A CONTRIBUTION TO THE KNOWLEDGE OF THE IMPORTANCE OF SODIUM FOR PLANT LIFE

INVESTIGATIONS WITH RADIOACTIVE SODIUM

BY

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Dit proefschrift met stellingen van

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6 november 1918, is goedgekeurd door de promotor,
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De Rector Magnificus der Landbouwhogeschool,
W.DE JONG

Wageningen, 24 januari 1957.

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PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR IN DE LANDBOUWKUNDE OP GEZAG VAN DE RECTOR MAGNIFICUS Ir. W. DE JONG, HOOGLERAAR IN DE VEETEELTWETENSCHAP, TE VERDEDIGEN TEGEN DE BEDENKINGEN VAN EEN COMMISSIE UIT DE SENAAT DER LANDBOUWHOGESCHOOL TE WAGENINGEN OP VRIJDAG 1 MAART 1957 TE 16 UUR

DOOR

J. M. WYBENGA

KANTOORDRUK DE GOEDE - WAGENINGEN

STELLINGEN

I

Voor het vervaardigen van makro-autoradiogrammen van planten of van plantendelen moet van snel, onder druk gedroogd, materiaal worden uitgegaan.

II

De in de plant aanwezige metaalionen worden niet alle even gemakkelijk tegen overeenkomstige nieuw opgenomen metaalionen omgewisseld.

III

Het valt te betwijfelen, of uit experimenten met afgesneden wortels een juist beeld van de ionenopname verkregen kan worden.

IV

De opneembaarheid van de voedingsionen moet gezien worden tegen de achtergrond van de dynamische processen in een bodemprofiel.

V

Zowel de bodem- als de landklassifikatie houden nog te weinig rekening met de kultuurtoestand van de grond.

VI

Voor een goede vruchtzetting bij *Arachis hypogaea* is het noodzakelijk, dat de gynofoor het benodigde calcium rechtstreeks uit de bodem opneemt, maar dit houdt geenszins in, dat dit eveneens het geval moet zijn met fosfor en kalium.

VII

Het is niet waarschijnlijk, dat de verhoogde latexproductie bij *Hevea braziliënsis*, tengevolge van de aanwending van stimulantia, veroorzaakt wordt door een uitbreiding van het bij de vloei betrokken bastareaal, maar deze moet vermoedelijk verklaard worden door een wijziging in het vermogen om assimilaten te mobiliseren.

VIII

Het optreden van gen mutaties en van breuken in de chromosomen moet meer worden toegeschreven aan de indirekte-, dan aan de direkte werking van de gebruikte ionizerende straling.

IX

De opvatting, dat natriumionen door de grassen moeilijk worden opgenomen, is in het algemeen niet juist.

AAN MIJN OUDERS

AAN MIJN VROUW

PREFACE (VOORWOORD)

Het verschijnen van dit proefschrift biedt mij de gelegenheid mijn dank te betuigen aan allen, die tot mijn wetenschappelijke vorming hebben bijgedragen.

Dit geldt in het bijzonder U, Hooggeleerde SCHUFFELEN, Hooggeachte promotor. Voor het feit, dat U het mij mogelijk hebt gemaakt te promoveren op een onderwerp, dat onder Uw leiding, maar niet op Uw laboratorium werd bewerkt, ben ik U zeer erkentelijk. Uw hulp bij het stellen van de problemen, Uw kritische zin bij het beoordelen van de resultaten en Uw onvermoeibare toewijding hebben zeer veel bijgedragen tot het totstandkomen van dit proefschrift. Met dankbare herinnering denk ik terug aan de prettige samenwerking en de persoonlijke gesprekken.

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Zeergeleerde LEHR, door Uw consciëntieus onderzoek werd de grondslag gelegd voor de thans verschenen studie. U hebt mij in staat gesteld dit onderzoek op het onder Uw leiding staande laboratorium, in volledige vrijheid en geheel naar eigen inzichten, uit te voeren. De prettige sfeer, Uw belangstelling voor het onderhavige onderwerp, de opbouwende kritiek en het delen in de verantwoordelijkheid voor de gang van zaken, waren voor mij van bijzondere waarde. Voor Uw medewerking ben ik U zeer erkentelijk.

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Waarde BUSSINK, je grote praktische landbouwkundige kennis en je diepe belangstelling voor het wetenschappelijk onderzoek gaf aan onze samenwerking wel een zeer bijzonder aspekt.

Dear MR.SELWAY, your great care and trouble to execute the huge task of translating the present are beyond all praise.For the conscientiousness and persistency with which you did this,I want to express my great gratitude and thankfulness.

Voor de toewijding en de zeer gewaardeerde hulpvaardigheid, bij het verlenen van technische assistentie door onderscheiden leden van het huidige en vroegere personeel van het Laboratorium voor Bemestingsonderzoek, kan ik niet dankbaar genoeg zijn.

CONTENTS

CHAPTER I

INTRODUCTION

In the middle of the last century it was demonstrated that it is possible to apply inorganic substances to the nutrition of plants. The theory of the mineral nutrition of plants evolved by LIEBIG was rapidly introduced into practice.

About 1880, physiological investigations showed the elements carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, calcium, magnesium, potassium and iron to be indispensable for the proper nutrition of the plant. In practical fertilization use was especially made of nitrogen, phosphorus and potassium, and these elements became so widely applied that about 1950 the world consumption of N, P_2O_5 and K_2O for fertilizer purposes was 4,000,000, 5,600,000 and 4,000,000 tons respectively per annum (221). It later appeared that a number of other elements were also necessary for the proper development of crops, namely, copper, manganese, zinc, boron and molybdenum. These have come to be known as the trace elements.

Apart from the elements in the two groups mentioned above, there are a number of others which, while stimulating growth, have not yet been definitely established as being essential for plant development. To these Cl^- probably belongs, BROYER *et al.*(46) having demonstrated that deficiency symptoms appear in plants to which this element is not available.

Na^+ should also be considered as belonging to this class. It is known that this element is always present in crops and further that certain of these show improved development when sufficient sodium is made available to them. This effect of the sodium ion is often attributed to the fact that it is able to replace, in part, the potassium in the plant. This may be the reason for the fact that the bean (a crop which takes up little sodium) could be cultivated by fertilization with sodium nitrate without the appearance of potassium deficiency symptoms, whereas such symptoms did, in fact, appear when calcium nitrate was the fertilizer used (see plates Ns. 1 and 2).

The phenomenon of potassium replacement is however less evident in beet, a crop which shows great preference for sodium. Deficiency symptoms did not appear with high potash fertilization plus sodium nitrate or even without potash fertilization, but they were present

when calcium nitrate was the fertilizer used (see plates Nos. 3, 4 and 5). Here sodium obviously produces an independent effect.

Deficiency symptoms manifest themselves in cases of serious shortage. However, long before such symptoms become apparent it is clear that something is wrong in the plant. We found that, when leaves of apparently equally healthy fodder beet seedlings, some of which had been fertilized with sodium nitrate and some with calcium nitrate, were placed in 70% alcohol, a blackish discoloration developed in those which had been treated with calcium nitrate.

Relatively little scientific investigation into the importance of sodium for the plant has been carried out. Although numerous trials have established that the sodium ion is capable of increasing the yields of certain crops, very little is yet known about the functions fulfilled by this element in the plant. In the past a great deal of research has been carried out at the Plant Nutrition Research Laboratory, Wageningen (The Netherlands), into the practical and physiological effect of sodium upon plant life. The purpose of this research was to obtain information about the sodium requirements of various crops and to ascertain to which crops sodium fertilization could, with advantage, be applied.

Despite the fact that a certain degree of insight into the physiological significance of sodium was gained from the numerous observations made in the course of this research, the need was felt for a more fundamental investigation - physiological and biochemical - which could contribute still further to the knowledge of the role played by this element in the plant. To this end it was decided to apply the technique involving tracer elements. In the physiological investigation - which has been carried out under the sponsorship of Professor A. C. Schuffelen - described in the following pages, an attempt has been made to extend the knowledge of the importance of the sodium ion in the life of the plant. With the aid of radioactive sodium, a study has been carried out of the uptake, outgo, translocation and distribution of the sodium ion in oats.

SODIUM AS A PARTIAL SUBSTITUTE FOR POTASSIUM

FRENCH BEAN LEAVES FROM AN EXPERIMENTAL FIELD WITH A LOW POTASSIUM LEVEL

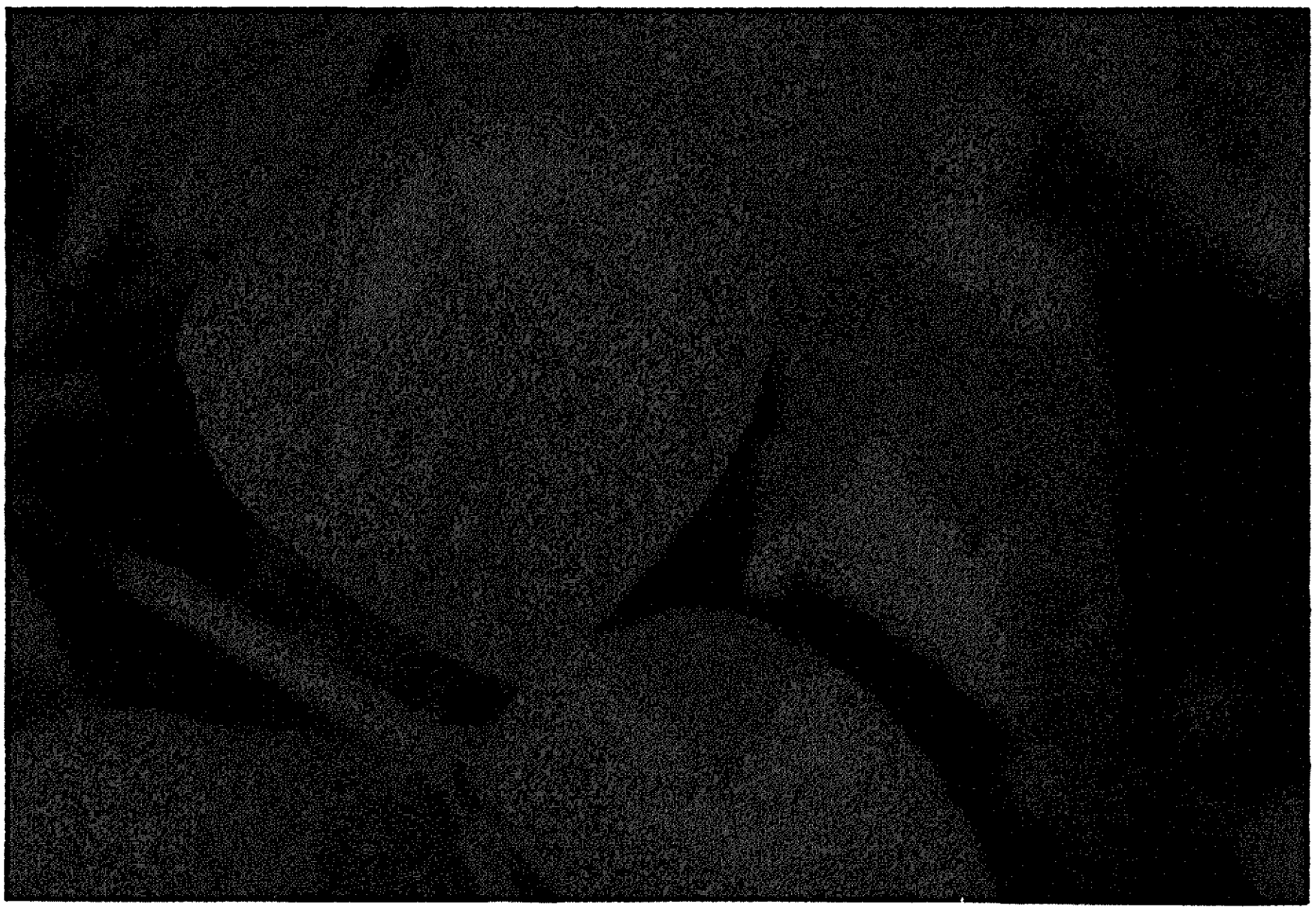

Plate 1. Treatment: Chilean nitrate of soda without potash. Healthy leaves

Plate 2. Treatment: nitrate of lime without potash. Leaves seriously deficient in potassium

INDEPENDENT EFFECT OF SODIUM ON PLANTS

FODDER BEET LEAVES FROM AN EXPERIMENTAL FIELD WITH A NORMAL POTASSIUM LEVEL

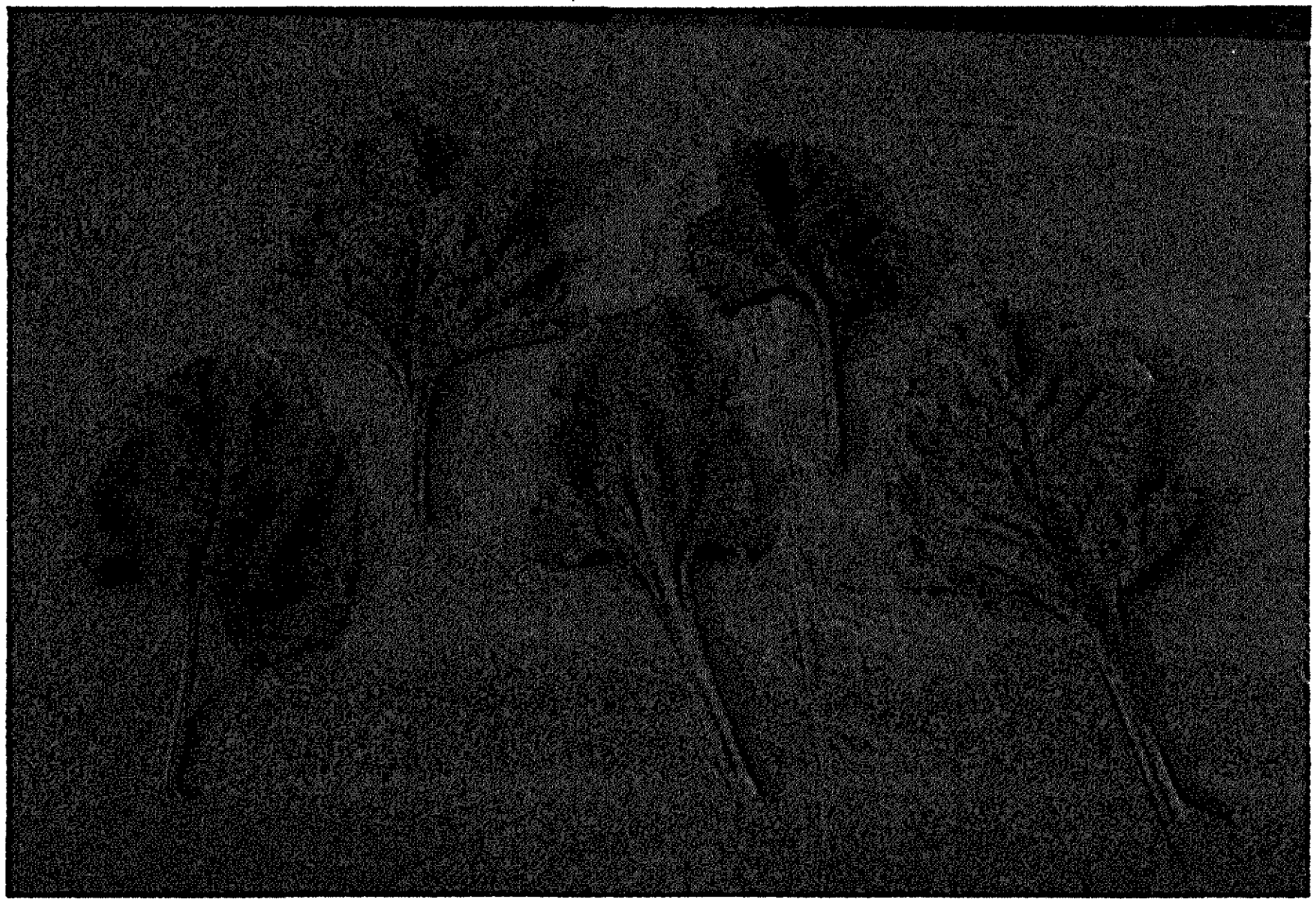

Plate 4. Treatment: Chilean nitrate of soda and 450 kg K_2O per hectare. Healthy leaves

INDEPENDENT EFFECT OF SODIUM ON PLANTS

FODDER BEET LEAVES FROM AN EXPERIMENTAL FIELD WITH A NORMAL POTASSIUM LEVEL

Plate 5. Treatment: Chilean nitrate of soda without potash. Healthy leaves

CHAPTER II

THE IMPORTANCE OF THE SODIUM ION IN PLANT NUTRITION

I. INTRODUCTION

As early as the beginning of the 18th century DUHAMEL DE MONCEAU (67) named sodium as a component of certain plants growing along seashores, but it was not for another hundred years or more that the first investigations into the importance of sodium for the development of plants were carried out, after LIEBIG had put forward the theory that such elements as sodium, magnesium, potassium and calcium fulfilled functions in the life of the plant. About this time also BOUSSINGAULT (33) observed: "On ne saurait douter de l'efficacité de la potasse et de la soude sur la végétation".

About 1860, the first fertilization experiments with sodium salts were commenced in Germany (27, 295); in England, the well-known fertilization experiments were laid down at Rothamsted in 1852, and in 1882 the now classic experiments with Chilean nitrate were started by the American experimental station, Rhode Island (290). Then followed a relatively large number of incidental investigations carried out at the end of the 19th and the beginning of the 20th century until, about 1940, the attention of investigators was being drawn to an ever increasing extent to sodium as a plant nutrient (26, 159, 243).

In the early stages of this "sodium - investigation" serious difficulties were encountered with regard to methods of chemical analysis for the determination of sodium and, indeed, for a long time such determinations were made in an indirect way. The indirect method was too inaccurate, however, to enable the quantitative determination of minute amounts of sodium in plants. Later, by means of the uranyl acetate method BERTRAND and co-workers (21, 22, 23, 24, 25) succeeded in studying the sodium contents of numerous different plants and parts of plants. Sodium is found, without exception, in all plants; in the different species, however, the sodium contents range widely from a few milligrams to 2 to 3 grams per 100 grams dry matter. Similarly, a considerable number of wild and cultivated plants were examined for their sodium content by American investigators (281), with the aid of the flame photometer. They discovered that the sodium content in the dry matter ranged from 0.00 to 3%. In view of the fact that this method has an accuracy of about 0.001 gram sodium per 10 grams dry matter and the available sampling material was often even less than 10 grams, it cannot be concluded from their investigations that sodium was completely absent.

BERTRAND's conclusion that all plants contain sodium would therefore appear to be correct.

By far the larger part of investigations with sodium salts has been directed towards the establishment of the agricultural importance of the sodium ion. To date, little attention has been given to

physiological investigation for the purpose of ascertaining the influence of sodium ions upon the plant's vital processes. In general, the agricultural investigation may be divided in three loosely defined parts, which may be characterized by the following questions:

1. What influence is exercised by the sodium ion upon soil?
2. What influence is exercised by the sodium ion upon the uptake of nutrient substances by the plant?
3. To what extent does the sodium ion influence the development of the plant?

The scope of the present work is not wide enough to allow all the various aspects of the sodium investigations to be discussed. We must be content therefore with summing up certain of the problems connected with sodium fertilization.

II. THE INFLUENCE OF THE APPLICATION OF SODIUM-CONTAINING FERTILIZERS UPON THE AVAILABILITY OF POTASSIUM IONS

Immediately following the fertilization of a soil with sodium, the ions of this element bring about a change in the ion equilibrium of the soil. Part of the sodium becomes adsorbed by the soil colloid and other ions are simultaneously exchanged. Another part remains in the soil solution. The more strongly an ion becomes adsorbed by a certain soil colloid, the less easily is it exchanged by other ions. The strength of the adsorptive bond with the soil colloid is dependent upon the kind of ion (37, 86, 212), the type of colloid (212) and the position taken up by the ion in the colloid (185). The order of affinity of the cations varies according to the type of soil and is dependent upon the type of clay mineral. It has been found that the order of strength of adsorptive bond for certain clay minerals is:

Beidellite	Li < Na < K < Mg < Ca < H	(86)
Montmorillonite	Li < Na < K < H < Mg < Ca	(212)
Kaolinite	Li < Na < K < Mg – Ca	(212)
Muscovite	Li < Na < Mg < Ca < K < H	(212)

With the exception of Li, the sodium ion has the least affinity; thus adsorbed K, Ca, Mg and H ions are not easily exchanged by sodium. On the principle of the complementary ion effect (as developed by JENNY and AYERS (121), according to whom the exchangeability and and hence the availability of an ion is greater, the greater the strength of adsorption of the other complementary ions) it follows that when the complementary ion is calcium the exchangeability of potassium is greater than when the more weakly adsorbed sodium is the complementary ion (120, 121). It may therefore be accepted that, in comparison with other ions, sodium ions applied in the fertilizer can play only a secondary role in making potassium ions available (78, 224, 225). For this reason, as has been stressed many times in the past (170, 188, 195, 217, 248), the favourable influence of sodium ions upon the development of various plants cannot be ascribed without further proof solely to an increase in the availability

of potassium ions. Were this the case, plants such as buckwheat and corn (102) which react strongly to potassium fertilization would react noticeably to the application of sodium when insufficient potassium is available. This, however, has not been established (35).

From the point of view of ion exchange and ion activity it might even be expected that sodium as complementary ion would strongly suppress the availability of other exchangeable ions. However, because of the considerable variation in the ability of different plants to absorb sodium under identical conditions of cultivation (35, 52, 100), the complementary ion effect is nullified (15). Although, in general, sodium tends to reduce rather than to increase potassium uptake (99, 103, 116, 206), circumstances can arise to cause sodium to stimulate the absorption of potassium (53, 100, 103, 157, 281).

The effect of a certain ion upon the absorption of another is, however, a matter in which the specific properties of the root play a very important role. It has been found (189, 272) that when the concentration of sodium is high in comparison with that of potassium, or when the potassium concentration is high and the ratio of calcium to potassium is low, calcium is able to increase the potassium absorption. In such a case, the influence of sodium is dependent upon the calcium concentration. But there is still another reason in terms of which the increase in potassium content under the influence of sodium fertilization can be explained. It appears that plants fertilized with sodium sometimes develop very extended root systems (53) which thus enable more potassium to be taken up (220). This phenomenon is observed in crops, such as alfalfa, which take up little sodium (53, 132, 282, 297).

The effect of the sodium dosage upon the potassium content appears to be dependent upon the type of plant concerned, upon the available amounts of sodium and potassium and upon the ratio of calcium to potassium in the soil.

III. THE INFLUENCE OF SODIUM IONS UPON THE AVAILABILITY OF PHOSPHATE

Among the numerous publications dealing with the solubility of phosphate in the soil and its availability to the plant (168, 287, 289, 293) various investigations will be found in which the sodium ion has played its part. The somewhat inconsistent and even contradictory experimental results obtained necessitate the arrangement of these investigations in accordance with the way in which the solubility and availability of the phosphate was measured. In certain cases the mobility of the phosphate was determined from the reaction of the plant including such factors as the development, the phosphate extraction and the phosphate contents of the plant. GRAČANIN (89), who carried out pot experiments with rye in soils of various degrees of acidity but all poor in water-soluble phosphate, found that the uptake of phosphate was increased by sodium nitrate. COLBY (51), using French Prune trees in water cultures, established that a large phosphate absorption was characteristic for trees which

were liberally treated with sodium salts.

Similarly, METZGER (165) found that a more complete utilization of phosphate by alfalfa occurred when both sodium nitrate and superphosphate were applied than when only superphosphate was applied. From the extensive pot and field experiments carried out by THUN (258) it appeared that the effect of sodium nitrate fertilization upon the development of various crops in various soils and under different conditions was not, in all cases, identical. The influence of sodium nitrate, as compared with that of calcium nitrate, was most pronounced when no phosphate fertilization was given.

It was found by THORNE (256, 257) that the phosphate content of the plant increased with increasing sodium level of the clay minerals. In the case of mangolds (284) it appeared that phosphate fertilization was more effective when sodium was also present. The same observations were made by SEMERGEI (236) who used cotton as the experimental crop. On the other hand it was found by HARMER and BENNE (99) using celery and sugar beet, and by SCHARRER and SCHROPP (215) using maize, winter rape and soya beans, that the application of sodium chloride had only a small effect upon the phosphate content. From the experiments of SCHARRER and SCHREIBER (213) it was found that sodium chloride applied to moderately light and heavy soils suppressed the phosphate uptake. VOLK (273) found that, in the case of oats and soya bean, the uptake of phosphate was scarcely influenced by sodium nitrate.

In pot experiments with winter oats (117a) it was found that in acid soils better results were obtained with ammonium sulphate and superphosphate than with sodium nitrate and superphosphate. The favourable effect of ammonium sulphate and superphosphate has been established in pot experiments on various occasions (62, 194, 244), but this effect has not been confirmed by field experiments (244). Only a very slight increase in yield was obtained in field experiments in which sugar beet was given sodium nitrate with no phosphate dressing. Using phosphate dressing in the form of phosphorite together with sodium nitrate a very much greater increase was obtained than with ammonium sulphate and phosphorite. In field experiments the combination of sodium nitrate and basic slag or superphosphate gave better results than ammonium sulphate with basic slag or superphosphate.

It appears from the above that the effect of sodium on the availability of phosphate is variable. This is, however, not surprising in view of the great differences between the experimental conditions, the application of various sodium salts and the fact that plants were used whose reactions to the sodium ion differ widely.

The measurement of the availability of phosphate from the plant itself raises the question whether sodium chiefly influences the physiological availability (the ability of the plant to assimilate soluble phosphates) or whether it increases the solubility of the soil phosphate. In this respect, the results of the investigation by PARKER and THORNE (187) are extremely interesting. They studied the mobility of water-soluble phosphate from suspensions of sodium and calcium bentonite clay and the permeability of the roots of

bean and tomato plants to phosphate throughout a pH range from 4 to 9. They discovered that the physiological availability of phosphate is a function of the pH. This is in agreement with the theory of VAN DEN HONERT (117) who suggested that only the primary phosphate ion was taken up by the plant. The permeability of the root to phosphate underwent no change in the pH range from 4 to 7, but on raising the pH to 8 a small reduction in permeability was brought about. Above a pH value of 8, the permeability of the root to phosphate was found to fall sharply. For the physiological availability of phosphate only the alkaline pH range is of importance, especially that between 8 and 9. From this it may be concluded that changes in the physiological availability of phosphate are of no importance in the majority of culture soils. The influence of sodium ions is, therefore, greater upon the uptake of the phosphate ions than upon their possible physiological effect.

In other investigations, the measurement of the solubility of the phosphate is carried out using water or acids of various strengths as extraction agent.

SCHULOW (223) states that ammonium sulphate exercises a stronger dissolving influence upon phosphorite than sodium nitrate does. In percolation experiments with these salts in a weakly acid subsoil BROWN (45) found that practically no increase in the penetration of the phosphate occurs. According to SEMUSHKIN (237) sodium carbonate increases the solubility of phosphates more than does calcium carbonate. Sodium chloride, sodium nitrate and ammonium salts caused the water solubility of calcium phosphate to increase (146).

It was observed by MIDGLEY (167) that in a weakly acid silt loam the penetration of superphosphate is strongly suppressed by calcium hydroxide and lightly suppressed by potassium sulphate and ammonium sulphate but increases considerably in the presence of sodium nitrate. DYER (68) found that the penetration of superphosphate was favoured by potassium sulphate and sodium sulphate.

The nature of the anion also appears to influence the solubility of phosphate. The solubility of rock and soil phosphate was found to be increased more by $NaNO_3$ and K_2SO_4 than by KCl and NaCl (90).

