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RELATION OF INCREASED WATER CONTENT AND DECREASED AERATION TO ROOT DEVELOPMENT IN HYDROPHYTES

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(WITH ELEVEN FIGURES)

The dependence of root development of most plants upon aeration is clearly shown by water-logging the soil. In a few days, the usual cultivated plants turn yellow, show wilting, and may ultimately die. If the water is kept well aerated, plants may survive though submerged for weeks. Exclusion of oxygen from the roots of most plants interferes with the respiration of the protoplasm of their cells. This results in the death of the cells and consequently the roots fail to function as absorbers for the plant (**22**).

The importance of aeration in plant development has long been recognized by plant physiologists and a very large number of investigations have been made. In 1921, CLEMENTS (**7**) summarized nearly 700 such papers in his mongraph on "Aeration and Air-Content." The long-continued work of CANNON has added much to an understanding of this subject and his "Physiological Features of Roots" (**5**) includes the most extensive recent contribution to this problem. The importance of aeration in the production of crops and the growth of forests has been emphasized by the extensive researches of HOWARD (**15**), HOWARD and HOWARD (**16, 17**), and HOLE (**14**) in India. A survey of the literature shows that, with rare exceptions, there is general agreement that the aeration of the roots promotes a better growth of tops. Most of the experiments were carried on in water cultures, *e.g.*, HALL, BRENCHLEY and UNDERWOOD (**12**), ANDREWS and BEALS (**1**), and BERGMAN (**3**), and some in soil, such as those of HUNTER (**19**), HOLE (**14**), HOWARD (**15**), and KNIGHT (**21**). The response of the plant in most cases has been measured by the development of tops and little account has been taken, especially in soil cultures, of the organs directly affected by the increased aeration. The work of BALLS (**2**), HUNTER (**19**), HOLE (**14**), and the HOWARDS (**16, 17**) are among outstanding exceptions. CANNON (**5**) measured the effect of inadequate aeration on root elongation and not on the development of the root system as a whole.

In devising a simple experiment for classes in plant physiology and ecology to illustrate the effect of aeration upon root and root-hair development, *Typha latifolia* was employed (**24**). It was selected because it grows naturally under a wide range of conditions, from water-logged soil to one that has a sufficiently low water content to be well aerated. Differences in root response under conditions of poor and good aeration were so marked that three other characteristic and widely distributed swamp and swamp-margin plants were also employed and an extensive study of their root behavior begun. The use of large containers furnished an opportunity to determine the normal nature and extent of the underground parts, a procedure which met with almost insurmountable difficulties where the plants grow naturally in soil covered with water.

Procedure

Rhizomes of *Typha latifolia, Scirpus validus,* and *Spartina michauxiana* were dug in quantity on April 5, before new growth had begun. They were kept in a refrigerator for a period of 14 days before planting on April 19. *Phragmites communis* was taken from a swamp at this time and immediately transplanted. Growth was just starting.

Four large galvanized iron containers, 30 cm. square in cross section, were used for each species. The following conditions of soil moisture and concomitant aeration were maintained: (1) saturated, no free air; (2) alternately saturated and drained, aeration poor; (3) optimum water content for land plants, aeration good; and (4) dry soil, aeration good. The depth of the containers necessary to accommodate maximum root growth was determined by preliminary experiments; those for conditions 1 and 4 were 60 cm. deep, the others 90 cm. A well screened, fertile, loam, potting soil was used. It was mixed with one-third of its volume of sand. This mixture had a hygroscopic coefficient of 10 per cent. and a water holding capacity (HILGARD method) of about 55 per cent.

In filling the saturated containers, the soil was thoroughly saturated and constantly stirred to permit the escape of air. After the soil had settled, an excess of water was added to the container so that a layer of clear water 2.5 to 5 cm. deep stood constantly above the soil. Losses by evaporation were replaced every two or three days by adding tap water from a sprinkler. Six liters of water were daily poured on the gravel mulch of the drained soil. The water slowly sank through the soil mass and disappeared from the surface after 10 to 30 minutes. It slowly trickled through 2.5 cm. of coarse gravel placed on the bottom and out through an opening on the side. Here it was caught in a container and again used. This prevented loss of nutrients or other substances from the soil by leaching. Since there was some loss by evaporation, fresh tap water was added from time to time as needed. The third set of containers had soil of optimum water content (25 per cent. based on dry weight) which was lightly tamped in filling. The soil was covered with a fine gravel mulch, as was the case with all the containers except the first lot. Only enough water was added to replace that actually lost by transpiration and surface evaporation. The dry containers were three-fourths filled with a dry soil which had only 12 per cent. water content. This was but 2 per cent. in excess of the hygroscopic coefficient. Above this was placed a 15-cm. layer of soil with a water content of 25 per cent. Only enough water was added to the upper soil to insure continued growth.

Before planting, the rhizomes were carefully selected and cut in such a manner that they were quite uniform in size, number of sprouts, etc. All of the roots were cut close to the rhizome and seven rhizomes were planted at depths of 3.75 to 7.5 cm. (varying with the species) in each container.

FIG. 1. Development of plants 17 days after transplanting the rhizomes. The sequence from left to right is dry, saturated, moist, and drained soil.

All of the plants, except *Phragmites,* rapidly developed. The growth of the reed, although transplanted when still young, was somewhat checked compared with the development of plants in the swamp (fig. 1). For the sake of clarity each species will be separately considered.

Results

TYPHA LATIFOLIA

The development of the aboveground parts of *Typha,* at the end of the 35 days they were permitted to grow, is shown in table I.

TABLE I

GROWTH OF *Typha latifolia* ABOVE GROUND WITH DIFFERENT MOISTURE CONDITIONS

CONDITION FOR GROWTH→	SATURATED SOIL	DRAINED SOIL	MOIST SOIL	DRY SOIL
Maximum height, cm.	111.0	106.0	86.0	66.0
Average number of leaves	8.4	8.1	7.6	7.0
Average height of leaves, cm.	46.8	42.3	33.0	27.5
Average width of leaves, mm.	13.0	12.4	9.5	9.4
Total dry weight of tops, grams	16.2	19.9	12.2	7.2

An examination of the table shows that in every way development decreased with a decrease in water content. The dry weight is only an apparent exception, since in the wet culture only 5 plants grew, but there were 7 in each of the others, except the dry soil where one plant died. Here, as among the other three species, the plants in the moist and dry soils had a darker green color throughout their period of growth, due probably, to the more favorable conditions for nitrification and nitrogen fixation. In the saturated and drained containers the roots were readily freed from adhering soil particles and their dry weight was obtained. The dry weight of tops and roots was in the ratio of 5.8 to 1 in the saturated soil and 5.6 to 1 in the drained.

