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DENSITY OF ROOT BRANCHING AS AFFECTED BY SUBSTRATE AND SEPARATE IONS

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INTRODUCTION

If the root system is studied in its relation to characteristics of the soil profile, the largest amount of roots per unit of soil volume is generally found in the most fertile layers or spots. This fact holds for both annual or perennial herbs: BENECKE (1903), DETMER (1872), GOEDEWAAGEN (1942), KAMPE (1929), KÖSTLER (1956), KRAUS (1892), NOBBE (1862), STEUBING, TORNAU and STÖLTING (1944) and for woody plants: KVARAZKHELIA (1931), WEAVER and CLEMENTS (1938).

Fertility, however, is a very complex condition, and is governed by a large set of separate factors. As the most important of these may be considered the level of nutrients, structure, pH, moisture supply and aeration.

In many of the more common soils used for agricultural purposes, except peat, fertility may be strongly related to the humus content of the soil. Also clay can be considered as a carrier of fertility in many cases. Evidence of this latter fact may be very clear in soils with alternating layers of sand and clay.

As clay and humus are so important as regards their influence on fertility and thus also on branching, they should have some properties in common. Both are colloidal substances with high adsorptive capacities, which enable them to carry a large supply of adsorbed nutrients. Also they can have a very favourable effect on soil structure, which may result in better aeration.

A good supply of oxygen indeed influences branching density. PREVOT and STEWARD (1936) have noticed the enhancing effect of aeration in waterculture and in soil. POLLE (1910) and DETMER (1872) mention denser branching to occur as a result of better aeration.

Clay and humus also effect soil fertility by means of their influence on the waterholding capacity. Although the effects of many other factors relating to soil fertility have been described, and all of them influence branching to some extent, attention is drawn to the three factors nutrient level, clay and humus.

In a large number of publications the occurrence of densely branched roots is more strictly related to a high level of nutrients: MC CREARY *et al.* (1943), DÉHERAIN and BREAL (1894), DETMER (1872), FRAAS (1872), GLIEMEROTH (1955), GOEDEWAAGEN (1932), LUNDEGÅRDH (1930), NOBBE (1862), POLLE (1910), SZEMBEK (1957), SOKOLOW (1956) and TORNAU (1944). It is here that a difficulty arises, for it is not specified what exactly is being considered. A high nutrient level implies a large amount of nutrients per unit volume of soil, but gives no idea as to the mode of occurrence of the nutrients. In this respect it is possible to distinguish between the large supply of adsorbed nutrients and the concentration of the soil solution. As they are not necessarily related, they must be considered as separate factors in their influence on branching.

The influence of nutrient concentration in solution can readily be investigated in solution-culture experiments. NOBBE (1862) already mentions the fact that on concentrated solutions a short, compact and densily branched root system is formed, while in dilute solutions and especially in water the roots are long, thin and more sparsely branched. MOELLER (1884) mentions the same kind of results. However, striking differences are not always obtained and our own experience confirms the latter fact. This need not be so very surprising as the possible range of concentrations of nutrient solutions is rather limited on account of the low solubility of the calciumphosphate compounds. Higher concentrations can only be obtained when the ordinary balance between the nutrient elements is disturbed. It may thus be concluded that the concentration of the soil solution cannot be the only factor governing density of branching.

Dense branching of roots in layers with a high content of humus or organic substance is mentioned by GOEDEWAAGEN (1942), KÖSTLER (1956), KROEMER (1918), STAHEL (1957), STEUBING (1949) and WEAVER and CLEMENTS (1938). This agrees with general observation in the field. That the occurrence of clay has a favourable influence on branching of roots is brought forward by BUTIJN (1955), CARLSON (1925), REDMOND (1954), STEUBING (1949) and WEAVER and CLEMENTS (1938). The influence of resinous ion-exchangers on branching has been noticed by NOSTITZ (1925).

Clay and humus are very often closely related to a high nutrient level on account of their high adsorptive capacities. So it was considered worthwhile to investigate the effect of clay and humus on branching with respect to their influence on the nutrient level. A second point which was considered to be of importance was the influence of separate ions on branching of roots, and so experiments were devised to study these factors as well.

EXPERIMENTS ON SUBSTRATE INFLUENCE

Technique

In order to be able to investigate the possible effect which contact with a soil colloid exercises on branching, the following technique was devised.

