frac{dx}{dy} = k(A - y) \tag{7}
\]

or

\[
\log_e(A - y) = \log_e A - c(x + b) \tag{8}
\]

where:  
\( c = “Wirkungsfaktor” \) or action produced by the nutrient element applied, 
\( A = \) maximum yield when \( x \) is not limiting, 
\( x = \) amount of nutrient element added, 
\( b = \) amount of available nutrient already present in the soil, 
\( y = \) yield obtained by application of nutrient element \( x \).

He argues, therefore, from the constancy of \( c \) that all plants must have at their disposal the same agent for the decomposition of difficultly soluble material and that this is \( CO_2 \) exclusively. In recent years he appears to have changed his views to some extent as a result of the following experiment (120), which is easily carried out. When a very dilute solution of HCl (0.0001 N) is added to root hairs observed under a microscope, at first local swelling up of the protoplasm can be observed, followed by a rupture and expulsion of the protoplasm into the surrounding medium. After some time new root hairs are formed, showing that the injurious effects of too high hydrogen-ion concentration have been overcome. These phenomena may, in part, be explained by the tendency of plants to change the reaction of the medium in the direction of neutrality as observed by Pantanelli (138), Hoagland (64, 65, 67) and Theron (185). The medium might be neutralized by the absorption of hydrogen-ions and the excretion of OH ions simultaneously, or, as Mitscherlich believes, the injurious effect of the acid may be counter-balanced by the liberation of substances of the nature of organic buffers. These ideas would coincide with Mazed’s (109) and also Comber’s view (26) that substances other than those of acid nature take part in the solubilization of mineral nutrients. That considerable organic matter is liberated from the root sap and root hairs sloughed off by plant roots is shown by the observations of Lyon and Wilson (105), but
these findings are not applicable as evidence to the exudations of intact root hairs. MINIMA's investigations (116) afford some evidence, although indirect, that organic acids are excreted by roots, on the basis that the period of maximum excretion of non-volatile organic acid buffers is coincident with that of maximum acidification of the soil.

Mitscherlich, in his earlier papers (118), held the view (146, 147) that the amount of P$_2$O$_5$ absorbed from rock phosphate by oats was identical with the amount dissolved by a saturated solution of carbon dioxide, and concluded (117) that the different "Aufschliessungs-vermögen" of different plants could be explained by differences exhibited in their ability to develop root systems, which, in turn, is proportional to the amount of carbon dioxide respired by them. More recently he has modified these views and has discarded chemical methods as being inadequate (119). Indeed, it has been found by numerous workers, especially by König (82) and Schloesing (168), that oats and other plants may absorb far more P$_2$O$_5$ from rock phosphate and other soil phosphates than can be dissolved by a saturated solution of CO$_2$. Frear and Erb (43) also drew similar conclusions with respect to the soil K$_2$O of the fertilizer plots of this Experiment Station.

In evaluating these opposing claims, it should be remembered that Stoklasa (180) and Stoklasa and Ernest (183) found that lactic, acetic, formic and oxalic acids were excreted only when the root system suffers from lack of oxygen; but as yet there are no critical experiments indicating whether or not under average field conditions, the system in immediate contact with the roots may not be relatively deficient in oxygen. The accumulation of these organic acids due to incomplete oxidation of the products of respiration has been found by Stoklasa to be highly toxic to plants. This view is further supported by Mazé's experiments (109) with peas in sterile cultures. That the problem of air renewal is a serious problem, especially in some of the finer textured soils, is apparent from technical remedies such as drainage and crop residues devised to meet it.

(b) Hall and Miller's experiments.—One of the arguments used by Hall (55) upon which to substantiate his conclusions that only CO$_2$ is excreted by the plant is based on the findings of Hall and Miller (57) that the net action of the plant upon the soil is to leave an excess of base in the soil. This result was arrived at by taking a balance sheet between the acid and bases contained within the completely developed plants (wheat, barley, sweeds and hay) of the Rothamsted rotation experiments on the Agdell field, and also of wheat and cabbage plants grown in culture solutions. These experiments, however, do not take into consideration the effect of hydrogen-ion concentration. As Theron (185) and others have empha-
sized, greater equivalent proportions of anions than of cations are absorbed on the acid side and on the alkaline side the reverse holds true. If Hall's statements had been made later, they undoubtedly would have been modified as a result of the recent progress in physical chemistry. Furthermore, the validity of the assumption made by Hall that all the nitrogen in the plant should be calculated as an acid on the basis that all the nitrogen enters the plant as nitrate may be questioned.

(c) Kappen's experiments on expressed root saps.—The procedure of Kappen (77) of determining the total acidity and hydrogen-ion concentration of the expressed sap of the roots of mature plants grown in field experimental plats is more pertinent; but even in these experiments values cannot be regarded as absolute, because—as we shall see later—of the existence of a hydrogen-ion concentration gradient (53, 195). Moreover, Kappen's experiments are open to the criticism that they do not distinguish between diffusion products and exudations of the roots. Considered, however, from the standpoint of the relative comparisons between total acidity and hydrogen-ion concentration of the respective root saps, Kappen's data indicating low hydrogen-ion concentration values but high titration numbers are instructive. Only 0.1 per cent. of the hydrogen-ions were found to be present in the ionic condition, the remainder being in the undissociated form. The inevitable conclusion is that the root saps must consist of a mixture of free organic acids and their alkali or alkali-earth salts. This point is of interest because such an arrangement would ensure the organism against too violent fluctuations in the degree of acidity of its sap, and is analogous to the conditions that exist with other physiological fluids, blood, urine, etc. Both Groh (49) and Pavlinova (143) come to the same conclusion as Kappen, but the deductions of the latter, unfortunately, are of limited application because only seedlings were used. They are of interest, however, in that they show that the older technique adopted by Czapek (28) is useless to determine the reaction of the water exuded by guttation.