SATURATED CULTURE.—The root systems were examined on May 23–25 when the plants were five weeks old. Those in the saturated soil were very shallow and consisted of two distinct parts, namely, soil roots and water roots. All originated from a basal node of the stem about 6 cm. below the soil surface and none from the old rhizome. The rhizomes shriveled upon the removal of accumulated food and in several cases they were decomposing, although the soil was not sour. The soil roots, 64 in number on one of the largest plants, pursued courses at all angles between the horizontal and the perpendicular in such a manner as to more or less thoroughly ramify a hemisphere of soil with a radius of 15 cm. Eleven of the longest extended to 28 cm. depth.

These shining white roots were 1.5 to 2 mm. in diameter and very turgid and brittle, especially the distal 10 cm. Branches were entirely absent on most of the roots or occurred only very rarely. On others, slightly brownish in color and probably older, thread-like laterals arose at the rate of 1 to 8 per cm. (rarely 14 on the best branched parts). These were exceedingly variable in their distribution, frequently long portions of the roots being bare. Laterals were 1 to 5 cm. (maximum 10 cm.) long, and entirely unbranched but much more abundantly furnished with root hairs than the main roots where they were relatively sparse.

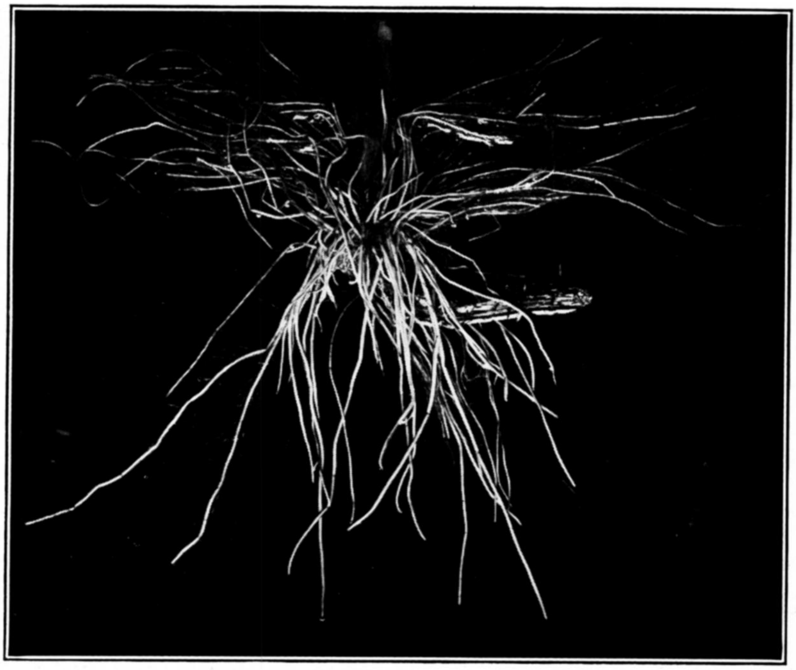

FIG. 2. *Typha latifolia* grown in soil covered with standing water, showing the sharp differentiation between soil and water roots. Photograph taken with root system under water in its natural position.

Approximately half of the root system (66 roots by actual count) consisted of water roots. These arose at a higher position on the node than most of the soil roots. While some ran obliquely upward, often at a 45° angle, many grew vertically and then turned at right angles after leaving the soil (fig. 2). Other roots ran horizontally about 8 cm. and then grew abruptly upward. The portions in the soil were like those described, but upon entering the water they greatly decreased in diameter and branched profusely, the distal part becoming extremely attenuated (figs. 3 and 4). They began to appear only 5 days after the rhizomes were planted and their growth was rapid, some reaching a length of 10 cm. in 3 days. By the expiration of 10–14 days all were greatly branched with laterals a centimeter or less in length. New roots continually appeared and branching increased throughout the period of growth. The older ones reached a maximum length of 30 cm. but many of them were only about one-half as long. When mature, they were branched to near the tips but there were no laterals of the second order. The very fine primary laterals, which occurred at the rate of 20 to 55 per cm., varied in length from 1.5 to 2.5 cm. and were en-

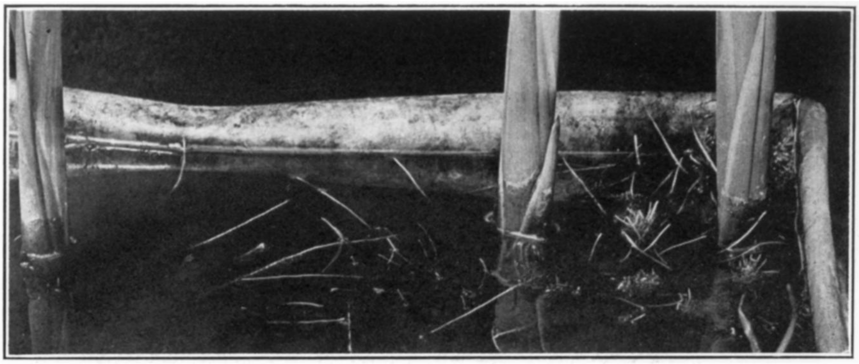

FIG. 3. Water roots of *Typha* about two weeks after transplanting the rhizomes.

tirely free from root hairs. These fine water roots and their very abundant branches enormously increased the absorbing surface in the aerated portion of the culture. Aside from frequent renewal of the water, an abundance of *Ulothrix* and *Mougeotia* increased the oxygen content. The former alga was so abundantly attached to the roots that it gave them a greenish hue.