The principle of the method is to lay a young, still unbranched lateral root over a series of varying substrates. All substrates along the whole root are soaked with a nutrient solution and, if necessary, have been equilibrated with it beforehand. The aim is to ensure an equal supply of free ions in solution along the whole root length, so that this factor was eliminated and contact effects could be observed.

For this purpose a perspex apparatus was devised, which consisted of four series of small compartments placed crosswise. Each series of compartments could be filled with a number of varying substrates and a root could be stretched out over them, guided by a few notches in the dividing walls (Fig. 1). A lid covering each series of compart-

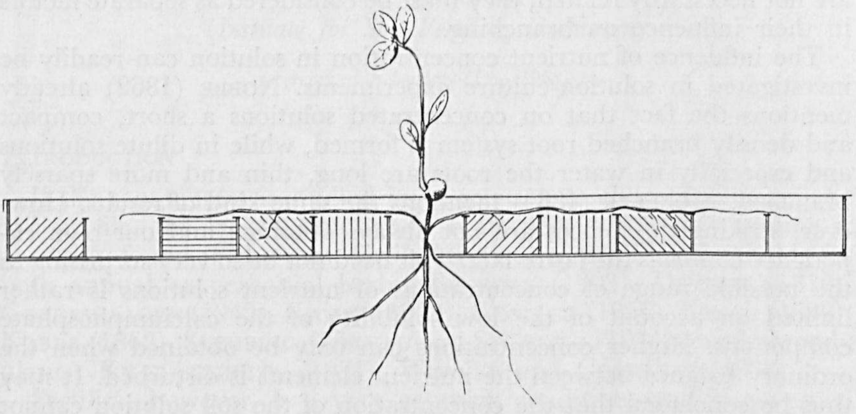

Fig. 1. Diagram of the experimental set-up to investigate the substrate effect on branching.

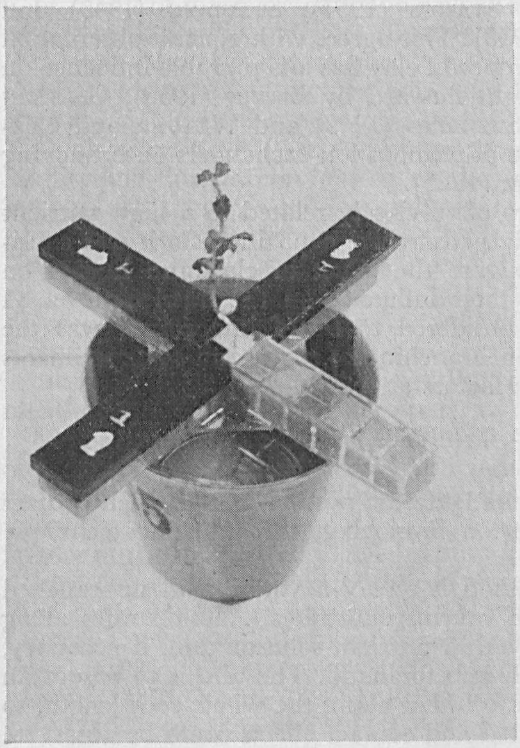

Fig. 2. Experimental set-up in investigating the influence of contact with varying substrates on branching.

ments was needed to eliminate evaporation of moisture and to keep the root in the dark as much as possible. This may be of importance as Detmer mentions that in light less laterals are formed than in the dark. In the center of the four arms a hole was drilled to hold a plant. A young pea plant which had been cultivated on tap water or on a dilute nutrient solution, could be mounted in the centre, and then four young lateral roots were laid out over the compartments. The remaining root system passed through the hole into a vessel containing water (Fig. 2). To reduce loss of water by transpiration and evaporation the apparatus with plant was placed in a moist glass chamber, which itself stood in the glasshouse.

As the root always shows a preference for branching at some distance behind the tip, this behaviour had to be taken into account. So in the experiments the separate substrates were used in alternating successions in each series of compartments. In this way a substrate would be applied to the tip of one root, to the centre of another root and to the base of a third root. In evaluating the results the zone of application has been taken into account, so that no "position effect" might obscure the effects obtained.

