

Factors Affecting Healthy Roots

CECIL H. WADLEIGH¹

Except for the ravages of insects and plant diseases, and the density of plant population, practically the only environmental factors we can control in the production of a crop of beets are those prevailing in the soil and thereby exerting their influence on the plant via the roots. The role of the root environment has been discussed so many times that the present discourse may seem trite. Yet the key importance of the environment about beet roots justifies reiteration of established principles and evaluation in terms of current physiological concepts. Since pathogens, nematodes, and insects may have major effects on roots of beets, this discussion will be confined to roots free of parasitism.

Primarily we look upon the soil as a reservoir for nutrients and water as well as a medium in which roots may grow successfully. Obviously, the effective utilization by the plant of this reservoir we call the soil depends in large measure on the degree of penetration and proliferation brought about by root growth. To be sure, the physical nature of soil will condition the extent to which the nutrient and moisture reservoir will be used by the roots, but comment on this point may well be deferred until certain general aspects of beet roots are first considered.

Andrews (1) found beet roots penetrating to a depth of more than 7 feet in an alluvial soil at Scottsbluff, Nebr. He reported that the roots completely filled the soil down to this depth, and then there was an especially high degree of proliferation in the surface foot of soil. Jean and Weaver (2) reported beet roots penetrating to a depth of 6 feet on irrigated soil at Greeley, Colo., and also emphasized a high degree of proliferation in the surface foot. These studies indicate the extensiveness of the root system and the mass of soil that is potentially available to a beet plant as a reservoir for water and nutrients. That is, the roots of a vigorous beet plant may occupy 8-20 cubic feet of soil.

It is essential that we also evaluate roots in terms of surface exposed to the soil mass permeated, since the primary activities associated with roots are surface phenomena taking place at the root-soil interface. The extent of the root surface determines the total capacity for the plant to take in water and nutrients at a given rate of entry per unit area of surface. It also gives us a measure of the extent to which the surfaces of the soil particles are actually contacted by roots.

No information is available on the total area of root surface of a maturing beet plant growing in soil; but it is of interest to consider the data obtained by Dittmer (3) from his measurements on the root system of a single winter rye plant grown in the greenhouse during the winter for four months in a container 12 inches square and 12 inches deep, filled with a dark loam. The roots were very carefully liberated from the soil at the end of the experiment, by spraying with water several hours. From detailed measurements of extensive samplings it was determined that this plant had approximately 13,800,000 roots, with a length of more than 385

¹ Head Physiologist in Charge, Division of Sugar Plant Investigations, Bureau of Plant Industry, Soils, and Agricultural Engineering, ARA, U. S. Department of Agriculture.

² Numbers in Parentheses refer to Literature Cited.

miles and a surface area of about 2,550 square feet. The root hairs of this plant numbered approximately 14,000,000,000 with a total length of more than 6,600 miles and a surface area of about 4,300 square feet. The data for the length and surface of the roots of this single rye plant appear to be astronomical, but Pavlychenko (4) has made similar observations.

It is recognized that the root systems of graminaceous plants tend to be more highly proliferated than those of most dicotyledonous crop plants. Yet, if one rye plant growing in one cubic foot of soil could have nearly 7,000 square feet of root surface, it seems conservative to estimate that the beets excavated by Andrews (1) and found penetrating to a depth of 7 feet would have at least 10,000 square feet of root surface per plant.

As a further basis for our proposed calculations, it is conservative to estimate that our typical beet plant grew at the rate of 50 grams fresh weight per day during the period of most vigorous vegetative growth. Let us assume that the plant contained an average of 0.5 percent nitrogen on the fresh weight basis. Then each increment of 50 grams of fresh weight implies that 250 milligrams of nitrogen would need to be taken in from the soil each day. On the basis of Avogadro's number (6.06×10^{23}), 11×10^{21} nitrate ions would need to enter the root systems each day to provide the 250 milligrams of nitrogen. This means that 1×10^{15} nitrate ions would enter each sq. cm. per day; or 100 million nitrate ions would enter each square millimeter of surface each second.

Thus, if our estimation of the total root surface of a beet plant seems fantastically high, it still means that ions have to enter a given unit area of roots at a seemingly high rate. Furthermore, we know that ineristematic parts of the root system are far more conducive to the entry of ions than the older suberized portions. Also, there are millions and millions of other ions entering each square millimeter of absorbing surface per second along with the nitrate ions.

This suggests that actually billions of ions are diffusing across each square millimeter of actively absorbing root surface per second along with many more billions of water molecules. Visual inspection of absorbing roots gives an impression of complete quiescence, but if one could view conditions at the root surface by a sufficiently powerful electron microscope it is clear that intense activity would be much in evidence.

It should be emphasized that ion entry into roots is in large measure not simple diffusion since ions of a given species are frequently accumulated against concentration gradients, and therefore require an expenditure of energy to effect net inward transfer. The mechanism by which the energy released in root respiration brings about ionic accumulation has been the subject of intensive study by numerous investigators (5, 6, 7, 8). Broyer (20) has recently presented an excellent review of this subject.

