

these objects shall be obtained we may easily estimate both our national intelligence and our peace-loving qualities.

Must it be the grim necessity of war only that shall awaken us to a nation-wide mobilization of all human forces for a single great purpose? Have we the mental capacity to be led by reason rather than driven by necessity "to sacrifice comforts, indulgences, and elegancies" for the purpose of acquiring the knowledge of self without which a practical preparation for living is impossible?

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THE ECOLOGICAL SIGNIFICANCE OF SOIL AERATION

DURING the past two years the writers have conducted, independently, laboratory investigations into the relation of plant roots to the composition of the soil atmosphere and especially to deficiency of oxygen or excess of carbon dioxide in this atmosphere. These investigations are still in progress and will be reported later. It seems, however, that certain features of the results already obtained have important ecological significance, and this phase of the matter is presented in the present preliminary paper.

One series of experiments was conducted by one of us (Cannon) in the Desert Laboratory of the Carnegie Institution of Washington at Tucson, Arizona, and in the Coastal Laboratory of the same institution at Carmel, California. Seedlings of *Prosopis velutina*, and cuttings of *Opuntia versicolor* were grown in glass tubes filled with sand and connected with a gas reservoir in such a manner that any desired gas or mixture of gases could be caused to replace the ordinary atmosphere of the tubes at will. Each tube was sealed with wax and usually a water seal was used in addition. By the use of appropriate thermostats the tubes were kept at any desired temperature. In all cases the shoots were exposed to the atmospheric conditions of the laboratory. The growth of individual roots was observed di-

rectly by means of a horizontal microscope. The experiments included tests with pure carbon dioxide and various mixtures of this gas with atmospheric air or with oxygen.

As a leading result it was learned that the roots of *Prosopis* and of *Opuntia* have unlike responses to carbon dioxide. Exposure to pure carbon dioxide causes cessation of growth in the roots of both species. However, the recovery on the admission of air is uniformly more rapid with *Prosopis* than with *Opuntia*. The two species respond differently, also, to percentages of carbon dioxide which are high but below 100 per cent. Thus mixtures of 50-75 per cent. carbon dioxide with 25-50 per cent. oxygen, do not stop root growth of *Prosopis*, but do stop that of *Opuntia*. Apparently excessive amounts of carbon dioxide in the soil atmosphere would act as a limiting factor for the latter plant, even if the oxygen content of the soil atmosphere was normal or above normal. Neither excess of carbon dioxide nor diminished supply of oxygen inhibits the growth of *Prosopis* roots, for growth did not wholly cease when an atmosphere containing less than 2 per cent. of oxygen was employed. However, entire deprivation of oxygen appears to inhibit growth since the roots did not grow in pure carbon dioxide. Thus while the effects of the undiluted carbon dioxide on root growth of the two species is apparently the same, namely, the cessation of growth, the responses leading to this effect may be quite different.

The conclusion that the root response to a variable ratio of oxygen to carbon dioxide in the soil atmosphere is a specific response, is supported further by the results of direct aeration experiments on several species of plants, among which were *Opuntia*, *Prosopis*, *Fouquieria splendens*, and garden varieties of cucumber and watermelon. An increased air supply to the roots of *Opuntia* and *Fouquieria*, if not excessive, favors root branching and probably accelerates the rate of root growth. In the case of *Prosopis*, increased aeration of the soil appeared not to affect the growth rate of the roots. The results with cucumber and watermelon were not consistent, although in the latter case the shoot growth appeared to be

more vigorous when the soil containing the roots was artificially aerated.

The other series of experiments was conducted by one of us (Free) under the direction of Professor B. E. Livingston in the laboratory of plant physiology of Johns Hopkins University. A technique has been devised by which plants of mature size can be sealed into tin cans of about two liters capacity, the shoot projecting through the seal into the open atmosphere. The root system, with the soil in which it grows, is inside the sealed space and the soil atmosphere can be replaced at will by an atmosphere of any desired composition. Water is supplied to the plant by the Livingston auto-irrigator. The controlled atmosphere inside the can is kept automatically at a pressure slightly (about 3 centimeters of water) greater than the general atmospheric pressure, changes of volume due to variable temperatures being compensated. This assures that any slight leakage will be outward and without effect on the experiment.

With this technique experiments have been made on four species: *Coleus blumei*, *Heliotropium peruvianum*, *Nerium oleander* and *Salix* sp. (probably *nigra*). With *Coleus* it is found that even a very small decrease of oxygen below that normal to the atmosphere is injurious to the plant. Thus a plant, the roots of which were supplied with gas consisting of 75 per cent. air and 25 per cent. nitrogen, was injured within three days and killed within 45 days. With lower oxygen content in the soil atmosphere injury and death are still more prompt. *Heliotropium* behaves substantially like *Coleus*, except that the period between initial injury and death is shorter. *Nerium* is much more resistant to oxygen deprivation. With a soil atmosphere of pure nitrogen, injury was first apparent in the shoot after 26 days. An atmosphere of 50 per cent. air and 50 per cent. nitrogen had produced no perceptible injury in 45 days when the experiment was stopped. Dilution of the soil atmosphere with carbon dioxide instead of nitrogen appeared to have a like effect. No evidence was observed of any specific toxic

effect of carbon dioxide, though such an effect is not excluded by the experimental results.