TABLE I

Amount of secondary laterals on pea roots formed in contact with different substrates soaked with nutrient solution

substrate	top zone	zone 2	zone 3	zone 4	whole root	branches per segment
A peat	15–14 1)	75–33	52–12	16–9	158–68	2.32
sand	15–12	36–12	49–23	22–10	122–57	2.14
IR 400 . .	13–20	31–13	48–20	13–6	105–59	1.78
Dusarit . .	17–16	14–15	13–12	36–14	80–57	1.40
Total . . .	60–62	156–73	**162–67**	87–39		
B clay	15–8	51–20	45–13	6–3	117–44	2.66
IR 400 . .	5–13	13–9	23–13	11–7	52–42	1.24
sand	7–15	11–9	10–8	20–8	48–40	1.20
IR 105 H .	7–17	4–14	4–7	2–2	17–40	0.42
Total . . .	34–53	79–52	**82–41**	39–20		

1) 15—14 = a total of 15 laterals counted in 14 observations (root segments).

Results of experiments

In Table I the results of a number of series of experiments have been summarized. As can be seen from the data either *Sphagnum* peat litter or clay are able to induce the densest branching as compared to a number of other substrates. These results were obtained with green peas.

Although the observed differences cannot be considered statistically significant, the conclusion as regards peat seems nevertheless to be justified on account of the fact that it proved to be the most effective in three series of experiments with some minor alterations. The effect induced by clay is significant.

If the branching per zone is summarized for all treatments, it can be seen that a certain "position effect" as regards the preferred zone for branching can be noticed. In these experiments laterals are most easily formed in the third zone behind the tip. This phenomenon is in accordance with what is usually seen if a root starts forming laterals.

A few experiments were made with some other plants, in order to substantiate the more general validity of the effects observed. A summary of the data is given in Table II. Although the number of observations is smaller and variability rather high, the average tendency is the same. Contact with clay again results in formation of the greatest number of laterals. It seems that the anion adsorbing IR 400 is second best in its effect.

TABLE II

Density of branching as a total of separate zones as induced by contact with several substrates.

Species	clay	IR 400	sand	IR 105 H
Pisum sativum	65-29 [1]	44-29	16-27	21-29
Vicia faba	9- 5	1- 5	3- 6	4- 4
Ranunculus repens . . .	18- 7	35- 8	18- 5	0- 5
Total	92-41	80-42	37-38	25-38

[1] 65—29 = a total of 65 lateral roots counted on 29 root segments, each about 16 mm long.

So it has been possible to substantiate in these experiments the stimulating effect of contact with clay or peat in inducing branching. The circumstances were such that the concentration of free diffusible ions along the whole root was the same.

If the anion adsorbing IR 400 is compared with the kation adsorbing substances, IR 105 and Dusarit, the first proves to be far more effective. This result can be easily understood when the results obtained on the effect of separate ions are taken into account. Analysis has shown that IR 400 adsorbs a very large amount of nitrate, the most active ion, while the kation exchange resin shows a very high calcium adsorption. This latter substance cannot be expected to have much influence on branching.

TABLE III

Amount of ions adsorbed by the different substrates used after saturation with Hoagland solution in mg per g substance.

	K	Ca	Mg	NO_3	PO_4	SO_4
cation exch. resin . . .	2.0	30.7	6.1	—	—	—
anion exch. resin	—	—	—	75.0	2.9	33.0
clay	0.23	2.6	0.02	0.4	0.15	1.9
peat	0.42	2.6	0.26	0.15	0.36	2.9

In Table III data are given on the amount of adsorbed ions on the different substrates expressed in mg ion per gram adsorbing substance.

EXPERIMENTS ON IONIC INFLUENCES

Technique

The availability of resinous ion exchangers makes it possible to administer a single ion, without giving also a diffusible counter-ion, which might also have an influence on the results.

As yet the experiments were restricted to an investigation of the effects of the six main nutrient ions. As experimental plant the pea (*Pisum sativum*, green pea) was chosen, because it has a root system with rather thick roots which are easy to handle.

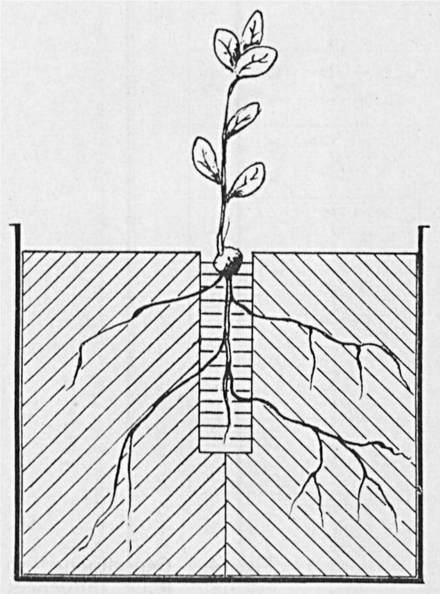

Fig. 3. Diagram of the technique used in investigating the effect of single ions on branching.