(d) Haas's experiments.—Haas (52) sought a solution of the problem of root exudation by determining simultaneously the hydrogen-ion concentration of solutions in which seedling plants were growing and also in controls without plants. After the CO₂ had been expelled by a current of pure H₂, the hydrogen-ion concentration of both series of cultures was identical. Although this method eliminates the possibility of confusing the exudation of living cells from those of dead cells, it is doubtful if the conclusion drawn by Haas from these experiments, viz., that plants do not exude other acids than CO₂, can be extended to mature plants. The mineral nutrient requirements of the 10 day seedlings with which Haas worked are, of course, much less than in more mature plants.
C. The influence of the degree of the acidity of the cell sap

In view of the emphasis placed by many investigators upon the influence of the degree of the sap acidity of cells as a determining factor in the feeding of plants, it is pertinent for us to inquire more closely into this phenomenon.

1. Does a hydrogen-ion concentration gradient exist

Although there is sufficient evidence to indicate that the hydrogen-ion concentration of the substrate has an indirect influence on the growth of plants, it is not definitely known what, if any, relation exists between the hydrogen-ion concentration of the medium and that of the metabolically active tissues. Jacobs (73, 74), in the case of isolated cells, found none. Hoagland's results (66) on barley grown in water, in sand, and also in soil cultures indicate that the pH values of the sap of the tops were almost identical, even though the pH of the nutrient media varied widely, viz., from 4.94 to 6.76 in water cultures and from 7.03 to 7.34 in soils. Reed and Haas (157, 158) report similar results from water culture experiments. The latter (157) and also THERON (185) have obtained comparable results in the case of the sap of tops, but in the roots THERON (185) noted that the pH increased with increase in pH of the medium (substrate). The existence of a definite hydrogen-ion concentration gradient in the case of algae has been shown by Child (23) and in some of the higher plants, grown in soils, by Haas (53) and in animal tissues by Gustafson (51). The regulatory influence of buffer systems, therefore, must vary considerably in different parts of the plant. The data of Haas (53) are illuminating. In Melilotus alba (second year growth), the following pH values were obtained: Soil extract, 7.68; root (6" portion below upper 2"), 5.82; root (2" of upper part), 6.46; leaves and petioles, 7.04; stems, 6.68. The pH of the mixed upper 3" of the tops, stems, leaves and buds was 8.0. As Reed and Haas (158) later pointed out, any hypothesis based upon differences of acidity of the plant sap and the external medium must account not only for the accumulation of inorganic elements within the roots but also for their movements to other portions of the plant. Investigators in this field must, moreover, take cognizance of the fact that marked change in the hydrogen-ion concentration usually occurs within an hour after expression of the plant sap (25, 50, 61, 195).

From the foregoing, it is apparent that we are not yet in possession of sufficient evidence to determine whether or not the cell sap of tissues possessing similar functions have hydrogen-ion concentration values that may be characteristic of the species. The assumption that root sap acidity values are a characteristic of the species formed the basis of much of the experimental work by the German investigators, (1, 89, 96) in their search
for a solution of the causative factors determining the "Aufschliessungsvermögen" of different species. Thus, the Gramineae and the Leguminosae were supposed to be sharply differentiated (96) on the basis of the acidity of their root sap, until KAPPEN (77) and later STOKLASA (181) showed very definitely that the distinction held neither for the titration nor hydrogen-ion concentration values. STOKLASA's experiments (181), if confirmed, would lead to the conclusion that the acidity of the sap of the roots of all cultivated plants is near neutrality, except when insufficient oxygen is present, under which latter condition the acidity increases. He emphasizes the significance of this fact for the development of the bacteria of the rhizosphere.

As we shall presently see, working on this assumption, TRUOG (194) considers that the feeding power of different plant species is a function of the different intensities of the acidity of the respective saps. Thus, buckwheat and clover are cited as types of plants with high and low acidities, respectively. The table below, however, taken from the data of TRUOG and MEACHAM (195), KAPPEN (77), HAAS (53), STOKLASA (181), and ABERSON (1), will show how impossible is such a classification, at least with the methods hitherto adopted.