DRAINED CULTURE.—The root system in the drained soil was much deeper seated although the roots were most abundant and most branched in the surface 9 cm., which was the best aerated. Here they formed a dense

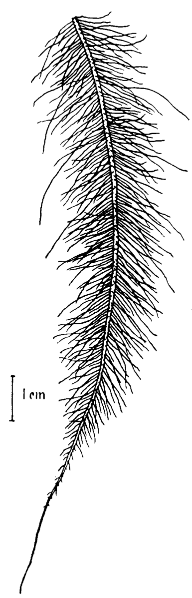

FIG. 4. Detail of water root of *Typha*. Note the attenuated tip and the profuse simple branching.

network. Roots were numerous to a depth of 30 cm. and some attained depths of 40 to 47 cm. (fig. 5). The general distribution of the roots was such as to occupy a more or less hemispherical mass of soil. They were rather clearly differentiated into three types as regards position, thickness, and degree of branching.

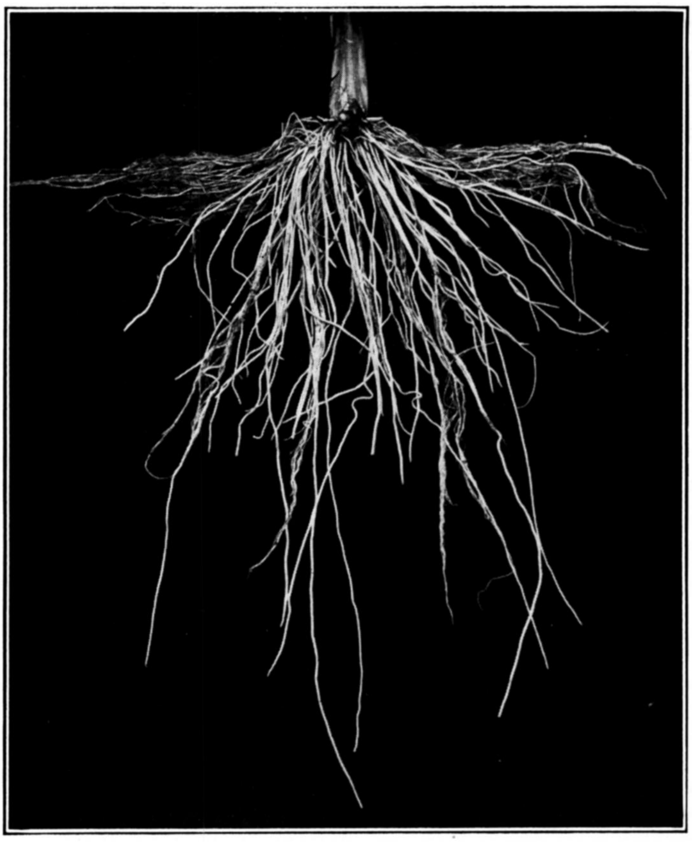

FIG. 5. *Typha* grown in drained soil. The finer, horizontal roots are near the soil surface.

One lot consisted of coarse, unbranched or practically unbranched roots which, as a group, penetrated deepest. Their diameters were 1.5 to 2 mm. throughout. A second lot was composed of roots with smaller diameters (1–1.5 mm.), some of which penetrated as deeply, or at least nearly as deeply, as the former. These branched profusely, often forming networks of laterals at depths of 30–36 cm. where branches 10 cm. long were found. The branching habit was variable; on some, only the proximal portion was branched, on others, the distal part. On still others the presence of branches and especially their density varied from place to place. The rate of branching was 6 to 25 laterals per cm. The branches ranged in length from less than 1 cm. to a maximum of 10 cm., although most of them did not exceed 3 cm. Nearly all of the primary laterals were simple; a few were branched to the first order, the branches seldom exceeding 3 or 4 per lateral, and a centimeter in length.

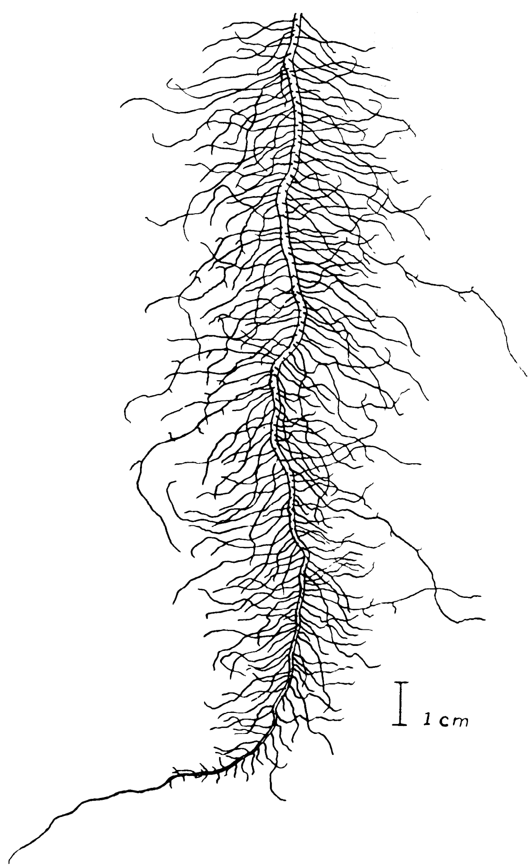

FIG. 6. Detail of one of the surface roots of *Typha* grown in drained soil.

A third type of root arose from the highest portion of the node at the base of the stalks and thus above the other roots. They thus originated at a depth of about 7 cm. and no portion of the root extended deeper than the point of origin. In fact, a few at first extended vertically upward but this tendency was not nearly so marked as in the case of water roots in the previous culture. Branches of these fine roots (which were 0.5 to 1 mm. thick) often occurred throughout, but in general they were most abundant and longest on the distal one-third to one-half. Laterals were 7 to 10 per cm. on the more thinly branched parts and 12 to 20 on those most thickly branched. These thread-like roots were shining white, and the longest were more abundantly furnished with laterals than were any in the deeper soil. Secondary branches were few. The main root and all its branches were well supplied with root hairs. These roots differed from the water type by having longer, coarser, and more crinkly laterals with some sublaterals and an abundance of root hairs (fig. 6). The last was in striking contrast to the water roots, which had none.

One of the larger plants had 56 of the deep, unbranched type, 33 of the deeply penetrating branched ones, and 43 of the fine, surface type which were most favorably situated as regards aeration.