The experimental set-up consisted of a cylindrical glass vessel of about 1 l size. The vessel was divided into 6 compartments, which however were not fully separated at the top (Fig. 3). Each sector could be filled with sand unto which 1–2 % of a saturated ion exchange resin (Amberlite IR 400 or IR 120) had been added. The sand used was course builders sand, which had not been pretreated in any way.

The mixture was kept moist by adding tapwater when necessary. A check was made to see if the different mixtures were at about the same pH. By using indicator strips the following values were obtained.

sand + K	8.0	sand + H_2PO_4	6.9
sand + Ca	7.8	sand + NO_3	7.9
sand + Mg	7.7	sand + SO_4	7.8

The fact that the pH is above neutral is the result of the carbonate content of the sand used. The variation in pH is not so that it could account for the differences in rooting obtained.

A germinating young pea was put into the centre and allowed to develop (Fig. 4). The tap root would grow downwards and along the bottom. The primary laterals formed at the base would be able to grow sideways into one of the compartments. As soon as a number of laterals were seen to be growing against the walls of the glass vessel, the roots in the sectors were washed free of sand and cut from the main root. The length of the lateral was determined and the number of secondary order laterals was counted.

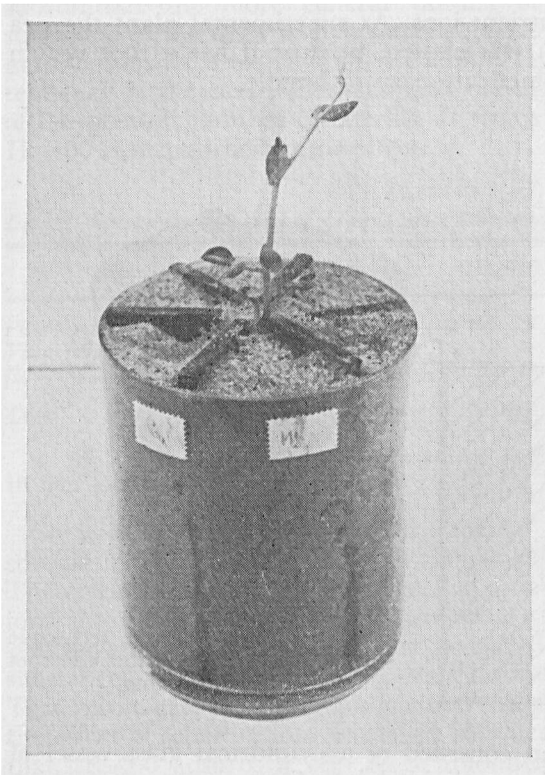

Fig. 4. Experiment to evaluate ionic influences on root branching.

Results of experiments

To evaluate the data the roots were classified according to their length. The oldest and longest primary laterals are always branched to a greater or lesser extent, and variation is considerable. So all roots exceeding 10 cm in length were not taken into account. Moreover, it was considered that the ionic effects would show up most clearly in the younger roots, which have just reached the stage of forming second order laterals. Table IV shows the results obtained in one single experiment, and demonstrates how the evaluation is achieved. For this purpose the number of branches occurring on all roots up to 10 cm in length are added up and the total number of roots is counted. By dividing the total number of branches by the number of observations a figure is obtained which is a relative measure for branching density. A high figure denotes dense branching and a low sparse branching. Table V summarizes the results of a number of experiments.

TABLE IV

Observations on branching density according to root length in a single experiment with peas.

Ion	Root length in cm															1–10	relative branching density	sequence of effectivity
	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1			
NO_3	28 1)	28	20	37	18,24 20		22		32,28	12, 6 5			8, 0	0		113/9 2)	12.57	1
H_2PO_4	22	16	0		29	7,14	16	11, 9	8,19	13,13	8, 9	7, 2	0, 0	0		136/16	8.50	3
K						18		27, 4			10, 6 9,17	13, 7 10, 4	1	9, 1 4, 5 4		151/17	8.88	2
Mg									14	3,14	2,10 8, 0	0	14, 0 0,14 10, 4	3		96/15	6.40	5
Ca							33	20	8	3,10	12, 7 8,11	10,19 2, 0 8	5,10	2, 1 2, 3 2, 1 0, 0	0, 3 0	180/27	6.66	4
SO_4				19		12			8	8	15, 5 7	4, 3 0, 1 8, 1 10	4, 0 5, 3	0		94/18	5.22	6

1) number of secondary laterals counted on 1 root.
2) 113/9 = a total of 113 branch roots counted on 9 roots (9 observations).