**TABLE III**

**pH of Buckwheat and Red Clover Roots Reported by Several Investigators**

<table>
<thead>
<tr>
<th>Investigator</th>
<th>Buckwheat</th>
<th>Red clover</th>
</tr>
</thead>
<tbody>
<tr>
<td>TRUOG and MEACHAM</td>
<td>4.0 - 4.03</td>
<td>5.6 - 5.9</td>
</tr>
<tr>
<td>KAPPEN</td>
<td>4.9 - 5.3</td>
<td>6.2</td>
</tr>
<tr>
<td>ABERSON</td>
<td>5.7 - 5.9</td>
<td>7.9 - 8.4</td>
</tr>
<tr>
<td>HAAS</td>
<td>4.8 (mature plant)</td>
<td>5.8 - 6.1</td>
</tr>
<tr>
<td>STOKLASA</td>
<td>5.4 - 5.9 (seedlings)</td>
<td>6.6</td>
</tr>
<tr>
<td></td>
<td>6.2</td>
<td>6.6</td>
</tr>
</tbody>
</table>

Further development of NĚMEC's work (125) on the hydrogen-ion concentration of the sap of seeds of a large number of different species of plants promises—from the practical standpoint—to clarify the whole situation. Seeds are more nearly constant in composition than other parts of plants, and NĚMEC found that the hydrogen-ion concentrations of the seeds of plants adapted to acid soils are relatively much higher than those adapted to alkaline soils. It is of interest to note that the saps from the seeds of barley, corn and peas were found to have the lowest hydrogen-ion concentration, pH 6.45 – 6.30.

It has been a matter of long observation that such plants as sweet clover, alfalfa and lettuce are adapted to grow on soils at or near the neutral point.
When soils to which these plants are adapted are allowed to go unlimed, they are replaced by others that are less sensitive to acid conditions. Camargo et al. (19) have recently shown in controlled experiments that the optimum growth of roots of the coffee plant is at pH 4.2, which affords an explanation of their adaptability to acid soils. The coffee plant is greatly injured by even moderate liming.

D. Theories proposed to explain differences in the feeding power of plants

1. The application of the Law of Mass Action

Tschirikow (196, 197) stressed the importance of the CaO/P₂O₅ ratio in the plant as an important factor in the ability of different plants to supply themselves with enough P₂O₅ from difficultly soluble phosphates. Plants having a high energy absorption for Ca would, according to him, depress the Ca concentration of the soil solution, resulting in an increased solubility of the phosphate. The smaller the amount of P₂O₅ necessary for the formation of one unit of organic substance of the plant (i.e., the smaller the percentage of P₂O₅ in the plant), the greater obviously would be the effect of P₂O₅. From this viewpoint the capacity of the plant to absorb difficultly soluble phosphates is directly parallel to the quantity of Ca absorbed and inversely parallel to the P₂O₅ requirement of the plant.

Truog (192, 194) has extended Tschirikow's views further and has invoked the concept of equilibrium between calcium phosphate and carbonic acid, on the one hand, and the products of their interaction, on the other, as expressed by the equation:

\[
\text{Ca}_3(\text{PO}_4)_2 + 2\text{H}_2\text{CO}_3 \rightleftharpoons \text{Ca}_3\text{H}_2(\text{PO}_4)_2 + \text{CaH}_2(\text{CO}_3)_2
\]  

He contends that plants such as buckwheat, which the majority of culture experiments show is capable of utilizing the phosphorus of rock phosphate in large measure, are supposed to be able to absorb both of the products to the right of the equation. It is to be inferred, moreover, as already stated (p. 462), from Truog's later expansion of this view that the rate of absorption is determined by the degree of acidity of the saps of these plants. Thus, buckwheat is characterized as a plant with "high internal acidity." In the case of plants having a low degree of sap acidity, one of the products to the right of the equation (calcium bicarbonate) is assumed to be incapable of absorption by the plant at a rate comparable with that of the other product (di-calcium phosphate); consequently, the operation of the reverse reaction will prevent the further solution of the rock phosphate. Corn and oats are placed in this class by Truog.

This view has been supported (6, 7, 53) and as vigorously disputed (30). In order to clarify our ideas, it should at the outset be remembered
that, although the possibility (p. 456) of absorption of salts in the undissociated form (133, 135, 137) must be considered possible under some conditions, e.g., in the case of detached cells, the weight of evidence (67) is that absorption in normal intact plants takes place in the ionic condition. Now there is ample evidence, as we shall see later, to show that not only do root hairs of different species differ in their degree of permeability to the same ion, but that the different relative velocities of the anion and cation of a salt may also be a factor in determining the equilibrium. We must then be prepared to consider ionic equilibrium, although the existence of such equilibria between the ions in the cells and the ions in solution has not as yet been established definitely.

2. Evidence for and against Truog’s views

a. Bauer’s sand culture experiments.—The results of Bauer (6) have been cited in support of Truog’s views. In these experiments corn was grown in sand cultures treated with rock phosphate (or acid phosphate) as the source of P, and NaNO₃ or (NH₄)₂NO₃ as the source of N; but the analytical data are insufficient to show that the improvement in growth in the leached pots was due to removal of calcium as the bicarbonate. Removal of toxic substances by leaching must also be considered a factor (119). Further critical experiments on this point should include pots without plants as controls.

b. The views of the California group.—Davis, Hoagland, and Lipman (30) cite Newton’s (126) results with peas and barley in water culture solutions, which grew normally without bicarbonates, and, moreover, in solutions at hydrogen-ion concentration at which bicarbonate ions could not exist to any extent. But this argument may be weakened by the fact that Hoagland (67) and others have later deduced evidence to show that rapid replacement of –HCO₃ ions by other ions may occur.

