The University of Chicago

DEVELOPMENT OF ROOT SYSTEMS UNDER DUNE CONDITIONS

A DISSERTATION
SUBMITTED TO THE FACULTY
OF THE OGDEN GRADUATE SCHOOL OF SCIENCE
IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

BY
WARREN GOOKIN WATERMAN

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DEVELOPMENT OF ROOT SYSTEMS UNDER DUNE CONDITIONS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 250

W. G. WATERMAN

(WITH SEVENTEEN FIGURES)

The attention of the writer was first attracted to this subject by the lack of knowledge in regard to the causes of the development and consequent extension of root systems.[1] This seemed the more surprising because this knowledge is important, not only from a theoretical standpoint, but also because of its bearing on the practical activities of plant production. All of the responses of plants to soil conditions, and some of those to atmosphere, are closely connected with the condition of their root systems, but in the past both botanists and agriculturists in the main have been satisfied to interpret results by observation of the shoots only. It is evident that in all cases where the chemical and physical content of the soil is not absolutely uniform, accurate interpretation of results must take into consideration the extension and general condition of the roots.

Recognizing the practical difficulties of root observations, a locality was chosen in which the character of the soil and the scattered stand of the plants would make it possible to observe complete root systems under natural conditions. It was soon found that the distribution of nutrient material was also an easily observed and very significant factor in this locality. The region also proved to have great geological and synecological interest, and since it has been described rather fully (44) elsewhere, it will be treated only briefly here.

In the figures the root systems are arranged as nearly as possible in the natural position in a vertical plane. A 10 cm. scale was the

[1] In this study the term "development" will be applied to the process of increase in size and branching of the roots, "extension" will refer to the size of the system, and "distribution" to the relative position of the system and its parts in the soil.

standard measuring stick. When missing from any figure, the scale is the same as that of the adjoining figure.

On account of the range of the subject and the relatively small amount of work done in it, the study has been largely a survey of the ground, and the results must be regarded as indications for future work rather than as final solutions of the problems.

The work was carried on under the direction of Dr. H. C. Cowles and Dr. Wm. Crocker, and grateful acknowledgment is made to them for their advice and general assistance; as well as to Dr. G. D. Fuller, Dr. Sophia H. Eckerson, and Messrs. H. C. Sampson, E. J. Kraus, and J. T. Buchholz.

Synecology of Crystal Lake bar region

GEOGRAPHY AND GEOLOGY

The region studied is located in the northwest corner of Benzie County, Michigan, and comprises a strip of land about 1 mile wide and 5 miles long between the west end of Crystal Lake and Lake Michigan. Geologically it is probably a harbor bar formed during Algonquin time between the ends of two glacial ridges extending from Lake Michigan southeastwardly on either side of Crystal Lake. There are some indications that this strip may have a morainic core, but if so it was worked over and its top leveled off during the Algonquin high water, so that from an ecological standpoint the situation would be the same.

Soon after the recession of the post-glacial lake waters, the winds began the work of piling up dunes. Apparently they were begun much farther west on land since eroded away by the lake. The group which may be called the Point Betsie complex starts in a point on Lake Michigan at the western end of the grounds of the Congregational Summer Assembly and spreads like a fan to the north, about 2 miles in length and half a mile in width at its widest part. At its southern extremity the dunes are fixed with a very uneven contour, showing dune ridges and outlines of former blowouts, and covered by a climax forest. Approaching Point Betsie the surface is lower and the fixed dunes give place to a complex of moving sand containing residual patches of the original forest. Above Point Betsie the dunes are fixed again and end with a definite lee slope just where the edges of the northern glacial ridge disappear under the level surface of the bar.

The glacial ridges consist of surface deposits of sand and gravel more or less water washed and stratified, but contain below at least one layer of laminated clay several feet in thickness. This layer appears on the Michigan shore bluffs and is occasionally exposed by erosion on hillsides and in ravines. On the shore end of the southern ridge is located a second small group of dunes about half a mile north of Frankfort. They are half a mile in length and one-fourth of a mile in width, and extend almost directly north from the shore, which at this point lies northwest and southeast. The group consists of small fixed dunes about 50 ft. in height, and the ridge is itself about 100 ft. above Lake Michigan. These fixed dunes have been blown out through the center in a long trough, which ends in a large, steep-sided, semicircular blowout popularly called the "Crater." For 100 yards or so from the edge of the shore bluff the sand has been blown away to or below the level of the glacial deposits, which are exposed in the bottom of the trough.

CHARACTER OF ENVIRONMENTAL FACTORS

CLIMATOLOGICAL.—So far it has been possible to obtain only incomplete and not entirely satisfactory observations, so that only a brief general statement will be given. There is nothing exceptional about the meteorological conditions of this region as to temperature, precipitation, or moisture in the air and in the soil. On account of the marked projection of Point Betsie into Lake Michigan, it is exposed both to southwesterly and northwesterly winds, which probably accounts for the large amount of moving sand around the Point. The wind also has an indirect influence on evaporation and temperature, especially in summer, as a marked difference in both is observed when a period of easterly winds is followed by a similar period of westerly winds.

SUBSTRATUM.—*Open dunes.*—On the dunes the blown sand is generally homogeneous in physical character, but a marked characteristic is the large percentage of calcium carbonate present in the form of residual grains formed by the grinding up of shells, apparently chiefly of gastropods. This calcium carbonate content varies from 1 to 5 per cent. The dune sand is also characterized by a very unequal distribution of organic material, in the presence not only of old soil lines, but also of buried plant remains and of patches and layers distinctly different in appearance and character from the ordinary dune sand. The old soil lines, which are familiar to all who have any acquaintance with dune regions, are usually quite extensive, but generally appear only as a dark layer on the sloping sides of blowouts. Only occasionally do they occur parallel to the surface of the sand at such a depth as to affect the roots of annuals or young perennials. The upper layers of the sand, however, are generally characterized by the occurrence of layers of a dark color, usually a few millimeters in thickness and covering less than a square meter in area. The cause of the color has not been determined definitely. It is apparently carbonaceous in nature, and its source might be attributed to thoroughly decayed organic matter, and sometimes also to unusual deposits of soot from steamers passing on the lake. There is some evidence that this soot accumulates on the snow in winter and is left on the sand when the snow melts in the spring. It has been noticed also that in periods of extreme dryness a very fine powder is formed from the attrition by the wind of the exposed dead roots and stems of plants, and this is unevenly distributed by the wind over large portions of the bare sand. When fixed by a sudden shower and covered by later deposits of blown sand, very thin interbedded dark layers might be produced. Other layers and patches are marly in nature, and appear to have been deposited in beds of dried pools in former pannes. Very rarely patches of rusty color, giving an iron reaction, are found. They are only a few centimeters in length and suggest a buried nail or possibly a bit of meteoric iron as their cause.