MOIST CULTURE.—The root system in the moist, well aerated soil showed no differentiation into parts; all of the roots were 1 to 1.5 mm. in diameter and about equally branched. There were no roots in the surface 7 cm. of soil. Long horizontal ones ran outward, sometimes to distances of 30 cm., but never turned downward. Others ran outward and downward to depths

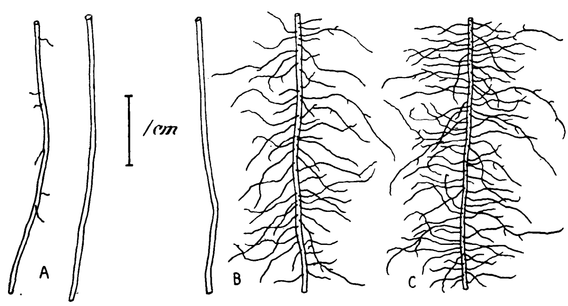

FIG. 7. Relative branching of roots of *Typha;* A, in saturated soil; B, in wet but drained soil; and C, in moist, well-aerated soil.

of 40 to 53 cm. All, except the shortest, were regularly branched except the rapidly growing, shining white distal 8 cm., upon which laterals had not had time to develop. Branches occurred at the rate of about 8 per cm. and varied in length from 1 to 2.5 cm. Secondary branches were only 1 to 3 mm. long and occurred sparsely and only on the longest primary branches (fig. 7).

DRY CULTURE.—The root system was very much like that in the moist soil but more abbreviated. Its extent was determined by the depth of the moist soil which varied from 16 cm. on one side of the container to 35 on the other. None occurred in the surface 9 cm. (fig. 8). The dwarfed plants had fewer roots (27 and 51 respectively on two of the largest plants) than in moist soil but they were much more densely branched, *e.g.* 10–35 laterals per cm., the longer ones having branches of the second order. The branches extended quite to the root tips where, owing to dry soil, further elongation was impossible. Where the tips had died, the roots gave rise to several long branches. In diameter, the main roots more nearly approached those of the moist soil than the thick roots of the wet soil (*i.e.*, they were mostly 1 mm. or less). They were more yellowish in color; root hairs were much more abun-

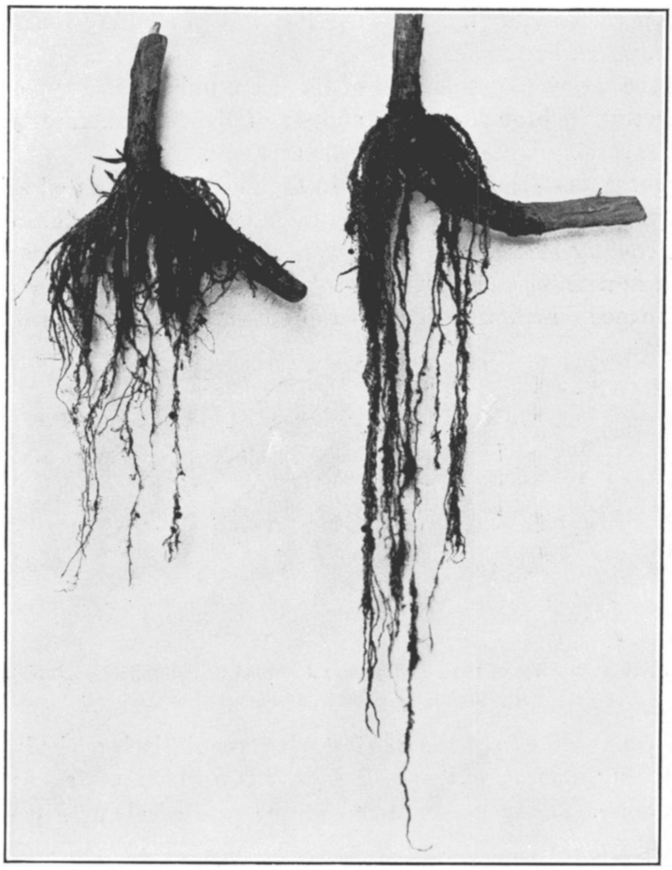

FIG. 8. Root system of *Typha* grown in dry soil. Short branches and root hairs are extremely abundant.

dant than in the drained soil, and, judging from the holding of the soil particles when excavated, more abundant also than in the moist culture. The root branches pursued markedly devious courses, in striking contrast to those in the wet and drained soils. One rhizome died without producing any growth, and another after some of its roots were only 10 cm. long.

RÉSUMÉ.—A survey of the preceding data shows that decreasing aeration on the one hand and decreasing water content on the other, has a marked effect upon root habit. In moist soil, the root system was uniformly developed throughout, spreading downward and outward below the level of the rhizome to a depth of 40–53 cm. In dry soil a similar root habit was found, although the number of roots on the dwarfed plants was fewer and root-hair development was more profuse and occurred to the root ends, whose further elongation was limited by the dry soil.

Where aeration was somewhat deficient in the alternately saturated and drained soil, the root system was somewhat shallower and differentiated into two distinct parts, one of these containing two types of roots. The surface root system consisted of a network of long, fine, profusely branched roots abundantly supplied with root hairs. This was confined to the surface 9-cm. layer of soil which was best aerated. The deeper part comprised both coarse and fine main roots, the latter only being much branched.

Where plants were grown in standing water, about half of the root system grew upward and developed into water roots. These were so fine and their primary branches so abundant that for their volume they presented a large absorbing surface for dissolved oxygen. They were destitute of root hairs. Similar root development has been observed in undrained marshes. The soil roots penetrated less deeply (30 cm.) than in the drained soil but were of the two types described for the latter. The chief differences were fewer, finer, and shorter branches that were more irregularly distributed, and a relative scarcity of root hairs.

SCIRPUS VALIDUS

Scirpus made a good growth even in the dry soil. Growth was again, with one exception, in direct proportion to water content as shown in table II.