TABLE V *Formation of secondary laterals as influenced by separate ions on pea roots.*

Experiment	NO_3	H_2PO_4	K	Ca	Mg	SO_4
1	20/11 [1] = 1.82	36/9 = 4.00	24/17 = 1.41	13/17 = 0.76	25/15 = 1.67	3/7 = 0.43
2	113/9 = 12.57	136/16 = 8.50	151/17 = 8.88	180/27 = 6.66	96/15 = 6.40	94/18 = 5.22
3	106/20 = 5.30	22/10 = 2.20	104/19 = 5.97	26/13 = 2.00	62/20 = 3.10	107/30 = 3.57
4	30/19 = 1.58	31/11 = 2.82	80/31 = 2.58	10/7 = 1.43	4/7 = 0.57	0/4 = 0.00
5	11/5 = 2.20	22/10 = 2.20	12/7 = 1.71	29/15 = 1.93	32/19 = 1.68	8/7 = 1.14
6	30/3 = 10.00	22/13 = 1.69	6/6 = 1.00	5/9 = 0.56	24/9 = 2.67	12/9 = 1.33
7	18/4 = 4.50	2/6 = 0.33	8/8 = 1.00	19/8 = 2.37	2/2 = 1.00	2/8 = 0.25
8	10/2 = 5.00	27/7 = 3.86	9/14 = 0.64	2/1 = 2.00	0/0 = 0.00	8/11 = 0.73

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1) 20/11 = number of counted laterals (20) formed on 11 roots.

As the results are rather variable, the sequence of effectivity can also be calculated for each separate experiment. By adding up all figures for each ion, the totals can be compared. The ion with the lowest total is the most effective one (Table VI).

The data demonstrate that nitrate is the most effective ion in inducing formation of second order laterals. Following in effectiveness are phosphate and potassium. Less effective are Ca and Mg, and sulfate only shows slight activity.

TABLE VI

Sequence of effectiveness of separate ions in the single experiments.

Experiment	NO_3	H_2PO_4	K	Mg	Ca	SO_4
1	2	1	4	3	5	6
2	1	3	2	5	4	6
3	2	5	1	4	6	3
4	3	1	2	5	4	6
5	2	5	1	3	5	5
6	1½	1½	4	5	3	6
7	1	3	5	2	6	4
8	1	5	3½	3½	2	6
9	1	2	5	6	3	4
Total	14½	26½	27½	36½	38	46

A statistical evaluation of the data given in Table VI by means of the method of Friedman showed that the observed sequence differs significantly from that to be expected on account of chance variation.

INFLUENCE OF ION DEFICIENT SOLUTIONS

Technique

In order to be able to investigate the more or less complementary effect of deficiency of a certain ion, a method was devised to test this also. The technique was derived from that of the "Kressewurzel-test" as used by FLAIG (1951).

In a plastic flowerpot 2 glassplates were placed that were covered with filterpaper. The vessel was filled with about 20 ml solution (Fig. 5). Seeds of the plant to be used in the experiment were put at the top of the glass plate and would usually stick to the moist filterpaper if small seeds were used. A lid was put over the pot and the seeds left to germinate in the dark at room temperature. After about 4 days the lid was removed and about another 2 days later the measurements could be performed.

The data obtained were individual root length, average root length and total number of laterals formed. From these data the sequence of effectivity of the solutions on the growth in length of the primary root and on formation of primary laterals could be calculated. The latter data can be totalized to obtain the mean effect of a number of experiments.