Reed and Haas (157) have also argued against Truog’s view on the basis of their experimental work with walnut and orange trees. In experiments with the former the effect of a solution of Ca(OH)₂ of pH 9.0 was determined. Although the percentages of Ca in the ash of the tops and roots were 14.60 and 9.80, respectively, the pH of their sap (5.26-5.48) showed no significant changes from values obtained when such plants were grown in complete culture solutions. This same argument, however, used by Reed and Haas to refute the existence of a relation (198) between the absorption of calcium and the degree of acidity of the sap, breaks down completely when certain experimental data (78) may be interpreted, by the same method of reasoning, to prove that calcium may be necessary for precipitating organic acids formed as a by-product, on the basis that
mottled leaves of citrus trees starved of calcium are considerably more acid and contain distinctly less calcium than normal leaves.

Again, Reed and Haas (158) are inclined to the belief that there is no evidence in support of the assumption by Truog (194) that absorbed materials are converted into insoluble compounds as rapidly as they accumulate in the plant, or that absorption necessarily depends on the precipitation of ions within the plant. The italics are the writer’s. But this conclusion is not justified from the experimental data supplied. Thus, Reed and Haas (158) find that in sand cultures the concentration of water-soluble K increases in the ash of leaves, trunk, shoots and stems, and that the concentration of soluble Ca increases in the leaves but decreases in the shoots, trunk and roots as the concentration of the nutrient solution increases. In soil cultures 45.82 per cent. of the Ca was soluble in the leaves, 15.03 per cent. in the shoots, and only 7–9.5 per cent. in the trunk, roots and rootlets. In buckwheat nearly all the calcium is insoluble in water (67). The fact that Nitella (69) contains large quantities of soluble potassium and calcium salts has also been used as an argument (30) against Truog’s views. But to what extent the extension of data obtained from such abnormal structures as Nitella to the higher cultivated plants is justifiable remains to be determined.

The work of Kostychev and Berg (88) has an important bearing in this connection. They have determined the forms in which Ca is present in the tissues of a number of plants. The following interesting data, table IV, are taken from their paper:

TABLE IV
FORMS OF CALCIUM IN PLANTS

<table>
<thead>
<tr>
<th>Plant</th>
<th>Percentage of the total Ca</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Soluble in water</td>
</tr>
<tr>
<td><strong>Trifolium repens</strong> (leaves)</td>
<td>42.4</td>
</tr>
<tr>
<td><em>Alchemilla</em> sp. (leaves)</td>
<td>35.6</td>
</tr>
<tr>
<td><em>Caragana arborescens</em> (leaves)</td>
<td>21.0</td>
</tr>
<tr>
<td><em>Solanum tuberosum</em> (leaves)</td>
<td>16.5</td>
</tr>
<tr>
<td><em>Lemna minor</em></td>
<td>11.6</td>
</tr>
</tbody>
</table>

In apple tree experiments (190) the writer has found in mature leaves relatively low percentages of the total Ca soluble in water, viz., 17.2 per cent., and relatively high percentages as the oxalate, viz., 54.3 per cent. The above data might, therefore, be just as readily used to support Truog’s views as to refute them.
CHIBNALL (22) has recently shown that one-tenth of the water-insoluble calcium of cabbage leaves consists of calcium phosphatide.

c. Some weak points in TRUOG’s theory.—

(1) The experiments of Parker—Bauer—Bartholomew.—According to TRUOG (194) plants with a slightly acid or neutral sap, like sweet clover and alfalfa, are more able to utilize the potassium advantageously from lower concentrations of the element than plants, like buckwheat, having a more acid sap; but PARKER (139) found that buckwheat absorbed relatively large quantities of soil potassium. Moreover, BAUER (6) found that both buckwheat and sweet clover readily absorbed calcium from rock phosphate. BARTHOLOMEW (4) also failed to find any relation between the amount (percentage) of calcium absorbed and the ability of these plants to feed on rock phosphate, although the substrate and nutrient medium were the same as that used by TRUOG (quartz sand).

(2) The effect of the destruction of the buffer systems.—No account has been taken of the buffer systems present, the destruction of which must of greater influence than the factors already noted. The buffer action of calcium bicarbonate, for example, is a function of the hydrogen-ion concentration of the medium, and is readily destroyed if the hydrogen-ion concentration varies from pH 7.5.

\[
\begin{align*}
\text{Ca(HCO}_3\text{)}_2 + \text{NaOH} & = \text{CaCO}_3 + \text{NaHCO}_3 + \text{H}_2\text{O} \\
\text{Ca(HCO}_3\text{)}_2 + \text{H}_2\text{SO}_4 & = \text{CaSO}_4 + 2\text{H}_2\text{O} + 2\text{CO}_2
\end{align*}
\]

(10) (11)

The destruction of Ca(HCO₃)₂ results, as shown by BUTKEWITSCH (16), in increased yields—in some cases as much as three times—and the amount of calcium in the medium decreases. The stronger the buffer action the greater the CaO/P₂O₅ ratio. From this standpoint, the inhibitory action of Ca(HCO₃)₂ on phosphate utilization may be regarded as that of paralyzing the root activity of the plant. In this sense and in this sense only may TRUOG’s view hold.