TABLE II

GROWTH OF *Scirpus validus* ABOVE GROUND WITH DIFFERENT MOISTURE CONDITIONS

CONDITION FOR GROWTH→	SATURATED SOIL	DRAINED SOIL	MOIST SOIL	DRY SOIL
Total number of stems	47.0	42.0	25.0	18.0
Average height, cm.	87.9	100.4	71.0	49.6
Average basal diameter, mm.	8.1	7.8	5.2	4.7
Dry weight of tops, grams	39.6	42.4	18.8	7.0

The panicles of the aerated (drained) culture were more abundant and further developed than those in the saturated soil. This accounts for the greater height and also for the greater dry weight. No flowers had formed in either of the other cultures, the tips of about one-third of the plants in each being dead. The ratio of dry weight of tops to roots was just the opposite of that of *Typha,* being 5.5 to 1 for the saturated soil and 7.4 to 1 in the drained soil.

SATURATED CULTURE.—At the time of root excavation, on May 29, the water-logged soil of the wet container had a distinctly sour odor. About

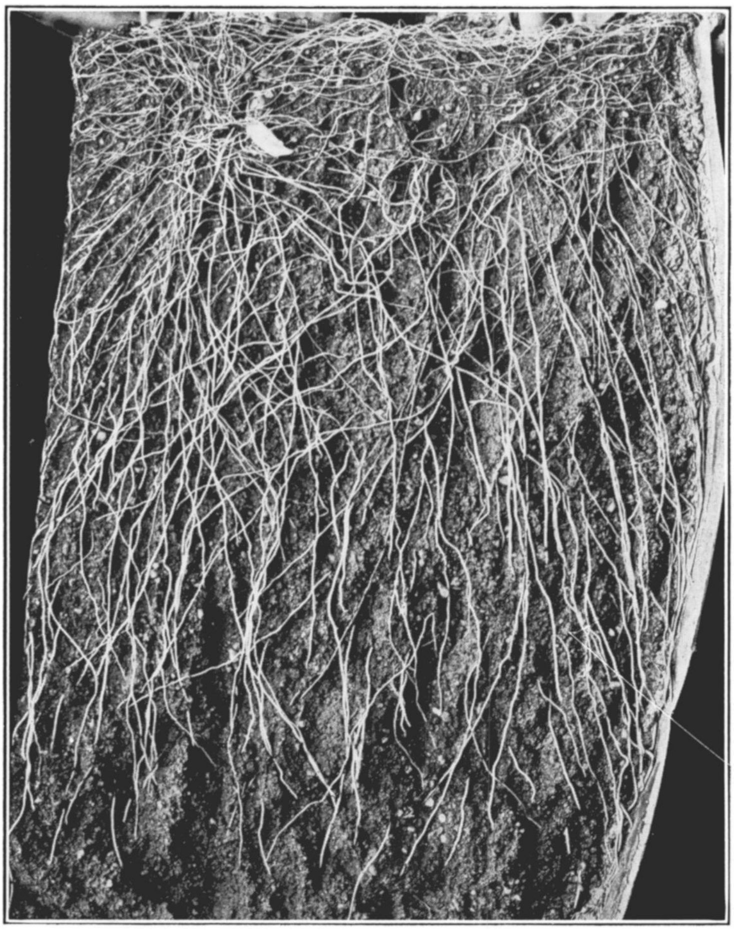

FIG. 9. Root development of *Scirpus validus* in water-logged soil covered with 5 cm. of standing water. The general root depth is about 38 cm.

half of the original rhizomes were still firm, the rest had decayed. The root system consisted of a glistening white mass of long fibrous roots that rather fully ramified the soil (fig. 9). All of these originated from the bases of the new shoots or from new rhizomes and none from the old ones except from the part directly below the shoot. Roots were abundant to a depth of 38 cm. and a maximum depth of 46 cm. was attained. As in the case of the cattails, the horizontal and obliquely ascending roots of the surface soil were much finer and very much more branched than the deeper ones. While most of these originated from the upper portions of the nodes, the roots were not sufficiently distinct to separate into groups as in the cattails. Although a few water roots 4 to 5 cm. long were formed, a week after transplanting, this portion of the root system failed to develop. The network of fine surface roots with extremely fine laterals occurring at the rate of 3–14 per cm., developed only in the surface 2 or 3 cm. of soil. The coarser, deeper roots, 1 mm. or less in diameter, were usually sparingly branched for $\frac{1}{3}$ to $\frac{2}{3}$ of their length. The branches were simple and rarely exceeded a cm. in length. The laterals varied from 1 to 9 per cm. and in general they decreased with depth. While the main roots throughout the container were sparingly furnished with root hairs, most of the branches had none.

Drained culture.—All of the rhizomes in the drained, unsoured soil remained firm and undecayed. As in the saturated soil, new rhizomes had made considerable growth, some a maximum of 7 cm. The root habit differed from the preceding in the following respects: the surface portion was very poorly developed, the deeper roots pursued a less devious course, and the depth of penetration was greater (fig. 10). Although some roots extended above their point of origin at the base of the shoot or rhizome, they were mostly short (10 cm. or less) and much less abundant than in the saturated soil. In fact, the surface 5 cm. of soil at a little distance from the base of the plant was only sparsely threaded with these fine roots.

In the deeper soil, the general root mass extended to 50 cm., roots were numerous at 55 cm. and a maximum depth of 59 cm. was attained. The younger roots usually reached lengths of 15 to 20 cm. before branching began and they possessed few or no root hairs. The older roots were usually branched throughout their proximal half and not infrequently almost to their tips. The branches were more numerous on the older roots, the number and length of branches being practically the same as that recorded for the saturated soil.