Ion accumulation dependent upon expenditure of metabolic energy is conditioned by four primary variables: Ion supply, aeration, temperature, and supply of respiratory substrate—largely sugars. Robertson and Wilkins (7) have presented a diagrammatic schema based on Lundegardh's (6) concepts to suggest the mechanism that may be involved in the energetics of ion accumulation. A modified version of this schema is presented in Figure 1. It represents an infinitesimal section of the outer layer of the cytoplasmic membrane of an absorbing cell of a root.

During the respiration of the sugar that has been translocated to the root cells, carbon dioxide is released; but what is more pertinent to the theory of ion accumulation is the fact that during the respiratory sequence the enzyme dehydrogenase liberates free hydrogen. The carbon dioxide diffuses outwardly into the substrate presumably along concentration gradients. The released hydrogen becomes ionized to hydrogen ions with the freed electrons going to the cytochrome system reducing ferri-cytochrome to ferro-cytochrome. In other words, the ferri-cytochrome adjacent to respiratory activity oxidizes hydrogen to hydrogen ions while becoming reduced to ferro-cytochrome. Electrons are presumably surface-transferred along the reduced cytochrome to the absorbing surface of the cytoplasm. At the outward surface of the cell, oxygen diffusing inward is used to oxidize the ferro-

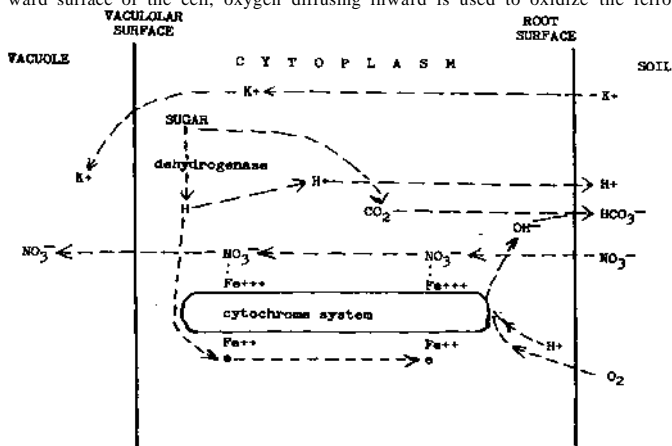


Figure 1. Schematic representation of the electron and anion transport system across the cytoplasmic membrane.

cytochrome by means of cytochrome oxidase. Hydrogen ions also enter the picture at this point with a release of hydroxyl ions. The oxidized ferri-cytochrome represents an increase in one positive valency for each ion atom oxidized. This added positive valency becomes a carrier for anions from the outer surface to the vacuolar surface where the cytochrome is reduced and the anion released to the vacuole. It is Lundegardh's concept that cations diffuse inwardly independent of energy released in order to maintain electrovent neutrality in the vacuole.

This brief mention of the postulated mechanism for the relationship between metabolism and ion accumulation is set forth to emphasize: (a) The utilization of sugar as the source of energy in nutrient accumulation, (b) the key demand for oxygen in the catabolic release of energy, and (c)

a favorable temperature for metabolic activity. These factors are of primary importance when water and nutrient supply is not limiting. It should also be mentioned that facilities for dissipation from the cell and root surface of carbon dioxide or bicarbonate ions produced by catabolism are essential for optimum root activity. An abnormal accumulation of bicarbonate in the substrate impairs the ability of tissue to accumulate ions (9).

It is evident in light of the foregoing that conditions inhibiting the transfer of sugar to the fibrous roots may also be detrimental, not only to root growth, but also to the capacity of roots to accumulate ions. Impaired carbohydrate synthesis or accumulation in the tops, pathogenicity of the phloem conductive tissue and low night temperatures may limit sugar transfer to the roots.

The temperature of the roots determines level of metabolic activity. If it is abnormally low, energy release from respiratory activity is low; and if it is abnormally high the rate of ground respiration may become sufficiently high to deplete the carbohydrate reserve. Physiologists distinguish between the ground respiration in root cells due to normal metabolic activity, and respiration associated with nutrient intake. When high temperatures of the roots result in carbohydrate depletion, there may be an inadequate supply of energy to effect ion accumulation.

The desirability of a well aerated soil for the vigorous development of beet roots is well recognized (10, 11, 12, 13), and oxygen demand of root as set forth in Figure 1 further emphasizes the essentiality of oxygen.

It is expedient to consider the soil conditions affecting oxygen supply at the roots. This may be done by reference to Figure 2 taken from the work of Gardner and Chatelain (19) depicting the relationship between the status of the moisture films about the soil particles and the hydrostatic head, i.e., vertical distance from the effective water table. At the water table all pores are filled with water, eliminating any channels for air transfer.