(3) Do the terms “high” and “low” acidity have any meaning?—The validity of TRUOG’s conception must necessarily rest also upon the accuracy of his classification of the relative acidities of the saps of plants into high, medium and low; but, unfortunately, we have no definite knowledge of the relative acidities of plant saps. As we have seen, the variation in different parts of the same plant is so great that it is not, as yet, justifiable to use the terms “high” and “low” in classifying plant saps. The hydrogen-ion concentration of the sap of seeds is much more constant; therefore, in any attempt to correlate hydrogen-ion concentration of plant tissues with nutrient supply, the examination of the sap of seeds would be the most profitable line of attack.
d. Lack of harmony of observation with theory.—Nevertheless, it is highly improbable that the results upon which Parker and Truog (142) based their classification of plants into (1) high Ca and high N, and (2) low Ca and low N are accidental, as has been contended (129). On the contrary, the preliminary studies of Storck and Rippe1 (134) support the existence of such a relationship between Ca and N. True, the analytical data presented by Parker and Truog represent the composition of plants grown under very varied and different conditions. But an examination of the paper (142) will show at once that the data have been collected with great care and, moreover, Truog has himself conducted carefully controlled experiments. He recognizes (193) that isolated analyses may be found that are relatively quite different from those used—especially of plants that have reached maturity or were cut as hay—due to losses of Ca, in part possibly by leaching (95).

If we accept this relationship between calcium and nitrogen as an actual fact, to what may it be attributed? Surely not to acids arising from the decomposition of proteins, as Truog assumes. The older physiologists (33) considered that "living" protein substance of the protoplasm functions as the immediate material for respiration, resulting in the production of the acids found in plants. But, as pointed out by Kostychev (87), this assumption contradicts an abundance of facts that have been established recently without question—that sugars are much more easily oxidized than proteins. Most of the plant acids arise from the carbohydrates and fats that serve as the fundamental sources of energy of respiration (156). As a matter of fact the amount of energy obtained by the decomposition of proteins is very small, and, moreover, the amino acids formed are readily converted by the plant again into proteins (176). Only after the complete consumption of sugars do plants begin to burn the protein material of their protoplasmic framework, and then the CO$_2$/O$_2$ ratio falls to 0.70–0.80.

The explanation of the Ca/N relations observed by Parker and Truog (142) is more probably to be explained by the antagonistic action of Ca and K resulting in an increased absorption of N and P$_2$O$_5$ (188).

e. Extent to which bases function as neutralizers of plant acids.—Truog and Meacham (195) and also Haas (53) have examined the hydrogen-ion concentrations of the tops of a large number of plants grown both in limed and unlimed plots, and, without considering the possibility that the results are within the limits of experimental error (185), it was found that with few exceptions the pH of the tops of the limed plants was higher than that of the unlimed. It might be argued from these facts (53) that one function of calcium is to adjust the pH of the soil solution so as to
enable the plant to secure a sufficiently rapid supply of bases to neutralize the injurious effect of too high acidity; but, apart from the fact that neither CLEVENGER (25) nor DUSTMAN (37) have been able to corroborate such a conclusion, there is absolutely no justification to assume that this function is more peculiar to calcium than the other bases, e.g., magnesium and potassium (90, 91). Moreover, it is not necessary to assume that the disappearance of acids is accomplished solely by the mechanism of neutralization, since ASTRUC (2) has shown conclusively that the disappearance of acids—which are always higher in the young plants—is due not so much to their "neutralization" as to the process of respiration and esterification.

f. Calcium requirements of plants are very different.—It is certain that plants cannot continue growth without calcium and, although different species respond differently to its presence, injury does not result if sufficient quantity of soluble salts are present in the media (157). The observation of LOEW (114), therefore, of the death of cells on treatment with salts that precipitate Ca must be interpreted accordingly.

The response of species to varying quantities of calcium appears to be an important ecological factor (201). Thus, SKEEN (175) has shown that Phaseolus vulgaris nanus must have large amounts of calcium and that Lupinus albus obtains its "neutralization" as to the process of respiration and esterification.

From the foregoing, we are forced to conclude that, although the suggested explanation (p. 467) offered to account for this Ca/N relationship may not explain all the facts, there is no sound reason for denying the existence of this relationship. It is unfortunate, from this standpoint, that the nitrogen content of the oat plants grown by SHEDD (171) on different soils and which showed such extreme ranges in calcium content are not known. This would have given us some valuable information.

3. Conclusions from recent more direct experiments

RUSSELL (162) considers that the critical problem is to know whether the concentration of the substrate (nutrient solution) with respect to calcium has decreased to a greater extent in the "high feeding" plants than in the "low feeders." Such experiments are at present being carried out by DOMONTOVITSCH and SCHESTAKOW (34), of which only the preliminary results have been published to date. In sand culture experiments with lupines, buckwheat, mustard, millet and oats—using rock phosphate (size of particles 0.1 mm.) as the source of P—the growth of the plants and concentration with respect to P2O5 and Ca were compared between pots containing mixed plants, viz., (1) buckwheat and oats, (2) lupines and oats, (3) lupines and millet, (4) mustard and oats, and pots containing an equal number of plants grown alone. The following table V gives the results of the preliminary work:—
The growth of oats and millet was scanty and not much greater than those plants without any phosphorus addition. In the mixed cultures with lupines the yield of oats and millet was increased 545 and 846 per cent. respectively, over the yields of these plants grown alone. Mustard and buckwheat also influenced the growth of these Gramineae to a remarkable extent. Unfortunately, calcium determinations are not reported in all cases; but it is evident that the mixed cultures with lupines have reduced the concentration of the calcium under that in the pots in which the Gramineae grew alone. The hydrogen-ion concentration of the medium in the mixed cultures is also much lower than that in the cultures of plants grown alone. These results indicate that the differences in the utilization of rock phosphate in these experiments are to be correlated with their effect on the hydrogen-ion concentration of the root medium and, perhaps, also with the unequal rates of absorption of calcium. The data for concentration of $P_2O_5$ show no relation between the rates of absorption of phosphate ion by the different plants.