Moist culture.—The root system in the moist soil was much deeper than under either of the preceding conditions. Roots were very numerous at 64 cm. depth and a maximum depth of 71 cm. was attained. They originated only from the portion of the rhizome adjacent to the growing shoot, or from the base of the shoot. The soil below the level of the rhizomes was filled with a mass of roots, although they were not so abundant as in the drained soil. In general, their course was rather directly downward. Many main roots in the upper soil were 10 cm. or less in length and the tips were dead. Short laterals, rarely exceeding 9 cm. in length, occurred regularly at the rate of 9–14 per cm. throughout the length of the main roots, except on the youngest 5–10 cm. of the root-ends. It appeared that the extremely abun-

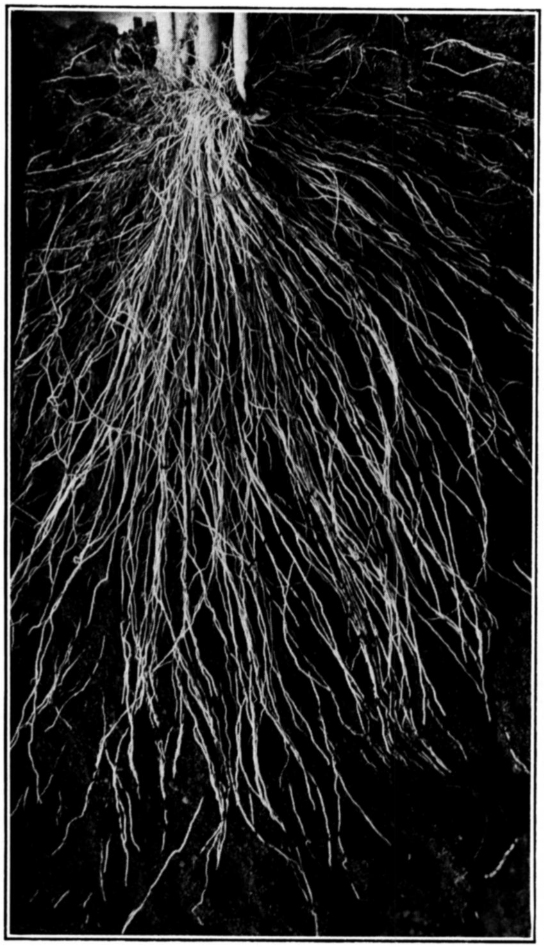

FIG. 10. Root system of *Scirpus* in drained soil (depth about 55 cm.). The development of a surface root system is much less marked than in figure 9.

dant roots were functioning throughout their entire course. Both the main roots and their branches were thickly covered with long root hairs. Portions of all of the old rhizomes showed decay and some were completely rotted.

DRY CULTURE.—The root systems in the dry soil were very much abbreviated as were also the tops. Roots were not only shorter but also fewer per plant, although more abundant in proportion to tops than in the wet soil. Insufficient water was clearly the limiting factor to growth since there was an abundant supply of food in the fairly well preserved rhizomes. As in the moist culture, there were many roots that extended horizontally or obliquely downward into the shallower soil but in no case were they found approaching the soil surface. The general direction of root growth was vertically downward or obliquely outward and then downward. The general level of root penetration was 30 cm., a few penetrating 10 cm. deeper. The older, deeper roots were profusely branched throughout but scarcely more so than in the moist container. Moreover, the branches were shorter, averaging only 3 mm. Since the main roots had ceased elongating, branches occurred to within 3 or 4 cm. of the tip. Although none of the primary laterals were rebranched, both they and the main roots were more densely clothed with root hairs than were those in the moist soil. Moreover, both branches and root hairs extended quite to the root tips. Hence, as shown in figure 11, the soil was held tenaciously.

RÉSUMÉ.—A comparison of the root behavior under the different environments shows, as in *Typha,* that under conditions of poor aeration there is a development of a fine, much branched network of surface roots and a consequent decrease in depth of penetration. The bulrush seems to emphasize the surface absorbing system somewhat less than the cattail. No water root system was formed and the surface system was less extensive, being confined to the first 3 cm. of soil. Moreover, in the drained soil it was very poorly developed. Here the deeper roots were straighter and penetrated about 12 cm. farther. Under both conditions branching was sparse and root hair development poor. In both the well aerated moist and dry soils, the surface root system failed to develop. Roots were 14 cm. deeper in the moist soil than in the drained, branching was quite profuse, and root hairs were abundant throughout. Relative to size of tops, the dry soil had the most roots. Their limited extent was compensated in part by the profuse development of short branches to the tips and by the very marked development of root hairs.

PHRAGMITES COMMUNIS

Phragmites made the poorest growth of all four species, a fact undoubtedly due to its being transplanted after growth began. The tops decreased in average height from 101 cm. in the saturated soil to 8 cm. in the dry soil where very little growth occurred. Total leaf production ranged in the same sequence from 61 leaves to only 4, notwithstanding the fact that the dry culture had the largest number of stems. Leaf area ranged likewise from 1,118 to 20 square cm., that of the drained soil exceeding the saturated. The dry weight of tops of the drained soil was also somewhat greater. The ratio of tops to roots was less in the drained than in the saturated soil.

SATURATED CULTURE.—When the container was opened for root study on June 3 it was found that the soil had a distinctly sour odor but none of the rhizomes were decayed. The root system was composed of two distinct parts, a very much branched surface system and a portion that would ultimately penetrate deeply. The roots of the latter generally originated from

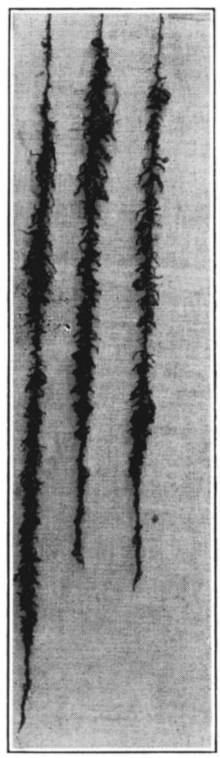

FIG. 11. Main roots of *Scirpus* grown in dry soil. Branches and root hairs occur to the root-tips.

the base of the rhizome branches, those of the former on the higher nodes of the shoot. Because of the repeated branching of the rhizomes at different levels, horizontal roots often originated more deeply than those that penetrated more or less vertically.

Some of the roots of the surface system arose as deep as 14 cm. and the surface soil was filled to its contact with the water with a mass of shining white rootlets. All were a mm. or less in thickness and none exceeded 28 cm. in length. While the younger ones often had unbranched ends several centimeters long, the older ones were profusely branched nearly to their tips. The branches were so very numerous (30 to 85 per cm., although only 0.5 to 10 cm. long and poorly rebranched) that the total surface for the absorption of water and oxygen was greatly increased.

The deeper roots had twice the diameter of the shallow ones. They extended to a depth of 21 cm. Only a few primary branches occurred and they were on the oldest part. Both main roots and branches of the entire root system were destitute of root hairs, except on a relatively small portion of the older ones.