Results of experiments

In these experiments the following plants have been used: *Lepidium*

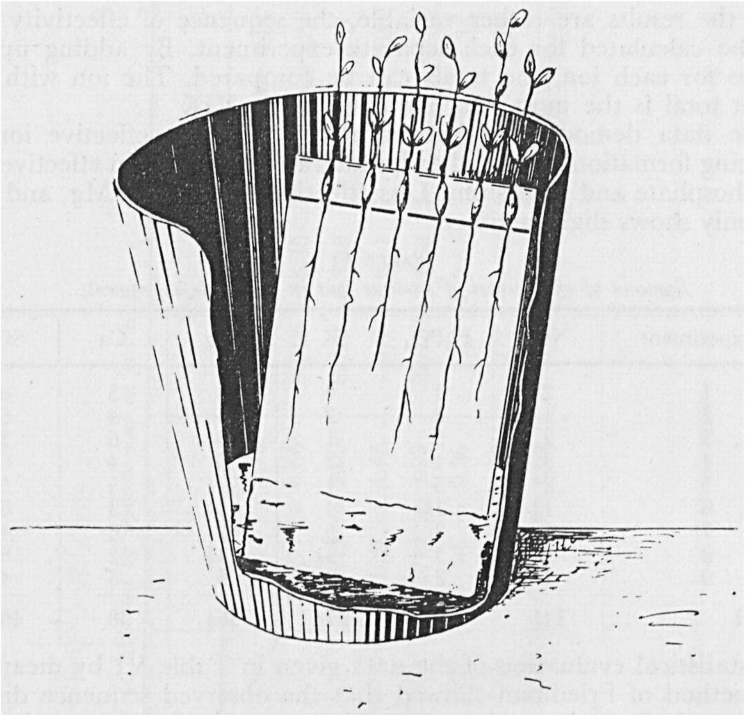

Fig. 5. Experimental technique in testing the influence of ion deficient solutions.

TABLE VII

Influence of ion deficient solutions on growth and branching of Lepidium sativum seedling roots.

Experiment	Average root length in mm in								
	-NO_3	dem. H_2O	tap water	-SO_4	-K	-Mg	-Ca	-H_2PO_4	Hoagl.
1	85	72	64	42	45	39	39	29	36
2	81	96	71	67	53	51	50	52	44
3	107	65	96	40	49	48	49	39	40
4	101	109	77	51	49	61	47	53	45
5	109	126	77	51	50	44	51	49	54
Total	483	468	385	251	246	243	236	222	219

Experiment	Branching, sequence of density								
	-H_2PO_4	tap water	-Mg	dem. H_2O	Hoagl.	-K	-Ca	-NO_3	-SO_4
1	1	4	6	2	3	6	8	5	9
2	1	4	6	7	2	3	4	9	8
3	1	4	1	3	5	9	7	8	6
4	5	2	3	1	4	7	8	6	9
5	6	1	4	8	9	3	2	7	5
Total	14	15	20	21	23	28	29	35	37

sativum, *Linum usitatissimum* and *Raphanus sativus* (radish). Peas and broad beans do not easily lend themselves to be used in this experimental set-up.

In Tables VII, VIII and IX the results are given. Although the variability is rather great, and there also seems to be some specifity according to the plant used, some general trends can be detected.

TABLE VIII

Influence of ion deficient solutions on growth and branching of flax seedling roots.

Experiment	Average root length in mm in								
	-K	$-NO_3$	$-H_2PO_4$	-Mg	$-SO_4$	dem. H_2O	-Ca	tap water	Hoagl.
1	59	52	50	43	44	47	43	46	35
2	74	55	42	42	50	34	38	40	43
3	53	42	44	40	36	38	31	27	30
4	63	56	59	64	56	62	40	37	37
Total	249	205	195	189	186	181	152	150	145

Experiment	Branching: sequence of density								
	tap water	dem. H_2O	Hoagl.	$-NO_3$	-Ca	-Mg	$-H_2PO_4$	$-SO_4$	-K
1	3	4	1	2	6	7	4	8	9
2	2	1	4	3	6	7	5	8	9
3	1	2	5	3	4	6	8	7	9
4	1	4	3	7	2	6	9	8	5
Total	7	11	13	15	18	26	26	31	32

TABLE IX

Influence of ion deficient solutions on growth and branching of radish seedling roots.

Experiment	Average root length in mm in								
	dem. H_2O	$-NO_3$	tap water	-Mg	Hoagl.	$-H_2PO_4$	-K	$-SO_4$	-Ca
1	84	52	51	43	50	37	41	31	35
2	114	95	93	60	67	55	51	47	53
3	80	71	71	53	42	51	44	49	42
4	81	88	65	75	53	75	60	71	66
5	91	55	70	47	49	40	47	43	38
Total	450	361	350	278	261	258	243	241	234

Experiment	Branching: sequence of density								
	-K	$-SO_4$	$-H_2PO_4$	Hoagl.	-Ca	-Mg	$-NO_3$	tap water	dem. H_2O
1	2	9	3	4	8	5	7	1	6
2	6	1	7	2	3	4	5	8	9
3	1	2	5	6	4	3	7	9	8
4	1	3	4	9	6	8	2	5	7
5	2	1	4	3	5	6	7	8	9
Total	12	16	23	24	26	26	28	31	39

Statistical significance can only be attached to the results obtained with flax. It is clear that a nitrogen deficient solution brings about long roots. In general those media which give rise to better growth in length of the root also result in sparse branching. This holds especially for nitrogen deficient or very poor media, except for flax, which seems to react somewhat differently.