Glacial deposits.—The upper layers of the glacial deposits are composed mainly of outwash material, sand with a few pebbles and an occasional bowlder. They are generally covered with humus, but in the crater blowout the erosion has been carried down to a gravel layer. This differs greatly from the dune sand in physical and probably in chemical constitution.

Humus.—The forested dunes as well as the glacial deposits are completely covered with a thin layer of leaf mold. This is surprisingly uniform in depth, rarely exceeding 10 cm. in thickness. The sand below this layer has been discolored for several decimeters and its chemical content is plainly affected by materials leached down from the humus above.

Moisture content.—The moisture content of the soil varies with the location and the character of the substratum, as is shown in table I. The 7 cm. samples were usually taken in the sand just below the lower edge of the humus, as it was thought that a centimeter of depth more or less would have less significance than an indeterminable admixture of humus.

TABLE I

Locality	Depth in cms.	Wilting coefficient	Average moisture content 8 weeks July and August 1916
Open dune summit............	7	0.5	2.0
" " "	25	0.5	2.5
Forested dune summit.........	7	1.8	2.1
" " "	25	0.3	1.3
Forested dune side............	7	1.0	2.2
" " "	25	0.3	1.2
Glacial moraine..............	7	3.3	7.5
" "	25	2.4	5.0

ECOLOGY

Climax forest.—The whole region, including at least part of the moving area, was originally covered by a heavy climax forest, which is still practically untouched in the southern tip and along most of the eastern edge of the dunes. The level ground on the Bar has largely been cleared, and is covered with second growth of forest trees and clearing pioneers, where not occupied by summer cottages. The climax forest is composed of beech, maple, and hemlock, with much yellow birch. The trees are tall and slender, with close stand and very little undergrowth where undisturbed. Occasional specimens of *Quercus rubra*, *Pinus Strobus*, and *P. resinosa* are found. Among the shrubs *Acer spicatum*, about at the southern limit of its range, *Viburnum acerifolium*, and *Taxus canadensis* are conspicuous. Characteristic species in the undergrowth are *Aralia nudicaulis*, *A. racemosa*, *Streptopus roseus*, *Clintonia borealis*, *Maianthemum canadense*, *Linnaea borealis*, and

Mitchella repens, with *Aspidium spinulosum*, *Adiantum pedatum*, and *Botrychium virginianum*.

Burned area.—The northern and central portions of the forested strip have been burned, in some parts repeatedly, in others not so recently. In the much burned portions the tree specimens are young and somewhat stunted. In the other portions the trees are larger and the undergrowth thicker. The species include *Betula alba*, *Prunus virginiana*, and *P. pennsylvanica*, with the more xerophytic relics of the mesophytic undergrowth, and much *Pteris* and *Equisetum*.

Border zone formation.—Where the climax forest, still untouched, extends to the shore, a zone 50–100 yards in width shows a very characteristic difference in species. The trees are *Thuja*, *Ostrya*, *Tilia*, and *Abies balsamea*, with *Celastrus scandens*. The line of demarcation is not sharp, but the climax trees, especially hemlock, mingle with the others almost to the edge of the cliffs. The characteristic border zone species are not found farther back in the climax forest.

Dune complex vegetation.—On the open dune complex there are found a number of forest patches, apparently growing in valleys between former fixed dunes whose summits have been entirely blown away. The interiors of these patches present all the characteristics of a heavy forest, and their evaporation rate is almost as low as that of the climax forest, but the vegetation is characteristic of the border zone already described, containing especially *Thuja* and *Abies*, and is marked by some trees reaching 2 ft. in diameter, but not over 30 ft. in height. The undergrowth is similar to that of the climax forest, but is especially characterized by *Viburnum acerifolium*, *Rhus toxicodendron*, and *Aralia nudicaulis*. On the edges, next to the open sand, are found *Arctostaphylos*, *Linnaea*, and *Juniperus horizontalis*. These apparently originate in the fixed area and extend out onto the sand, forming a protective covering, which frequently contains also *Juniperus communis*. Buried trees and occasional graveyards are to be found all over the moving sand area.

There is not much forest reproduction on the moving sand, and, unlike some similar regions, there are no young stands of *Pinus*

Banksiana, nor any cottonwood dunes similar to those of the Indiana-Michigan region. There are practically no panne colonies, but a few isolated oval groups, chiefly of *Thuja* and *Betula alba*, which seem to have originated from pannes, growing upward as the sand accumulates around their stems. A few other patches have reached the low conifer stage, but seem chiefly to have been invasions from the relic patches previously described. On the open sand the vegetation consists of characteristic pioneer herbs, *Ammophila* and *Calamovilfa* among grasses, with *Lathyrus maritima*, *Artemisia caudata*, *Campanula rotundifolia*, *Cirsium Pitcheri*, some *Hudsonia*, and *Zygadenus chloranthus*. There are frequent mounds protected by *Calamovilfa*, *Prunus pumila*, *Salix syrticola*, and *Cornus stolonifera*.

The growth of grasses, especially *Ammophila*, is quite extensive, and frequently approaches the character of fixed grass dunes. This is especially noticeable on the advancing lee slopes, where the complex is overwhelming the climax forest.

Literature

In view of the state of our knowledge of the general subject, the literature was reviewed rather fully, but only a brief summary of the results will be given here. The survey covered only the extension and distribution of soil roots, and the questions of absorption, structure, and effects of environmental factors were considered only as they affected extension. Owing to the range of the subject, the matter was treated from the standpoint of lines of work followed rather than that of historical development. These will be summarized and general conclusions indicated.

Intensive study of root systems.—This line has been followed mostly by German workers, and was directed chiefly toward the questions of structure and function, either in different roots of the same maturity or in the same root at different stages of its development. The leading workers along this line were von Alten (1), Freidenfeldt (16, 17), and Tschirch (43). Kroemer (24) has made the most thorough study of the "biological" significance of structure, and concludes (1) that the root is divided longitudinally into zones characterized by greater or less suberization in the different layers of the root, and (2) that the distances of these zones from the root tip are specific. Specialized types are also reported: "contractile" (RIMBACH 30); "deciduous" and "rudimentary" (CANNON 6). Root systems are classified as "intensive" and "extensive" by BÜSGEN (4), and he regards these as hydrophytic and xerophytic, respectively.