DRAINED CULTURE.—The soil in this container was also sour but none of the rhizomes were decayed. With one exception, the depth of penetration was the same as before, but the following differences were plainly evident. The surface root system, although well developed, was not nearly so pronounced as in the saturated soil. Primary laterals on the entire root system were finer, longer, more numerous on the deeper parts, and more profusely branched, but rarely to the second order. Root hairs were abundant throughout the soil mass on both the main roots and practically all of the branches.

MOIST CULTURE.—The root system had made a poor growth in this container as had also the tops. Two rhizomes had died, one had not developed, and another had developed three short aerial shoots but no roots. The horizontal, surface root system consisted of wire-like, profusely branched roots, some occurring at a depth of 15 cm. That they were young was indicated not only by the absence of branches near the root-ends but also by the fact that approximately half of their laterals were simple. Moreover, they were not abundant. Of the few roots that penetrated downward, all but two were less than 16 cm. in length; the longest extended 34 to 37 cm. Root hairs were abundant throughout.

DRY CULTURE.—The poor growth showed that even the surface soil in this container was too dry for much development. Two rhizomes had decayed, three had developed short, erect stems but no roots, one had rooted and died. The others had from 3 to 6 roots each that varied from 1 to 20 cm. in length, but they were mostly less than 10 cm. The two types of roots were in evidence but neither was as well developed as in the preceding container.

RÉSUMÉ.—In the saturated soil, *Phragmites* developed a network of fine, extremely well branched roots which filled the surface 10 cm. to its contact with the water. The coarser, more or less vertically penetrating roots extended to about twice this depth and branched but little. There were no root hairs except on a small portion of the oldest roots. In the better aerated, drained soil the root habit differed only in a less pronounced development of the surface root system and in the fact that root hairs were abundant on practically all of the main roots and their branches. In well aerated, moist soil the surface root system was represented by only a few horizontal roots, some of those of the deeper portion reaching nearly twice the depth attained in the poorly aerated culture. Few roots grew in the dry soil.

SPARTINA MICHAUXIANA

Spartina made a rapid growth, the plants in the saturated and drained cultures both reaching an average height of 75 cm., in comparison to 55 and 35 respectively for the drier soils. Dry weight of tops again decreased directly in the sequence of decreasing water content of soil except that the moist soil produced slightly more dry matter than the drained. The top-root ratios of the saturated and drained soils were 8.2 to 1 and 5.6 to 1 respectively.

SATURATED CULTURE.—The root system was more or less differentiated into a shallower and a deeper portion. The former consisted of a large number of fine, profusely branched, horizontally placed roots, some 20 cm. in length, that ramified throughout the shallower soil extending to its surface. Many of these ended without turning downward. They were branched abundantly with long laterals but root hairs were very sparse.

The deeper portion of the root system was chiefly composed of numerous coarse roots nearly 2 mm. thick that extended vertically downward or ran obliquely downward with little change in the direction of their course. Many ended at 28 cm. depth, a few extended 5 to 10 cm. deeper. Some of the shining white younger roots were only 10 cm. long, and entirely unbranched but sparsely clothed with root hairs. The last 10 cm. of the older roots was likewise frequently free from branches. Otherwise branching occurred at the rate of 9–16 laterals throughout. These varied in length from 1 to 10 cm. Root hairs were sparse and found on only relatively few branches. Short secondary branches occurred only on the longer laterals. Another lot of the deeper roots was much finer and could not be distinguished except by position from the fine surface roots. They were evidently older than those just described. All were abundantly clothed with fine laterals usually 0.5 to 3 cm. in length. Only the longer ones were rebranched and root hairs were sparse. Many new rhizomes had originated from the base of the clumps, but none exceeded 7 cm. in length.

DRAINED CULTURE.—The development of the rhizomes and general extent of the root system were very similar to those of the saturated soil, general root extent being only 5 cm. deeper. The surface portion of the root system was the same as in the previous culture but in neither were the roots densely matted as in *Typha* and *Scirpus*. Not only was the rate of branching somewhat increased but also the primary branches averaged twice as long and fairly extensive laterals occurred even on the shorter rootlets. The roots were branched more nearly to their tips. Moreover, root hairs were much more abundant than in the saturated soil. Thus, the effects of increased aeration were clearly apparent.

MOIST CULTURE.—Quite in contrast to the abbreviated root system of the wet soil, 90 per cent. of the roots extended to the bottom of the container, thus having a length of nearly 90 cm. Moreover, none were found in the surface soil, all penetrating vertically or obliquely downward. Many of the coarse, rapidly growing roots were 2 mm. thick and the distal 15–25 cm. were unbranched. There was a decrease in thickness to approximately 0.5 mm. on older roots, and an increase in the degree of branching, long branches occurring close to the root-ends. Laterals occurred at the rate of 6–14 per cm.; branches exceeding 10 cm. in length were not abundant and most were shorter. The longest laterals (20–30 cm.) were found in the last 20 cm. of soil. Secondary laterals were common and root hairs abundant throughout. Where the roots entered the coarse gravel at the bottom of the container, their diameter was doubled and the branches were much coarser.

DRY CULTURE.—The roots had penetrated quite beyond the 20 cm. of moist soil and through the dry soil to the bottom of the container at 58 cm. In one case this was true of 14 roots from a single rhizome. In many cases they extended 5–14 cm. along the bottom of the container and gave off great clusters of long branches very nearly to their tips.

The roots were distinctly smaller in diameter than those in the wet soil, none exceeding a mm. and some were only $\frac{1}{3}$ as large. This was in striking contrast to the thick, rapidly growing roots of the moist soil.

All of the numerous coarse roots ran either vertically or obliquely downward so that there were none in the surface 6 cm. of soil. Branching was very similar on all of the roots, being uniform and profuse throughout the soil mass. It was somewhat more profuse than in the moist culture, and many branches, especially near the root-ends, were longer. Branches occurred at the rate of 9 to 22 laterals per cm. on both main roots and primary laterals. The primary laterals usually extended out horizontally 2–4 cm., although many, especially near the root-ends, were longer. Branches of the third order were not infrequent, all of the smaller branches being very fine.

RÉSUMÉ.—*Spartina* reached the same height in saturated and drained soils. Decrease in dry weight of tops accompanied decrease in water content, except that in the moist soil dry weight was slightly greater than in the drained.