Another investigation (288), however, gave indications that the effect of sulphates is less pronounced than that of chlorides and nitrates. The solubility of the phosphates appears to be much higher in soils where sodium predominates than in those where calcium holds sway (82, 160, 187, 197, 247, 256, 294). RAVIKOVITCH (198) found the following order for the effect of cations upon the availability of adsorbed phosphate:

$$Na > K > NH_4 > H > Mg > Ca.$$

This phenomenon is also described by LEHR and VAN WESEMAEL (140). They demonstrated that the points of difference which are to be found in the literature in connection with the influence of neutral salts upon phosphate availability in soils are attributable to the fact that the behaviour of phosphates varies according to whether or not soil is included in the system. In a system containing no soil, neutral salts of univalent cations generally promote phosphate solu-

bility. On the other hand, in a system containing soil, reduction in phosphate solubility is practically always caused by salts of both univalent and bivalent cations, the degree of reduction increasing in the order of the lyotropic series. They attribute this influence, in the case of soils of the temperate zones, to the liberation of calcium ions from the adsorption complex. Sulphate, however, has a stabilizing effect upon phosphate solubility and this is held to be due to the suppression of the concentration of calcium ions on account of transgression of the solubility product of $CaSO_4$. The experiments of LEWIS (145) indicated that the availability of soil and fertilizer phosphate was increased by application of sodium ions, whilst administration of calcium ions caused a stronger phosphate fixation to occur. In laboratory experiments HEBERT (109) found that both in calcium-rich and calcium-poor soils more phosphate was liberated by sodium nitrate than by calcium nitrate.

After discussing the extensive long-term experiments carried out by various American experimental stations, FRANKLIN (79) comes to the conclusion that sodium ions promote the solubility of phosphate. In his opinion this is brought about by a reduction in the degree of acidity of the soil and also by the direct influence of the sodium ion itself.

The fact that, apart from an increase of pH caused by sodium salts, the sodium sometimes exercises a direct influence upon the availability of phosphate was also demonstrated by PARKER and THORNE (187) and by RAVIKOVITCH (198).

From the foregoing it is clear that many investigators have found that the sodium ion favourably influences the solubility of phosphate.

In view of the numerous factors which can influence the availability of phosphate (168, 293) and the widely differing experimental conditions used in the various investigations, it is scarcely surprising that the results relative to the degree to which sodium can affect the solubility of phosphate also differ greatly. In general, it can be said that, of the neutral salts, those of sodium least suppress the solubility of phosphate (140, 162, 163, 288). Moreover, apart from the phosphate-dissolving effect brought about in certain cases by sodium salts through the increase in pH, the sodium ion itself exercises a favourable influence upon the availability of phosphate (78, 79, 187, 198). As a result, not only the solubility but also the mobility and thus the availability of the phosphate will increase. The effects peculiar to the sodium ion itself may be regarded as a phosphate-dissolving influence which is dependent upon the pH (187), and an ability to mobilize phosphate through the agency of the sodium humate which forms in the soil (78). A third possibility was voiced by ANDREWS (6). In the purification of water, tricalcium phosphate is used to precipitate fluorine (147), causing the formation of calcium fluorphosphate. With the aid of a dilute soda solution it is possible to separate out the fluorine again from the calcium fluorphosphate. As practically all soils contain fluor (168), ANDREWS considers it possible that the

sodium of the nitrate of soda in the fertilizer zone can prevent the formation of fluorphosphate.

IV. THE IMPORTANCE OF SODIUM IONS FOR THE STRUCTURE AND HABIT OF THE PLANT

From investigations into the cause of the lodging of cereals and into the factors which influence the structure of fibre crops (20, 141, 172, 182, 263), it has been clearly established that mineral nutrient substances affect the structure of the plant. The effect of the nutrient ion is dependent not only upon the type of plant and upon the nature of the ion itself but also, and to as great an extent, upon the rate, chemical form, time and method in which application of the element is made (148). Moreover, studies of the ontogeny of plants have also shown that mineral nutrition has an effect. In summarizing this, LOEHWING (148) states that "although mineral nutrients are not the initial and primary causes of tissue differentiation or inception of reproductive processes, they are often controlling in the implementation of the plants' developmental potentialities".

The element potassium has been used in many investigations in connection with the sturdiness of the stalk and the formation of fibres (1, 2, 5,169, 218, 254, 261, 262,268, 292). Potassium appears to promote the rigidity of the stalk and the formation of fibres. The influence of sodium in this respect has been the subject of very few investigations, but here and there in the literature reference is found to a few experiments designed to investigate the effect of this element upon plant structure. Moreover, other references are found to investigations into the structural influence of potassium in which sodium has been applied with the dressing.

In this laboratory* LEHR's observation (134) has established on many occasions that the influence of sodium finds expression in the habit of the plant. Thus with sugar and fodder beet, for instance, it is possible to differentiate between a "calcium type is and a "sodium type" (134, 139). The calcium type is "thick-set" in appearance and has stiff, upright leaf-stalks and more slender leaves, whereas the leaves of the sodium type are luxuriant, pliable and drooping. In general, plants dressed with sodium salts have bigger, broader and darker green leaves (49, 59).

In the case of flax a positive influence attributable to sodium was established, which was reflected in an improvement in quality and yield of the fibre (41).

NESZLER (176) found that by the application of sodium chloride to hemp a better, tougher and more pliable bark was obtained.

VERONA and TREGGI (271) and TREGGI (265) investigated the influence of sodium upon the anatomy of wheat and lupin. In these plants sodium was found to affect the formation of vascular and supporting tissues. HAYWARD and LONG (105) found, in the case of tomato, that with increasing concentrations of sodium chloride or sodium sulphate in the nutrient solutions, thicker cell walls of the mechanical tissues resulted.

* Plant Nutrition Laboratory, Wageningen, The Netherlands.

A deficiency of potassium results in the citrus fruits developing thick skins (71), and this appears also to be the case when these fruits are dressed with ammonium sulphate. Dressing with sodium nitrate, on the other hand, produced thin-skinned fruit (164). This difference is attributed by VAN DER MERWE (164) – not without some justification, presumably – to the difference in chemical form of the applied nitrogen. However, in view of the fact that sodium is known to influence the structure and habit of the plant and affects the development of citrus fruits (94), it is very probable – especially since sodium acts in the same way as potassium – that sodium contributed to the formation of thin-skinned fruits in the investigation of VAN DER MERWE. In earlier investigations with fibrous crops, in which much sodium was applied simultaneously with the potash dressing in the form of kainit, the influence of the potash dressing was unjustly ascribed entirely to the potassium ion (see compilation by LEHR and WYBENGA, 141).

From the results of investigations it may be generally concluded that sodium promotes development of the supporting tissues. The relationships of the mineral nutrients with photosynthesis, enzyme effect and other functions vital to the regulation of the growth and development cycle of the plant appear to be less intimate than that of the inorganic ions with the action of the phytohormones and other specifically morphogenetic compounds (144, 148). Since the minerals do not directly affect the reproductive processes but exercise their influence through the metabolism, they must necessarily take part in the metabolic process if they are to have an effect upon the tissue formation. In this way, sodium will also play a role in the metabolism of the plant.

V. THE INFLUENCE OF SODIUM IONS UPON THE WATER ECONOMY OF THE PLANT

The amount of water required by the plant is greater than that of other necessary nutrients. The majority of this water, however, is again taken from the plant by evaporation. The water balance of the plant is governed by the factors which control the water uptake through the roots, the water-holding capacity of the plant and the transpiration. The difference between the suction tension of the roots and of the soil which is partly determined by the salt concentration in the soil solution is of great importance for the water uptake.

As can be concluded from many investigations (69, 105, 106, 107, 149,154, 177, 207) the availability of water is strongly influenced by the osmotic forces, even in cases of low osmotic values of neutral salt solutions. An increase of the osmotic pressure of the soil solution goes hand-in-hand with a decrease in the physiological availability of water to the plant.

In conformity with this many investigators (83, 84, 153, 155, 177, 276, 277) attribute the toxicity of salts largely to osmotic effects.

'It appears from various investigations, including that of EATON (69) who used corn and tomato plants as experimental crops, that, if the water uptake is dependent solely upon the osmotic pressure of

the salt solution, the composition of isotonic salt solution could have practically no influence upon the water uptake.

On the other hand, it has appeared from other investigations (36, 63, 70, 108, 124, 177, 275) that, apart from osmotic pressure, the nature of the salt has, in fact, some influence upon the regulation of the water uptake. Dependent upon the concentration and the proportion of cations and anions in the nutrient solution, histological and physiological changes may occur in the plant (126, 132, 216, 265, 271). Dependent upon the nature of the plant, a given salt is able to influence the water and ion uptake more strongly than the osmotic pressure of the nutrient solution, as affected by that salt.

In this way, also, the influence of sodium upon the water uptake is explained by the changes which have taken place in the plant as a result of sodium absorption (49, 59, 144, 265, 271). But neither the effects of different sodium salts nor the effect of a specific sodium salt are identical for all plants (126).

The extensibility and the permeability of the protoplasm are influenced by sodium. By comparing various nitrates SEIFRIZ and PLOWE (235) found, in the case of epidermal cells of the onion *(Allium cepa)*, that the various cations were able to cause structural changes which altered the properties of the plasma. ($Ca^{++} > Sr^{++}$ promoted the elongation and $Na^{+} > Li^{+} > K^{+}$ decreased it).

1). The influence of sodium ions upon the permeability of the plant cell

The permeability of the plant cell varies with the age and position of the cell (43, 44, 191, 208, 209, 269) and is, moreover, influenced by various chemical and physical factors (123), namely, the *pH* (92, 234), temperature (92, 233), salts (114, 125, 217, 232, 233) and changes in metabolic activity.

It was found by SEEMAN (234), that the presence of salts results, in general, in an increase in permeability. The supposition that sodium and potassium change the permeability of the cell was confirmed by the investigations of GUTTENBERG and BEYTHEIN (91). Univalent cations such as Na^{+} and K^{+} pass the cytoplasmic membranes more easily than the bivalent and trivalent cations do.

The investigations with *Laminaria* carried out by OSTERHOUT (183) indicate that the ions $Li^{+} > Na^{+} > K^{+} > NH_4^{+} > Cs^{+} > Rb^{+}$ all promote permeability whilst Ca^{++}, Ba^{++}, Si^{++}, Mg^{++}, Fe^{++}, La^{++}, Fe^{+++} and Al^{+++}, in combination with the univalent anions, first suppress permeability and later increase it.

Similar effects upon the permeability of the cytoplasm of epidermal cells of onion bulb scales to water were found by DE HAAN (93).

In the investigation of RABER (196) on the influence of the anion upon permeability, various sodium salts all gave indications - though not in the same degree - of increased permeability. Dependent upon the anion, equimolar concentrations of various sodium salts stimulated the permeability in accordance with the lyotropic series, citrate > PO_4 > tartrate > SO_4 and acetate > Cl > NO_3 > Br > I. The polyvalent anions had more effect upon the permeability than the univalent anions had.

to the role of sodium in the nutrition of the plant. The present trend of development dates from about 1860 when sodium was described as a non-essential element but was recognized at the same time as being able to function in the place of potassium to some extent. In more recent times much material has been collected - and in this, the Plant Nutrition Research Laboratory, Wageningen, The Netherlands, has also made its contribution - from which it has appeared that the role of sodium is not confined solely to its ability to substitute for potassium but may, in fact, be regarded as independent and partly specific in nature. The development of ideas on this subject has been sketched by LEHR in a series of three lectures (138a), in which he traces the gradually increasing appreciation of sodium throughout its various stages. We are shown how, from the earliest conception of sodium as a 'make-weight' or ballast substance, then as a substituting element and, still later, as a stimulating element, the trend has moved steadily towards its recognition as an essential plant nutrient. Although this latter stage has not yet been reached, still more new facts have been revealed in recent years which strengthen the likelihood of sodium ultimately being recognized as having a specific function in plant life. In agricultural investigations, much consideration has been given to the possibility of potassium and sodium ions being mutually exchangeable in the plant.

In itself, there is nothing exceptional about the interchangeability of ions in living organisms.

It occurs also with the elements calcium and strontium (17), magnesium and beryllium (252), potassium and rubidium (202, 203).

In cases of potassium deficiency, three elements, namely, rubidium, sodium and lithium, appear to be capable of fulfilling the functions in the plant normally fulfilled by potassium. The accumulation of amino acids and amides, for instance, is prevented by these three elements in the same way as by a sufficiency of potassium (204). In plant nutrition sodium, however, plays a role different from that of rubidium or strontium.

In oats cultured in nutrient solutions containing equivalent amounts of potassium and sodium, the absorbed amounts of these elements are in the ratio of 20 : 1. When the sodium concentration is reduced 400 times, the amount of absorbed sodium is found to be reduced by only 33 times. With rubidium in the presence of potassium and with strontium in the presence of calcium, a reduction of the concentration of rubidium or strontium in the nutrient solution results in a proportionate reduction in the absorption of these elements (52). From this it appears that, in contrast with rubidium and strontium, sodium is selectively absorbed and therefore it has apparently still a physiological function other than that performed by potassium. This phenomenon has also been observed by other investigators (100, 184).

In all probability, one of the reasons why so much stress has been laid upon the interchangeability of potassium and sodium is the fact that, in their chemical properties, these elements are very similar.

Another logical reason is that it has appeared from many observations that a saving in potash fertilization can be achieved by the application of sodium-containing products (143). On the basis of results from investigations into the interchangeability of potassium and sodium, attempts have been made to classify crops in accordance with their reaction to sodium as influenced by the potassium supply (101, 132). In this connection reference is also made to the tentative scheme of classification of crops according to potassium-replacing power of sodium (138).

HARMER *et al.* specified four groups which enable crops to be classified as follows:

1). Little or no reaction to sodium in the case of insufficient potash supply. These crops include : buckwheat, corn, potato, spinach, white bean (101), tomato (178).
2). Slight to medium reaction to sodium in the case of insufficient potash supply. These crops include: alfalfa, asparagus, carrot, oats, tomato (101), cotton (130).
3). Slight to medium reaction to sodium in the case of ample potash supply. These crops include : cabbage, celeriac, pea, wheat (101), potato (133), cotton (54, 55, 158), oats (136, 137, 286), flax (132, 141), barley, Westerwolds ryegrass (136) and tomato (174).
4). Large reaction to sodium in the case of ample potash supply. These crops include : celery, mangold, sugar-beet, turnip (101), spinach (135).

Because the findings of different investigators are not always in agreement, the above classification has only limited significance. Differences in results may be attributed in part to differences in the external conditions under which the experiments were conducted and in part to the fact that considerable varietal differences in sensitivity to sodium can occur within a plant species (136). On comparison of the classification of plants grouped according to their sensitivity to sodium (101) with the classification according to their sensitivity to potassium as given by HARTWELL (102), it will be found that plants which react strongly and less markedly to sodium are placed in plant-groups which react strongly, moderately and slightly to potassium. Favourable effects from both potassium and sodium do not, therefore, necessarily go together. This means that the reaction to sodium cannot always be considered as being dependent on the reaction to potassium: this can be seen most clearly with plants which display a slight reaction to potassium and a marked reaction to sodium (e.g., oats). It is therefore very probable that the sodium ion exercises an influence of its own which is independent of the potassium-replacing effect. The similarity existing between these two ions has, most probably, led to the conception of the replacement of potassium by sodium and this has, in turn, led to the differences between them being lost sight of.

In this way it was too readily accepted that agreement also exists between the functions which each element fulfils in the plant and

between the way in which they combine - temporarily or permanently - with the substances present in the plant cell.

TABLE 1

	Radius hydrated Ion A^0	Radius crystal A^0	Molar refraction gas, c.c.,	Ionic potential charge/radius	Dissociation constant polyphosphate
K^+	1.98	1.33	2.25	0.75	0.50
Na^+	2.56	0.96	0.47	1.00	0.05

From the above table - based upon data given by STEINBACH (249)- it can clearly be seen that considerable differences exist between the sodium ion and the potassium ion. In respect of rate of diffusion, the measurement of the hydrated ion is, of course, important and the sodium ion will diffuse less rapidly than the potassium ion. The tendency to form tight complexes with large anionic material is dependent upon the ionic potential, being increased as this potential increases (74). Since the ionic potential of sodium is greater than that of potassium the former element forms complexes better than the latter. This can also be deduced from the differences between the dissociation constants of polyphosphate complexes of sodium and potassium (74, 285).

The conclusions which certain investigators (175, 280, 296) have drawn from their experiments relative to the replaceability of potassium by sodium have not, in all cases, been correct. For instance, MULLISON and MULLISON (175) interpreted the results of their investigation with barley as follows : 'Sodium itself is utilized in place of the potassium when the latter is present in insufficient amounts'. The experimental results, however, did not justify this conclusion. In their investigations, nutrient solutions were used containing ascending amounts of potassium (from 0 to 180 p.p.m.) and descending amounts of sodium (from 180 to 0 p.p.m.), in such a way that a total of 180 p.p.m. sodium plus potassium was present in each nutrient solution.

Thus, the actual amount of sodium present was greater in the lower potash levels than in the higher potash levels. The highest yields were obtained from potassium concentrations of 20 to 60 p.p.m. with sodium concentrations of 160 to 120 p.p.m. while, when no sodium was present (the experiment was also carried out with the same potash levels but with no addition of sodium), the yields were lower at all potash levels. There appears to be no justification, therefore, to assume that, in the case in question, sodium acts solely as a 'potash replacer'. On the contrary, it might be assumed much more readily that the sodium, as such, played an active role in increasing the yields. WOLFF (296) is of the opinion that an equivalent replacement of sodium by potassium in the plant can-

not be considered a possibility, but he observed from his experiments (which cannot be regarded as very reliable) that equivalent, part-exchange of potassium by sodium in the nutrient solution had a favourable, rather than unfavourable, influence upon the development of the plants. This was also found in experiments with tomatoes in sand cultures carried out by WALL (280), who based his investigation upon the conclusion of NIGHTINGALE *et al.*(178), that, in the case of tomato plants, sodium is unable to replace potassium.

Accordingly, in the discussion of the experimental results, this possibility was left entirely out of account. But considering the fact that the ash contents of the various groups of plants (tests were made on four groups of plants cultured in nutrient solutions containing sodium and potassium in ratios of 0 : 351; 104 : 176; 181 : 44 and 207 : 0 p.p.m. respectively) were practically identical, the replacement of potassium by sodium is actually mentioned as the possible cause. Plants cultured in a nutrient solution containing concentrations of 181 p.p.m. sodium and 44 p.p.m. potassium exhibited the best vegetative development. It would certainly not be misplaced here to assume that a replacement of potassium by sodium had occurred and even that the sodium had exercised an influence of its own.

The above-mentioned arguments strongly indicate that the sodium ion has a specific action, but give no answer to the question whether the sodium ion is essential for the plant.

The criteria which an element must satisfy in order to be regarded as essential for the plant have been formulated by ARNON and STOUT (13) as follows:

1) A deficiency of it makes it impossible for the plant to complete the vegetative or reproductive stage of its life cycle.
2) Such deficiency is specific to the element in question and can be prevented or corrected only by supplying this element.
3) The element is directly involved in the nutrition of the plant quite apart from its possible effects in correcting some unfavourable microbiological or chemical condition of the soil or other culture medium.

According to PIRSON (190) the first criterion embraces not only the appearance of visually observable deficiency symptoms to which the lack of the essential element gives rise, but also requires, especially when none of these outward deficiency symptoms occur, that all biochemical and enzymological processes in the living subject, which are functions of this essential element, should be checked. The latter requirement is difficult to meet in the case of elements such as sodium, where the biochemical functions for which they are responsible are not known.

In order to create the specific deficiency symptoms it is advisable to start with a culture which is practically free from the element which it is desired to study in relation to its indispensability for the plant. It is desirable to chose as the experimental plant one which is known to have a relatively high requirement

of the element concerned. When an experiment designed in this way gives no positive results, it is still essential to be extremely careful in the interpretation of the result since, despite all precautions, it is never quite certain that the element in question was completely absent (13).

Especially in the case of elements such as sodium, which is present almost everywhere, not only is the preparation of a sodium-free nutrient solution far from simple, but great difficulties are also encountered in keeping such a solution, once prepared, free from sodium. It may be readily accepted that the possibility of the prepared solution still containing a relatively large amount of sodium - despite all efforts - is far from excluded. In addition, uptake of sodium from the air must be prevented in these experiments and that is also far from simple. That this latter is not a difficulty to be underrated came to light from the experiment with sugar-beet in water cultures carried out by VAN SCHREVEN (220), which was designed to study the replacement of potassium by sodium. It appeared later that the supposedly sodium-free experimental plants and cultures contained, in fact, considerable amounts of sodium. In this connection, it is interesting to note the remark by STEINBERG (251) to the effect that an element may not be considered as non-essential if it is present in the nutrient solution in concentrations greater than one part per thousand million.

It will be appreciated from the foregoing that to produce evidence that sodium is an essential element for the plant, it is, if not practically impossible, at least insuperably difficult to proceed in this way with the present-day technique. Moreover, the difficulties of proving sodium to be an essential element are increased by the possibility of partial interchanging of the elements sodium, potassium, calcium (122), rubidium and lithium. Chemical analysis of plant material has definitely established that sodium is always present in fairly large amounts in the organs of plants, and relatively large quantities are found in the roots even of those plants which appear to contain little sodium in their aerial parts when supplied with a sufficiency of the element (95, 163a). However, the fact that sodium (as also manganese (133)) in contrast with potassium, is found in such widely different amounts in different plants, is evidence that the essential requirement of the element can differ greatly between one plant and another. Although sodium has not been tested sufficiently (if at all) against the three criteria given above, the available data support the opinions of various investigators that sodium must, in fact, be considered as an essential element for the plant. On the one hand, plants receiving an amply supply of potash have been found to develop better when sodium is added to the substrate (11, 87, 99, 100, 116, 118, 134, 175, 211, 214, 220, 240, 253, 266, 279, 291) and on these grounds or in the light of the fact that sodium has no influence upon the

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movement of potassium within the plant (121), a function of its own is attributed to sodium.

On the other hand, a few investigators have observed sodium deficiency symptoms in beet which had received a sufficient supply of potash (95, 138, 205, 283).

This was described by WALLACE (283) as follows: 'Where sodium is in short supply for these plants (sugar-beet, mangolds and turnips) the leaves are dark green, rather dull, wilt rapidly in drought and may tend to grow out horizontally from crown of plant. Some marginal brown scorch may develop.'

With this observation the second criterion of ARNON and STOUT (13) is met. In connection with the third criterion laid down by these workers, it should be mentioned that it has not yet been demonstrated that the disappearance of deficiency symptoms has not been brought about by the correction of any unfavourable conditions which may have been present in the culture medium.

The problem of determining whether or not an element is essential can be approached from two directions. The direct way is based upon the ability or non-ability of the plant to develop without it; the other approach is to determine whether or not the element in question forms part of an essential component of the plant cell or is involved in a crucial biochemical reaction (13). Using the latter route, it then becomes necessary to establish a vital and irreplaceable function of the element and if this is successful that element may be said to be essential. If the element does, in fact, form part of an essential component of the cell, it must be present in the cell in a bound form. The conception that ion accumulation, selective absorption and ion translocation must be connected with specific bindings to cell substances has been put forward on various occasions (8, 9, 150, 151, 152, 184).

It is, in fact, known that certain cations are present in the cell in bound form. It was found with *Chlorella pyrenoidosa*, for instance, that the part of the magnesium which was present in strongly bound form in the cells was greater than that which was present in the chlorophyll (227). Calcium and pectic acid form calcium pectate in the middle lamella of the cell wall.

From investigations with radioactive isotopes it has appeared that, in contrast with the generally accepted ideas, potassium and sodium are also able to combine with cell substances. Which substances in the cell are actually involved is not known, however; research into this question is still rather limited.

In *Chlorella pyrenoidosa*, potassium is so strongly bound that it cannot be washed out with distilled water or with the chlorides of sodium, potassium or magnesium (227). OLSON (180, 181) found that in beech leaves, 30% of the total amount of potassium could be present in bound form and suggested that this potassium might be combined with proteins.

From investigations with *Escherichia coli* (56, 206) it was deduced that substances exist which have high affinity for potassium and low affinity for sodium. The potassium uptake of *Bacterium lactis*

aerogenes was considered by EDDY et al. (72) as a specific binding by active centres which are necessary for growth.

In research with animals (see the summaries of STEINBACH (249, 250)), selective bindings of potassium and sodium with cell substances are repeatedly being established. If potassium in bound state occurs in the plant it is justifiable to assume that sodium may also occur in this form (see Table 1). Moreover, in inorganic literature, at least one compound is known (empirical formula $K_2Na(PO_3)_3$) which selectively and preferentially combines with sodium rather than potassium (129, 156). This compound is undoubtedly related to the polyphosphates important in biology. The observations on *Ulva lactuca* to test the applicability of the postulated role of glycolysis in cation regulation reflect a largely ionized cellular potassium and a partially bound sodium (228, 229).

It was found by CARR and TOPOL (50) that, under alkaline conditions, casein is able to bind considerable amounts of sodium. In studies in connection with the source of energy necessary for the contraction of muscles, FLECKENSTEIN (76, 77) observed that sodium is usually bound in an outer envelope. HOLM-JENSEN *et al.* (115) found that sodium was strongly adsorbed in the cell wall. From investigations with air-dried plant tissues of alfalfa, McGEORGE (161) found that part of the sodium was soluble in water. According to BROOKS (42) it appears that potassium, sodium and other salts of alkaline metals act on some intermediates or enzymes by momentary or more lasting combination with them.

It is known from the investigations of SCHWEIGART (226) that sodium is able to reactivate amylases. Furthermore, REED and HAAS (200) found that the percentage of water-soluble sodium and phosphate in citrus leaves decreases as the leaves age. It appears therefore that, on several occasions, sodium compounds which are not soluble in water have been discovered. It was demonstrated by ALLEN and ARNON (4) that sodium is essential for the blue-green alga *Anabaena cylindrica* and that its sodium requirement is specific.

From the present author's investigations with radioactive sodium and oats, which are described in the following pages (Chapter VI), it also appeared that sodium in bound form is present in the plant and that this sodium is bound partly selectively and partly specifically. The latter cannot readily be replaced by other sodium ions. This signifies that sodium plays a role of its own in the plant. Whether this function of sodium is of great importance for the higher orders of plant life has not yet been demonstrated. It is to be expected, however, that when a certain element has a specific function in the living organism, that element is also of importance for the existence of higher organisms. There is, therefore, every reason to subject the role played by sodium in the existence of higher orders of plant life to further research.

From this review of the literature relevant to sodium, the following conclusions may be drawn:

1) Sodium is selectively absorbed by the plant;

2) Specific sodium deficiency symptoms are observable in the plant;
3) Given optimal potash supply and insufficient sodium, certain plants develop less satisfactorily than when sufficient sodium is available;
4) Sodium is present in the plant partly in bound form.

CHAPTER III

THE METHOD OF INVESTIGATION

I. INTRODUCTION

For the experiments described in the following pages, use was made both of water cultures (Chapters V and VI) and of dusarite-silica sand mixtures (Chapter VII).

The water cultures were employed for experiments of relatively short duration (ca. 4 weeks) and the dusarite-silica sand mixtures as culture media for the experiments of longer duration.

II. WATER CULTURES

The plant material used for the water-culture experiments was obtained as follows:

Oat seed was sown in a seed box filled with silica sand which had been previously washed clean with tap-water, and the seed was then covered with a thin layer (<2 cm.) of the same material. As soon as the plants had attained a height of 9 cm. (after ca. 12 days) they were lifted from the sand and the roots were rinsed with extreme thoroughness, first with tap-water and then with demineralized water (conductivity <6 x 10^4 m.h.o.). They were then transferred in the manner described below to enamelled cultivation trays (46 x 36 cm.) each of which contained 4 litres nutrient solution prepared in accordance with the formula of HOAGLAND and BROYER (113). Before transfer to the cultivation trays, the seedlings were first graded according to height development; this made it possible to employ experimental plants which were, as nearly as possible, all equally developed.