EXTENSION.—The largest amount of agricultural work has been done by KING (23), TEN EYCK (39), SHEPHERD (36), and GOFF (18): Their conclusions were largely along practical lines and in many cases simply confirmed conclusions already reached by empirical methods. SCHULZE'S (34) work is especially to be commended for carefulness of records and character of photographs. CANNON (6, 9) has done the most comprehensive work on arid regions. His records are very complete, but his method of recording is not uniform and no scales were photographed with his plants. In several cases photographs manifestly of different enlargement were included in the same plate. On other wild herbs the best work was by WEAVER (45) on about 20 species of prairie plants. The observations were carefully made and well recorded, and the plants were photographed with scales attached. This work promises well for his "Ecology of roots" (46), soon to be published by the Carnegie Institution. This latter study was undertaken to determine the root habits of dominant and subdominant plants that were growing under a wide range of climatic and edaphic conditions; to find the root relations of the plant communities as units of vegetation; and to determine the root distribution and root competition of the individual species in their relation to other species in the vegetational group. Other aims were to determine the relation between the root habits of plants in various communities and their successional sequence; and to obtain a more definite knowledge of the indicator value and significance of various species used in classifying lands for grazing or for agriculture; as well as to aid the forester in selecting sites for afforestation or reforestation. The investigation extended over 4 years, during which time more than 1150 individual root systems of about 160 species of shrubs, grasses, and non-grassy herbs were excavated and studied on the prairies of eastern Nebraska, the chaparral of southeastern Nebraska, prairies of southeastern

Washington, plains and sand hills of Colorado, the gravel slide, half gravel slide, and forest communities of the Rocky Mountains of Colorado. Among other interesting observations on roots incidental to studies of other features, HITCHCOCK (21), PAMMEL (27), and SHERFF (37) might be mentioned. Very little work has been done on the root systems of trees. BÜSGEN (5) was not accessible to the writer. PULLING (28) describes the root systems of certain trees of the northern coniferous forest, but does not attempt much explanation of the phenomena observed.

EFFECTS OF ENVIRONMENT.—The main records of the influence of soil on the extension of root systems are incidental to other subjects, as CANNON (6, 8), HILGARD (20), HELLRIEGEL (19), and others. CRAIG (12) observed the effects of frost on the root systems of fruit trees; TOLSKY (40) made some careful experiments with oats grown at 25° and 8°, respectively; and TRANSEAU (42) observed the results of different temperatures on the growth of seedlings in bog water. CANNON (10) discusses the relation of temperature to rate of root growth. As to the depth of water table, CANNON (7) made observations on the root systems of desert plants and also on development of seedlings in relation to the water supply. CANNON and HILGARD give some information on the effects of drought, but the most extensive article by ROTMISTROV (31) was accessible only in the review in the *Experiment Station Record.* BENNETT (3) offers evidence that roots of certain land plants are not aërotropic, and CANNON (8) concludes that in mesquite and *Fouquieria* aëration within limits favors root growth and shoot development. NOYES, TROST, and YODER (26) conclude that excessive CO_2 is detrimental to normal root development, and agree with CANNON and FREE (11) as to the importance of soil aëration.

Since the work of NOBBE (25) and STOHMANN (38), HÖVELER (22), BENECKE (2), and TOTTINGHAM (41) have done the most comprehensive work on chemicals. On the whole, such work has been chiefly on the roots of seedlings, and the question at once arises whether the results would have been the same with mature root systems. BENECKE quotes PROBST to the effect that "observations on mature plants gave results opposite to those in plants less mature, but even then the evidence seems somewhat contradictory." BENECKE concludes that, on the whole, scarcity of chemical nutrients tended to increase root length, calling this effect "hunger etiolation." HÖVELER reached similar conclusions by growing plants in alternating layers of sand and humus. SEELHORST (35), by counting the number of roots found in fertilized and unfertilized patches, decided that "in the fields investigated, plants strongly fertilized not only produced stronger roots, but also roots penetrating to lower levels." RUSCHE (32) used various salts on 8 groups of plants and concluded that the different groups responded somewhat differently, but that on the whole sulphates produced the longest and nitrates the shortest root systems. TOTTINGHAM made a thorough study of the effects of various salts on young wheat plants in water cultures by varying the proportions of the components of Knop's solution. He included observations on length and weight of roots developed, but drew no general conclusions. DACHNOWSKI (13, 14, 15) and RIGG (29) conclude that toxins in bog waters and in decaying rhizomes respectively cause stunting of roots and therefore xerophily or death of plants.

SCHREINER and REED (33) conclude that roots of healthy growing plants excrete substances deleterious to root growth, especially in plants of the same species.

Conclusions from literature

1. There has been comparatively little work done on extension of root systems as such, and the value of the results is lessened by the lack of uniformity in recording, which makes it practically impossible to compare the results of different workers. The use of vague descriptive terms in characterizing the branching of roots is also unsatisfactory.

2. Much variability of roots as a result of the action of the environment is reported, but most of this action is destructive, as the results of frost, drought, hard soil layers, etc. The experimentation with chemicals shows differences in length and weight of roots, but does not offer any definite evidence as to the causes of root extension in general or of differential extension within a single root system.

3. The elaborate studies of the structure of roots are marked in the main by great freedom of inference as to the functions of these structures. There would seem to be need of further evidence, experimental or otherwise, to give a more certain foundation for the statements as to function.

4. It seems evident that extension of root systems should be interpreted in the light of the structure and function of the roots in question. The length of a root is of little importance unless we know how much of it is functioning for the plant. Great length, also, or closeness of branching, may have very different causes and effects in different species or under different conditions, and so a very different meaning to the plant.