The fact that a calcium deficient solution gives rather short roots is in accordance with the favourable effect of Ca on growth in length of roots as studied by BURSTRØM (1954).

The effect of —NO_3 is just the opposite of the results obtained with NO_3-Amberlite and confirms our expectation. On account of the favourable effect exercised on branching by phosphate, it could be expected that a P-deficient solution would give rise to rather long and sparsely branched roots. This, however, does not happen to be the case in the experiments with *Lepidium* and radish.

In general a complete nutrient solution has the tendency to bring about short roots, which are rather well branched.

DISCUSSION

In the experiments where pea roots were brought into contact with a number of substrates, it was possible to demonstrate the favourable influence on density of branching of peat and clay. As the roots were laid out on top of the different media, a difference in aeration must be considered as excluded. As all substrates are kept soaked with nutrient solution, it must be assumed that the concentration of solutes in solution is the same along the whole root. As the observed effects cannot be due to concentration differences of the dissolved ions they must be due to some other effect of the media. The main results are in complete agreement with what has been observed in the field (see introduction).

It might be conceived that the effect of peat is brought about by one or more soluble compounds it contains, especially as FLAIG and co-workers have observed growth-promoting effects of humus components. In these experiments, however, this cannot be the explanation, as was brought forward in a few trials where roots were grown in gravel mixed with peat and gravel only. The same nutrient solution was continually percolated through both media in succession, so that soluble substances would come into contact with all roots (WIERSUM, 1957). Yet even in this case a favourable effect of peat is noticed.

In our opinion the effect humus and clay have in common in inducing dense branching is related to the adsorptive capacity of these substances. As they are both able to adsorb cations and to a lesser degree anions also the activity of the ions in the boundary layer of the colloids will be considerably raised. It is this high ionic activity, which far exceeds that in the nutrient solution, that is considered to be the causal factor.

This idea is supported by comparing the effects obtained with the two types of ion exchange resins. The one which brings about high ionic concentrations of the most effective ions by adsorption is the most effective on branching. Indeed, Amberlite IR 400 is more effective than IR 120, because the first mentioned substance adsorbs the very effective nitrate and phosphate ions.

The fact that first order laterals have been used in these experiments may have been an advantage, as Tornau and Stölting remark that the number of second order laterals of Phaseolus increases in rich and fertile soil, whilst the number of first order laterals increases in poor soil.

The sequence of effectivity of single ions was observed to be $NO_3 >$ H_2PO_4, K $>$ Ca, Mg $> SO_4$. These observations are in accordance with those of GLIEMEROTH (1955), who noted that the effect on branching and root hair formation was $N > P > K$.

If experiments of a complementary nature are performed, a nitrogen deficient solution has the opposite effect, i.e. roots are long and more or less sparsely branched. Also there is a general tendency to form long and sparsely branched roots on very poor media such as demineralized water or tapwater. All these results agree with what has been noticed in the field or in many agricultural trials with fertilizers. Increase in root length in cases of nitrogen deficiency has also been found by Bosemark.

The favourable effect of a high N content on dense branching was already well known. For data in the literature reference may be made to DASSONVILLE (in BENECKE, 1903), EL HINNAWY (1956), GLIEMEROTH (1955), STEUBING (1949), STOHMANN (in BENECKE, 1903), VERMAAT (1950), and WEAVER and HIMMEL (1929). Localized application of N in bands can also effect this phenomenon.

Many results of these experiments indicate that there usually is a more or less inverse relationship between growth in length of a root and the number of laterals. Kroemer also mentions this fact.

The effect of P on branching has also often been noted by others such as TOTTINGHAM (in LUNDEGÅRDH, 1930) and BENECKE (1903). Attention, however, must be drawn to the fact that a P-deficient solution does not have the opposite effect of a high P-level. DASSONVILLE (in BENECKE, 1903) mentions that P-fertilization may result in a relative N-deficiency and that in this case grain crops react with enhanced growth in length of their roots. SOKOLOW (1956) also mentions the same observation. The results obtained in this investigation lead to the same view regarding this possible interaction between N and P. A P-deficient solution may lead to less growth in length and more formation of laterals: its effect is then the same as that of a high N-level.