Flat, paraffin-waxed corks (diameter 4.5 cm.) each bored with seven holes (diameter 0.9 cm.) were taken. Into each of these corks, six seedlings were transplanted and fixed with cotton in the usual manner. (The purpose of the seventh, centrally placed hole was to take the capillary tube by which the nutrient solution was aerated. During the three weeks' cultural period the nutrient solution was not aerated and, in order to obtain low-salt plants, it was also not renewed). The corks containing the seedlings were then placed in the culture trays containing the nutrient solution, 24 corks (144 seedlings) to a tray, and the cultural period commenced.

After the cultural period the corks, together with the plants, were transferred to 200 c.c. experimental pots (diameter 5.5cm.),

(KNO_3, 0.0025 M; $Ca(NO_3)_2$, 0.0025 M; $MgSO_4$, 0.001 M; KH_2PO_4, 0,0005 M). The iron tartrate used by Hoagland and Broyer was replaced by a single application of 7 p.p.m. ferric potassium ethylene diamine tetra-acetate (119) per litre nutrient solution. The advantage attaching to the use of this iron compound is that the iron remains in solution in the nutrient solution over a wide pH range.

the roots having first been thoroughly rinsed with demineralized water. The plants from the remaining corks were harvested.

Dependent upon the experiment, the experimental pots were filled with 150 c.c. of a nutrient solution containing 0.1, 2 or 4 m.e. Na in the form of sodium sulphate, and 0.05 m.e. $CaSO_4$ per litre. These solutions were aerated by means of a capillary tube 10 cm. in length and 0.1 mm. in internal diameter. The air, at 0.5 atmosphere overpressure, was passed through a reservoir containing water and glass-wool and thence distributed over the pots. The rate of aeration was approximately 12 cu. ft. per day for each pot.

After the experimental period the plants were taken from the corks, pot by pot, and the roots were thoroughly rinsed with demineralized water, squeezed out and dried for a few seconds between filter paper.

The culms* were separated from the roots, and the fresh and dry weights of the parts were determined.

III. DUSARITE-SILICA SAND CULTURES

For these experiments, use was made of glass cylinders (diameter 12.5 cm.; height 25 cm.; volume 2.5 l. (222)), filled with a mixture of 2.4 kg. silica sand and 100 g. dusarite.**

To these dusarite-silica sand mixtures the phosphate in dry form, and the other fertilizers in solution, were added whilst continually mixing with the hand. Finally an amount of demineralized water was added, such that, together with the water of the fertilizer solution, the mixtures were at 40% of their water-holding capacity. The cylinders were filled with these substrates, which were then covered with a 3 cm. thick germination layer of damp pure silica sand (moisture content equivalent to 40% of the water-holding capacity).

In this germination layer 18 oat seeds were embedded uniformly over the surface area. After germination and when the seedlings had attained a height of about 9 cm., they were thinned out to leave 12 per cylinder. By gradually adding demineralized water, the media were brought up to 60% of their water-holding capacity. To reduce evaporation from the culture medium, the germination layer was covered to a depth of 1 cm. (ca. 200g.) with silex (French quartz). To compensate for evaporation as determined by weighing, the cylinders were replenished with demineralized water twice a day. To compensate for the increasing weight of the plants increases in the rate of water supply were made three times during the experiment. Water was added to the pots by means of a glass tube (diameter 37 mm.) with 5 outlet vents at its lower end which was placed in the

* The term culm denotes stem plus leaves

** Dusarite is an activated char coal, which is used as cation exchanger. It has an adsorption capacity of ca. 2 m.e. per g. at a pH of 6.5. The 100 g. dusarite was added to the sand as Ca, K, Mg and Na dusarite in amounts which were dependent upon the experimental design. The dusarite mixtures were brought to a pH of 6.2 with hydrogen dusarite.

centre of the cylinder 8 cm. below the surface of the substrate. The tube was filled to a height of 8 cm. (i.e., to the level of the surface of the substrate) with silica sand (222). The cylinders were borne on trollies which normally stood in the open air during the day but could easily be pushed into the greenhouse at night and during rainy weather. The position of the cylinders was changed daily in accordance with a constant rotation system. At the end of the cultural period the fresh and dry weights of the plants were determined.

IV. THE APPLICATION OF RADIOACTIVE SODIUM

The radioactive sodium, Na^{22}, was obtained through Philips Roxane from the Instituut voor Kernphysisch Onderzoek, Amsterdam, in the form of a solution of sodium nitrate. The amount required for each experiment was calculated and weighed out with a small known excess in a small weighing bottle.

The contents of the weighing bottle were then transferred to a flask. Before use with water cultures the radioactive sodium nitrate solution was diluted from 5μc.** per 1 c.c. to 1/40 μc. per 1 c.c. The amounts of radioactive sodium required for the pot experiments were pipetted from this diluted solution. After the nutrient salts had been pipetted into the pots, the contents of the latter were brought up to 150 c.c. with distilled water. A similar method of applying the radioactive sodium was also followed in the case of the dusarite-sand cultures. The radioactive sodium (1.5 μc. per pot) was given as top-dressing together with nitrogen.

In order to determine the radioactivity of the solution used, 1 c.c. is pipetted into a small aluminium dish (diameter 2.7 cm.; thickness of aluminium 0.01 cm.), and evaporated to dryness at room temperature. The radioactivity of the residue is then measured. The standard so obtained is used in the measuring of the radioactivity of the samples.

V. THE PREPARATION AND MEASUREMENT OF THE HARVESTED PLANT MATERIAL

After drying, the plant material was finely crushed in a mortar and then ashed in the muffle furnace for 2 hours at 500°C. Part of the ash was used for the flame-photometrical determination of sodium, the remainder for the determination of radioactivity.

1. The chemical determination

The sodium was determined in accordance with the method normally employed in this laboratory, using the Lange flame photometer:

2 c.c. 2*N*HCl was added to a specific amount of ash and the mass was then evaporated to dryness on a water bath. A few drops of

* Institute of Nuclear Physics.

** 1μc. is that amount of a radioactive element which disintegrates at the rate of 3.7×10^4 atoms per second. The radiation from 1.839×10^{-10} g. Na^{22} is equivalent to 1 μc.

concentrated HCl were then added and the ash was again evaporated to dryness on the water bath. This last-mentioned treatment was repeated once. Subsequently 1 c.c. 0.1*N* HCl was added and the mass was quantitatively transferred to a 50 c.c. flask which was then filled with distilled water and shaken. The whole was then filtered through coarse filter-paper into a 100 c.c. Erlenmeyer flask and 20 c.c. of the filtrate pipetted into a centrifuge tube. To the solution in the tube 200 c.c. of a 2% ammonium oxalate solution was added.

After being allowed to stand for 30 minutes this solution was centrifuged. After the calcium oxalate had been centrifuged off, the top liquid was poured into a flame-photometer tube and the sodium determined.

2. *The physical determination*

For the physical determination of the radioactivity of the ash, the method used was as follows:

20 mg. of the ash was weighed out and placed on a small aluminium dish (diameter 2.7 cm.; depth 0.2 cm.; thickness of aluminium 0.01 cm.). In order to prevent loss from scattering by air currents the ash was moistened with a drop of distilled water as soon as it had been weighed off. When a certain series had been thus treated, 1 c.c. distilled water was added to each dish. Using a needle, the contents of the dishes were carefully stirred in order to give the sodium the opportunity to dissolve in the water.

The solutions were then evaporated to dryness at room temperature. In this way, an even distribution of the ash over the bottoms of the dishes was obtained, while the sodium which was dissolved in the water settled on top of the ash during evaporation.

The advantage of commencing with equal amounts of ash is that the counts obtained can immediately be compared with each other. If the thickness of the layer of ash is increased by using any amount from 5 to 20 mg., no reduction in the number of counts per mg. ash occurs. Within this range of ash thicknesses, therefore, no absorption in the ash takes place and no correction factor need be used.

The samples made in this way were counted by means of the Philips G.M. 4810 three-decade electronic counter in conjunction with the P.W. 4020 high-voltage unit. The G.M. 18514 tube had a window (mica) thickness of 3.5 - 4.5 mg./cm.^{2}, an effective area of 6 cm.^{2}, a dead time of 240 μsec. and a background of 40 imp./min. (shielded).

The counting tube was enclosed by a 3-cm.-thick lead castle, which was also fitted out as sample carrier.

The distance between the bottom of the aluminium dish and the window was ca. 4 mm. Before making counts of the plant ash, the characteristic of the counting tube was determined with the aid of a matured U_3O_8 sample* . From this it appeared that, having regard

* This sample is obtained by the ashing of uranyl nitrate. 200 mg. U_3O_8 is placed in an aluminium dish and covered with liquid plastic as protection against moisture adsorption.

to the plateau of this characteristic, the most suitable operating voltage was 750 V. Since the results of the counts will be influenced by various factors connected with the apparatus and with the pre-treatment and arrangement of the sample, the possible influence of these factors upon the number of counts must first be ascertained. The main factors which can influence the results of the counts are as follows:

(1) Variations in the voltage of the tube,
(2) Background,
(3) Dead-time and recovery time of the tube and the resolving time of the counter,
(4) Varying efficiency of the counting tube,
(5) Thickness of the window,
(6) Area of the window,
(7) Temperature,
(8) Material of the sample carrier,
(9) Absorption losses in the sample,
(10) Sample geometry,
(11) Time at which measurements are made,
(12) Statistical errors.

In view of the facts that a constant arrangement and the middle voltage of the plateau was used, that all measurements were made with the same tube at room temperature, that the aluminium dishes used as sample carriers were identical and, finally, that a constant amount of ash, pre-treated as described above, was measured, the influence of factors (2), (3), (4), (11) and (12) only need be further considered:

(2) Background

As a result of cosmic radiation the counter registers a certain number of counts even when no radioactive material is deliberately brought into the vicinity. The count obtained from a sample includes this background count. Since the background is not constant but varies with the prevailing conditions from 35 to 45 c.p.m.* , its value is determined after each measurement and subtracted from the total count to obtain the true value for the sample.

(3) Dead-time and recovery time of the tube and resolving time of the counter

Upon penetrating the sensitive volume of the tube, the kinetic energy of an electron is increased as a result of the potential between the anode and cathode of the tube. After each collision with the gas molecules, part of the electron's energy is expended. When the electron approaches the wire (anode) stretched tautly through the centre of the tube, it enters a zone having a greater field strength and, as a result, its kinetic energy increases in the period between two consecutive collisions. At a critical distance from the anode, the electron, in the period between two consecutive col-

* c.p.m.: counts per minute.

lisions, acquires, for the first time, sufficient kinetic energy to cause the ionization of the gas atom with which it collides, this ionization resulting from the splitting off of an electron from the gas atom. Further collisions between these two electrons and gas atoms occur and give rise to still more electrons which all tend to move towards the anode, until the repetition of this process finally gives rise to an avalanche of electrons. At the same time, however, since each collision liberates a positive ion, the anode becomes surrounded by a mantle of positive ions. The space-charge of this mantle reduces the field strength to a value less than that required to give a new electron coming into the tube sufficient kinetic energy to cause ionization. From the moment the positive ion mantle is formed, the tube becomes insensitive for the new electrons which enter. The time which is necessary for the positive ions to diffuse sufficiently towards the cathode so that the voltage gradient at the anode is restored to the minimal value necessary for resumed ionization is a period during which no registration of electrons entering the tube can take place.

This is known as the dead-time. Additionally, a certain time is necessary for the voltage gradient to recover fully. This is the recovery time. Electrons entering the tube during the recovery time do, in fact, cause ionization but the impulse is weaker than normal. When the sensitivity of the apparatus is great enough and the time required by the amplifier to resolve an impulse - known as the resolving time - is short enough, impulses occurring during the recovery time are registered.

Since no registration of the electrons entering the tube during the dead-time took place and the radiation sources measured were of various strengths a correction for the dead time had to be made. The dead-time of the tube used in this investigation was 240 μsec. whilst the resolving time could be regulated from 50 to 500 μsec. For the relevant counts, an insensitive period of 300 μsec. was employed. Under 1,000 c.p.m., the correction factor is small enough to be neglected. For the determination of the correction factor, the following formula is applicable:

$$N_d = \frac{N_g}{1-TN_g}$$

in which T is the dead-time and N_g the number of c.p.m. measured.

(4) Varying efficiency of the counting tube

By the efficiency of the counter is understood the ratio of the number of registered particles - corrected for the dead time - to the number of particles actually entering the tube. The efficiency of a good tube is approximately 100%, but after long and continual use efficiency may fall. In order to test the efficiency of the counting tube after measuring three samples, the uranium oxide (U_3O_8) standard was measured. The variation in efficiency of the tube was found to range from 0 to 4%. The counts were, therefore, also corrected for this variation.

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(11) Time at which measurements are made

Because of the disintegration of the isotope, it is essential that the results of all measurements made at various times should be recalculated to values applicable to a single specific date. As correction factor for this drop in radioactivity, the following well-known equation may be used:

$$N_t = N_o\ (1 - e^{\lambda t}),$$

in which,

N_t is the number of atoms remaining from the original number N_o, after a period t; λ is the disintegration constant of the isotope; e is the basis of the Napierian logarithm.

It is, however, simpler to make the corrections with the aid of the measurements made with the standard sample of the relevant isotope. The radioactivity of this standard is repeatedly determiped after the measurement of three samples. The interim periods between these measurements may, in view of the half-life of the Na^{22} used (3 years), be completely disregarded. Using these measurements, the recalculation of the counts to the date on which the experiment was commenced incorporates the correction for the efficiency of the tube.

(12) Statistical errorss

The fluctuations in the radioactive decay (a random process) follow Poisson's law of distribution.

The probability (P_n) that, per unit of time, n counts are actually made, while the average number of counts is $\bar{n}$, is given by the equation:

$$P_n = (\bar{n})\ e^{-n}\ n!$$

In measurements of radioactivity it is usual to relate the statistical fluctuations to the standard deviation of a single observation.

In the case of strong radioactive samples the standard deviation can be computed by taking the square root of the number of counts. This method is, however, too inaccurate in the case of weak samples, since the weaker the radioactivity, the greater is the influence of the background upon the statistical error. With such samples, therefore, the combined error is taken as the square root of the sums of the squares of the individual errors.

In order to increase the precision of the counting date each sample is measured three times. For strong samples the period of observation was invariably 10 minutes, while weak samples were counted for 30 or 60 minutes. The standard deviation of the mean, including the background, is calculated from the formula:

$$T = \frac{\Sigma n\ (x_k - \bar{x})^2}{n\ (n - 1)}$$

in which, x_k is the individual count, $\bar{x}$ the arithmetic mean and n the number of times that the sample is counted. The deviation of the background (T_o) is determined in the same way. The deviation of the average counting date of the sample is then found as $T^2 + T^2_o$. The maximal deviation of the counts thus obtained was 3%.

VI. THE TECHNIQUE FOR THE PREPARATION OF AUTORADIOGRAPHS

By an autoradiograph is understood the image which is formed by radioactive objects on a photographic plate. Autoradiography is based upon the phenomenon, known since 1896 (Becquerel), whereby radioactive radiation produces a blackening upon a photographic plate (242). The radioactive plant is laid upon a sensitized plate, a certain exposure time is allowed and the plate is then developed. An image is thus obtained which shows the distribution of radioactive substance in the tissues of the plant. With the aid of autoradiographs of plants, parts of plants or even tissue sections, it is possible to carry out both qualitative and quantitative determinations. The quantitative determination is based, in principle, upon the measurement of the blackening on the photographic plate, this blackening being dependent upon the radioactivity and upon the thickness of the tissue. This method was evolved by ODEBLAD (179) but in its execution various difficulties are, apparently, encountered. In the present investigations quantitative determinations from autoradiographs were not carried out; quantitative distribution of sodium throughout the experimental plants was determined by the method described above. The autoradiographs were made for the purpose of ascertaining the differences in the distribution of sodium in the various plants, to which end the qualitative comparison of corresponding tissues is eminently suitable.

The quality of autoradiographs is influenced by various factors:

1. The properties of the radioactive isotope employed

The sensitivity of the photographic plate to the various types of radiation which the radioactive isotopes are able to emit is not constant. For the localized ionization of the emulsion of the photographic plate, α-particles are 10,000 and β-particles 100 times as effective as γ-radiation. The Na^{22} used in this investigation radiates both β-particles and γ-radiation.

The β-radiation is chiefly responsible for the effect obtained. The better a β-particle is localized in the emulsion, the sharper is the image obtained. Should the intensity of the radiation from the tissue be too strong, this can be reduced by the insertion of a thin aluminium plate (0.1 mm. thick) between the object and the photographic plate.

2. The properties of the photographic plate

It will be seen from the foregoing that far higher requirements in connection with the density and reaction speed of the emulsion will need to be set for gamma radiation than for beta and alpha radiation. Of the various sorts of photographic plates which were tested during the investigation, the Kodak X-ray plate was found to be the most suitable for the β-radiation involved. This plate has an emulsion layer on both sides.

3. The exposure

The time during which it is necessary for the radioactive plant

to be in contact with the photographic plate, in order to obtain a satisfactory image, is dependent upon the radioactive isotope being employed and the amount of radioactive material present in the plant. Since one plant takes up sodium more readily and satisfactorily than another plant it is not possible to decide in advance what length of exposure will be required. Too short an exposure results in a weak, vague image while too long an exposure gives a diffused, poorly defined picture of the tissue. The exposure must be determined at the commencement empirically, making several autoradiographs of the same object with different exposures. The method by which the radioactive plant is placed between two photographic plates has been very successful. The one plate is developed after a few days and, dependent on the quality of the image obtained, the other plate is left exposed for a longer period. From previously empirically determined exposures and from counts made from the plants or plant parts, it is possible, after sufficient experience, to make very reasonable extimates of the exposure required even when armed only with the available knowledge of the sodium (or other element) uptake of a given plant. After exposure, the plates were developed with Kodak Rapid X-ray Developer at 21°C., fixed for 20 minutes with Rapid Fixer U II and washed for 30 minutes.

4. The thickness of the plantpart and the state in which it is autoradiographed

When a rather abrupt transition in thickness occurs between two organically connected plant parts, it is extremely difficult to make a true autoradiograph of an intact plant as contact of the plant with the plate at the point of transition leaves much to be desired. In such cases, it is advisable to sever the plant at the transition point and to autoradiograph the parts side by side or, where the difference in thickness is very pronounced, separately.

In order to achieve close and uniform contact between the plant and the plate the following procedure was used:

A strong, rectangular cardboard box, having a bottom equal in area to the size of the photographic plate, was taken. The bottom of the box was covered with a piece of hardboard and on top or this foam-rubber sheet covered with tissue-paper was laid. The photographic plate was then placed in the box. The plant parts to be autoradiographed were placed between two sheets of tissue-paper and laid on the plate, after which the whole was covered first with another foam-rubber sheet and finally with hardboard. The box was closed, sealed in an envelope and set aside for 4 to 8 days under a pressure of 40g./cm^2. The tissue-paper prevented the plant from adhering to the photographic plate or the foam-rubber.

It is possible for a thick plant part to contain more sodium than a thin part, even though the sodium concentration in each is equal. It is necessary, therefore, to compare only similar tissues with each other. With oats, for instance, a sodium concentration was found in the nodes. As these parts are thicker than the rest of the culm, nodes and adjacent parts of the culm were checked for their radioactivity with the Geiger counter.

TABLE 2

RADIOACTIVITY IN THE VARIOUS PARTS OF A FULL-GROWN OAT STEM
per 100 mg. dry matter

Part of the Plant (From the base to the tip)	*Radioactivity* (c.p.m.)
Stem (base)	1,096 ± 10.4
Node	1,220 ± 11.0
Stem	1,094 ± 10.4
Node	1,585 ± 12.6
Stem	627 ± 7.8

From the table it will be seen that more sodium per 100 mg. dry matter is, in fact, accumulated in the nodes than in the adjacent parts of the stem.

In the preparation of the first autoradiographs the plant was brought into contact with the plate in the fresh state and between sheets of pliofilm. When making an autoradiograph of spinach in this way a peculiar phenomenon was revealed, namely, that the sodium was distributed throughout the plant in localized patches (XXVI)*.

Since the amount of calcium present in spinach is sufficient to neutralize only one third of the oxalic acid (61), it was considered possible that, in the circumstances, the sodium in this plant might be present in the form of a sodium oxalate or a sodium potassium oxalate. In order to ascertain whether or not this is so, the autoradiographed plant was immersed in water for one week, the water being renewed every day. It was then rapidly dried and again autoradiographed. It was found that the water treatment had considerably reduced the illumination but had not caused it to disappear entirely. From this test it may be supposed that sodium is present in spinach in the form of sodium oxalate, sodium bioxalate or a sodium potassium oxalate.

It is, however, also possible that sodium was present as an impurity in the calcium oxalate crystals. To test this, calcium chloride was added, in excess, to a radioactive sodium nitrate solution, whereby calcium with ammonium oxalate was precipitated. After centrifuging, the precipitate was washed with a dilute ammonium oxalate solution and again centrifuged. This treatment was repeated six times in all, after which the precipitate was dried. In order to measure its radioactivity the precipitate was placed in a small aluminium dish. The 26 mg. calcium oxalate gave an average of 52 ± 1.5 c.p.m., the background being 45 ± 2.6 c.p.m. Thus it appeared that the calcium oxalate was in fact polluted with a little sodium. The question remained, however, whether or not this pollution was great enough to cause the effect found on the autoradiograph of the spinach plant (XXVI). This problem was investigated as follows:

The precipitate was spread over a piece of tissue-paper and placed

* Roman numerals refer to the autoradiographs in Chapter IV.

on the X-ray plate. Even after an exposure of three weeks the calcium oxalate polluted with radioactive sodium did not cause a blackening on the photographic plate, despite the fact that the radioactivity of the medium in which it was precipitated had been so chosen that it exceeded the radioactivity of the plant.

From the results of these various tests it was considered highly probable that the presence of sodium and sodium potassium oxalate crystals in the plant was responsible for the above-mentioned, peculiar radiographic image. It is, however, still difficult to suppose that sodium occurs in spinach as sodium oxalate, distributed in localized patches. Since the plant was brought into contact with the plate in the fresh state and therefore died during the period of exposure, it is possible that, as the semi-permeability of the cell walls gradually diminished, the sodium and the oxalic acid obtained greater mobility. Simultaneously, however, the plant dried out causing an increase in concentrations in the plant and giving rise to a situation which, at a certain moment, is favourable for the formation of sodium oxalate nuclei. It was logical to suppose that, if this line of reasoning was correct, a rapidly dried spinach plant would give a different image. This was, indeed,. found to be the case. Rapid fixation of an identical plant was achieved by drying it with an electric iron and when it was autoradiographed an entirely different picture was obtained (XXVII).

The spinach plant represented in XIV was also autoradiographed after rapid drying. From these two autoradiographs it will be seen that the strongly localized radiation had disappeared and that the sodium is much more uniformly distributed than in the plant autoradiographed in the fresh state (XXVI). From then on during the investigation, all plants were autoradiographed in the fresh and the dry state for the purposes of comparison but in no case was such a marked difference apparent as with spinach.

Certain plants (see Chapter IV) were autoradiographed after they had been cultured in nutrient solutions containing various amounts of calcium and potassium for the purpose of studying the sodium distribution under conditions of abundant calcium or potassium. One such plant was mustard (XX is of a plant in the fresh state and XVII of a plant rapidly dried). In the two autoradiographs . the distribution of sodium is identical; the image of the fresh plant is, however, weaker than that of the dried plant. The reason for this phenomenon must be sought in the higher moisture content of the fresh plant whereby part of the radiation becomes absorbed.

A similar phenomenon was also observed with fresh and rapidly dried plants cultured in nutrient solutions with higher potassium or calcium levels. In the case of the fresh plants the radiation of the sodium appeared to be more strongly suppressed by potassium than by calcium; in the case of the rapidly dried plants, the images showed the situation to be exactly reversed, that is, the radiation of the sodium was more strongly suppressed by calcium than by potassium. Here again the higher moisture content of the fresh plants liberally supplied with potassium (XXII) caused stronger radiation absorption than that which occurred in the drier fresh plants given an excess of calcium (XII).

In general, it may be concluded that in order to obtain trustworthy autoradiographs rapidly dried material should be used in preference to fresh material as, on the one hand, the moisture content influences the quality of the image unfavourably and, on the other, in plants autoradiographed in the fresh but slowly dying state, an element such as sodium appears to be able to shift its position. For this reason, all plant material to be autoradiographed in this investigation was rapidly dried by placing it between filterpaper and "pressing" it with an electric iron.

CHAPTER IV

THE DISTRIBUTION OF SODIUM IONS THROUGHOUT THE PLANT AS ESTABLISHED FROM AUTORADIOGRAPHS

I. INTRODUCTION

During research designed to ascertain the influence of a nutrient upon the living organism the important question of the distribution of that nutrient between the various organs of the plant in question must inevitably arise. In this respect the literature is not particularly informative about sodium as a nutrient element. While it tells us that, with plants like oats, the sodium content in the leaf decreases from the base to the tip, it is silent on the question whether this phenomenon is common to all types of plants. Yet the matter is of considerable importance; from a knowledge of the way in which sodium is distributed throughout the plant it is not impossible that conclusions can be drawn in respect of the function fulfilled by the element in that plant.

In order, therefore, to form an idea of the distribution of sodium between the organs of various types of plants the technique described in Chapter III for the preparation of autoradiographs was developed and applied. This method was chosen in preference to the more usual analytical method not only because less time and labour is involved but also because it can be carried out with whole, undissected plants.

To avoid confusion it is pointed out that the nutrient solution - prepared in accordance with Hoagland (Chapter III) - with which the plants were cultured, contained no sodium. The radioactive sodium taken up by the plants originated from a nutrient solution containing only 0.1 m.e. Na and 1.5 μc. Na^{22} per litre solution. This low concentration was expressly chosen in order to eliminate the possibility of the sodium taking up specific positions in the plant by reason of its quantitative superiority over calcium and potassium.

For a proper study of the autoradiographs it is necessary to bear in mind that tissues of different thicknesses, such as mesophyll and leaf-veins, may be compared only for the qualitative distribution of sodium. Quantitative comparison is only possible when the autoradiographs relate to plants (or the same plant parts) of the same age, which received the same amount of radioactive sodium and were in contact with the substrate for the same length of time.

More than 120 autoradiographs were prepared from the plants, or plant-parts, of barley *(Hordeum vulgare)*, wheat *(Triticum vulgare)*, oats *(Avena sativa)*, rye *(Secale cereale)*, perennial ryegrass *(Lolium perenne)*, bean *(Phaseolus vulgaris)*, pea *(Pisum sativum)*, lupin *(Lupinus luteus)*, spinach *(Spinacia oleracea)*, beet *(Beta vulgaris var. rubra)*, orach *(Atriplex hortensis)*, chicory *(Cichorium intybus)*,

celery *(Apium graveolens)*, tomato *(Solanum lycopersicum)*, flax *(Linum usitatissimum)*, mustard *(Sinapis alba)*, savory *(Satureja hortensis)*, carrot *(Daucus carota)*, cotton *(Gossypium hirsutum)*, tobacco *(Nicotiana tabacum)*, maize *(Zea mays)*, jute *(Corchorus capsularis)*, roselle *(Hibiscus sabdariffa)*, aster *(Aster sinensis)* and red pepper *(Capsicum annuum)*. From these autoradiographs a choice was made in such a way as to obtain a clear idea of the differences in sodium translocation and distribution in different species of plants.

II. TRANSLOCATION OF SODIUM IN VARIOUS SPECIES OF PLANTS

There were found to be considerable differences in the degree to which sodium is translocated from the roots to the aerial parts of the different plants. In this respect clear distinction can be made between three groups, namely:

Group A

Plants in which, despite the fact that the roots appear to have taken up considerable sodium, the sodium is translocated reluctantly and sluggishly to the stems and leaves.