Hoagland has recently reported that with the same source of rock phosphate, buckwheat was able to make normal growth, whereas tomato plants were almost entirely unable to obtain phosphate from this source—yet the tomato plants had a much higher percentage of calcium than the buckwheat plants (68). The conclusion is drawn that the solid phase of the soil and its ability to keep the soil solution supplied with calcium is an important factor. Results obtained by Mazé (109) may be similarly interpreted. It would be of interest for investigators in this country to conduct experiments similar to those of Domontovitsch and Schestakow’s work and, in

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**TABLE V**

Data from Domontovitsch and Schestakow

<table>
<thead>
<tr>
<th>Nr. der Gefäße</th>
<th>$P_2O_5$-Quelle und Pflanzenart</th>
<th>pH</th>
<th>$P_2O_5$ in 100 cc. der Lösung</th>
<th>Ca in 100 cc. der Lösung</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>Rohphosphat Hafer</td>
<td>7.43</td>
<td>0.020</td>
<td>95.0</td>
</tr>
<tr>
<td>16</td>
<td>Hirse</td>
<td>7.14</td>
<td>0.018</td>
<td>111.93</td>
</tr>
<tr>
<td>6</td>
<td>Buchweizen mit Hafer</td>
<td>5.43</td>
<td>0.041</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Buchweizen</td>
<td>6.25</td>
<td>0.036</td>
<td></td>
</tr>
<tr>
<td>11</td>
<td>Lupine</td>
<td>5.34</td>
<td>0.767</td>
<td>30.85</td>
</tr>
<tr>
<td>12</td>
<td>Lupine mit Hafer</td>
<td>5.17</td>
<td>0.679</td>
<td>75.89</td>
</tr>
<tr>
<td>17</td>
<td>Lupine mit Hafer</td>
<td>4.80</td>
<td>1.350</td>
<td>48.59</td>
</tr>
<tr>
<td>26</td>
<td>Hafer</td>
<td>7.21</td>
<td>Spuren</td>
<td></td>
</tr>
<tr>
<td>36</td>
<td>Senf mit Hafer</td>
<td>6.35</td>
<td>grössere</td>
<td></td>
</tr>
</tbody>
</table>
addition, to determine the content of the plants in Ca and PO₄. It is well to bear in mind, however, the possibility that the carbon dioxide exuded by roots may, under the artificial conditions of many of the experiments reported, be of far greater importance than under normal conditions and for this reason it is undoubtedly more advantageous to use soils as the substrate.

E. The influence of the extent of the root system

1. Is there any relationship between feeding power and extent of roots

That great differences exist with respect to the extent of the root system among different types of plants is a common observation. A review of the literature has been given by Miller (115). This difference in the growth of plant roots outwards, together with the differences in their respiration energy, is regarded by some authorities (30) as an important factor in the mechanism of absorption of ions by plants.

Truog has also clearly recognized that differences in the extent of root system may be a factor in the absorbing power of plants. This is quite evident from a statement in one of his earlier papers (193) to the effect that “the feeding power of a plant for lime depends largely on the extent and character of the root system.” From the results of experiments carried out later, Truog modified this view and, as we have seen, stressed the internal acidity of the sap as a more important factor in plants like buckwheat, which have a very restricted root system.

But there are several experiments (84, 152, 154, 155, 192) that indicate no evidence of the existence of any relationship between feeding power and the extent of the root system. In quartz sand cultures with rock phosphate as the source of phosphorus (84, 152, 154, 155, 192) much larger yields and a much higher percentage of P₂O₅ were obtained in the case of the legumes (peas and lupines) and also of buckwheat than of the cereals. In other words, in these experiments buckwheat—with a small root system—(145, 146) utilizes rock phosphate better than the cereals which have, relatively, a very extensive root system. Parker’s data (139) are of interest in this connection. Comparing the absorption of sorghum and cotton under similar conditions, it was found that the latter absorbed more than double the amount of ash constituents than the former. If, as the majority of field observations tend to indicate, sorghum has a more extensive root system than the tap-rooted cotton plants, differences in absorption of mineral constituents cannot, in Parker’s experiments, be attributed to differences in extent of root systems. On the other hand, Davis et al. (30) cite Newton’s experiments (126) to show that the extent of root system is an important factor in the absorption of ions from soil. This conclusion is based on
Newton's experiments in which peas and barley were grown together. Under these conditions the peas absorbed more calcium than barley from soil cultures; but there was no similar difference in solution cultures. It is argued, therefore, that if barley and peas differed considerably in extent of root system such results would be expected to follow. Data on the growth of the respective root systems in these experiments are not given. In a later experiment (128) on the evolution of CO₂ from barley and peas, the dry weights of the roots of peas were found to be less than those of barley. Newton himself (128), however, is inclined to attribute these differences to the much larger respiration energy of peas over barley than to differences in the extent of root systems. But Hoagland (67) later pointed out that comparisons of extent of root systems have only a very limited value, because the general appearance and size of a root system is not necessarily an accurate index of the total active absorbing area. In this connection it is of interest to note that Russell (162) is of the opinion that the whole question of the supply of nutrients involves both root spread and replacement of ions, although no experimental evidence is cited.