Hence, we find numerous observations to the effect that nearly saturated soils tend to asphyxiate roots. At just a few inches above the water table, only the largest pores are free of water, and most of the interstices are still filled with water. Gaseous transfer would be impeded, and, accordingly, there are many instances noted in which maintenance of soil moisture above filled capacity is inhibitive to plant growth. At a greater distance above the water table, the largest pores and many of the medium sized pores are free of moisture so that the contiguous air passages prevail. At this point, which we may regard as a moisture content slightly below field capacity, the moisture films are still sufficiently large and contiguous to maintain an abundant supply of water to the roots.

When we proceed to greater distances above the water table, approaching conditions supposedly corresponding to the permanent wilting percentage, the pore spaces are sufficiently free of water to provide excellent gaseous transfer; but the moisture films are so thin and confined to the smallest interstices that contact of rootlets with these films may be impaired, in addition to the fact that the energy retention of the moisture in the fine interstices may restrict movement of water molecules into the roots. That is, Figure 2 presents a clear picture as to the manner in which moisture content of soil affects aeration. The effect of soil status on gaseous transfer

was emphasized since Raney (14) has shown this to be the primary consideration in evaluating aeration of soils.

Absorption of moisture and nutrients is the primary physiological function of roots, and it follows that the efficiency with which the roots may accumulate water and nutrients from the soil mass will be contingent upon the extent to which the roots proliferate and contact the minute soil particles.

It was previously mentioned that Dittmer (3) estimated that the roots of a single rye plant exposed a surface of about 7,000 square feet when grown in a single cubic foot of loam soil. Such a soil may have a specific surface of around 20 square feet per cubic centimeter, so that the cubic foot of soil used by Dittmer had a total particle surface of around 500,000 square feet.

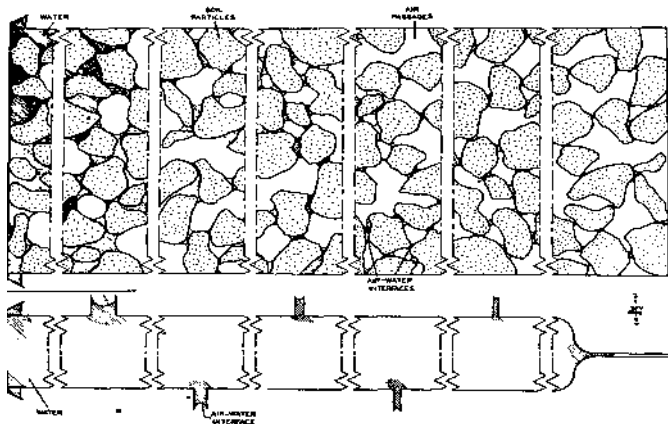


Figure 2. Diagram illustrating the change in air-water interface with increasing hydrostatic head.

Since soil is completely interspersed with minute interstices, it is obvious that all the surface of a root system is not exposed to soil particles; but some of the root surface is contiguous with air space. Thus, we find that less than 0.2 percent of the soil surface in Dittmer's culture was in direct contact with roots. This means that, for effective utilization of moisture and nutrients in the soil mass, there must be a certain degree of surface flow of these entities over soil particles to root surfaces. This situation may be more readily apparent on discussion of Figure 2.

In this microscopic picture of a soil presented in Figure 2, we note that the soil particles are pictured so as to show an abundance of minute air spaces among them. If we look at the section of this diagrammatic soil

at the moisture condition just above the water table, we note that the soil particles could be packed more densely, and also that there would be plenty of moisture present to lubricate and facilitate particle transfer to the more dense packing. Accordingly, we frequently find that mechanical agitation of wet soils transfers them into a "puddled" conditions. In this stage, the more closely packed particles in the "puddled" state contribute to lowered facility for gaseous transfer, more mechanical resistance to root penetration, and lowered capacity for storing available water. Consequently, plant growth may be seriously weakened (15, 16).

There are numerous instances where adverse physical condition of the soil has been shown to be a serious limiting factor in the growth of sugar beets (*loc. cit.*). Even though it is well recognized that beets respond to improved tilth in soils, this fact needs further emphasis in the light of modern tendencies to use heavy machinery during certain operations. This is especially the case during harvests on exceedingly wet soils. As studies by Gliemerth (17) have shown, use of tractors and heavy machinery under such conditions may have seriously adverse effects upon the soil.

The Experiment Station of the Hawaiian Sugar Planters' Association (18) has recognized the seriousness of this problem. It is conducting soils engineering tests on the important soil types to determine the "fluid flow" zone of the compaction curve, so that the heavy Tournahaulers will not be used on the soils when they are in a sufficiently moist state to be seriously damaged by this heavy mechanical equipment.

Although the importance of good soil tilth for the production of sugar beets has long been recognized, current information on the physiological processes in roots and the danger of the adverse effects on soil from the use of heavy equipment emphasize the need for continually watching the factors affecting healthy roots.

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