To this group belong, for example, jute, aster, red pepper, maize (I)* and bean (II and III).

The reason for this sluggish translocation is not known. According to the carrier theory, which attributes active translocation to cytoplasmatic carriers (7), the carrier responsible for conveying sodium to the xylem in the root becomes so obstructed that the movement of sodium practically ceases.

In the case of phosphate it has been found that certain substances such as potassium cyanide and iodo-acetate have a restraining influence on translocation (8). It cannot, however, be accepted as likely that these substances - which are known to be enzyme inhibitors - occur in greater quantities in this group than in plants in which considerable translocation of sodium appears to take place.

Another possibility is that these plants produce certain substances - either entirely absent or else present in smaller amounts in plants of the other groups - which control translocation and perhaps affect or inactivate the sodium carrier. If this is the case the effect upon the translocation of sodium would almost certainly be similar to the influence exercised by the growth regulator 2-methyl-4-chlorophenoxyacetic acid.d (M.C.P.A.) (201) upon the distribution of potassium. When this compound is added to the culture medium the translocation of potassium to the shoots or its redistribution between roots and shoots is influenced. The potassium content of the aerial parts decreases, that of the roots increases and there is a considerable decline in the total potassium content of the plant. That something similar occurs in respect of the translocation of sodium within the plants of this group should certainly be recognized as a possibility.

Despite the fact that sodium translocation in these plants is very poor a certain amount of the element does eventually find its way

* Roman figures refer to the autoradiographs.

into the aerial parts where it accumulates - in the case of the bean, in the pod-wall and the pericarp.

Group B

Plants in which sodium is translocated in considerable amounts to the stems and leaves.

To this group belong plants such as winter wheat, winter rye, winter barley, oats (IV), carrot (V), pea (VI), tobacco (VII), perennial ryegrass (VIII), tomato (IX), mustard (XVII, XVIII, XIX), flax (XXIII, XXIV, XXV), roselle and lupin.

From the point of view of their capacity for the translocation of sodium the Gramineae are certainly not identical. Sodium is much more easily translocated in winter barley, oats and perennial ryegrass, for instance, than in winter wheat or winter rye. In the rest of the plants named above, the differences in capacity for the translocation of sodium are very small.

Group C

Plants in which large quantities of sodium are translocated to the stems and leaves and in which the amount accumulated in the mesophyll is large in comparison with that accumulated in the leaf-veins.

Among the plants belonging to this group, in which, as a result of strong translocation, the amount of sodium which accumulates in the mesophyll is large in comparison with the amount accumulating in the leaf-veins, are: beet (X), cotton (XI), orach (XII), chicory (XIII) and spinach (XXVI, XXVII, XIV).

Relationship between translocation and reaction to sodium

The classification of the various types of plants according to their ability to convey sodium, as drawn up from the relevant autoradiographs, is in complete agreement with the classification based upon these plants' reactions to sodium fertilization as deduced from the results of pot and field experiments (101, 132). It thus appears that the relationship which exists between the plants' ability to translocate sodium and their reaction to sodium fertilization may be expressed as follows:

Ability to translocate sodium	Reaction to sodium fertilization
Group A - poor	Little or none
Group B - good	Moderate to good
Group C - very good	Very good

It may be concluded from these results that the use of radioactive sodium is an excellent means of determining the reaction to sodium fertilization to be expected of any given crop. Apart from its reliability the method is considerably less costly than methods used hitherto and is, moreover, quickly carried out.

III. DISTRIBUTION OF SODIUM IN VARIOUS SPECIES OF PLANTS

In nearly all plants it was found that, irrespective of their re-

action to sodium, the amounts of sodium in the different parts decreased in the order: roots, stems, leaf-veins and mesophyll.

1. Distribution in the aerial parts

In connection with the distribution of sodium, plants may be roughly divided into two groups, viz.

(1) Those in which the sodium is distributed uniformly throughout the stem and leaf. This group comprises the plants which react very strongly to sodium, such as beet (X), cotton (XI), chicory (XIII), spinach (XIV) and celery.

(2) Those in which the sodium is unevenly distributed throughout the stem and leaf. This group comprises the plants which react moderately strongly to strongly to sodium, such as oats (IV), peas (VI), tobacco (VII), perennial ryegrass (VIII), tomato (IX), flax (XXIII, XXIV, XXV), mustard (XVII, XVIII, XIX); and those which react only slightly or not at all.

To summarize, it appears in general that:

(1) In plants which react very well to sodium, accumulation with uniform distribution occurs in the leaves, e.g., beet (X) and cotton (XI).

(2) In plants which react well to sodium, considerable translocation takes place but distribution throughout the plant is irregular, e.g., oats (IV) and tomato (IX).

(3) In plants which react moderately to sodium, moderate translocation takes place and distribution throughout the plant is irregular, e.g., lupin and winter rye.

(4) In plants which react only slightly or not at all to sodium, very little translocation takes place and distribution throughout the plant is irregular.

The irregularity of the distribution reveals itself in a progressive decrease in the amount of sodium from the base of the leaf towards its tip, and in accumulations at specific points in the plant. In plants such as oats, pea, perennial ryegrass, chicory and flax (IV, VI, VIII, XIII and XXIII respectively), sodium accumulations are found in the merismatic parts such as the nodes, the junctions of leaf-blade and leaf-sheath and the junctions of stem and petiole. In plants such as tobacco (VII), sodium is able to accumulate in the margins of young leaves.

In older tobacco leaves, it is uniformly distributed. In general, sodium accumulation occurs at the growing points.

2. Distribution in the roots

The distribution of sodium in the roots is also irregular. In one and the same plant sodium accumulation can occur at the tip of one root and towards the base of another. It would appear that the places in the root which are suitable for sodium uptake are not all equally active at any given moment and an autoradiograph only records the sodium disposition obtaining at one moment.

In all plants, however, sodium accumulations occur at the junctions of side roots with the main root (XIV).

Autoradiographs were made of longitudinal and transverse sections of a red table beet (XV) which had been cultivated in a sandy soil fertilized with nitrogen in the form of a solution of Chilean nitrate containing 3μc. radioactive sodium as sodium nitrate per 6kg. potsoil. From this autoradiograph it appears that sodium is accumulated in the red beet in concentric bands, the positions of which coincide with the phloem. The largest amount of sodium is, however, contained in the root-wall.

This investigation gave rise to the question how, when a seed germinates, the sodium in the seed becomes distributed between the root and shoot. In order to ascertain this, seed was obtained from oat plants cultured in a dusarite-silica sand medium (see Chapter III) dressed with a nitrogen fertilizer to which radioactive sodium had been added. The seed was allowed to germinate on moist filter-paper in Petri dishes and as soon as a shoot and leaf had developed, an autoradiograph was made (XVI). From this it could be seen that, on germination of the plant, the sodium contained in the seed is practically all translocated to the roots.

3. *Distribution at high and low calcium and potassium concentrations in the plant*

As has previously been remarked, the amount of sodium made available to the plants from which autoradiographs were made, was very small in comparison with the amounts of calcium and potassium supplied. Despite this, doubt arises whether the excesses of Ca and K (the normal concentrations were 5 and 3.5 m.e.* respectively) in the nutrient solution containing 0.1 m.e. Na (from which the sodium accumulation originated) were sufficiently large to prevent the sodium from taking up specific positions in the plant.

It was for this reason that the translocation and distribution of sodium in spinach, mustard, flax and oat plants was investigated using both normal calcium and potassium concentrations (Hoagland's nutrient solution) and high calcium and potassium concentrations.

The concentration of each of the two elements was trebled, the plants in question being cultured in nutrient solutions in all of which the sodium concentration was held constant at 0.1 m.e., but which contained three different ratios of calcium and potassium, namely, 5 : 3, 15 : 3 and 5 : 9, expressed in m.e.

In general, it appeared that the sodium uptake of plants with higher calcium or potassium levels is less than that of plants with lower levels.

The high calcium concentration was found to suppress the sodium uptake to a greater extent than the high potassium concentration did (XVII, XVIII, XIX).

It was further observed that the different species of plants developed better in the nutrient solution containing the high concen-

* 0.5 m.e. K originates from the KH_2PO_4, which amount is not trebled in the nutrient solution containing Ca and K in the ratio of 5 : 9 m.e. per litre.

tration of calcium, namely, the 15 Ca : 3 K solution than in the 5 Ca : 3 K solution, and that this was especially true of flax. Thus the reason why the flax plants cultured in the 5 Ca : 3 K solution took up less sodium than did those in the other solutions must apparently be sought in the fact that they were rather poorly developed compared with those in the other solutions (XXIII, XXIV and XXV).

Despite the effect of the calcium and potassium upon the sodium uptake, the presence of higher concentrations of these elements in the nutrient solution exercised no influence upon the distribution of the sodium in the plant. Irrespective of whether the concentrations of calcium and potassium in the plants were high or low the plants were found to have accumulated sodium in precisely the same places. This indicates that any given type of plant has its own specific distribution system for sodium. Such a distribution system is difficult to explain except by regarding it as functional and therefore connected with the functions (known and unknown) which sodium fulfils in the plant.

The results obtained from the study of the autoradiographs may be summarized as follows:

(1) The autoradiographic technique provides a rapid, inexpensive method for the determination of the influence of sodium upon the development of the plant.
(2) With regard to the translocation of sodium, plants may be classified in the following three groups:
    (a) Plants which react only slightly or not at all to sodium.
    (b) Plants which react moderately strongly to strongly to sodium.
    (c) Plants which react very strongly to sodium.
(3) Sodium accumulates in the plant at those places where great cell activity prevails, viz. growing points, root-walls (beet), nodules (pea) and leaf margins (tobacco).
(4) The calcium and potassium levels of the plant have no influence upon the distribution of sodium.

IV. AUTORADIOGRAPHS

As already stated, all solutions contained 0.1 m.e. Na and 1.5 μc. Na^{22} per litre. The normal concentrations of Ca and K were 5 and 3 m.e. per litre respectively. In the case of spinach, mustard, flax and oats only, solutions with Ca and K concentrations of 15 and 3 m.e. respectively and 5 and 9 m.e. respectively were also used.

A description of the autoradiographs, with particular reference to the translocation and distribution of sodium, is as follows:

I. Maize (Zea mays) - roots

After an uptake period of one week, the translocation of sodium to the stem and leaf of the 5-week-old plant was so slight that no autoradiograph of the aerial parts was obtained after an exposure of 10 days. Distribution in the root is irregular. Accumulation occurs in the tips of the roots and at the points of origin of side roots.

II. Bean (Phaseolus vulgaris) - roots

The distribution of sodium in the roots is irregular. In the main root accumulation occurs in those places where many side roots have their origin; in the side roots it occurs at the points of origin, in the middles and at the tips.

Accumulation occurs at the base of the stem at the origin of a side root. Translocation from the root to the stem does not occur readily (see also III).

III. Bean (Phaseolus vulgaris) - stem and leaves

Stem and leaves excised from the root shown in autoradiograph II. Insufficient radioactive sodium was present in the leaves to enable registration upon the photographic plate. During an uptake period of one week, translocation from the root to the stem and leaves was extremely slight. This plant was treated in precisely the same way as the pea shown in VI and the two plants are therefore comparable in all respects.

IV. Oats (Avena sativa)

The distribution of sodium in the leaf of the 8-week-old plant is irregular, the amount decreasing from the base to the tip. Accumulations takes place in the stem, the nodes and the junctions of leaf-sheath and leaf-blade.

V. Carrot (Daucus carota)

Accumulation of sodium takes place in the root at the base of the stem, and at the junction of the petiole with the stem. Good translocation to the stem and leaf occurs.

VI. Pea (Pisum sativum)

The translocation of sodium to the stem and leaf can be said to be very good. Distribution in the mesophyll is uniform . Accumulation in the nodules is a noteworthy phenomenon.

VII. Tobacco (Nicotiana tabacum)

Sodium appears to accumulate in the margins of the leaves of the young tobacco plant.

VIII. Perennial ryegrass (Lolium perenne)

Very considerable translocation of sodium from the root to the stem occurs in plants of a few weeks old. The element accumulates in the nodes.

IX. Tomato (Solanum lycopersicum)

In the young plant translocation to the stem is very good but it is less good to the leaves in which distribution is irregular, the amount decreasing from the base to the tip.

X. Red table beet (Beta vulgaris var. rubra) - leaves and cotyledon

Leaf of red table beet some month old cultivated in a sandy soil.

The accumulation of the evenly distributed sodium in the mesophyll is quite considerable as compared with that in the leaf-vein. Strong accumulation occurs in the cotyledon.

XI. Cotton (Gossypium hirsutum)

Leaf of a young plant. Translocation from the stem to the leaf is very good. The sodium is uniformly distributed in the mesophyll.

XII. Spreading orach (Atriplex hortensis)

Very good translocation to the leaf occurs in young orach. Sodium accumulates especially in the young leaf and at the growing point.

XIII. Chicory (Cichorium intybus)

In young plants translocation to the stem and the leaf is good. The sodium accumulates at the growing point and in the mesophyll.

XIV. Spinach (Spinacia oleracea)

Spinach seedlings cultured in a nutrient solution with a calcium/potassium ratio of 15 : 3. Accumulation in the mesophyll is good in comparison with that in the leaf-vein. The distribution in the leaf is uniform. Accumulation occurs at the junction of the side roots with the main root.

XV. Red table beet (Beta vulgaris var. rubra)

Longitudinal and transverse sections. The beets from which the exposures were made were some months old and were cultivated in sandy soil. The sodium accumulation in the root occurs in the root-wall and the phloem.

XVI. Oats (Avena sativa)

Seedling from radioactive seed. Seeds from radioactive oat plants were placed in Petri dishes to germinate. After germination it appeared that practically all the sodium had been utilized for the development of the root.

XVII. Mustard (Sinapis alba)

Mustard seedlings cultured in a nutrient solution with a calcium/potassium ratio of 5 : 3 and autoradiographed in the dry state. Otherwise, the plants are in all respects comparable with those of XVIII and XIX. Very considerable uptake and translocation to the leaf took place and distribution in the leaf is fairly uniform. Accumulation occurs in the leaf-tips.

XVIII. Mustard (Sinapis alba)

Mustard seedlings cultured in a nutrient solution with a calcium/potassium ratio of 15 : 3 and autoradiographed in the dry state. Moderate uptake and translocation of sodium took place. The amount taken up is less than with the calcium/potassium ratio of 5 : 3 (XVII) or of 5 : 9 (XIX). Accumulation and distribution are the same as in XVII.

XIX. Mustard (Sinapis alba)

Mustard seedlings cultured in a nutrient solution with a calcium/potassium ratio of 5 : 9 and autoradiographed in the dry state. Very considerable uptake and translocation of sodium took place. The amount taken up is less than with the calcium/potassium ratio of 5 : 3 (XVII) but greater than with the ratio of 15 : 3 (XVIII). Accumulation and distribution are the same as in XVII and XVIII.

XX. Mustard (Sinapis alba)

The seedlings were cultured in a nutrient solution with a calcium/potassium ratio of 5 : 3 and are in all respects comparable with those of XVII. They were autoradiographed in the fresh state, in contrast with the plants described under XVII. The distribution of sodium is the same as in XVII, but the amount taken up is apparently considerably less. The apparent difference in sodium accumulation results from the radiation-absorbent effect of the water in the fresh plant. For the same reason the accumulation of sodium in fresh plants from a high-potassium solution (XXII) appeared to be less than that in plants from a high-calcium solution (XXI), whereas it was in fact greater (XIX and XVIII respectively).

XXI. Mustard (Sinapis alba)

The seedlings were cultured in a nutrient solution with a calcium/potassium ratio of 15 : 3 and were autoradiographed in the fresh state. They are in all respects comparable with the plants autoradiographed in the dry state (XVIII). The distribution of sodium is identical with that in the plants of XX and XVIII. Accumulation is somewhat greater in the plants autoradiographed in fresh state.

XXII. Mustard (Sinapis alba)

The seedlings were cultured in a nutrient solution with a calcium/potassium ratio of 5 : 9 and were autoradiographed in the fresh state. They are in all respects comparable with the plants autoradiographed in the dry state (XIX).

The distribution of sodium is identical with that in the plants of XIX. Accumulation is, however, considerably less than in the dried plants (XIX).

XXIII. Flax (Linum usitatissimum)

Flax plants cultured in a nutrient solution with a calcium/potassium ratio of 5 : 3. Sodium is accumulated at the junction of the leaf and stem and at the growing point. The plants are less well developed than those in the nutrient solution with a calcium/potassium ratio of 15 : 3 (XXIV).

XXIV. Flax (Linum usitatissimum)

Flax plants cultured in a nutrient solution with a calcium/potassium ratio of 15 : 3. Sodium uptake is better than with a calcium/potassium ratio of 5 : 3 (XXIII) and less good than with a ratio of 5 : 9 (XXV). Distribution is the same as in XXIII.

XXV. Flax (Linum usitatissimum)

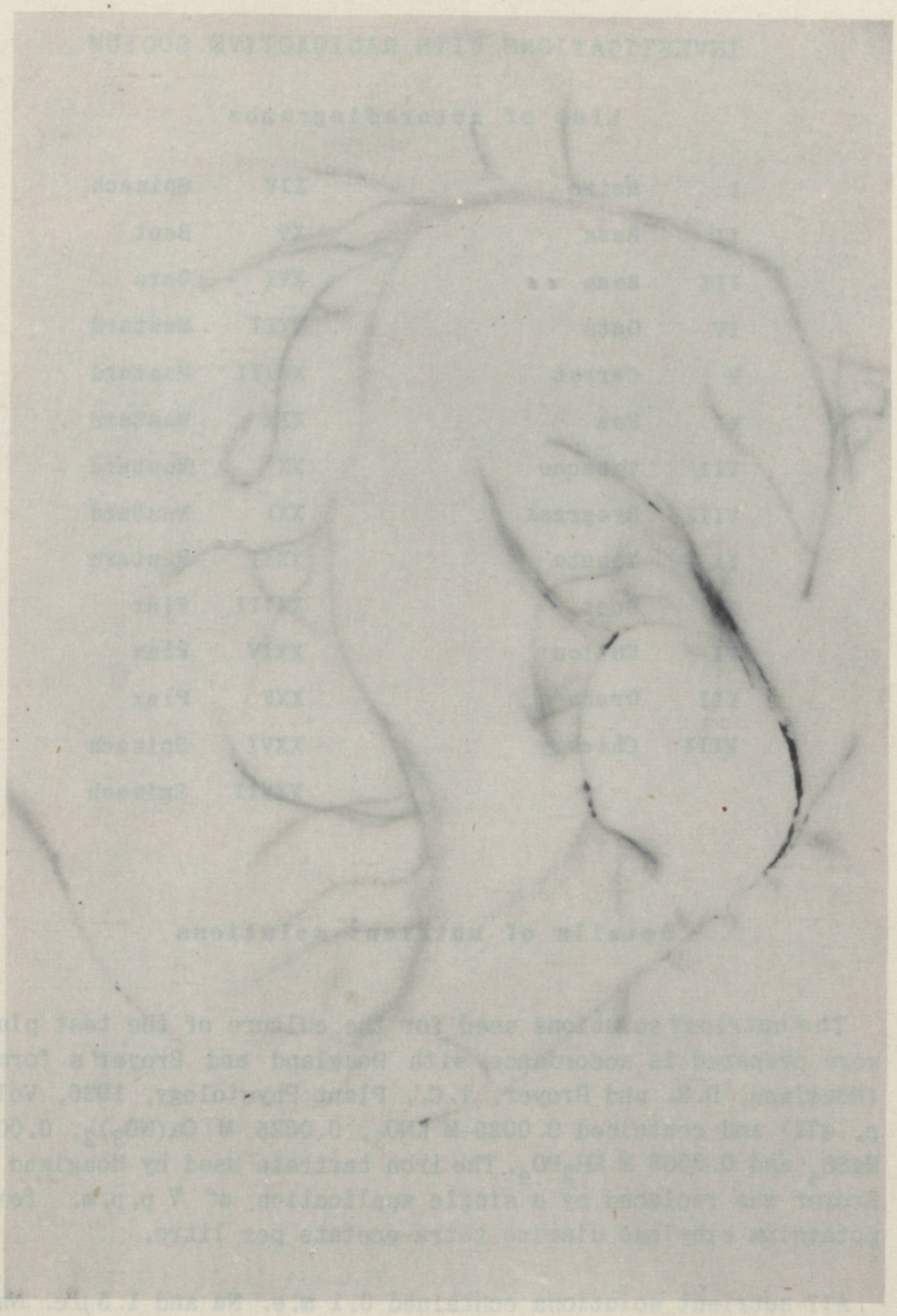
Flax plants cultured in a nutrient solution with a calcium/potassium ratio of 5 : 9. Uptake and translocation of sodium are better than with a calcium/potassium ratio of 5 : 3 or 15 : 3. Distribution is the same as with a calcium/potassium ratio of 5 : 3 (XXIII) and of 15 : 3 (XXIV).

XXVI. Spinach (Spinacia oleracea)

Spinach seedlings autoradiographed in the fresh state. The peculiar accumulation of sodium in the leaf, petiole and stem is very probably caused by the formation of sodium oxalate crystals.

XXVII. Spinach (Spinacia oleracea)

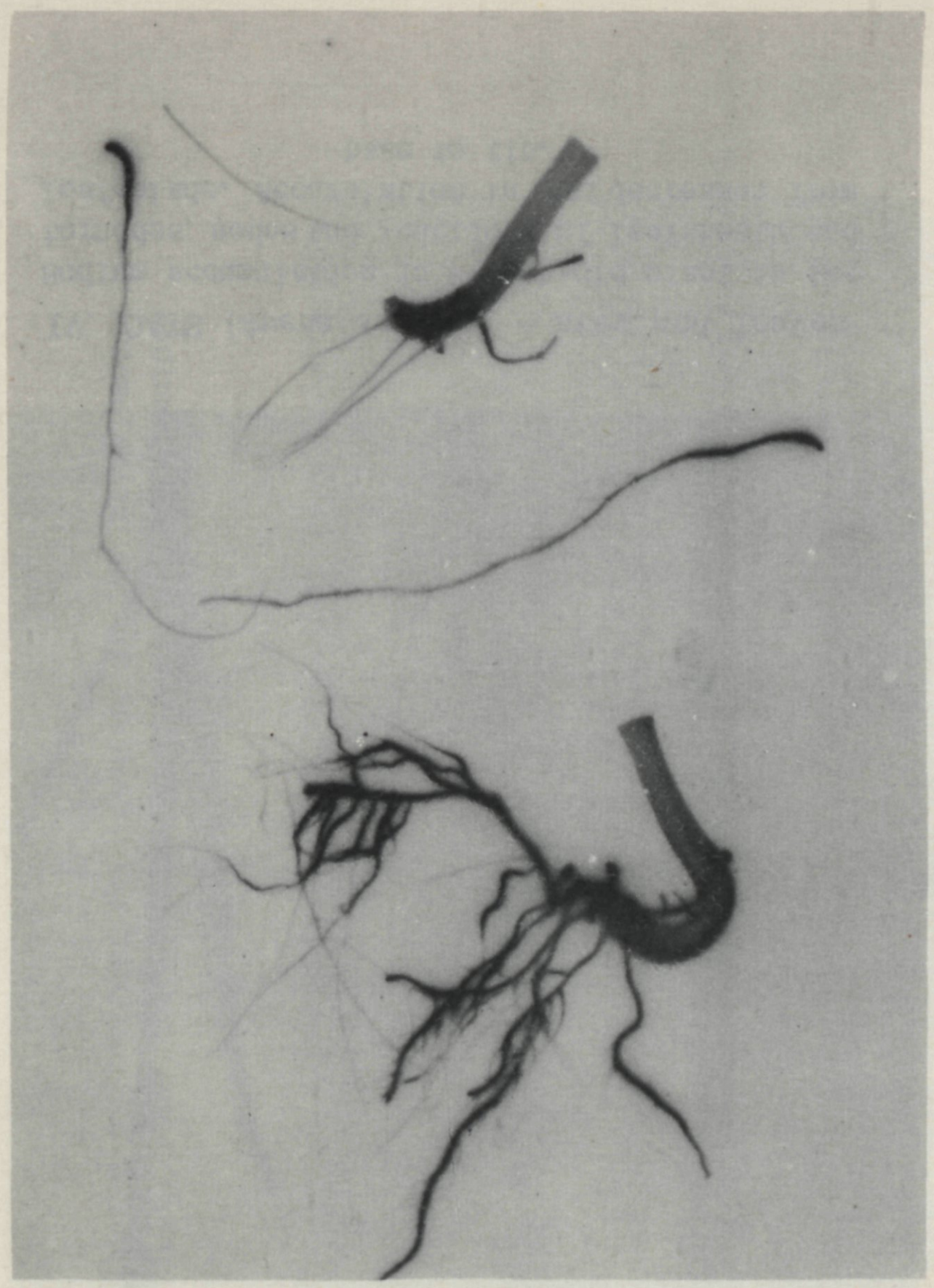
The seedlings are in all respects comparable with those of XXVI but they were autoradiographed after having been dried rapidly, by which means the position of the sodium in the plant is fixed. No large crystals of sodium oxalate could have formed.



x 1⅓

I. MAIZE *(Zea mays)* - roots

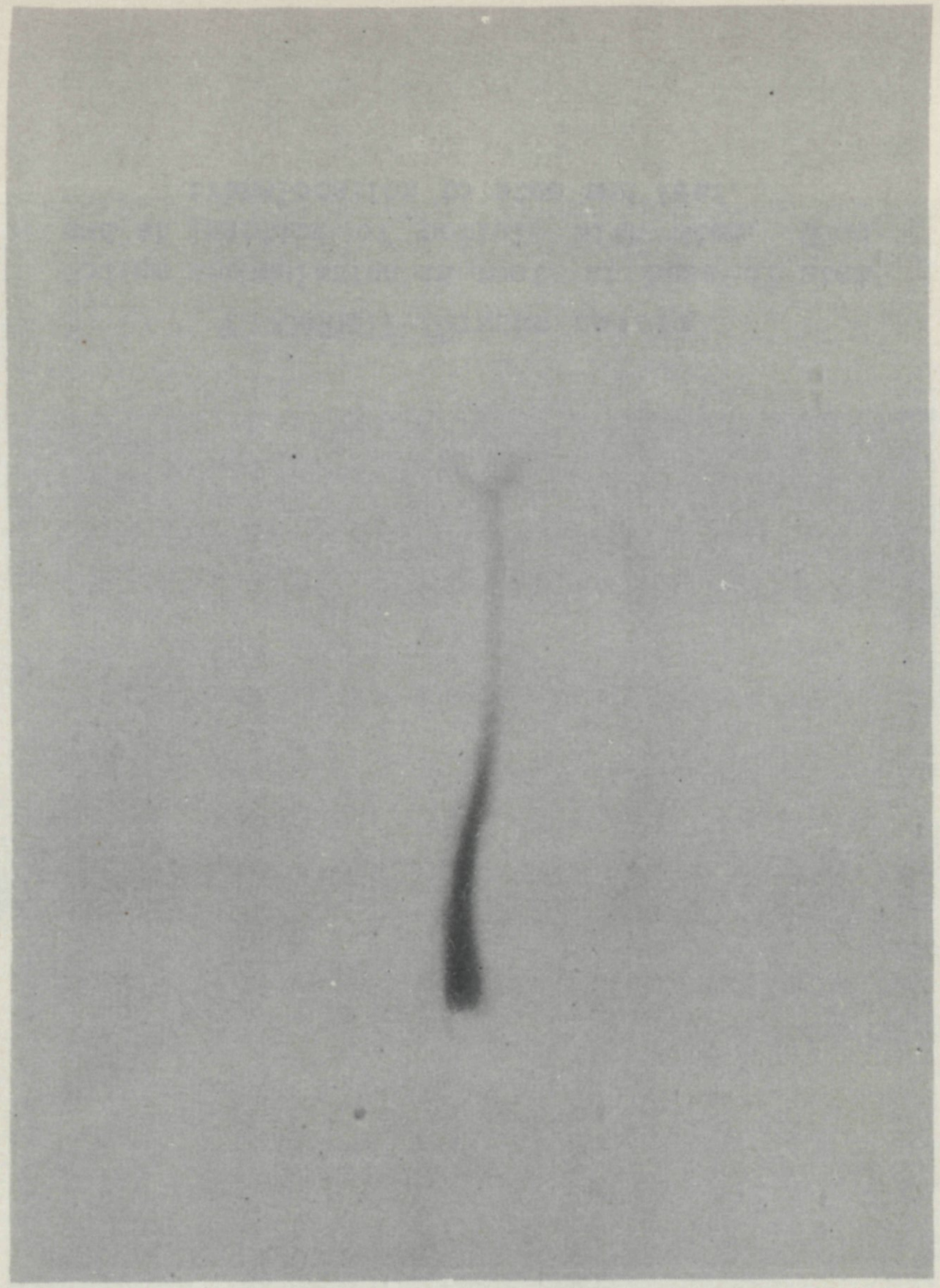
Sodium distribution irregular. Accumulation in root tips
and at points of origin of side roots.



x 1

II. BEAN *(Phaseolus vulgaris)* - roots

Sodium distribution irregular. In the main root, accumulation where many side roots arise; accumulation at bases, middles and tips of side roots.