Root systems of dune plants

GROWTH HABITS OF ROOT SYSTEMS

METHODS.—From the consideration of the literature, it becomes evident that the extension of root systems means very little ecologically unless interpreted in the light of function and of probable causes of that extension. Studies which include simply the extension of root systems, without considering the conditions of their development and in some way evaluating the absorbing power of their different parts, omit a large part of the significant elements of the problem. For these reasons it seemed better not to attempt to study the extension of the root systems of all possible plants found on the dunes, but to confine the attention more intensively to a few species. Within the limits of the present paper it will be possible to study only the development of roots in relation to the factors of their environment. This can best be done by beginning with the germinating seed and tracing the probable course of development with the influence of the environmental factors always in mind. From this viewpoint length and weight of roots would be of less importance than the determination of a "normal" root system and the interpretation of the modifications actually found. The question of structure and function, while equally important, cannot be considered in the present paper, but must be left for future study.

General description of certain species.—*Prunus pumila.*—This was the species first investigated because, as a perennial well distributed over the Betsie complex, it showed promise of a permanent and well marked root system. On investigation it proved to have not only these features but other characteristics which admirably fitted it to serve as a basis of comparison with other species. As usually observed on the dunes, the plant has more or less of a shrub habit, with many stems caused by vegetative reproduction of parts buried by the sand. Under these conditions it frequently functions as a sand binder and forms a protected knoll or hummock. On the other hand, where the sand is being blown away, a long straggling stem will be produced, more or less prostrate and with little branching. In general the shrub type seems to fruit best, and seedlings are most abundant at the base of a shrub or around a knoll, although the fruits sometimes roll or blow some distance before being covered with sand.

The only conditions of germination seem to be burial over a winter in 1 or 2 inches of sand. In the laboratory the seeds germinated readily in a sterile moist chamber on filter paper, after the stony pit and the seed coat had been removed.

After 3 months' growth on the dunes the root system shows the general type illustrated in fig. 1, while a 3-year-old seedling is shown in fig. 2. The root system, however, does not usually develop along these lines. The more usual form is extremely asymmetric and develops very unevenly, as indicated in fig. 3. All the seedlings show wide individual diversity of form, and these specimens are not at all exceptional in their eccentricity. An examination of these asymmetric forms shows that their irregularities are connected with the distribution of more or less decayed plant parts under the sand. A typical illustration of this is shown in fig. 4, where horizontal laterals are shown passing through and exploiting bits of stems, branches, etc. When a seedling grows in the vicinity of a dark layer already described, its laterals are generally found in these layers, and they are more branched and longer than those in ordinary dune sand; in fact, a layer of this sort will generally be found to contain many rootlets of various species of plants, while the sand on either side is almost completely free from them. An interesting case was found in the sand at Miller, Indiana, shown in fig. 5. A 3-year-old specimen (*b*) grew within the field of such a layer, and the effect is seen in its well developed horizontal laterals. The carbonaceous layer in question was absent in the neighborhood of

FIG. 1

FIG. 2

FIGS. 1, 2.—*Prunus pumila:* fig. 1, 3 months old; fig. 2, 3 years old

FIG. 3.—*Prunus pumila*, showing asymmetric habit

the 2-year-old specimen *a*, barely 2 ft. away, and the absence of prominent laterals is very marked. Cases of extreme elongation were occasionally observed, as in fig. 6. In the specimen figured, the root came in contact with a decaying grass rhizome and turned back at a sharp angle, following the rhizome for about 60 cm. In a similar case the root did not make such a sharp angle, but followed the rhizome for an even greater distance. It should be noted in

Fig. 4

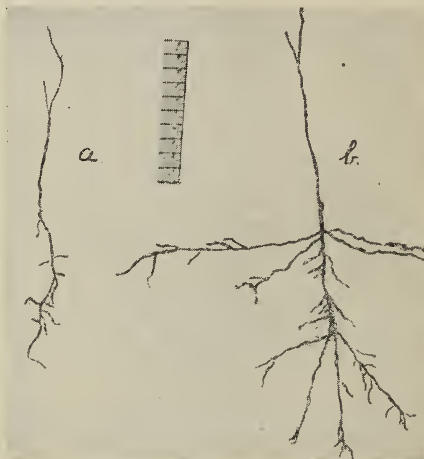

Fig. 5

Figs. 4, 5.—*Prunus pumila:* fig. 4, showing relation of roots to buried plant parts; fig. 5*a*, 2 years old, which grew in normal dune sand; *b*, same, 3 years old, which grew in sand with interbedded black layers.

both cases that the size of the shoot was not at all in proportion to the length of the root.

In these cases the relation of the root to the organic matter is not clear. Generally there is little penetration of the tissue of the decaying organ. There are occasionally short laterals clasping the foreign body, frequently passing under a sheathing leaf or a disorganized epidermis, and in cases of extreme decay adjusting themselves to the easy passages formed by the disintegration of the middle lamella of the cell walls. There are no indications of haustoria or of actual penetration of cell walls. In black layers and patches in the sand there are cases of extreme development of small rootlets with close branching.

The development of the shoot is more or less connected with the presence of these plant parts. Seedlings whose roots do not come in contact with such organic matter have few and small leaves, and in general it would seem that the securing of food from such organic matter is essential to the development and maturity of the plant. Most of the plants which have reached the shrub stage are found to have stems which have apparently come up through superposed masses of sand, and while it has not been possible to demonstrate the presence of organic matter at the base of such shrub systems, such presence is very strongly connoted by the appearance of the plant and the evidence from the smaller specimens excavated. The condition of the shoots with very long roots will be considered later.

FIG. 6.—*Prunus pumila* with long lateral developed in contact with dead *Ammophila* rhizome.

In the sphere of inhibiting factors very little evidence was observed. On account of the scattered stand the roots seldom come into contact with roots of other plants, but occasionally they were found exploiting bits of buried plant material in company with and unaffected by roots of (*a*) other species. In one case, however (fig. 7), a *P. pumila* seedling had sent its roots down almost into a thick mat of willow roots (*b*). Here there seems to have been a very definite dwarfing of the root system, either from the presence of injurious excretions or because of the removal of water or nutrient material by the willow roots.

The presence or absence of the water table seemed to have no directive effect on the *P. pumila* roots; in fact several seedlings were found growing in the water on the edge of a pool, with no apparent effect on the roots. Observations near Miller, Indiana, on *P. pumila* and *Populus deltoides*, seemed at first to show such effects (fig. 8). The seedlings were growing in very wet sand with the water table only 8–10 cm. below the surface. On inspection the water table zone proved to be very mucky and foul, and the effects on the tap-roots seemed to be a rotting due to the action of micro-organisms, with a proportionately increased development of laterals.