Consequently, views on the relation of extent of root system to feeding power are necessarily speculative until more critical data are forthcoming. The method of determining the actual absorbing surface such as that employed by Dustman (37) and others is unquestionably the most accurate. A critical discussion of the relative merits of the various procedures has been given recently by Weaver and Himmel (202).

F. The influence of other factors

1. Permeability

In an earlier paper (187) the writer has discussed some of the factors involved in "membrane" permeability. Until sufficient quantitative and qualitative data, obtained under rigid control of all the variables are available it is improbable that views on the subject can be anything but speculative. Possibly, a satisfactory working hypothesis may be formulated only when data, based upon cataphoresis experiments, have accumulated from a wide variety of materials carrying no charge (99). The importance of securing more qualitative information is indicated by the interesting properties of the phosphatide \((\text{RO}_2 \cdot \text{C} \cdot \text{CH}_2\text{OH} (\text{C} \cdot \text{R'}\text{O}_2) \text{CH}_3\text{O} \cdot \text{PO}_2\text{H})\) isolated by Channon and Chibnall (22). It forms a fat-soluble calcium salt but a water-soluble sodium salt; and, accordingly, cell permeability could be conceived to be altered by a change in the proportion of calcium to sodium salts.

From thermodynamic considerations and also from the kinetic theory it can be deduced that ionic pairs having the higher mobility will pass through a membrane in proportionally the greater quantity, and also that
the permeability of an ion is increased by the introduction of another electrolyte possessing a common ion. Thus, many investigators (100) have found that the absorption of K from KCl is increased by the addition of NaCl; and the effect of the NaCl has been shown to be dependent on the hydrogen-ion concentration of the medium. Since hydrogen and hydroxyl ions have the greatest velocity, the addition of acids (decrease of pH) will increase the diffusion of anions; the addition of alkalies (increase of pH) that of cations (46, 47, 48).

The influence of the hydrogen-ion concentration of the medium on the absorption of weak acids and bases and their salts by living cells has been investigated by Jacobs (73, 74). The pH of the medium to which a cell is exposed was found to bear no necessary relation to the pH produced by that medium within the cell itself. The higher permeability of living membranes to undissociated acids and bases results in a higher physiological activity of weak acids and bases compared with stronger ones. Conditions favoring the formation of undissociated molecules, therefore, will promote their penetration into membranes to which they are permeable. The result of these influences may, as Loeb (100) has shown, be to modify the properties of the cell wall in such a way as to accelerate the rate of diffusion of certain ions and retard the rate of diffusion of other ions. CaCl₂ and NaCl are important factors in causing such selective diffusion.

From the practical standpoint it is interesting to note that Stoklasa (183) finds that different plants have different selective abilities towards cations and anions, respectively. The Gramineae, in his experiments, absorb anions more than cations; potatoes and beets more cations than anions; legumes anions and cations equally. Of course, further confirmation of such results is necessary.

2. Ion Antagonism

There is sufficient evidence to show that Ca and Mg, which precipitate sols, cause contraction and impermeability and that K and Na, which stabilize sols, cause relaxation on the one hand, and greater permeability on the other. The antagonistic effects between univalent and divalent cations in colloidal systems have been studied by Meulen and Riemann (113, 159), by Weiser (203), and also by Höber (71). Simms (173) has derived a mathematical expression for the antagonism between Na (or K) and Mg (or Ca) in true (non-colloidal) solutions of oxalate. One might expect—although it has not been demonstrated—that the activity of proteins would show a similar antagonism.

It is essential, however, for the investigators to keep in mind the fact that the effect of a mixture of two or more cations (or anions) on cell permeability may be quite different from the effect of one alone when the activity of the ions is due to different combining proportions of the cations.
(or anions) in a mixture (such as the soil solution), in proportion to the relative combinations in solutions of each alone (174). Some of the practical agricultural applications of ion antagonism between Ca and K have been investigated by Lipman et al. (98), by McCool and Weldon (106) and by Fonder (42).

3. Gibbs-Donnan distribution law

In systems containing a non-diffusible ion, a marked effect is observed on the unequal distribution of inorganic electrolytes on either side of the cell membrane. A non-diffusible electro-negative ion will produce a greater concentration of diffusible electro-positive ions and a lower concentration of electro-negative ions on its own side of the membrane than on the other. A non-diffusible electro-positive ion will produce the opposite effect. At equilibrium the product of the concentrations of each pair of oppositely charged diffusible ions is the same on either side (35, 36). The distribution of an electrolyte in such a system will be expressed by the equation:

$$\frac{x_i y_i}{v_i^2} = \frac{x_e y_e}{v_e^2}$$

where $x_i$ and $y_i$ represent the amounts of cation and anion, respectively, within the membrane at equilibrium; and $x_e$ and $y_e$ the equilibrium amounts of the same pairs of ions in the external solution; $v_i$ and $v_e$ the volume of the solvent on either side of the membrane.