III. BEAN *(Phaseolus vulgaris)* - stem and leaves

Translocation to stem and leaves very slight, even after an uptake period of one week.

x1

IV. OATS *(Avena sativa)* - stem and leaves

Sodium accumulation in 8-week-old plant in internodes, nodes and junctions of leafsheath and leaf-blade. Accumulation in leaf decreases from base to tip.

x1

V. CARROT *(Daucus carota)*

Sodium accumulation in root, at base of stem and at junction of petiole with stem. Good translocation to stem and leaf.

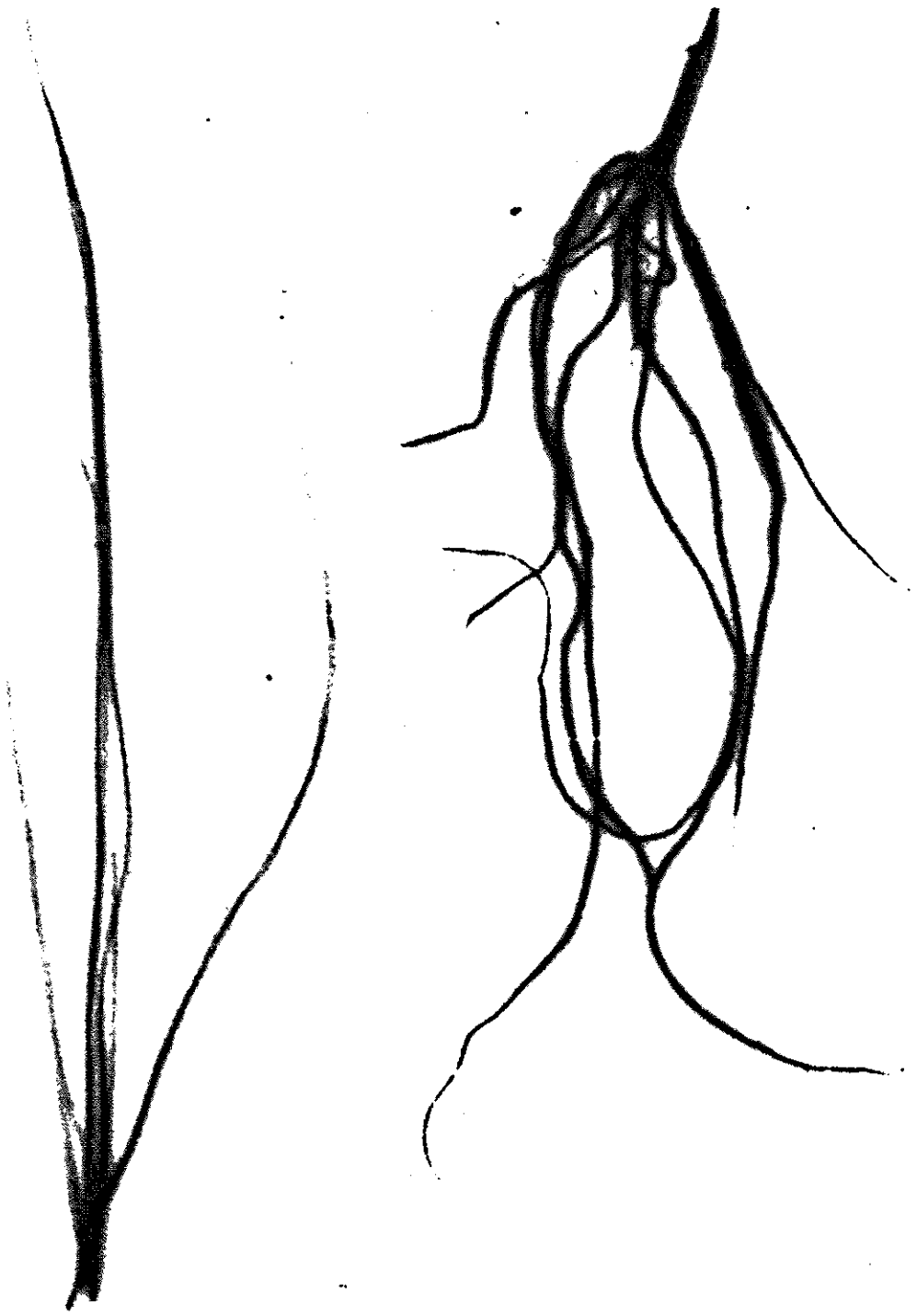
x 1

VI. PEA *(Pisum sativum)*

Sodium translocation to stem and leaf very good. Striking accumulation in the nodules. Distribution in mesophyll is uniform.

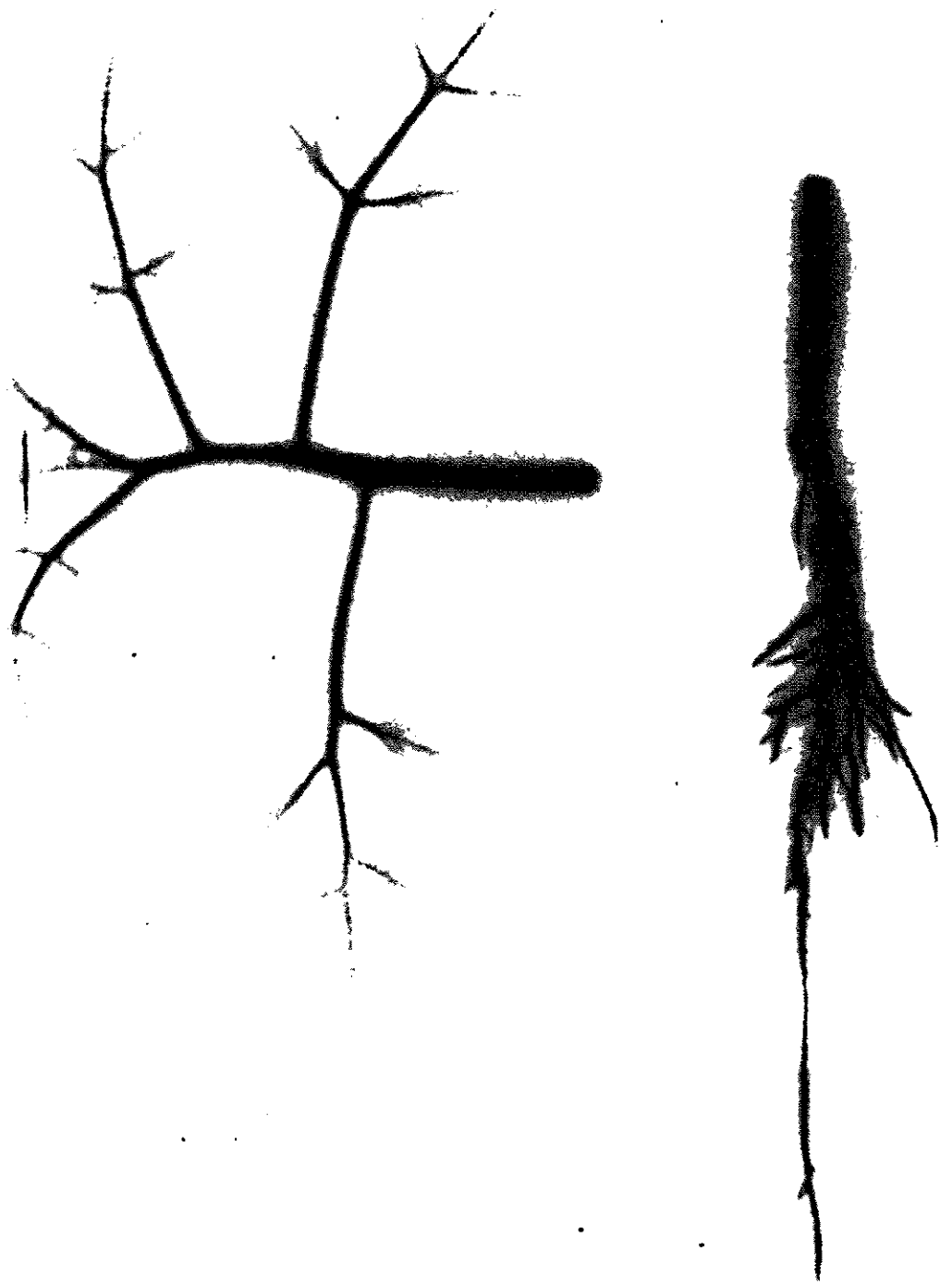
x 2

VII. TOBACCO *(Nicotiana tabacum)*
Sodium accumulation at the margin of a young leaf.



x ¾

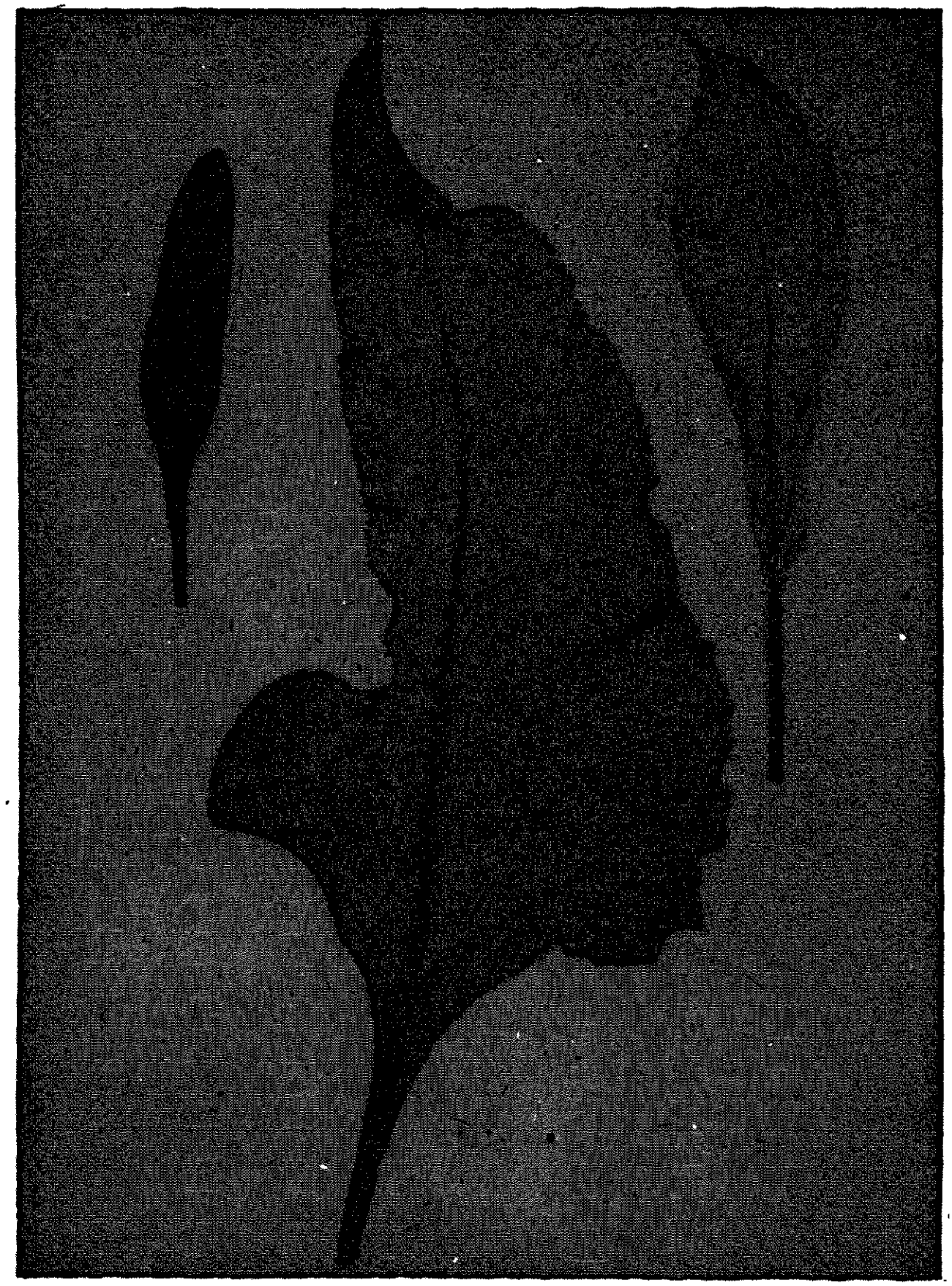
VIII. PERENNIAL RYEGRASS *(Lolium perenne)*
Very considerable translocation of sodium to stem in young plant with accumulation at nodes.



x ¼

IX. TOMATO *(Solanum lycopersicum)*

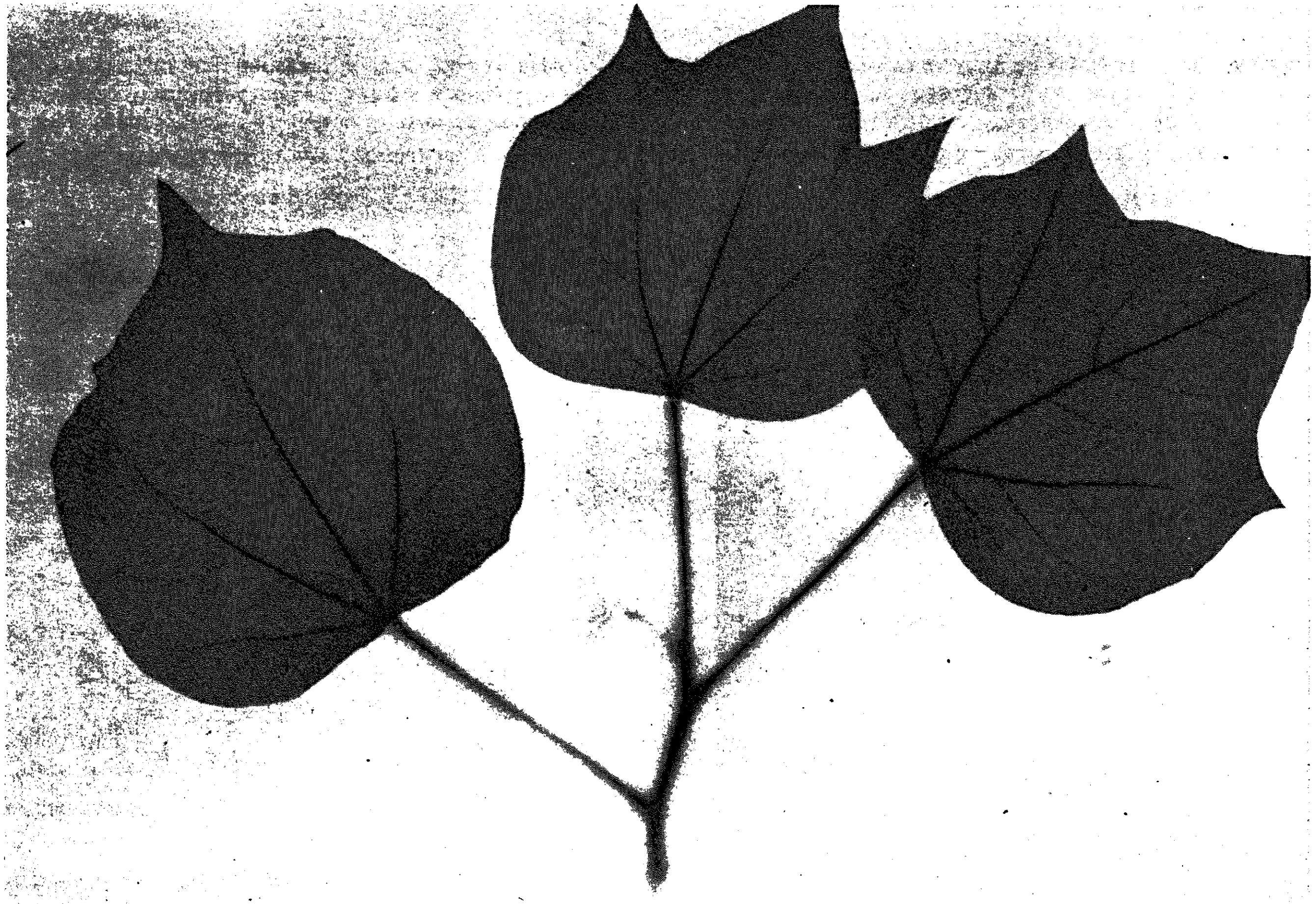
Good translocation of sodium to stem in young plant. Translocation to leaves moderately good with amount decreasing from base to tip of leaflets.



x 1

X. RED TABLE BEET *(Beta vulgaris var. rubra)*

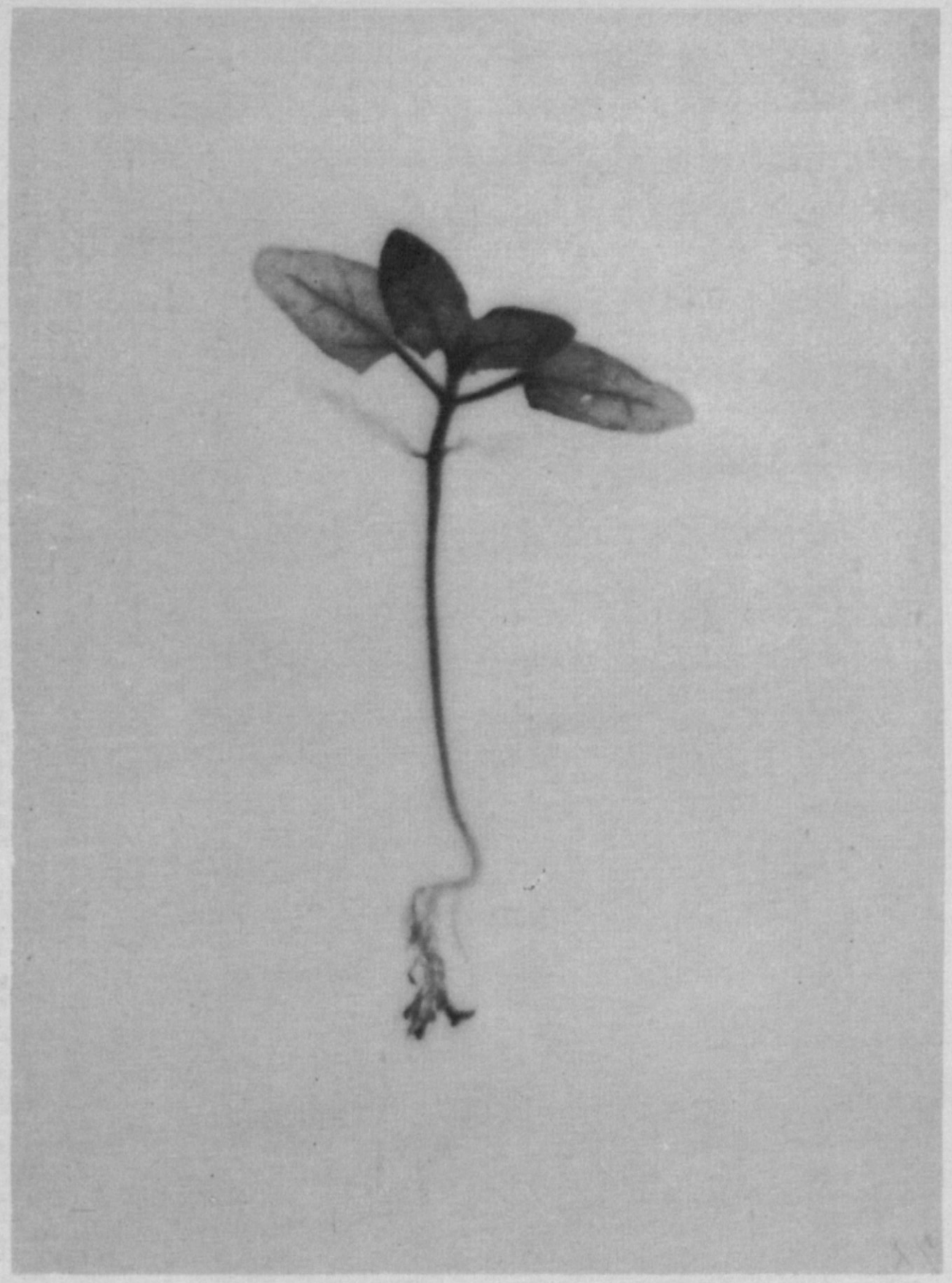
The accumulation of the evenly distributed sodium in the mesophyll is quite considerable as compared with that in the leaf-vein. Strong accumulation in cotyledon (top left-hand corner of radiograph).



x 1

XI. COTTON *(Gossypium hirsutum)*

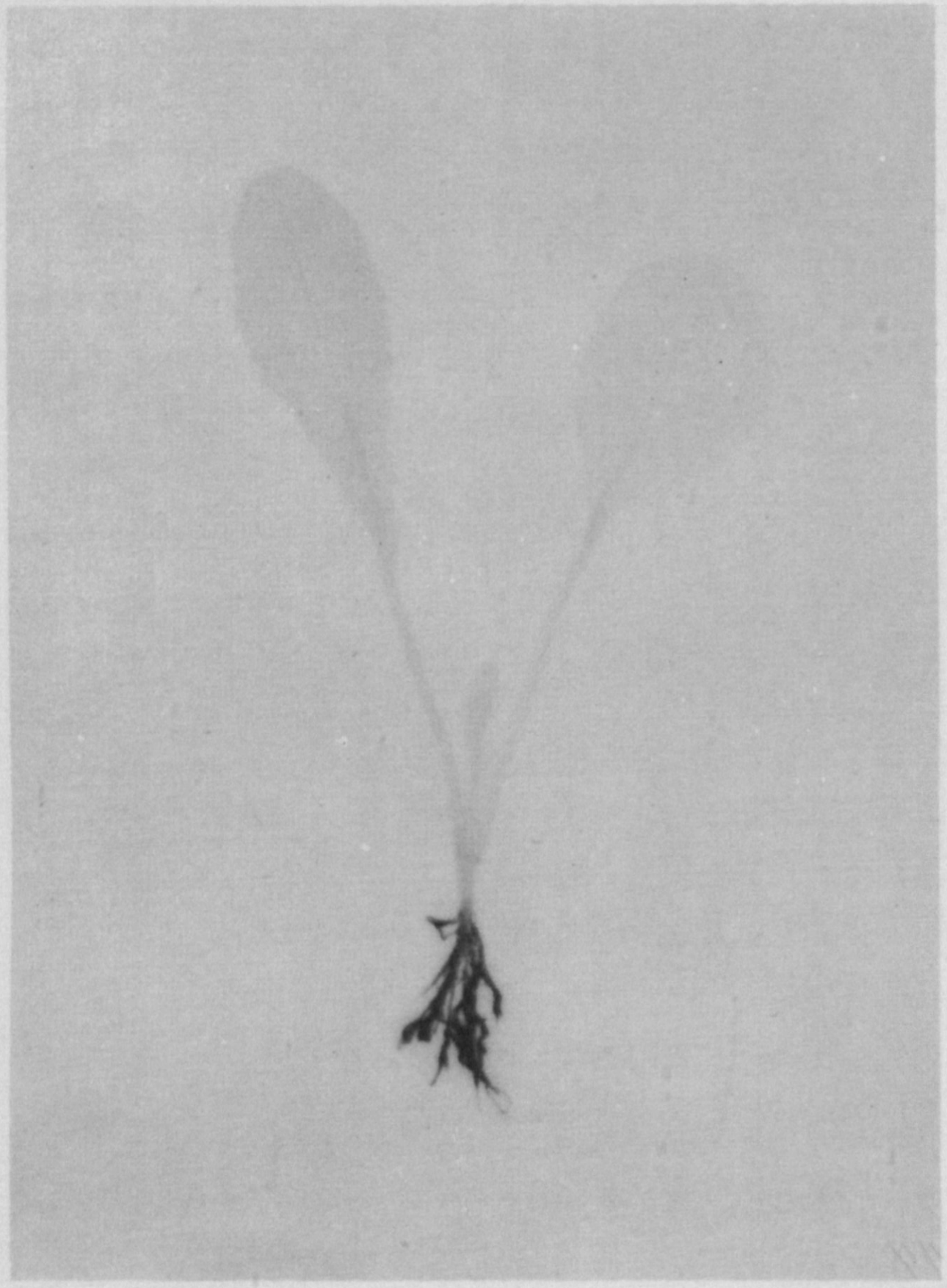
Sodium translocation from stem to leaves of young plant very good.
Uniform distribution in mesophyll.



x 1

XII. SPREADING ORACH *(Atriplex hortensis)*

Very good translocation of sodium from stem to leaf.
Accumulation in growing point and young leaves.



x 1

XIII. CHICORY *(Cichorium intybus)*

Good translocation of sodium to the stem and leaf.
Accumulation in mesophyll and at growing point.