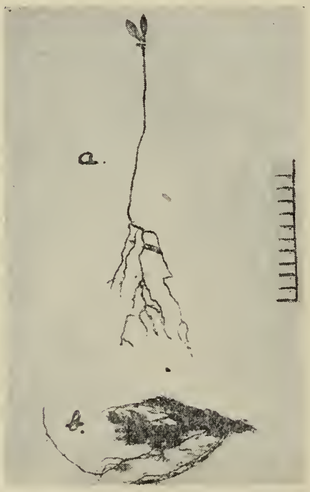

FIG. 7

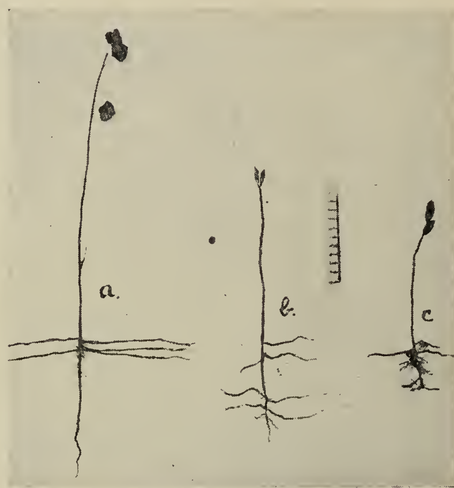

FIG. 8

FIGS. 7, 8.—*Prunus pumila:* fig. 1*a*, with stunted root system; *b*, horizontal layer of matted willow roots in approximately natural position with relation to *P. pumila* roots; fig. 8, root systems showing effects of high water table, Miller, Indiana: *a*, *Populus deltoides; b* and *c*, *Prunus pumila*.

Ammophila arenaria.—While this is the typical plant of the open dunes, its seedlings are difficult to find, and its reproduction is mostly vegetative through rhizomes. The spikes are thoroughly exploited by insects, and when gathered late in the season very few seeds will be found untouched. For this reason the seedlings are very scanty, except in dense colonies where mature spikes have been buried by fresh sand, and even then there are seldom over 6 seedlings from a whole spike. In the mature plant, as is well known, there is a long slender rhizome producing usually 2 roots and a bud at each node. The bud frequently does not develop, but the roots range widely under normal conditions through fresh blown sand, often reaching a length of several meters. They are thickly set with short laterals which bear abundant root hairs. At times the tips of these roots are much enlarged for about 10 cm., gradually tapering in both directions and without branches. All the roots are extremely wiry and tenacious, and on account of their fineness and length cannot well be shown in a figure.

It has generally been recognized (WESTGATE 47) that *Ammophila* ordinarily requires annual supplies of fresh sand for its best development. Field observations in this region would indicate also that it does not thrive in sand possessing an appreciable amount of humus, and that its colonies do not extend across the border into such a region (sand containing humus). In at least one case a colony seems to be dying out in the presence of a competing colony of *Calamovilfa*, which has not been studied closely, but which seems to be more humus tolerant than *Ammophila*. Excavation shows that the roots of mature plants of *Ammophila* exhibit little response to organic material, following black layers only slightly and frequently passing obliquely through them. A study of the seedlings would seem to indicate that the extension of their roots may to some extent be inhibited by the presence of decaying plant parts. In fig. 9, *a* grew in pure sand, but in *b* all the roots came directly into contact with buried *Ammophila* leaves and stems, and in *c* the upper roots developed in pure sand and the lower in plant remains. It will be noted that in *b* and *c* the roots do not extend beyond the

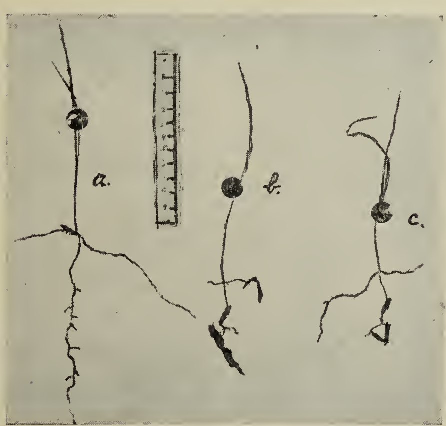

FIG. 9.—Seedlings of *Ammophila arenaria*, 2–3 months old: *a*, in homogeneous dune sand; *b*, all roots in contact with buried plant parts; *c*, upper roots in sand, lower in contact with buried plant parts.

decaying plant parts. Great care was taken in excavating these specimens, which are simply typical of a number of cases found, and there can be no question that in every case the roots stopped in the decaying plant parts as figured.

Artemisia caudata.—This species germinates freely on the open dunes, and also in the edge of the forested sections. It is described by Gray as not perennial, but the character of the mature specimens found on the dunes would indicate that there at least it has a perennial habit. Two series of plants are shown, one grown in pure sand (fig. 10), the other in sand containing some admixture

Fig. 10

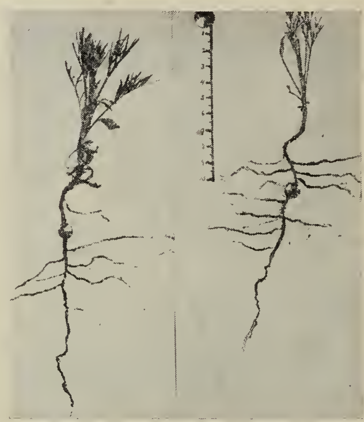

Fig. 11

Figs. 10, 11.—*Artemisia caudata:* fig. 10, which grew in pure dune sand, showing stumps only of long laterals; fig. 11, of apparently same ages as in fig. 10, but in sand containing some humus; laterals very short.

of humus (fig. 11). In the former may be observed the stubs of the characteristic laterals, which in mature specimens extend 20–30 ft. No attempt has been made to show in the figure the full extent of these laterals, but rather their relation to each other and to the taproot. In pure sand this species shows some of the asymmetry of *Prunus pumila*, but the causes are not so evident. In some specimens very long laterals develop almost on the surface of the sand, and are so shallow that they are often exposed and killed by the blowing away of the upper dry sand layer. In other specimens it is one or more of the deep seated laterals which shows extreme elongation. The superficial laterals show marked parallelism with the upper surface of the sand, even in plants growing on slopes; where the laterals join the main root at different angles, they are acute on the upper side and correspondingly obtuse on the lower. The position of these laterals seems to be on the relatively constant plane separating the upper layer of dry sand from the moist sand which constitutes the remainder of the substratum. In general the system is characterized by extreme shortness of taproot, but occasionally the taproot becomes very prominent.