The importance that the Gibbs-Donnan distribution law may have in the equilibrium conditions and consequent selectivity of nutrients by plants has been mentioned by Hoagland (67), Pierre and Parker (148), and also by Briggs and Petrie (14). It will be recalled (187) that Parker (141) found that the displaced soil solution from many of the experimental fields in America were too low in inorganic phosphorus to support growth in the nutrient media when the phosphorus in these soil solutions was used as the source of phosphorus. One of the explanations offered by him to explain this anomaly is that a Donnan membrane equilibrium may exist, resulting in a higher concentration of phosphorus in the solution on the surface of the soil particles than in the soil solution itself. The mechanism involved has already been discussed by the writer (132, 187). But the exact experimental verification of Donnan's law in the case of specific plant tissue is difficult, for it is impracticable to measure the $x_i$, $y_i$, and $v_i$ accurately, since a calculation of the amount of ions absorbed by means of the difference between their concentration before and after equilibrium is reached does not take cognizance of the amounts of these ions already present in the tissue (14). Hence, extension of the methods of Osterhout (135) and of Osterhout and Dorcas (137) on the absorption of CO$_2$ by Valonia do not afford a basis for generalization, for even here the average
concentration of the ions in the cell, as a whole, is not considered but only that in the cell sap.

As Briggs and Petrie (14) point out, in the plant cell we are dealing with a polyphase system. The Donnan equilibrium applies to free ions only. In the cell there is evidence that some of the ions are present as undissociated salts of proteins or other substances, or again some of the ions may be physically absorbed. We should expect, therefore, that the simple Donnan equation would not hold in such systems. That this is the case is apparent from the results of Briggs and Petrie's experiments on the absorption of 0.1 M KCl and NH₄Cl from carrot tissues (14) and from Wright's (214) work on the secretion of high amounts of calcium in milk from the relatively low concentration of this element in the blood plasma. The latter finds that both the degree of dissociation of the protein salts and the establishment of a Donnan equilibrium must be taken into account in explaining the inequalities of the products in the distribution of inorganic elements in living tissues, whereas the former (14) have deduced that the apparent ionic internal product, resulting from the collective effect of all the phases within the tissue, must have a higher value than that of the external media. Briggs and Petrie (14) point out that "the plant cell is not a simple system, composed of a mere membrane enclosing a homogeneous solution, one of the ions of which is indiffusible; there are at least three phases between which the ions may be distributed—the external medium, the cytoplasm, and the vacuoles. Within the cytoplasm also, and perhaps in the cell-sap, there are micelles, or gel-particles, which can constitute yet other phases."

Butkewitsch and Butkewitsch (17, 18) have advanced as a reason for the inequality of the products of the diffusible ions on each side of a membrane in systems containing a non-diffusible ion, that the degree of permeability of the plasma membrane is not the same in both directions. This has been shown to be the case by Wertheimer (204, 205) for certain types of membranes. In such a case the equation of membrane equilibrium will contain, besides the concentration product of diffusible ions, a factor corresponding to the velocity of migration of the corresponding ionic pairs. Thus, if a solution, say of KCl, is separated by a membrane permeable in the two directions, we have:

\[
\begin{array}{ccc}
x' & K^+ & x'' \\
y' & Cl^- & y'' \\
p' & \rightarrow & p'' \\
\end{array}
\]

where \( x' \ y' \ p' = x'' \ y'' \ p'' \)
where \( x \) and \( y \) represent the concentration of K and Cl ions and \( p \) a permeability factor.

By this means it can be calculated (17) that in OSTERHOUT’s experiments on *Valonia* (134) the permeability of the plasma membrane for Na in one direction is one-fifth that in the opposite direction and in the case of K the difference is 45 times.

Within the limitations already discussed it is possible to interpret the experiments of BUTKEWITSCH and BUTKEWITSCH (17) on the influence of colloidal silicic acid upon the absorption of phosphorus by maize plants by DONNAN’s principle. When small amounts of \( \text{P}_2\text{O}_5 \) are present in the nutrient medium, growth and absolute amounts of \( \text{P}_2\text{O}_5 \) increased by the additions of silicic acid in the nutrient medium; but the percentage of \( \text{P}_2\text{O}_5 \) remained about the same. It follows that a functional replacement of \( \text{P}_2\text{O}_5 \) by \( \text{H}_2\text{SiO}_3 \) in the plant does not occur, but that the favorable action of \( \text{H}_2\text{SiO}_3 \) on the development of the plants is due to its effect in increasing the absorption of \( \text{P}_2\text{O}_5 \) in a medium that contained minimum amounts of phosphorus for growth (189).

4. THE EFFECT OF DIFFERENCES IN POTENTIAL BETWEEN SOIL AND PLANT

Since the breaking down of carbohydrates sets free electromotive force, part of the energy stored in the plant must be electrical and used in growth. The work of Groh (49) is important. He attributes the different behavior of different plants toward different degrees of hydrogen-ion concentration in the medium to a difference in potential between the plant and soil solutions, which results in a decomposition of the nutrient material. This hypothesis is supported by the following experiment. Peas and also barley were grown in sand and also in soil cultures to which \( \text{Ca(NO}_3\text{)}_2 \) were added. During growth individual plants were connected with a galvanometer with one of the platinum electrodes immersed in the soil and the other connected to the plant. The E.M.F. produced varied with conditions—from 0.01 to 0.20 volts. The greater the distance from the roots, of the electrode connected to the plant, the greater the current registered. This shows that the difference of potential existing in the plant itself is much less than that existing between the plant and the soil. The degree of vegetative development apparently was not a large factor in determining the degree of the difference of potentials noted. Groh’s work, although of a preliminary nature, is suggestive and should be considered in connection with OSTERHOUT’s (136) more refined work on the potential difference in *Valonia* and *Nitella*.

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