x 1

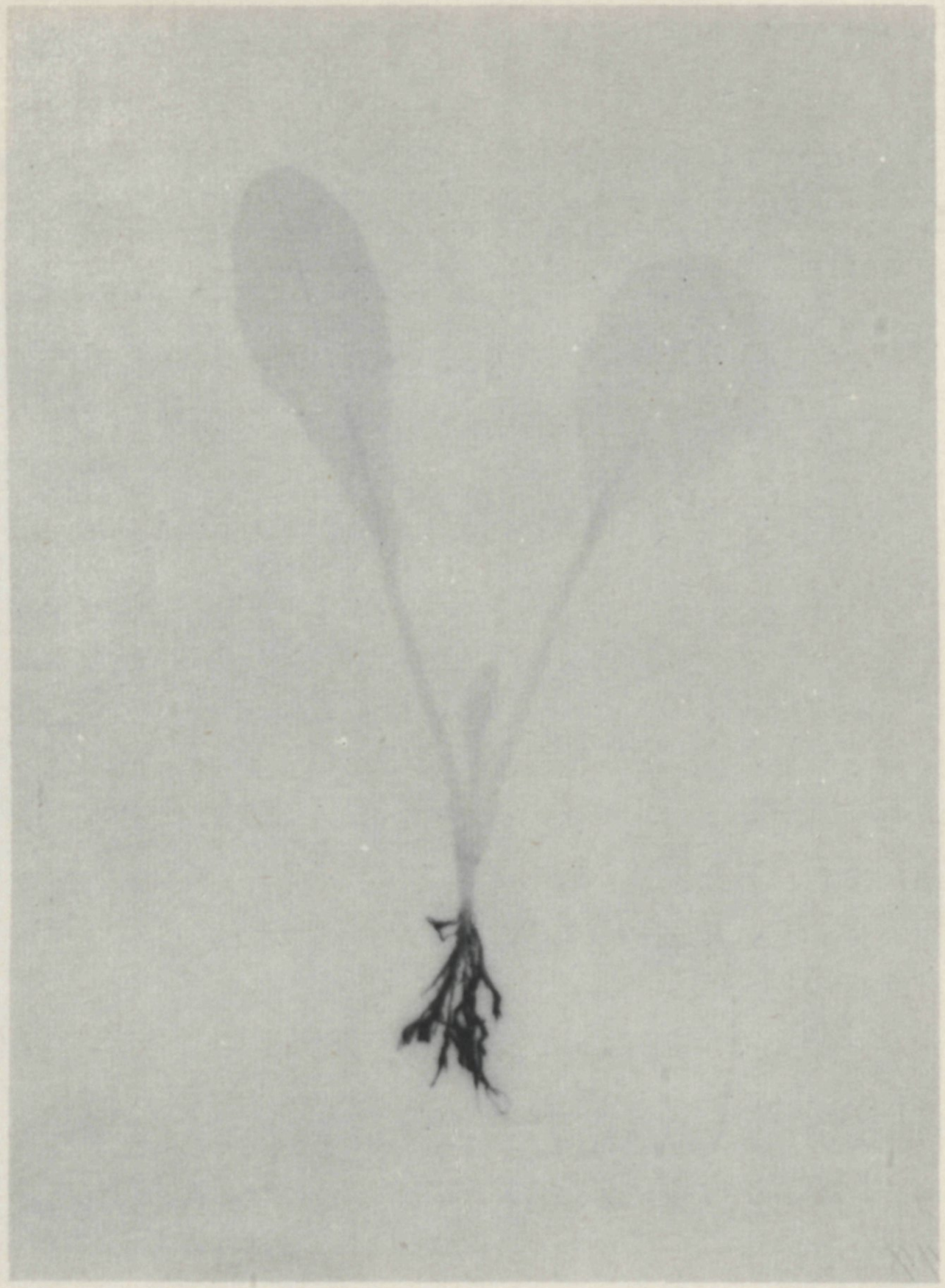
XI. COTTON *(Gossypium hirsutum)*

Sodium translocation from stem to leaves of young plant very good.
Uniform distribution in mesophyll.

x 1

XII. SPREADING ORACH *(Atriplex hortensis)*

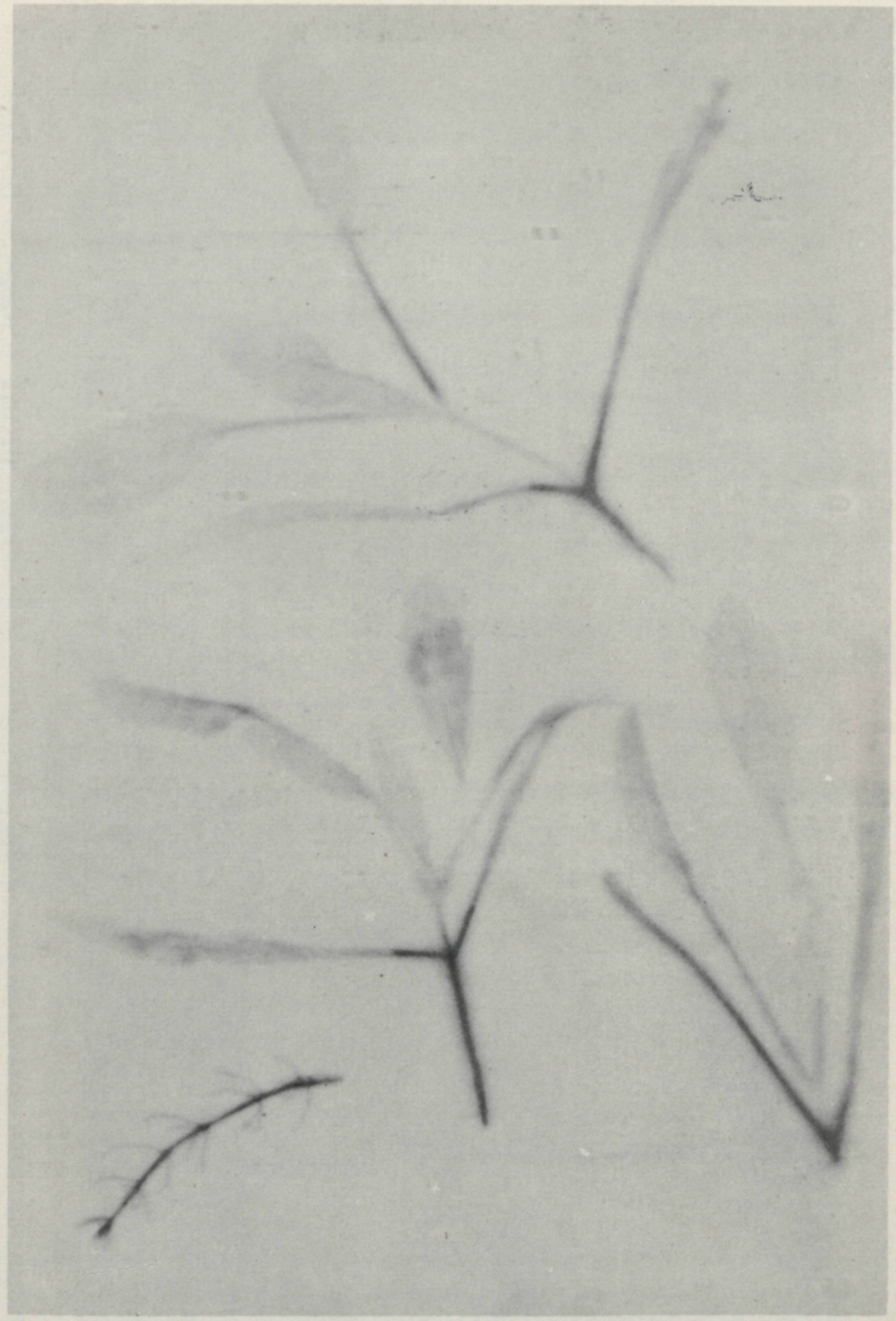
Very good translocation of sodium from stem to leaf.
Accumulation in growing point and young leaves.



x 1

XIII. CHICORY *(Cichorium intybus)*

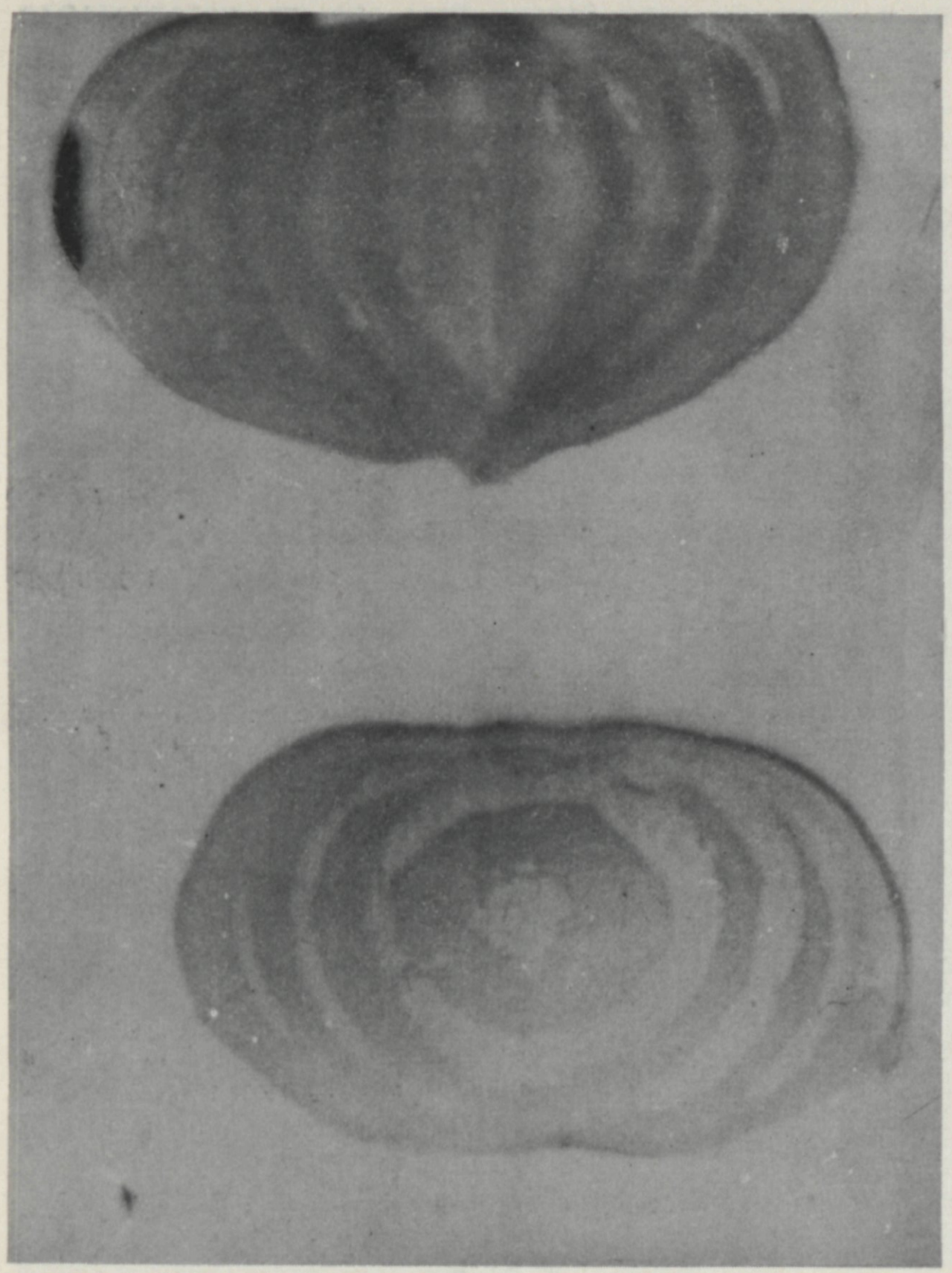
Good translocation of sodium to the stem and leaf.
Accumulation in mesophyll and at growing point.



x 1⅓

XIV. SPINACH *(Spinacia oleracea)*

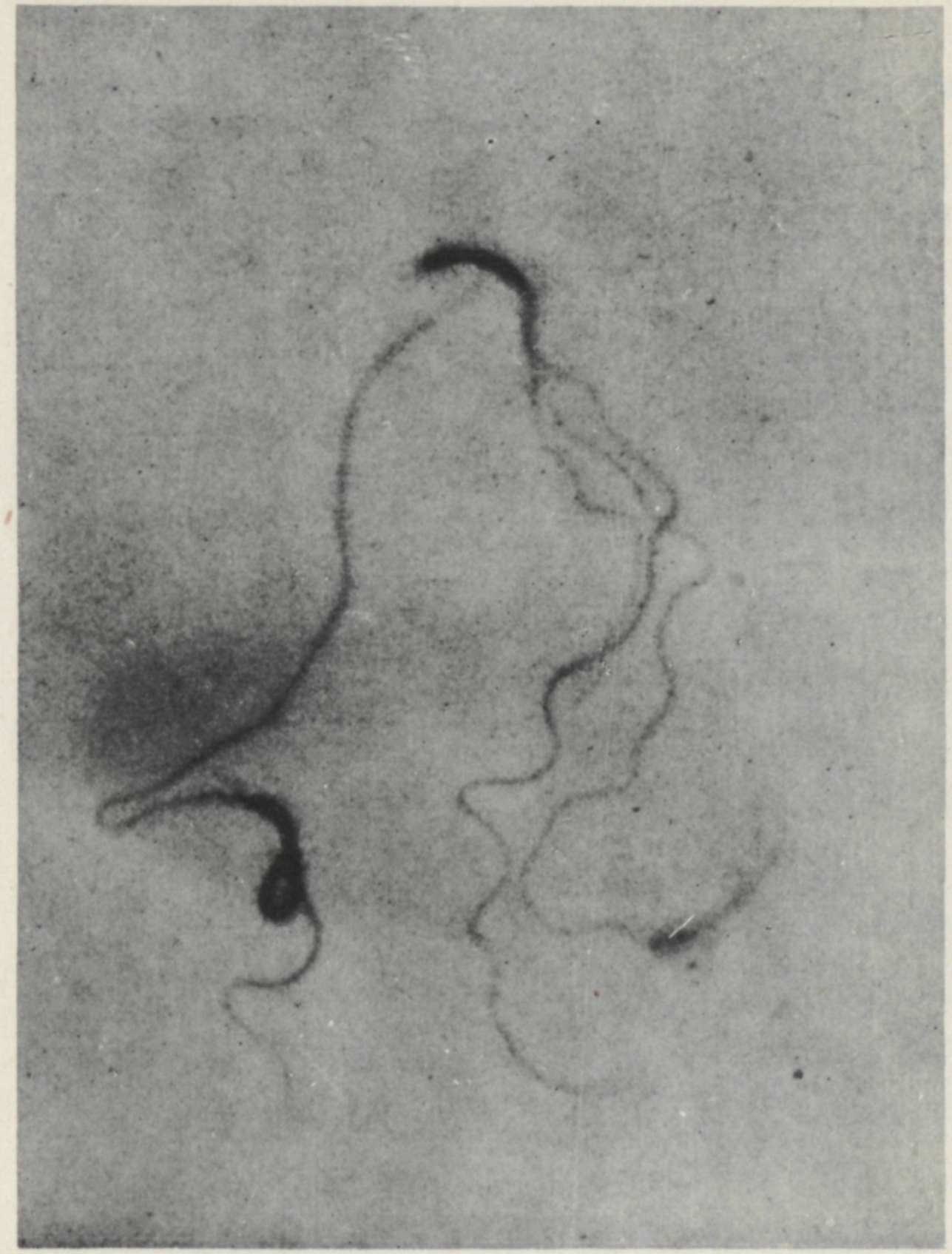
Seedlings cultured in a nutrient solution with a Ca/K ratio of 15 : 3. Sodium accumulation in mesophyll is uniform and good in comparison with that in the leaf vein. Accumulation at junction of side roots.



x 1

XV. RED TABLE BEET *(Beta vulgaris var. rubra)*

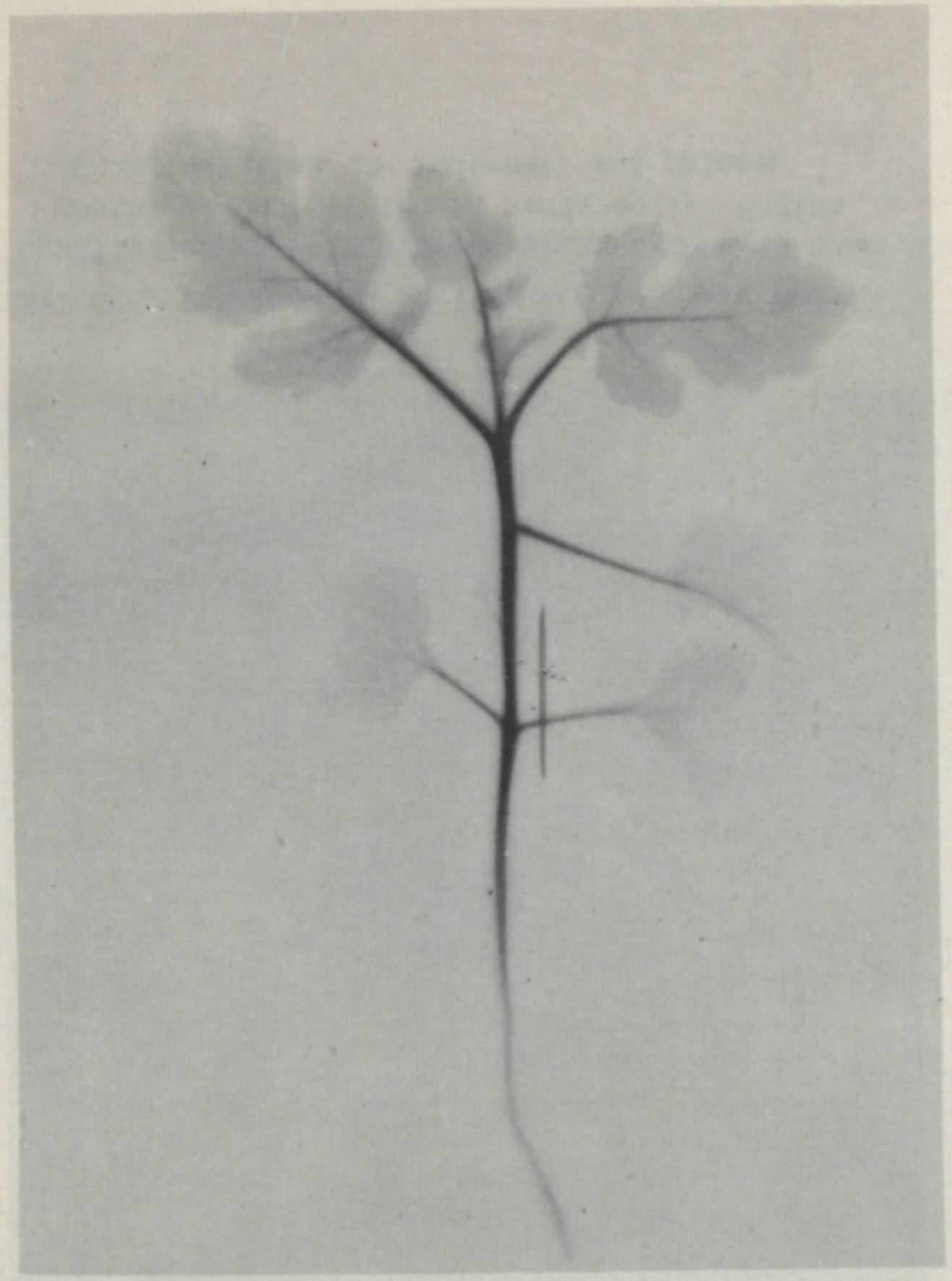
Longitudinal and transverse sections of beets some months old cultivated in sandy soil. Sodium accumulation in root-wall and phloem.



x 1½

XVI. OATS *(Avena sativa)*

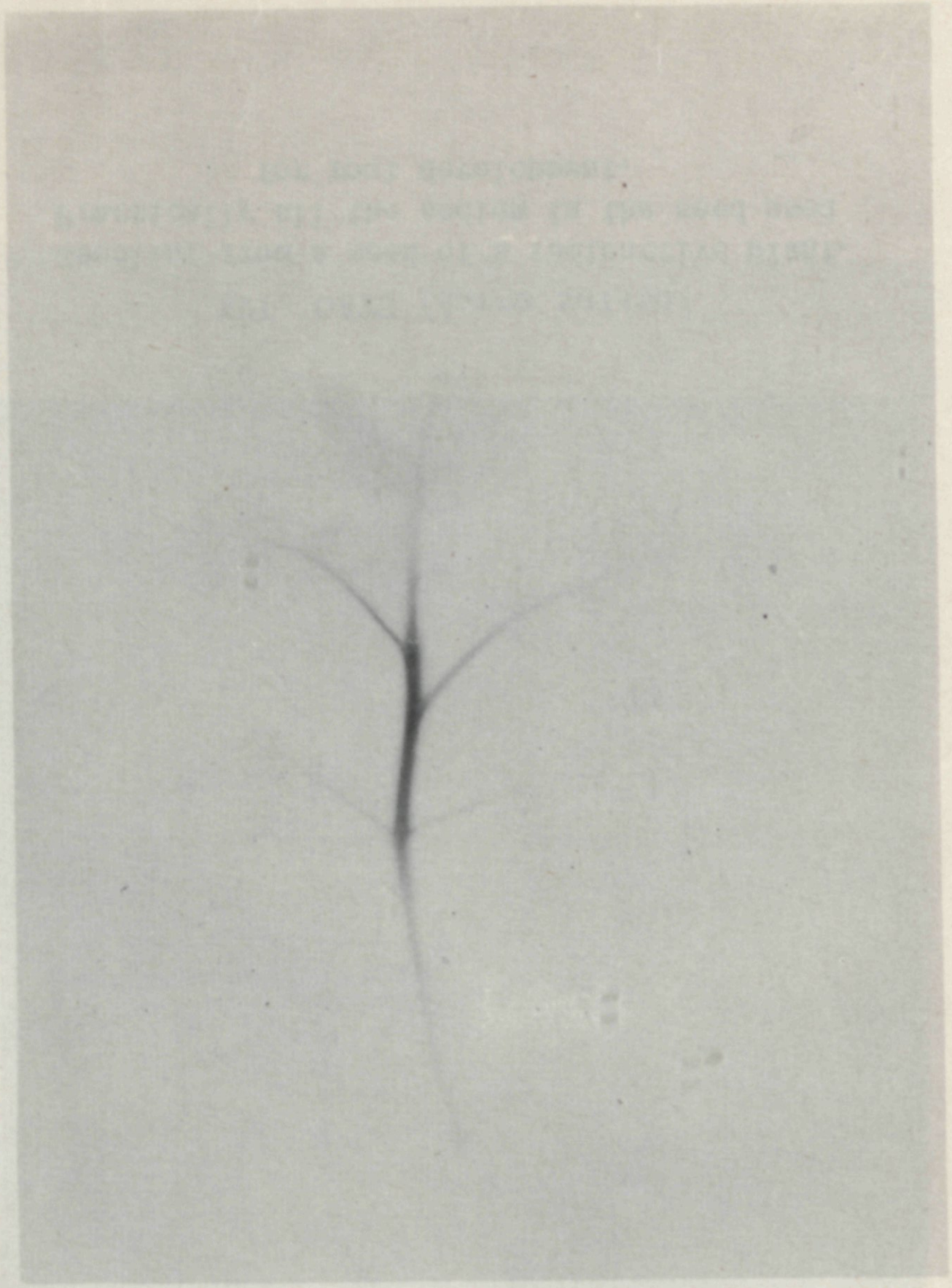
Seedling from a seed of a radioactive plant. Practically all the sodium in the seed used for root development.



x1

XVII. MUSTARD *(Sinapis alba)*

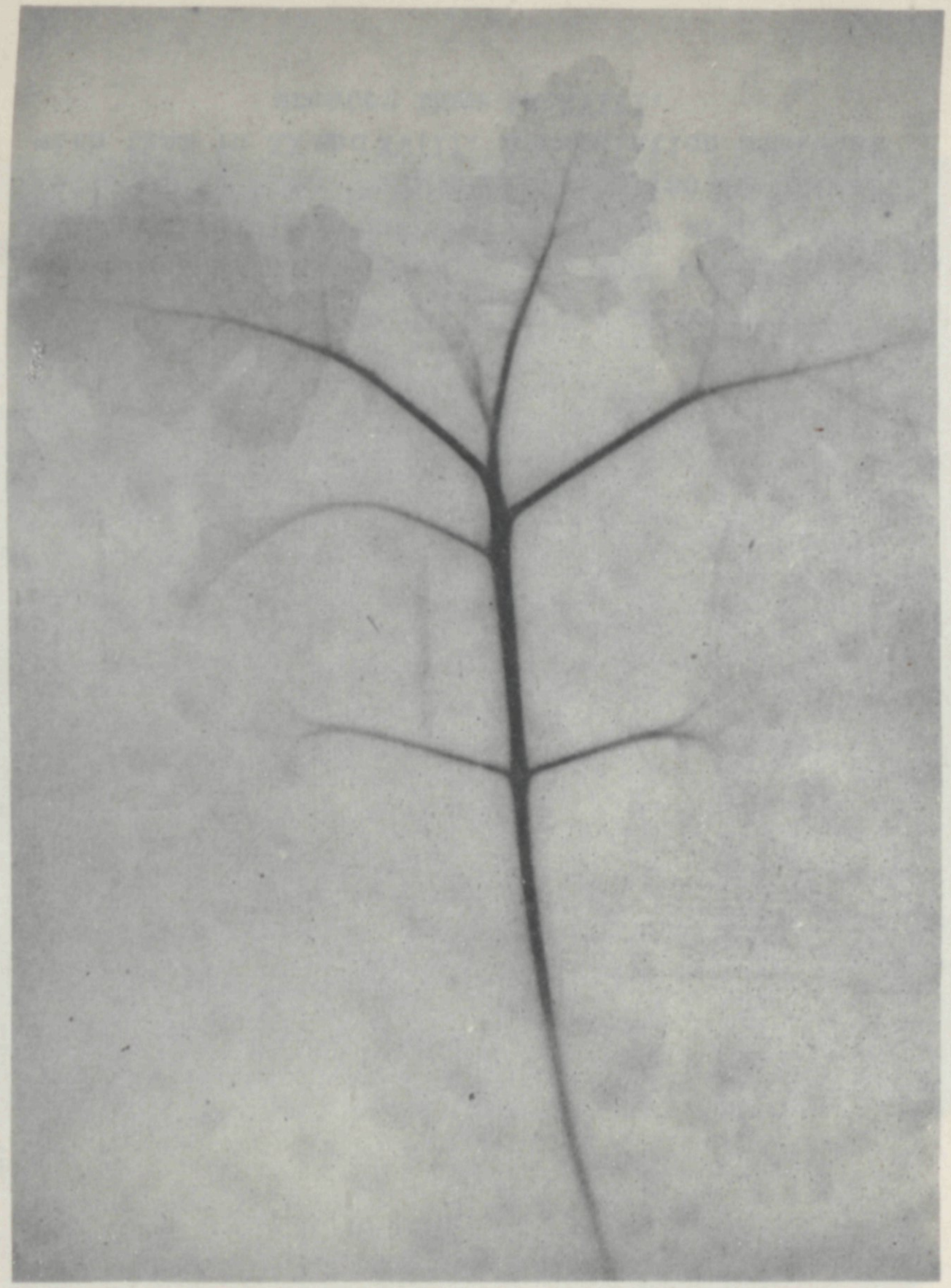
The seedlings in XVII, XVIII and XIX were autoradiographed in the dry state in contrast with those in XX, XXI and XXII. Those shown in XVII were cultured in a nutrient solution with a Ca/K ratio of 5 : 3. Very considerable uptake and translocation of sodium. Distribution in the leaf fairly uniform with some accumulation in the leaf tips.