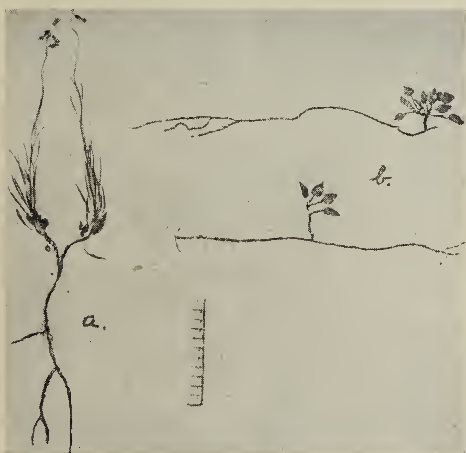

FIG. 12

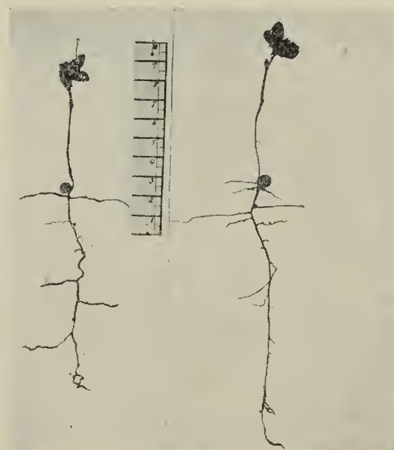

FIG. 13

FIGS. 12, 13.—Fig. 12, *Campanula rotundifolia: a*, normal root habit; *b*, young plants on exposed edge of horizontal marly layer; fig. 13, seedlings of *Lathyrus maritima*, showing remains of seed and root tubercles.

Artemisia resembles *Ammophila* in the reduction in length of roots in the presence of organic matter or humous layers, and its roots are not attracted by decaying plant parts. It will be noted in fig. 11 that the laterals of this series, which grew in sand mixed with humus, are finer, more branched, and with none of the very long laterals of the pure sand specimens. The fact that the roots are not attracted by decaying plant parts was distinctly shown in one case where a mature plant with laterals up to 6 ft. in length was growing near a decaying log. One lateral passed a few inches below the log in a zone of leaching, bent first away, then toward the log, then away again, and showed in general no effect attributable to the presence of the log. A marked attraction would have been expected if the plant had been *P. pumila*.

Cirsium Pitcheri.—This is apparently ecologically similar to *Artemisia caudata* as to locality and general conditions of growth, but it differs in having a strongly developed taproot with very few and inconspicuous laterals. Occasionally, for no apparent reason, a single lateral becomes prominent, as in *Artemisia*.

Campanula rotundifolia.—This species is not uniformly distributed, but apparently germinates freely in restricted localities on the open dunes, as well as in open places of a humus bearing substratum. Its marked characteristic on the dunes is the long taproot with U-shaped insertion of laterals (fig. 12*a*). In one case where a buried marly layer was exposed on a slope a row of seedlings was observed growing along the exposed edge of the layer, and the roots were found to have grown horizontally inward through the marly layer (fig. 12*b*). They have not been observed in contact with the dark layers, so their reaction to them cannot be stated.

Lithospermum Gmelini.—This is a fairly well distributed plant on the open dunes, and is characterized by a very long, thick, black taproot, with almost no laterals. A study of the structure might reveal some interesting features as to the absorbing power of this root.

Lathyrus maritima.—This species is frequently the companion of *Ammophila*, but it differs in root development in some important respects. It germinates freely on the open dune, producing numerous seedlings. No marked seedlings have been followed over winter, but from the scarcity of 2-year-old plants they do not seem to survive well, either on account of sand movement or possibly because of lack of nutrition. The mature plant develops a wide ranging rhizome, deeply placed and difficult to excavate unless exposed in a blowout. The roots are scattered and usually not over 10–20 cm. in length. Root tubercles are early developed in dune sand (fig. 13), but less in some localities than in others, possibly on account of unequal distribution of infecting organisms. When present the tubercles occur only near the surface of the sand, they do not occur in a humous layer, and in humus the roots are longer than in sand.

Several species found more or less frequently on the open sand, but especially along the borders of forested patches being blown out, have in general similar characteristics, and will be described together. These are *Thuja occidentalis*, *Cornus stolonifera*, *Arctostaphylos Uva-ursi*, *Vitis* spp., *Betula alba*, *Tilia americana*, and *Juniperus horizontalis*. These rarely germinate on the open sand, although *Thuja* and *Betula alba* are occasionally found germinating on the edges of blown out patches, and regularly germinate, when present, on the floor of these same patches. A study of their root systems shows that the roots regularly follow and exploit the carbonaceous layers and old soil lines, and the plants remain stunted unless their roots find such plant remains.

Populus deltoides.—This species is very rare in this region, and its ecological equivalent, *P. balsamifera*, is found sparingly along the shore of Lake Michigan, more frequently on Crystal Lake beach, and in the burned part of the forested dune area.

Salix spp.—The willows were not included in this study, although their roots were frequently met, and certain points may be noted. They showed a positive and vigorous hydrotropism, which was observable in the neighborhood of pannes and also of Lake Michigan. Several times roots were found descending with the slope of the surface of the sand until they finally entered the water table and passed under the pool in the panne. They also show in marked degree the ability to form a small bunch of closely branched rootlets in small dark patches in the sand.

GENERAL OBSERVATIONS

Root systems in glacial gravel layers.—In the blown out portions of the Crater group gravelly layers of the glacial substratum had been laid bare and bore a scattered vegetation similar to that of the dunes. There was some excavation of *Prunus pumila* and of *Artemisia* in this locality, and indications seemed to point to a closer and more regular branching. There were of course no buried plant parts, so that asymmetric development would not be expected (fig. 14).

Mycorrhiza.—The question of symbiotic fungi suggested itself early in the investigations, but there was no opportunity for a detailed study. Slight examination of a few species was made, but did not show evidence of the presence of such fungi.