Favourable effects on rooting density effected by Ca have been noticed a number of times: LONGENECKER and MERKLE (1952), LUNDEGÅRDH (1930), POHLMAN (1946) and WOLF (in POLLE, 1910). If, however, Ca is applied to the soil a number of characteristics may be affected. Usually a change in pH may be the result, and in some cases there is an influence on structure. The results obtained in this investigation strongly suggest that neither Ca nor Mg as such have much influence on branching. So the observed effects mentioned elsewhere must be related to the influence of the secondary changes induced in the substrate.

It may be mentioned that KRUYT (1954) observed an effect of Fe^{+++} on root habit. This fact might be taken into consideration as regards part of the favourable effect of humus or peat in the field. Iron complexing compounds might play a role.

The observations made in this investigation all concern the fact of certain characteristics of the root medium acting as a stimulus in enhancing the formation of many laterals. It should be worth while, however, also to consider the manner in which these effects might be induced. So some possibilities will be indicated to show how the effects may be linked to what has been found in research concerning hormone regulation of root growth and branching.

First of all attention can be drawn to the fact that growth in length and density of branching are mostly inversely related. This fact has also been noticed by DI AMATO (1948), BOLL (1955), and ZIMMERMAN (1935), who were studying root growth. BURSTRØM (1950) mentions the observation that growth of laterals is impeded by accelerated elongation of the root.

Evidence on the role of auxins in regulating formation of lateral roots can be derived from experiments where varying auxin concentrations have been applied in the medium. BERTOSSI (1954), DELARGE (1946), FRIES (1951), PILET and WENT (1956), SLANKIS (1950), WILDE (1951) and ZIMMERMAN and HITCHCOCK (1935) have all noticed enhanced branching under the influence of applied auxin. TORREY (1950) and also GEISSBÜHLER (1953) mention that this effect may be dependent on the auxin level the root naturally contains. KANDLER (1950) draws attention to the fact that formation of primordia also is influenced.

It must be clear that auxins have a regulative activity on the process of root branching. But there are some other substances, which also have an influence. DELARGE (1946) draws attention to rhizocaline and FRIES (1951) to the influence of amino-acids. GEISSBÜHLER (1953) demonstrates the necessity of nicotinic acid. LEOPOLD (1955) mentions that formation of root primordia can only occur if sufficient IAA, thiamine, nicotinic acid and adenine are present.

As all the above mentioned substances are N-containing it could easily be conceived that enhanced N supply in the root medium would result in a higher level of these compounds in the root. The latter fact would then account for increased branching (BOSEMARK, 1954).

As some humic compounds (FLAIG and OTTO, 1951) and chelating agents (HEATH and CLARK, 1956) are recorded to have activities comparable to growth substances, part of the influence of humus might be explained in this manner.

KANDLER (1950) suggests that the growth substance induces increased respiration, and that this results in the formation of laterals.

If this may be true, the effect of phosphate can easily be understood as it is closely linked with respiration. Also it is well known that the presence of ions in the medium may generally enhance respiration, since LUNDEGÅRDH (1930) drew attention to the "Anionen Atmung". Recently, Epsteins results demonstrate that there may be a cation respiration as well. Thus we might have the sequence high ionic level → increased respiration → more laterals formed.

Thus, although it seems possible to suggest some intermediary links in the sequence of reactions leading to increased formation of laterals under influence of higher activities of all or certain ions in the medium, further research will have to elucidate this.

SUMMARY

An experimental technique has been devised to investigate the possibility that the colloidal substances in the soil, such as humus and clay, might have some specific influence on density of branching of roots. Results were indeed obtained which demonstrate that in model experiments peat and clay stimulate the outgrowth of many laterals.

By using resinous ion exchangers it has been possible to investigate the effect of a single ion on root branching. Complementary experiments, in which the influence of nutrient solutions deficient in one element, were tested, were also performed. The techniques used have been described. It could be demonstrated that the sequence of activity is $NO_3^- > H_2PO_4^-$, $K^+ > Ca^{++}$, $Mg^{++} > SO_4^{--}$.

These results were obtained with peas. N-deficient solutions have the opposite result as NO_3 alone. Indications were obtained that a deficiency in P may result in effects comparable to those of high N.

The effect of peat and clay in these experiments is ascribed to the high ionic concentrations of the adsorbed ions. This explanation of our results seems justified by comparing the effects of an anion exchange resin with that of a cation exchange resin.

A discussion of the results is given.

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