x1

XVIII. MUSTARD *(Sinapis alba)*

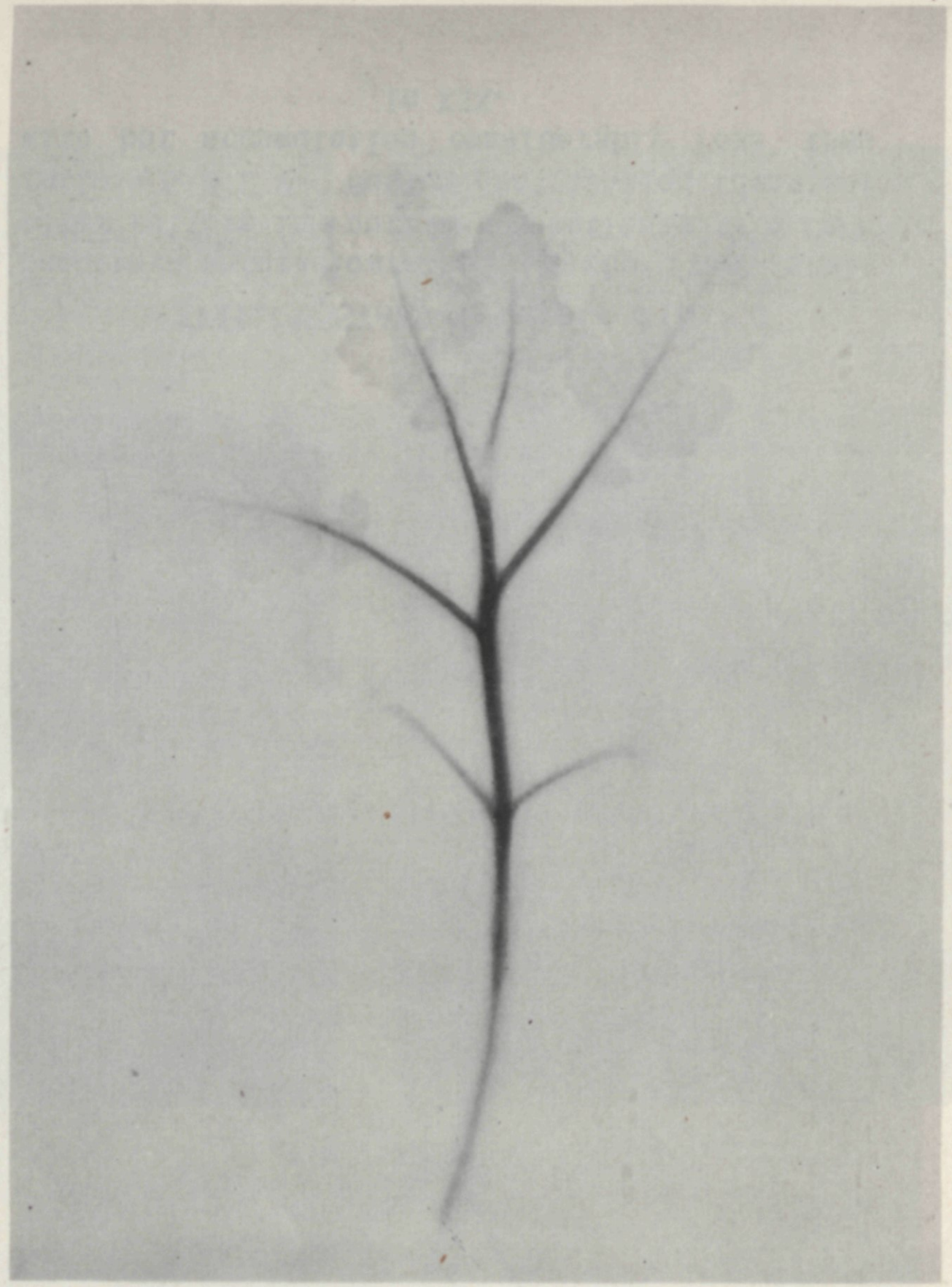
Seedlings autoradiographed in the dry state after culture in a nutrient solution with a Ca/K ratio of 15 : 3. Uptake less than with a Ca/K ratio of 5 : 3 (XVII) or of 5: 9 (XIX). Accumulation and distribution as in XVII.



x1

XIX. MUSTARD *(Sinapis alba)*

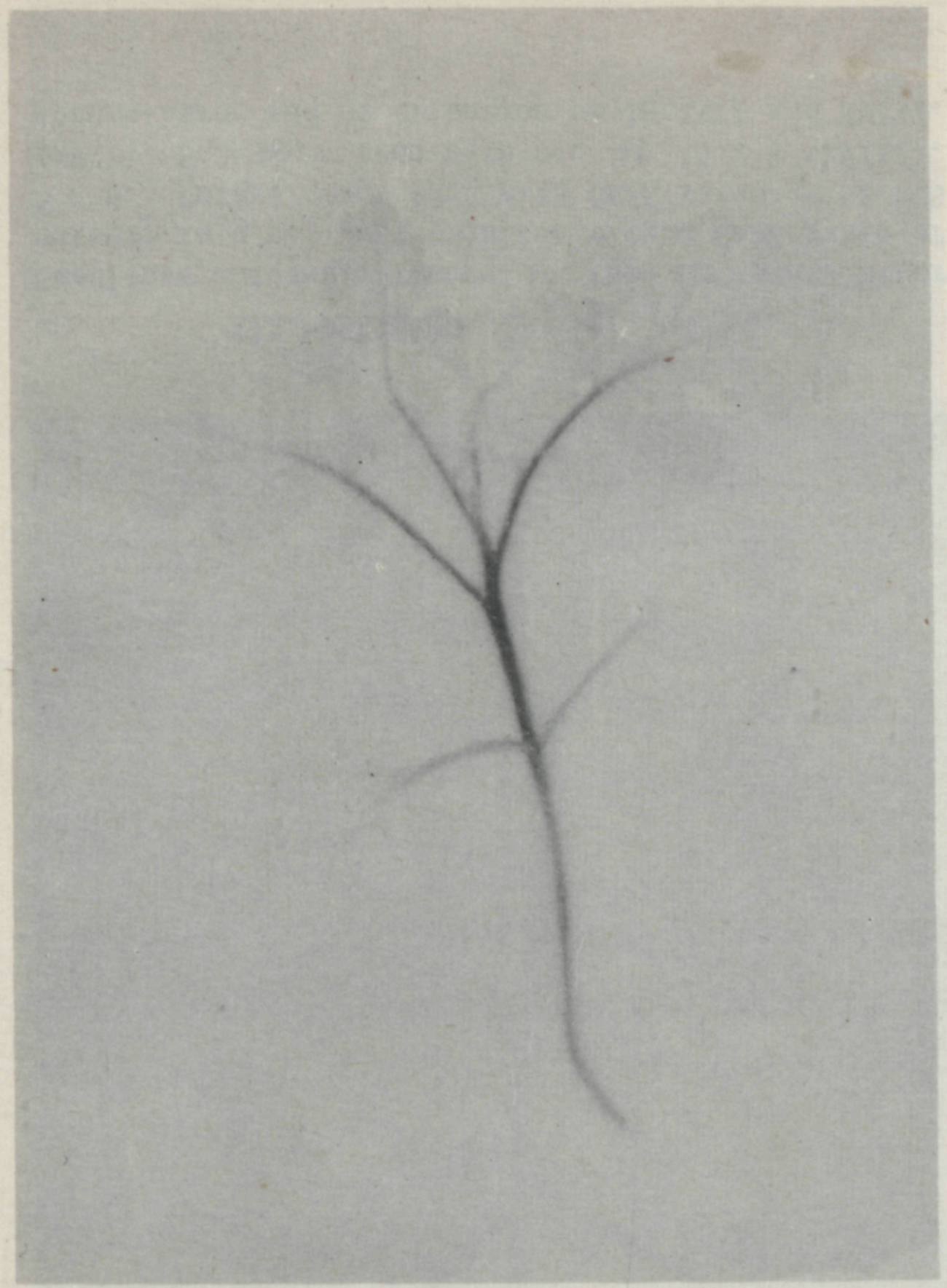
Seedlings autoradiographed in the dry state after culture in a nutrient solution with a Ca/K ratio of 5 : 9. Uptake less than with Ca/K ratio of 5 : 3 (XVII), but more than with one of 15 : 3 (XVIII). Accumulation and distribution as in XVII and XVIII.



x1

XX. MUSTARD *(Sinapis alba)*

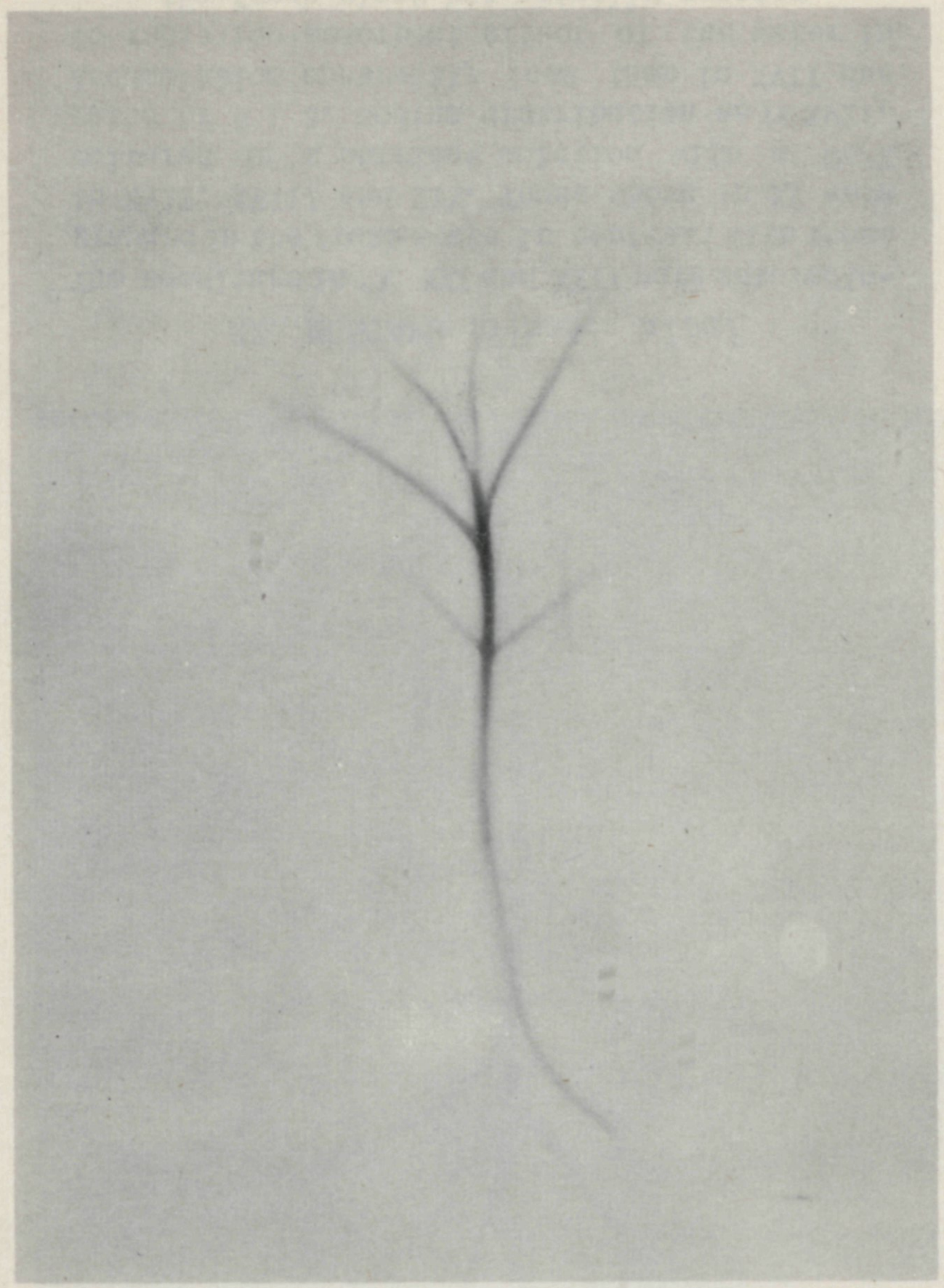
The seedlings in XX, XXI and XXII were autoradiographed in the fresh state in contrast with those in XVII, XVIII and XIX. Those shown in XX were cultured in a nutrient solution with a Ca/K ratio of 5 : 3. Sodium distribution as in XVII. Accumulation apparently less than in XVII due to radiation-absorbent effect of the water in the fresh plant but actually greater.



x 1

XXI. MUSTARD *(Sinapis alba)*

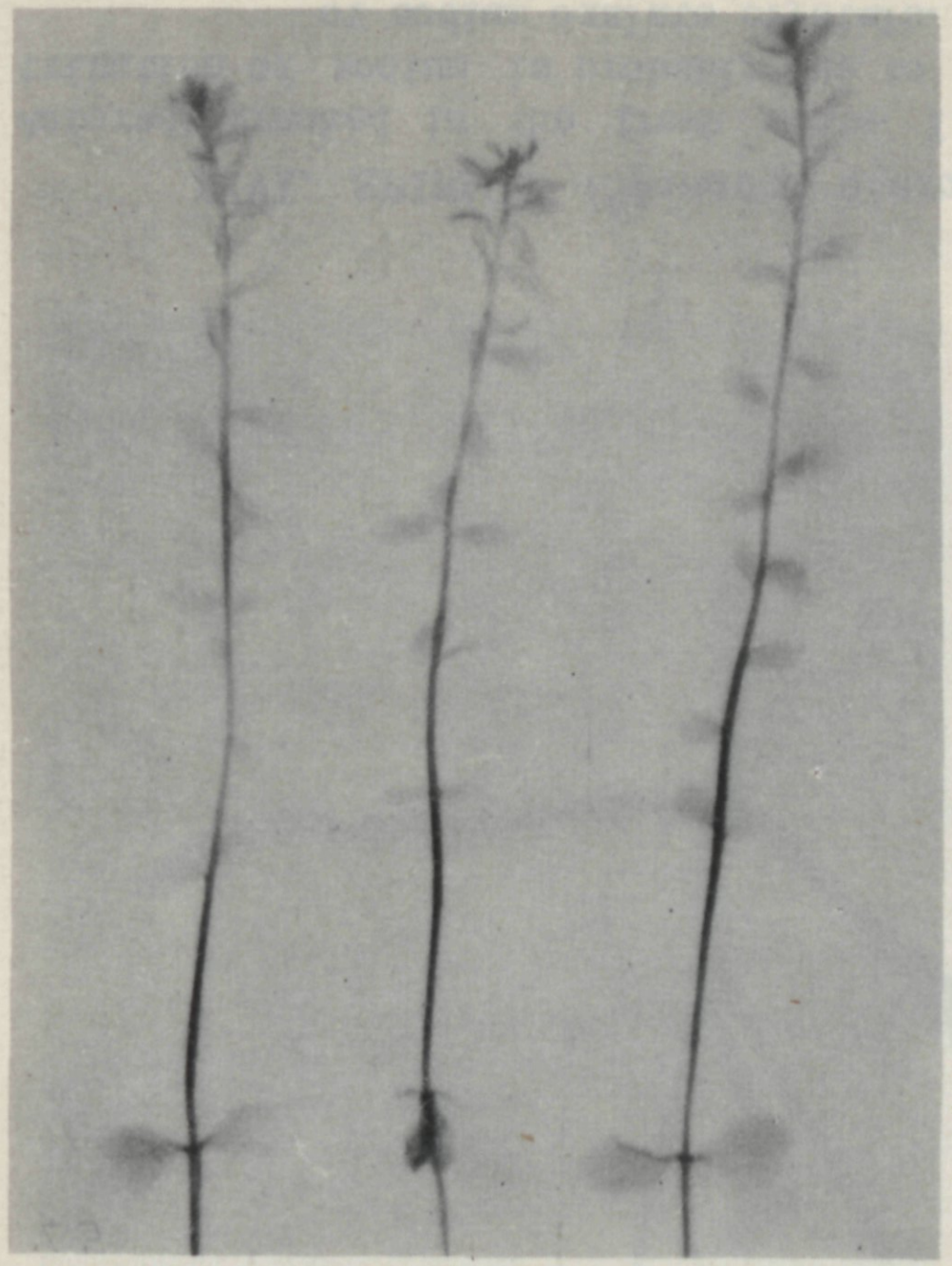
Seedlings autoradiographed in the fresh state after culture in a nutrient solution with a Ca/K ratio of 15 : 3. Sodium distribution identical with that in XX and XVIII. Accumulation somewhat greater than in XVIII.



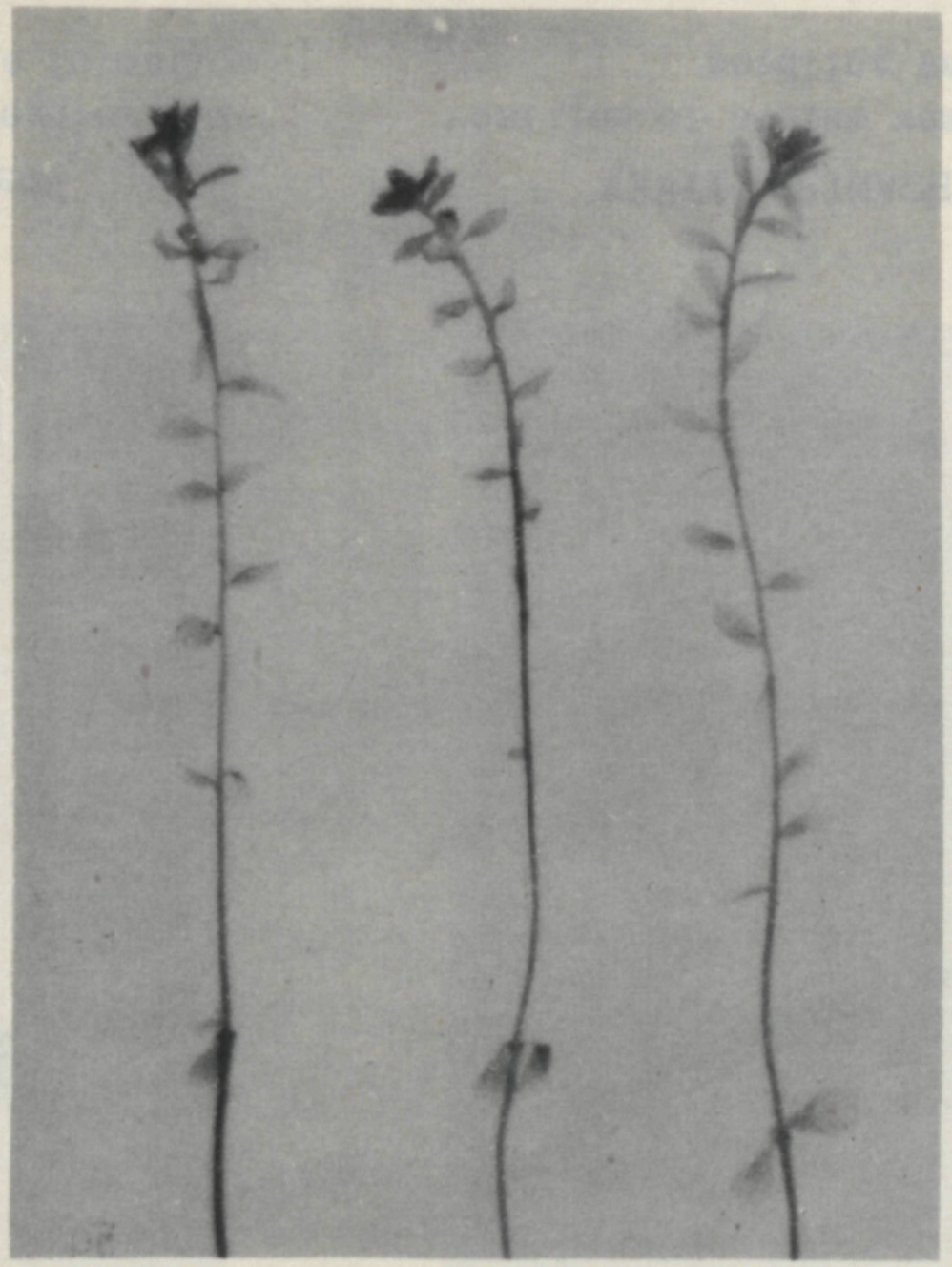
x 1

XXII. MUSTARD *(Sinapis alba)*

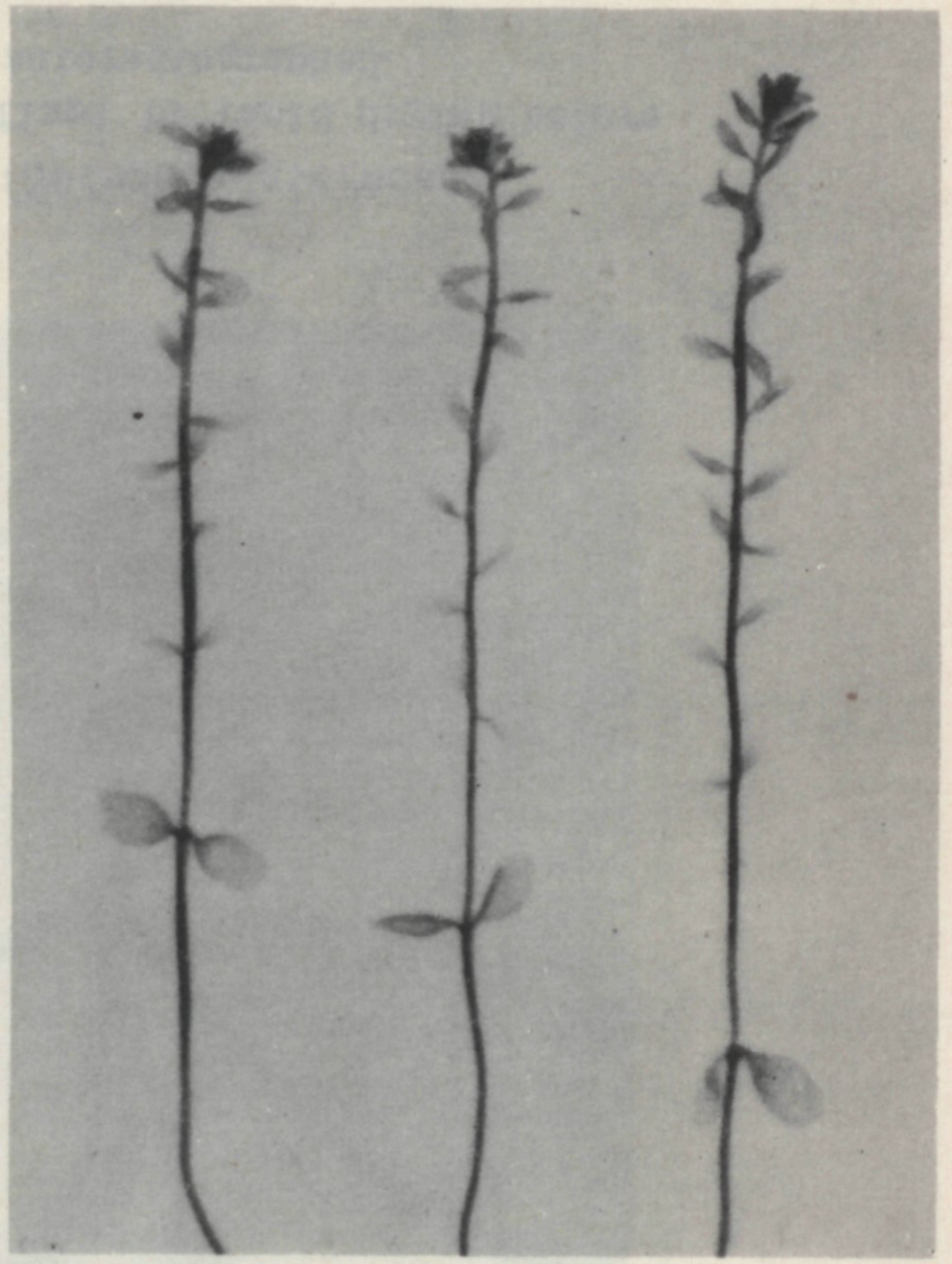
Seedlings autoradiographed in the fresh state after culture in a nutrient solution with a Ca/K ratio of 5 : 9. Sodium distribution identical with but accumulation considerably less than in XIX.



XXIII x ¾



XXIV x ¾



XXV x ¾

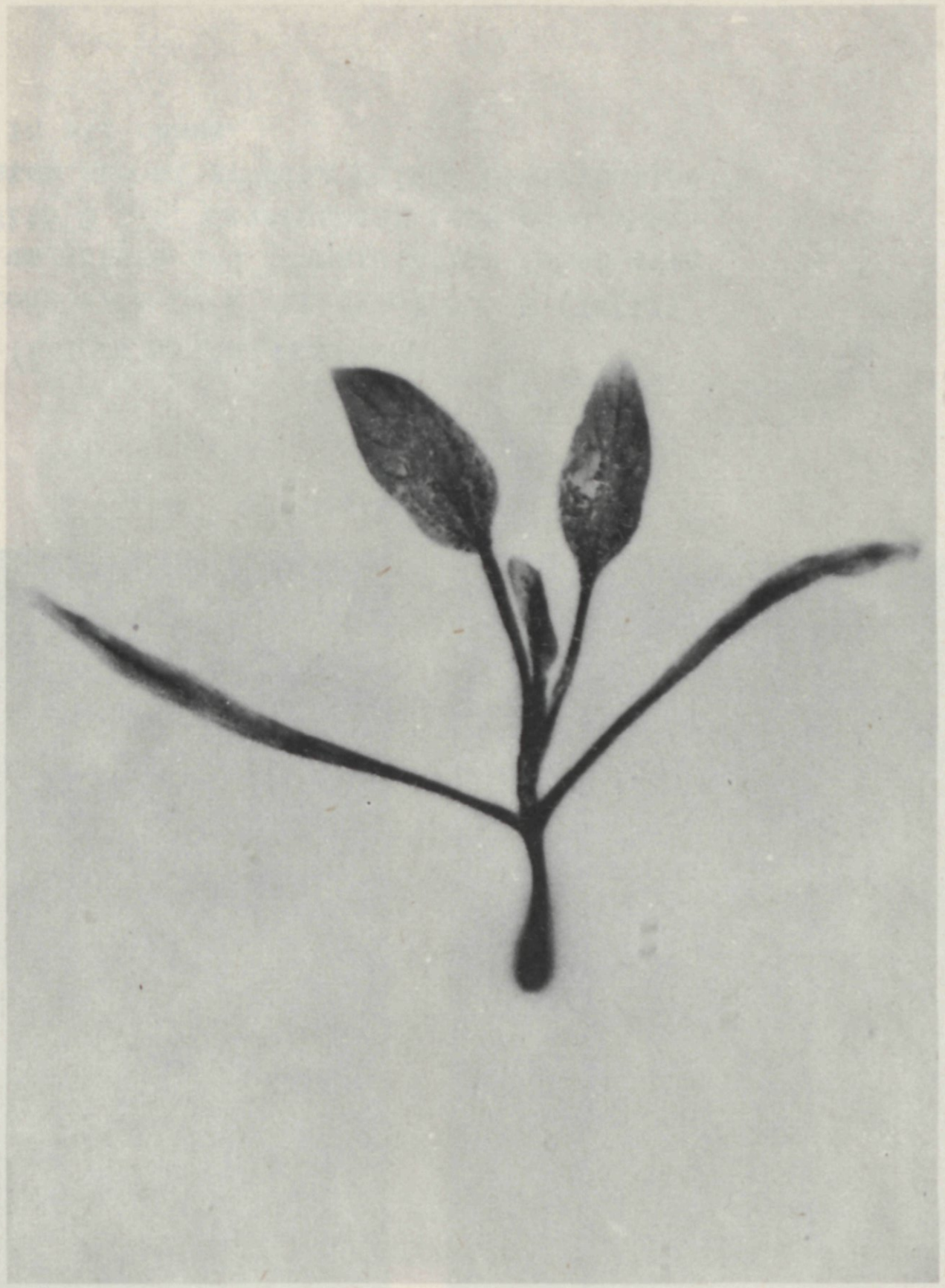
XXIII – XXV. FLAX *(Linum usitatissimum)*

Plants cultured in nutrient solutions with Ca/K ratios of 5 : 3 (XXIII), 15 : 3 (XXIV) and 5 : 9 (XXV). Sodium uptake and translocation least with 5 : 3 and greatest with 5 : 9. With 5 : 3, development less good. Accumulation at junction of leaf and stem and at growing point. Distribution the same in all cases.

x 1

XXVI. SPINACH *(Spinacia oleracea)*

Autoradiographed in the fresh state. Irregular distribution of sodium is probably due to the formation of sodium oxalate crystals.



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XXVII. SPINACH *(Spinacia oleracea)*

Position of sodium was fixed by rapid drying before seedling was autoradiographed.

CHAPTER V.

THE INFLUENCE OF CONCENTRATION OF RADIOACTIVE SODIUM AND OF DURATION OF UPTAKE UPON DRY-MATTER PRODUCTION AND UPON UPTAKE AND DISTRIBUTION OF SODIUM IN THE LEAF, STEM AND ROOT OF THE OAT PLANT (Avena sativa var. Marne)

I. INTRODUCTION

The determination of the uptake* and outgo** of sodium ions by the roots of a plant during a given period of development is possible only when use is made of radioactive sodium. The question is, however, whether it is possible to obtain real values for the uptake by the application of this technique.

The opinions of investigators differ concerning the positive or negative effects of small quantities of radioisotopes upon plants.