The grass responded to poor aeration by the development of numerous fine, long, well branched horizontal roots extending to the soil surface. This part of the root system was less poorly developed than in either *Typha* or *Scirpus*. The deeper portion of the root system was only slightly more extensive in the drained soil, but here it was furnished with more and longer branches. Root hairs were sparse in water-logged soil but more abundant in the drained.

No surface aerating roots developed under good aeration in moist soil, but the others grew to almost three times the depth attained in the intermittently water-logged soil. Branches were more numerous and root hairs very abundant throughout. Roots and branches in the coarse, well aerated gravel, were of much greater diameter. In the drier culture the roots penetrated soil of only 2 per cent. available water content, their extent being limited by the size of the container. Branching was most profuse here and the number of branch orders greatest. Root hairs were much more abundant also than in the moist soil.

Discussion

Of the four species investigated, three are characteristic of the reed-swamp stage of the hydrosere, all being very widely distributed. *Scirpus* grows in the deepest water, sometimes in excess of 6 feet, and *Typha* in shallower places. *Phragmites* usually occupies wet areas which are submerged at least for a part of the growing season, while *Spartina* represents a very late stage of the hydrosere and forms a transition between swamp plants and more mesophytic vegetation. Owing to changes in water level resulting from drought, flooding, and other causes, the above sequence is not absolute and relicts of cattails and bulrush often occur intermixed with the reed. In fact, the great extremes of water and air content endured by the plants, once they are thoroughly established, are indeed remarkable. *Spartina,* in these experiments for example, flourished in water-logged soil and also, after growth was started, made a fair development in soil with only 2 per cent. available water content.

These experiments show clearly that plants growing naturally in poorly drained and poorly aerated habitats are much less sensitive to the composition or absence of a soil atmosphere than are those in naturally well drained soils. In water-logged soil the oxygen supply must be very low or practically nil. Oxygen diffuses slowly through water, so that the supply is not quickly replenished by diffusion alone. The addition of tap water through a sprinkler to that standing on the soil surface together with the photosynthetic activity of the algae considerably increase the supply of dissolved oxygen. It has been demonstrated by several investigators that algae may bring about the supersaturation of lakes and streams as a result of photosynthesis, at the same time preventing the accumulation of large amounts of carbon dioxide, in consequence of the same process (**3, 13**).

All four species showed a distinct aerotropic response by the development of a superficial root system with a very extensive absorbing area. *Typha* was the only species, however, that extended its roots into the water layer above the soil. This development of an aerating portion of the root system and its absence under conditions of good aeration is in accordance with the findings of WILSON (**26**). He observed that the number and size of "knees" of the bald cypress (*Taxodium distichum*) were determined by the height of the water and the duration of the flooding. Young roots often grew directly upward until they reached the surface when they again turned and developed beneath the water. In dry soil the trees showed no trace of such development. Similar structures occur about the bases of trunks of Tupelo gum (*Nyssa aquatica*) in swamps, the roots bending sharply upward to a distance of 6 to 8 inches above the surface of the water and then turning downward into it again.

The production of adventitious roots which run horizontally above oxygen-free swamp soil, as in *Alnus, Fraxinus,* and various other land species, is well known (cf. **8**). But less exact information is available on the root behavior of true hydrophytes, although upright roots have been developed on *Rumex* and *Nymphaea* when these were planted too deeply (**11**).

In considering root response to aeration it must be kept in mind that species vary widely, a substratum of water or water-logged soil may furnish sufficient oxygen for certain hydrophytes, while under similar conditions most plants would succumb. CANNON (**4**) has shown that the temperature relation is of great importance in problems of aeration, the species studied demanding better root aeration as the soil temperature became higher. Since these cultures were grown under a moderate and rather uniform soil temperature (about 70° F.) the temperature factor need not be considered. Although there is some evidence that the rate of root respiration in hydrophytes is lower than that of land plants (**10**), the capacity of marsh plants to grow in water-logged soil is undoubtedly due to their extensive development of aerenchyma in leaves, stems, and roots (**25**). The continuously open stomata in many of them (*e.g., Typha* and *Scirpus*) would facilitate rapid gaseous diffusion. The extent to which aerenchyma develops when the roots of grasses like *Spartina* are continuously submerged remains to be determined, although a marked increase of intercellular spaces in roots of corn, etc., under such conditions has been clearly shown (**20**). The dependence of root-hair development of various plants upon the presence of oxygen has been pointed out by several investigators (**6, 23**). Although water roots are commonly without hairs, they may readily be produced on some plants in an aqueous medium provided that calcium is present (**9**). Root elongation in nearly all plants is likewise retarded by a deficient oxygen supply.

Summary

Plants of great bulrush (*Scirpus validus*), cattail (*Typha latifolia*), reed (*Phragmites communis*), and tall marsh grass (*Spartina michauxiana*) were grown in large containers under four sets of conditions of aeration and water content, *viz.*; water-logged soil, soil alternately saturated and drained, moist soil, and dry soil.

Growth of tops in *Typha,* as measured by number and size of leaves and total dry weight, increased with increasing water content until a condition of saturation was reached. More and larger *Scirpus* grew in the saturated soil but because of earlier flower-stalk production in the drained soil, both height growth and dry weight of tops were greatest in that culture. Both *Phragmites* and *Spartina* grew about equally well in the water-logged and drained soils but like *Typha* and *Scirpus* they became progressively poorer as the soil became drier.

The ratio of tops to roots (based on dry weight) was less in the drained than in the water-logged soil, except in *Scirpus.*

Typha alone had roots that developed in water. These were of small diameter and possessed so many fine laterals that they presented a large surface for the absorption of dissolved oxygen.

A response to poor aeration was shown in all four species by the development of a shallow root system of fine, much branched roots which presented a large surface area in proportion to volume. This did not develop in well aerated soil, except to a limited extent in *Phragmites.*

Aside from this surface portion of the root system, the development of lateral roots increased with an increase in aeration. Where dry soil hindered or prevented root elongation, branching occurred to the root tips.

Root depth increased with decreasing water content until the soil became too dry for root growth.

Root hairs were absent in water, few and irregularly distributed in saturated soil, but progressively more abundant as aeration became better with decreasing water content.

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