The most interesting result was with *Salix*. With this plant entire deprivation of oxygen appeared to be without injurious effect. In an experiment three times repeated the plant grew normally with a soil atmosphere of pure nitrogen, one of the experiments lasting for ten weeks. Replacement of the nitrogen with carbon dioxide and the use of various mixtures of carbon dioxide and air were also without perceptible effect. It appears that this species of *Salix* is quite independent of the content of oxygen in the soil atmosphere. That the respiration of the root cells can be anaerobic is less certain, but is strongly suggested by the data.

The two series of experiments outlined are sufficient to show that different species of plants may differ markedly in their response to variations in the composition of the soil atmosphere, and hence to changes in soil aeration. The effects of diminution of oxygen are manifest and the results with *Opuntia* indicate a direct and specific effect of carbon dioxide in addition to the effect of the dilution of the oxygen.

Though many details are lacking it is known that the composition of the soil atmosphere is neither the same as, nor so constant as, the composition of the general atmosphere. The presence of living matter in the soil, including bacteria, fungi and protozoa, as well as the roots of higher plants, tends to decrease the oxygen of the soil atmosphere and to increase its content of carbon dioxide. Doubtless there are chemical reactions associated with the decay of dead organic matter and which have the same or similar results. This tendency toward impoverishment in oxygen and enrichment in carbon dioxide must be counteracted by diffusion between the soil atmosphere and the general atmosphere, assisted, no doubt, by changes in barometric pressure and in temperature of soil and air. The importance of these assisting agencies is difficult to estimate but the effect of diffusion alone has been shown by Buckingham¹ to be extremely slow. Doubt-

¹ Bulletin 25, U. S. Bureau of Soils (1904).

less in normal cases the soil atmosphere is always slightly higher in carbon dioxide and slightly lower in oxygen than is the general atmosphere. Since the diffusion processes are effected very markedly by the average size of the interspaces between the soil particles, the difference in composition between the soil atmosphere and the general atmosphere will be greatest in the soils of fine texture and least in those of coarse texture. The similar effect of the soil water is obvious, especially the effect of the water existing as films about the grains in diminishing the size of the spaces available for gas diffusion.

The ecological bearing of these facts is manifest. Although deficiency in aeration has frequently been suggested as an agricultural difficulty, or as the reason why certain species do not grow upon soils of heavy texture, it does not appear that this suggestion has had any exact experimental basis, nor does it seem to have been appreciated that different species may have great differences in the oxygen requirement of their roots and widely variant responses to differences in soil aeration, responses which appear to be quite as specific and significant as the responses to temperature and to available water which form the present basis of ecological classification. The importance of root-habits in ecology has long been recognized on the basis of their characteristic and specific reaction to the features of the soil environment included under temperature and water relations. Thus it has been shown that the general distribution of the cacti as a family is closely related to the response of the roots to the temperature of the soil. It seems probable that soil aeration must be added as a factor of no less importance than temperature and water. Thus in the matter of local distribution of cacti, it is probable that the restriction of this family to habitats which have a relatively well-drained soil, in which the accumulation of carbon dioxide during the season of most active root growth is probably relatively slight, may be owing in part to the inability of the roots of these forms to grow well in an atmosphere charged heavily with carbon dioxide. On the

other hand, the distribution of *Prosopis* and *Nerium* along the river bottoms, and of *Salix* in swamps, indicates that the presence of a relatively large amount of carbon dioxide in the soil does not act as a limiting factor to these species. Again, Howard² notes that the general distribution of the gram (chick-pea) as a crop in India is closely associated with the fact that the roots of this species require a relatively large amount of air. It accordingly occurs only, or mainly, where the soil and the system of cultivation provide an amount of air sufficient for its root growth.

In many semi-arid regions the physiography is such that there are relatively large and shallow basins without outlet, the central portions of which are flooded during rainy seasons but are dry for most of the year. Usually the central flats or playas of such basins have soils composed largely of fine silt or clay, and which puddle easily. It is characteristic of these playas that they are void of plant life during all, or most, of the year, and that no perennials are to be found in the lowest places, even when no excess accumulation of salts in the soil has occurred. It is here suggested that the probable reason for the absence of plant life on such playas is directly traceable to insufficient soil aeration at the time when the soil is suitably moist and of a temperature suitable for the growth of plants. It is interesting, also, that around such playas the plants frequently occur in well-marked bands or zones. Where the zones are found there is probably little difference in the available moisture or the soil temperature and it is suggested that the zonal differentiation may be a result of unlike response of the roots of the plants comprising the zones to the atmosphere of the soil. Whether zonation is to be associated with the relation of roots to the soil atmosphere in places outside the arid regions remains to be seen, but this may well be the case.

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² Howard and Howard, Bulletin 52, Agricultural Research Institute, Pusa, 1915.