Enlarged root tips.—A frequently observed feature of many of the dune species was the marked enlargement of some root tips. The tip rapidly increased to 3 or 4 times its normal diameter and then gradually tapered away again, the extreme length of the enlargement being 20–30 times its greatest diameter. This enlargement seemed to be confined to the central tip of the larger branches only,

FIG. 14.—*Prunus pumila* plants in sandy morainic substratum

and especially in those which showed a marked and rapid extension into new territory, for which reason the name "pioneer" or invading root tip has suggested itself for this type. It was found under apparently normal conditions both in pure sand and in humus, but in the sand it seemed to be increased in some species by the chemical solutions used, and even by distilled water. The largest tips found were in the case of *Juncus balticus*, where in shape and size they resembled large angleworms. It was not possible to make a microscopic examination of fresh material, but sections of tips preserved in 4 per cent formaldehyde showed no signs of symbiotic fungi or animal forms. The enlargement seemed to be due to increase in size and number of the parenchyma cells.

In several cases there were indications that taproots and laterals gave different reactions to the same stimuli. In these species taproots were never deflected by horizontal black layers or plant parts, while laterals were apparently free to move in any direction. Typical species showing this habit were *Artemisia* and *Cirsium Pitcheri*, while in *Prunus pumila* and notably in *Campanula* the taproots, if such they could be called, showed marked variability in a horizontal direction. Whether this difference was structural

FIG. 15

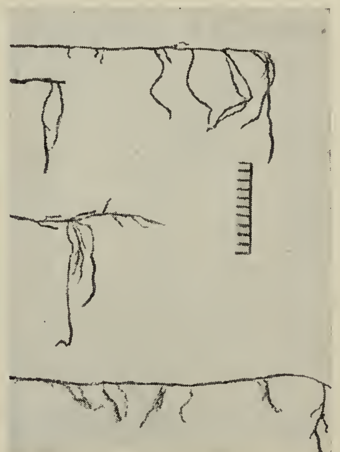

FIG. 16

FIGS. 15, 16.—Fig. 15, *P. pumila* root system after 2 months' irrigation with Knop's solution; round black spot represents location of center of diffusion and dotted circle apparent limits of influence; practically all new roots found within the circle; fig. 16, *Thuja occidentalis:* new root tips grown under irrigation with Knop's solution.

or due to a difference in quantity or quality of the stimulus was not evident.

EXPERIMENTATION

A consideration of these observations would suggest several possible factors as causes for the observed characteristics of root systems of dune plants. Chief among these would be the distribution of chemical materials not normally found in dune sand, also the distribution in the sand of moisture and of oxygen and the varying penetrability of the sand. As the chemical factor seemed most likely to be the controlling one, some experiments were carried on in the endeavor to clear up this point if possible, and to indicate the nature of the chemicals producing the different results.

Experiments with plants in situ.—The first question to be settled was, can root extension be stimulated by the presentation of nutrient material either to the root tips or along the more mature roots? This was investigated by diffusing Knop's solution from porous cylindrical cups (old atmometer cups in this case) which had been buried in the sand near the roots of growing plants. The cups

Fig. 17.—*P. pumila*, 3 months' seedlings grown in pots: *a*, irrigated with rain water; *b*, with Knop's solution; *c*, grown in rotted barnyard manure and humus.

were located at a distance of 5–10 cm. from large lateral roots near a portion of the root practically without secondary laterals. The cups were filled about 3 times a week with 0.6 Knop's solution and were dug up after 2 months. In every case there was a marked development of laterals in the zone of diffusion of the solution. This was tried with *Prunus pumila* and with *Thuja occidentalis* (figs. 15, 16). The contrast between the old bunched roots and the new slender ones is striking. Controls with distilled water showed no abnormal development.

Pot cultures with nutrient materials.—Pot cultures with *P. pumila* seedlings were grown in dune sand watered (1) with distilled water, and (2) with Knop's solution, and (3) in a substratum of rotted barnyard manure. The results are shown in fig. 17. While the root systems in (1) and (2) seem rather similar in extension, an examination showed that (2) was more closely branched than (1) and had nearly twice as many absorbing root tips. The striking feature of (3) was the much greater development of the shoot. Attempting to reproduce more closely the natural conditions, a seedling was grown in the laboratory in a pot of sterile dune sand in which a small patch of rotted manure had been included. Here the most marked extension of rootlets appeared under the patch of organic matter in a space stained by leaching from the material above.

Pot cultures with inorganic salts.—Experiments on the directive influence of inorganic salts have showed so far only indications and suggestions. Rusche (32) has already shown differences in extension produced by different salts, and attempts were made to extend his results along the line of directive influence. The technical difficulties of finding suitable seedlings and of presenting the chemicals in solution from one side only, along with the uncertainty as to the direction and extent of diffusion of the solution through the sand, have so far prevented reaching any conclusive results. Indications of a tendency to react in accordance with the sequence of the liatropic series were observed and definite specific differences were also evident.

Discussion and conclusions

The most marked feature of these observations is the varied reactions of different species to apparently identical environmental conditions. These showed sufficient constancy within a species, but with such differences in different species as to suggest that the reactions are specific and that the controlling factor is heredity. Their general character also strongly suggests their relation to a former habitat or condition of growth. It would seem possible that species which had varied in the direction of an extended root system in sandy soil had survived there and had become adjusted to that environment, and that when germinating in soils richer in nutrients these root systems would be less extended. On the other hand, species which had similarly become adjusted to the richer soils had thereby become dependent on these soils for the development of extended root systems, and were therefore stunted in sandy soils. While a relation to past conditions may not be the true explanation for this specificity, the facts are evident and certainly indicate very definite relations to present conditions. These should be of great value in selecting species for revegetating exposed areas and other localities where the humous content of the soil is slight or unevenly distributed, as well as in the cultural treatment of species which may be regarded as worthy of development for their economic value.

On this basis it would follow that general statements in regard to the root habits of dune plants as a class are dangerous, and that the so-called "dune pioneers" are not all on the same footing; that in fact they should be put into two widely different groups with a series of types occupying intermediate positions. In one group would be the *Prunus pumila* type, which does not have the power of extending root systems widely in pure dune sand, but is stunted and does not reach maturity unless its roots find buried organic matter. In the opposite group would be the *Ammophila* type, which reaches maturity in pure dune sand and whose root system is limited in extension by the presence of decaying plant materials. Similar to *Ammophila* would be *Artemisia*, *Cirsium*, and *Campanula*, with *Calamovilfa* and other grasses, and probably species of *Solidago* and *Aster*. *Lithospermum* is similar ecologically, although with a very different root habit, while *Lathyrus maritima* occupies a peculiar position on account of its relationship to the nodular bacteria. From these observations it would seem that *Ammophila* is the only plant which can reasonably be expected to thrive successfully on the normal dune substratum.

In seeking for the causes of the asymmetric development of root systems observed, it is evident that the only factors to be considered are those working in the soil and exerting an unequal or one-sided influence in the system as a whole. These may be limited to four, namely, moisture, chemicals, oxygen, and density or penetrability of the soil. In the case of a few plant groups, as the willows, which are recognized as having a hereditary hydrotropic tendency, there will be little question as to the dominant factor, but the evidence in the cases of the species previously described must be considered somewhat carefully.

Taking up first the possibility of moisture as the main factor, it should be noted that below the first few centimeters water is evenly distributed in dune sand, and cannot be regarded as the causal factor in the development of the asymmetric root systems described. It might be assumed that the following of humous layers and dark patches by plant roots should be attributed to the presence of a greater amount of moisture in those patches than in the adjoining sand. Granting the power of humus to absorb greater amounts of water than can the pure sand, it would be difficult to prove that water was held by these patches beyond the quantity required by their increased wilting coefficients. The patches are so small and the medium so unstable that it would be practically impossible to collect from adjoining patches pure samples large enough for accurate determination of their respective moisture contents and wilting coefficients. In the experimental work the adjustment of the water supply was a difficult matter. As a result there were occasional reactions which seemed to point to the influence of moisture, but even in these it could not positively be stated that chemical influence was not the dominant factor with moisture as contributory only.

Approaching the question from the chemical side, we find definite evidence, both from observation and from experimentation, that, with the species considered, variations in chemical solutions produced changes in root development, while variations in water supply produced little or no evidence of such changes in development. Perhaps the most conclusive evidence was found in the case of a patch of humus in a pot culture of *Prunus pumila*. Here the abnormal development of laterals occurred under the patch of humus in a zone stained by leaching of organic matter rather than in the free region on either side, where the moisture content should be the same as in the region under the organic patch.

We find also marked differences in elongation of root systems in the presence of decaying plant parts. Contact with or even coming into the zone of influence of these plant parts seems to cause elongation of the roots of some species, but inhibition in those of others. The determining factor here might be a direct chemical stimulation, the furnishing of organic material, or in opposite cases the presentation of some injurious or inhibiting chemical product of decay. No deciding evidence has as yet been secured along this line. There were some indications that the roots of seedlings are more sensitive to inhibiting factors than are those of mature plants.

Oxygen.—There was little evidence of unequal distribution of oxygen through the dune substratum. The only exception would be in connection with a high water table, and there the evidence was not conclusive. The slight effects observed were inhibitory in nature, and, in one case at least, referable to destructive action of micro-organisms rather than to a direct reaction of the plant tissue to the absence of oxygen.

Penetrability of the soil.—It is quite possible that the substratum may be more penetrable in some localities, either on account of differing densities of certain layers or of the disintegration of buried plant parts. This would be difficult to prove either way, but there was no evidence of any tendency of the root tips to be turned back by a less penetrable layer when accidentally wandering too near to the borders of a dark layer, as would be the case if the dark layer had been the more penetrable medium. In fact the only observed case of a probable difference in penetrability was that of a soil layer which apparently contained a percentage of wind-blown clay. In this case certain roots were distributed along the upper surface of this layer when normally they might have been expected to pass directly down through it. As already indicated, the difference of penetrability of the moist sand under the soft sand mulch may be the determining factor in the distribution of *Artemisia* laterals. This distribution, however, may also be explained by the difference in moisture content of the two layers of sand.

There is no clear indication as to the method by which the chemical substances act on the root, whether by direct stimulation or by removal of some inhibition; neither are the relative rôles of organic and inorganic substances more than suggested. The cases of marked elongation of roots in one direction would seem to indicate the possibility that roots under certain conditions can make use of organic matter directly; in other words, that green plants may be somewhat saprophytic in nature. A careful microchemical study of the contents of the root at different points along its length would be necessary in order to get any definite information on this point. It would probably occur only when the root found materials exactly suited to its needs, and would be proportionately greater as the increasing length of the root made transportation to the shoot increasingly difficult.

Under these stimulating influences abnormal lengthening and thickening of roots occur to such an extent as to call in question the value of the common method of estimating root development by measuring the length and weight of roots. In fact, if the explanation of direct local use of organic material of the root be accepted, the abnormally long root may be a detriment instead of a benefit to the plant as a whole. It would seem as though there could be developed some method of evaluating the absorbing power of roots through study of the structure of the different parts of the root system which would give more dependable results than the length and weight method.

The evidence cited emphasizes the unique character of the dune substratum, in that pure dune sand is the only soil in which mineral salts, with the exception of calcium carbonate, are practically absent, and organic matter is so rare and scattered that as a general factor it is practically negligible. This is in strong contrast with many arid deserts in which large quantities of desirable mineral salts are present, needing only the addition of water to make them available for plant use. While irrigation is the main need of many desert stretches, it would not solve the problem of plant culture on a dune area.

Summary

1. The study of the literature shows that the work done on extension and development of root systems has been surprisingly little, in view of the importance of the root in the utilization of moisture and chemicals in the soil. This study also emphasizes the necessity of interpreting the extension of root systems in the light not only of structure and functions, but also of the causes of such extension.

2. The study of the habitat selected shows that dune sand as a substratum for plant growth is almost unique in uniformity of texture and in absence of mineral salts required by growing plants. It is homogeneous chemically, but contains not only old soil layers but minute streaks and patches, apparently of carbonaceous and organic origin, as well as dead plant parts, very unequally distributed.

3. The roots of dune species react differently to the elements of this heterogeneous structure, extension being increased in some species by the buried organic matter, while others seem unaffected or even inhibited by it.

4. These reactions are specific and hereditary, and may reflect the conditions under which the ancestral plants grew. They must be regarded as of great importance in the choosing of species for introduction into conditions where the humous content is uneven.

5. Giving due weight to the possibility of moisture, oxygen content, and penetrability of the sand as influencing factors, the evidence seems to point conclusively to nutrient or at least chemical influence as the cause of variability in symmetry in the extension of roots under dune conditions.

6. Under certain conditions the root apparently utilizes organic matter directly, at the expense of its shoots. Extreme lengthening and thickening of roots occurring under these conditions call into question the value of the common method of estimating plant growth by measuring the length and weight of roots.

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