Radiation effects can be caused by either external or internal irradiation (264). As a result of these, genetic and biochemical changes can take place in the plant cell. Any effect to which internal irradiation may give rise will influence the cell activities in the meristematic parts of the plant -in which phosphate and sodium accumulate- to a greater extent than in any other part. However, whether or not radioactive radiation is able to influence the plant in any way, a possible effect is dependent upon the amount of radioactive material which is present in the plant and, therefore, upon the ratio of non-radioactive to radioactive element in the substrate and upon the capacity of the plant to accumulate the element in question. Moreover, the type of radiation emitted by the element is of importance. It appears from the relevant literature (3, 16, 19, 29, 30, 31, 32, 41, 57, 58, 60, 64, 65, 66, 73, 75, 80, 81, 85, 110, 111, 112, 123, 131, 142, 173, 176a, 186, 230, 231, 238, 245, 264) that radioactive isotopes have a neglible effect when they are applied to the culture medium in small amounts in the presence of a large excess of the non-radioactive isotopes. Because practically nothing is known about the effect of radioactive sodium upon plant development it was necessary first to conduct an exploratory experiment to ascertain whether plant development is in fact influenced by radioactive sodium and to obtain some information on the way in which radioactive material should be employed and on what could be discovered about sodium uptake and outgo.

In this experiment it was ascertained:

(1) Whether development of the plant had been influenced by the radioactive isotope,

(2) Whether the total amount of sodium present in the plant after the experiment had been influenced by the radioactive isotope,

* Uptake : the amount of sodium taken up through the root of the plant during the uptake period.

** Outgo : the amount of sodium returned to the nutrient solution through the root during the uptake period.

(3) Whether it was in fact possible to measure the uptake of sodium by means of Na^{22},
(4) How the total amount of sodium and the radioactive sodium taken up was distributed in the root, stem and leaf,
(5) What concentration of Na^{22} in the nutrient solution and what period of uptake could best be used for the definitive experiment.

II. THE DESIGN AND EXECUTION OF THE EXPERIMENT

Since the possible effect upon the plant of radiation from a radioactive isotope is a function of the isotope concentration in the substrate and of the irradiation period (i.e., of the duration of uptake), these two factors were varied in the experiment. In this way it was possible to establish the minimal amount of radioactive sodium which must be applied to give a measurable radioactivity in the plant ash.

The experiment was carried out in 1953 without replication. Oat plants were cultured for 3 weeks as described in Chapter III in a nutrient solution prepared according to the formula of HOAGLAND and BROYER (113). They were then transferred to experimental pots containing nutrient solutions which included 4 m.e. Na as Na_2SO_4, 0.1 m.e. Ca as $CaSO_4$ and either 0, 1/3, 1, 3, 9 or 27 μc. Na^{22} per two litres.

After accumulation* periods of 1/3, 1, 3, 9, 27 or 81 hours, six plants from each of the various nutrient solutions, which differed only in their contents of radioactive sodium, were harvested and the roots were separated from the shoots. In the case of the plants allowed an accumulation period of 27 hours, root, leaf and stem were divided into two halves on harvesting. Information about the experimental design and method is given in greater detail in Appendix 1.

III. THE EXPERIMENTAL RESULTS

The influence of the radioactive isotope upon the plant was ascertained from the fresh weights, dry-matter yields, dry-matter percentages, total contents and percentages of total-sodium and of uptake-sodium of culm and root resulting from the various isotope concentrations in the nutrient solutions and the various accumulation periods. In this unreplicated experiment one of the two variables must be regarded as the replication. In view of the fact that the differences in the figures per uptake period between treatments with various amounts Na^{22} were very small and irregular, while greater differences were found between the various uptake periods, the former variable was taken as the replication.

Every effort was made to select plant material which was uniform. For the series with 27 and 0 μc. Na^{22}, however, insufficient iden-

* Accumulation = the uptake minus the outgo = the amount of sodium present in the plant after the experiment less the amount of sodium present in the plant prior to the experiment.

tical plant material was available and it was therefore necessary to use plants that were better (series 27 μc.) or less well (series 0 μc.) developed than those used in the other series. The fact that the average fresh weights and dry-matter yields of these two series differ somewhat from those of the other series (Tables 3 and 4) is attributable to the use of plant material which differed slightly in its degree of development.

1. The influence of the concentration of the radioactive isotope and of the duration of uptake upon the production capacity of the plants

In Tables 3 and 4, hereunder, the fresh weights, dry-matter yields and dry-matter percentages of culm and root are recorded.

TABLE 3

FRESH WEIGHTS, DRY-MATTER YIELDS AND DRY-MATTER PERCENTAGES OF THE CULM

FRESH WEIGHTS (in g.)

No. μc. Na^{22} per 2 l. nutrient solution	0	1/3	1	3	9	27
Uptake period in hours						
1/3	4.12	4.65	5.61	4.--	4.80	5.17
1	3.40	5.23	5.80	4.51	6.12	5.58
3	3.27	4.77	4.14	4.74	5.96	5.12
9	3.46	5.45	3.74	5.14	5.17	6.56
27	4.91	3.78	4.96	4.53	5.04	5.65
81	7.49	5.82	5.18	5.13	4.82	6.16
Average	4.44	4.95	4.91	4.68	5.32	5.73

DRY-MATTER YIELDS (in g.)

No. μc. Na^{22} per 2 l. nutrient solution	0	1/3	1	3	9	27
Uptake period in hours						
1/3	0.54	0.56	0.70	0.57	0.60	0.66
1	0.50	0.68	0.72	0.56	0.75	0.68
3	0.48	0.62	0.59	0.62	0.81	0.69
9	0.51	0.65	0.54	0.70	0.68	0.89
27	0.63	0.50	0.68	0.58	0.53	0.69
81	0.89	0.67	0.64	0.59	0.55	0.71
Average	0.59	0.61	0.65	0.60	0.65	0.72

DRY-MATTER PERCENTAGES

No. μc. Na^{22} per 2 l. nutrient solution	0	1/3	1	3	9	27
Uptake period in hours						
1/3	13.-	12.-	12.6	13.-	12.4	12.9
1	12.5	13.-	12.5	12.5	12.4	12.1
3	14.6	13.2	14.2	13.2	13.6	13.6
9	14.7	13.-	14.5	13.5	13.1	13.6
27	12.9	13.2	13.8	12.8	10.5	12.3
81	11.9	11.4	12.3	11.6	11.5	11.5

TABLE 4

FRESH WEIGHTS, DRY-MATTER YIELDS AND DRY-MATTER PERCENTAGES OF THE ROOT

FRESH WEIGHTS (in g.)

No. μc. Na^{22} per 2 l. nutrient solution	0	1/3	1	3	9	27
Uptake period in hours						
1/3	1.87	1.83	2.32	1.72	2.46	2.10
1	1.59	1.51	2.51	2.19	2.07	2.12
3	1.61	2.13	1.65	1.94	2.47	2.88
9	1.35	2.96	1.66	2.36	2.39	3.27
27	2.40	1.49	2.13	1.94	1.89	2.37
81	3.08	2.72	2.09	2.54	2.19	2.64
Average	1.98	2.11	2.06	2.12	2.24	2.56

DRY-MATTER YIELDS (in g.)

No. μc. Na^{22} per 2 l. nutrient solution	0	1/3	1	3	9	27
Uptake period in hours						
1/3	0.23	0.22	0.26	0.22	0.24	0.22
1	0.21	0.26	0.28	0.24	0.29	0.25
3	0.21	0.22	0.24	0.22	0.26	0.31
9	0.20	0.28	0.21	0.27	0.24	0.30
27	0.25	0.21	0.25	0.22	0.25	0.28
81	0.28	0.25	0.22	0.24	0.21	0.25
Average	0.23	0.24	0.24	0.24	0.25	0.27

DRY-MATTER PERCENTAGES

No. μc. Na^{22} per 2 l. nutrient solution	0	1/3	1	3	9	27
Uptake period in hours						
1/3	12.4	11.8	11.-	12.6	9.6	10.6
1	12.9	17.3	10.9	10.7	13.8	11.8
3	13.1	10.3	14.5	11.5	10.9	10.6
9	14.5	9.5	12.4	11.2	10.2	9.3
27	10.5	14.1	11.9	11.5	13.2	11.6
81	9.-	9.2	10.4	9.4	9.7	9.6

The analyses of these tables are given in the Appendix 2 (Tables I to VIII).

No important differences are observable either between the fresh weights or between the dry-matter yields with the various concentrations of radioactive sodium or with the various uptake periods (Appendix 2 : Tables I to IV).

The radioactivity of the nutrient solution had no important effect upon the dry-matter percentages of root or culm. The influence of the uptake period was far greater, however (Appendix 2: Tables V and VII). The differences between the dry-matter percentages of the culm after uptake periods of 3 and 9 hours and those after uptake periods of 1/3, 27, 1 and 81 hours may be regarded as very considerable (Appendix 2: Tables VI and VIII).

The influence of the uptake period upon the dry-matter percentages was much less in the root than in the culm. The highest dry-matter percentages from culm and root were found after an uptake period of 81 hours (Appendix 2: Tables VI and VIII).

It cannot be deduced from the data on fresh weights, dry-matter yields and dry-matter percentages of culm or root that a stimulating or suppressing influence was exerted by the radiation emitted by the various amounts of radioactive sodium made available to the plants through the nutrient solutions.

2. The influence of the concentration of the radioactive isotope and the duration of uptake upon the percentages and the total contents of sodium in culm and root

In Tables 5 and 6 respectively, the sodium contents per 100 g. ash and the total contents of sodium in culm and root are recorded.

The analyses of these data are given in Tables IX to XVI of Appendix 2.

TABLE 5

SODIUM PERCENTAGES (in mg. per 100 mg. ash)

	Culm						Root					
μc. Na^{22} per 2 l. nutrient solution	0	1/3	1	3	9	27	0	1/3	1	3	9	27
Uptake period in hours												
1/3	1.5	1.3	1.5	1.6	1.3	1.6	2.9	1.1	3.2	2.8	3.1	2.8
1	1.1	1.3	1.3	1.5	1.5	1.2	2.4	3.4	2.3	3.2	2.-	2.6
3	1.5	0.8	1.1	1.3	1.4	1.4	3.0	0.9	3.2	2.5	2.3	2.8
9	1.7	1.4	2.1	1.1	2.-	1.4	3.9	3.1	3.6	2.1	4.-	4.3
27	1.8	2.6	1.7	2.1	2.-	1.9	4.3	4.4	4.6	5.4	4.2	4.5
81	2.-	2.3	2.5	2.2	2.3	2.2	5.1	6.-	5.-	7.1	4.6	6.1

TABLE 6

TOTAL CONTENTS OF SODIUM (in mg.)

	Culm						Root					
μc. Na^{22} per 2 l. nutrient solution	0	1/3	1	3	9	27	0	1/3	1	3	9	27
Uptake period in hours												
1/3	1.11	1.09	1.54	1.18	1.24	1.53	0.96	1.05	1.25	1.00	1.16	1.06
1	0.83	1.49	1.51	1.21	1.75	1.15	0.81	1.71	1.13	1.12	0.96	1.18
3	0.94	0.71	0.82	1.02	1.51	1.28	1.01	1.01	1.11	1.01	1.05	1.42
9	1.12	1.32	1.47	0.95	1.80	1.71	0.95	1.20	0.95	0.86	1.07	1.65
27	2.07	2.16	1.47	1.82	1.76	2.21	1.75	1.44	1.79	1.68	1.72	1.64
81	2.56	2.57	2.40	1.95	1.96	2.29	1.96	2.24	2.--	1.99	1.43	2.34

The percentages and total contents of sodium per unit of time did not appear to be correlated systematically with the concentration of radioactive sodium. On the other hand, they did appear to be correlated with duration of uptake, though the relationship only became noticeable with the longer uptake periods of 9, 27 and 81 hours.

The percentages and total contents of sodium in culm and root did not appear to be influenced appreciably by the concentration of radioactive sodium (Appendix 2: Tables IX, XI, XIII and XV) but they were influenced appreciably by the duration of uptake, as is clearly seen from the differences in the aggregate percentages and total contents (Appendix 2: Tables X, XII, XIV and XVI).

During the first three hours of uptake, the percentages and total contents of sodium in culm and root decrease somewhat. In view of the fact that before the experiment the plants were cultured in a nutrient solution which contained no sodium, and that during the experimental period their nutrient solution contained only 2 m.e. sodium and 0.05 m.e. calcium, it is reasonable to suppose that the decreases in the percentages and total contents of sodium were due to the time which must necessarily elapse before the plant adapts itself to the changed situation.

During the first 9 hours of uptake, however, the total content of sodium in the root fluctuates irregularly. In the case of both culm and root, the greatest increase per unit of time in the sodium percentage occurs in the period between the 3rd and 9th hour of uptake and it is also during this period that the greatest increase in the total content of sodium in the culm takes place. In the case of the root, however, the greatest increase per unit of time in the total content of sodium occurs between the 9th and the 27th hour of the uptake period, that is, after the 3rd to 9th hour during which the greatest amount of sodium per unit of time is translocated via the root to the culm.

The differences between the percentages and total contents of sodium in culm and root found after uptake periods of 81 or 27 hours and those found after shorter periods of uptake are very considerable.

To summarize, it may be concluded that the accumulation of sodium in culm and root is not influenced by concentrations of radioactive sodium of 0 to 27 μc. per two litres nutrient solution with 2 m.e. sodium and 0.5 m.e. calcium per litre and that these concentrations have no appreciable influence upon the development and production capacity of the plant.

3. *The influence of the concentration of the radioactive isotope and of the duration of uptake upon the sodium taken up by culm and root during the experimental period*

By means of the known radioactivity of the 2 m.e. sodium in the nutrient solution the uptake-sodium (i.e., the sodium taken up during the experimental period) is calculated from the counts obtained from 20 mg. ash (see Chapter III), corrected and reduced to total ash of culm and root. The question is, however, whether the actual sodium uptake can, in fact, be determined from the radioactivity of the plant as, apart from the effect of the active isotope uptake, the radioactivity of the plant may have been increased by isotope exchange.

The variations in the amounts of sodium taken up in uptake periods of 1/3, 1, 3, 9, 27 and 81 hours from nutrient solutions containing 1/3, 1, 3, 9 or 27 μc. radioactive sodium per litre were not systematic.

These variations are, to some extent, ascribable to the experimental error. When measuring the radioactivity of weaker radioactive material (i.e., material obtained when short uptake periods are combined with low concentrations of radioactive sodium in the nutrient solution) the background influences the results to a relatively greater extent than when stronger radioactive material is measured. For this reason, the uptake values found for weaker radioactive material are less reliable and subject to greater variations than those for stronger radioactive material.

TABLE 7

SODIUM UPTAKE BY CULM AND ROOT (in mg.)

	Culm					Root				
$\mu c.$ Na^{22} per 2 l. nutrient solution	1/3	1	3	9	27	1/3	1	3	9	27
Uptake period in hours										
1/3	0.08	0.07	0.03	0.02	0.02	0.40	0.44	0.41	0.44	0.31
1	0.15	0.13	0.08	0.11	0.09	0.61	0.73	0.59	0.59	0.47
3	0.14	0.18	0.16	0.18	0.14	0.65	0.64	0.71	0.80	0.87
9	0.59	0.47	0.44	0.48	0.51	1.--	0.56	0.76	0.69	1.02
27	1.04	0.93	0.83	1.02	1.07	0.79	0.82	0.80	1.02	1.18
81	1.42	1.46	1.47	1.37	1.41	1.51	1.45	1.41	1.40	1.50

It will be seen from Table 7 that the uptake increases with the duration of uptake. As previously mentioned, however, since no systematic correlation appears to exist between uptake values and concentrations of radioactive sodium, the treatments with different

concentrations of radioactive sodium and constant period of uptake were regarded as replications in analysing the results.

In the case of both culm and root only the duration of uptake appreciably influenced the uptake (Appendix 2: Tables XVII and XIX).

The differences between uptake of culm and of root, totalled for the various aggregate amounts of radioactive sodium, increase with the duration of uptake (Appendix 2: Tables XVIII and XX). In the first 27 hours of uptake, the root receives a larger share of the uptake-sodium than the culm. After this period, however, the root and culm share equally in the uptake (Fig. 1). That is to say, after

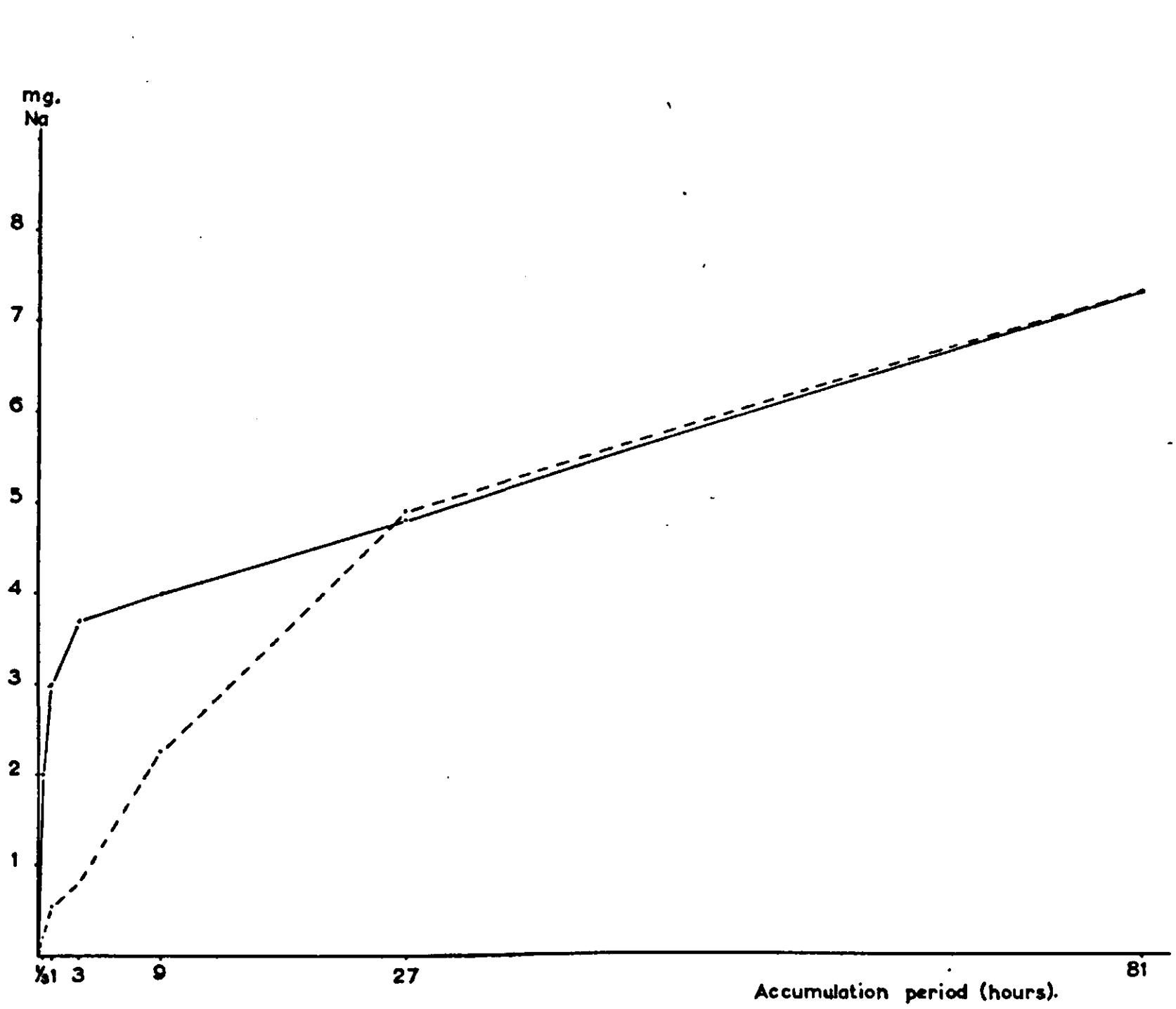


Fig. 1. Uptake-sodium in culms and roots totalled for the replications

---- Uptake-sodium in the culms —— Uptake-sodium in the roots

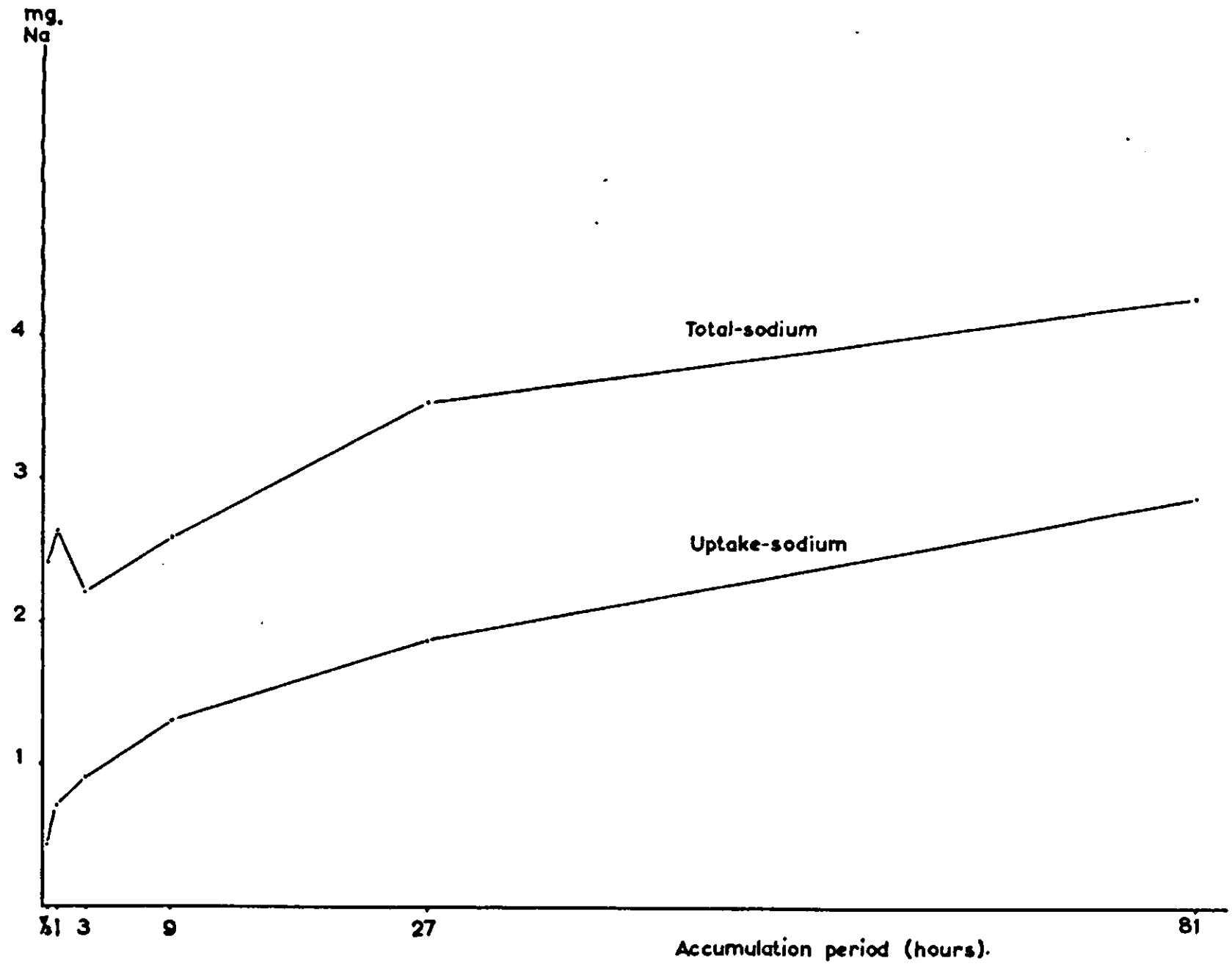


Fig.2.Average contents of total-sodium and uptake-sodium in plants

27 hours, considerable translocation of uptake-sodium from the root to the culm occurs and, at the same time, the uptake-sodium in the root not only maintains its level but actually increases in amount.

The fact that the culm receives less uptake-sodium than the root in the initial stages of uptake indicates that before considerable translocation of uptake-sodium to the culm can occur, part of the sodium which was present in the root before the commencement of the experimental period must first be transferred to the culm. This conception is supported by the fact that the content of total-sodium -that is, uptake-sodium plus original sodium- is consistently higher in the culm (except after an uptake period of 1/3 hour) than in the root (Appendix 2: Tables XIV and XVI) while, although the amount of uptake-sodium entering the culm during the first 27 hours of uptake is appreciable, it is considerably less than the amount retained by the root (Fig.1).

It is possible, however, that, as a result of isotope exchange, the uptake values found were too high.

If the total-sodium in culm and root is equated with the accumulation, it follows that in all plants of these treatments the actual accumulation has increased by the same amount of sodium. If the uptake values were in fact correct, the outgo values must also

have been increased by the same amount, since accumulation is equal to uptake minus outgo.

The trend of the outgo curve will therefore remain unchanged during the uptake period of 81 hours. Since it has been experimentally found that accumulation and uptake exhibit the same trend in that both diminish as duration of uptake lengthens (Fig. 2), and in view of the relationship between uptake and outgo, this same trend must also apply to outgo. It appears, therefore, that during the uptake period, the uptake and outgo have the same trend as the sodium accumulations determined by flame photometer.

This allows of the conclusion that the sodium uptake during the experimental period can, in fact, be measured by means of radioactive sodium and that the isotope-exchange process has therefore very little influence upon the uptake. It has, moreover, previously been demonstrated (Appendix 2: Table XVII and XIX), that the concentration of radioactive sodium in the nutrient solution has no appreciable influence upon the sodium uptake. Thus the values found for the uptake may be accepted as true. In this type of experiment, in which low-salt plants are used, the isotope-exchange process plays a very unimportant role in comparison with that of ion uptake. Hence it may be concluded that the determination of the uptake by means of physical measurements is justifiable.

4. The distribution of the content of total-sodium and of the sodium taken up during the experimental period (uptake-sodium) in leaf, stem and root after an accumulation period of 27 hours

After an accumulation period of 27 hours the plants of this series were grouped in accordance with the concentration of radioactive sodium (i.e., 0, 1/3, 1, 3, 9, 27 μc.) in the nutrient solution and harvested. The leaves, stems and roots were divided into upper and lower halves for analysis purposes while the rhizomes which were over-developed owing to the seed having been planted too deeply, were analysed separately.

TABLE 8

DISTRIBUTION OF TOTAL-SODIUM IN THE PLANT AFTER AN ACCUMULATION PERIOD OF 27 HOURS (in mg.)

	a							b						
	Per total ash of plant part						Average	Per 100 mg. ash						Average
μc. Na^{22} per 2 l. nutrient solution	0	1/3	1	3	9	27		0	1/3	1	3	9	27	
Part of the plant Upper half of leaf-blade	0.23	0.16	0.20	0.25	0.32	0.42	0.26	1.1	1.1	1.1	1.2	1.3	1.4	1.2
Lower half of leaf-blade	0.50	0.45	0.42	0.40	0.33	0.49	0.43	1.7	1.8	1.5	1.7	1.5	1.5	1.6
Upper half of stem	0.32	0.50	0.25	0.40	0.30	0.50	0.38	1.5	2.3	1.6	2.-	2.1	2.5	2.-
Lower half of stem	1.03	1.06	0.60	0.77	0.80	0.82	0.85	3.7	5.1	2.5	3.6	3.1	3.2	3.5
Rhizome	0.33	0.45	0.52	0.54	0.52	0.41	0.46	4.2	4.7	5.1	6.5	4.8	4.6	5.-
Upper half of root	0.91	0.50	0.80	0.51	0.73	0.91	0.73	3.5	2.8	3.6	3.1	3.1	4.5	3.4
Lower half of root	0.35	0.43	0.34	0.42	0.33	0.32	0.37	5.2	6.6	5.0	6.6	4.8	4.3	5.4

TABLE 9

DISTRIBUTION OF UPTAKE-SODIUM IN THE PLANT AFTER AN ACCUMULATION PERIOD OF 27 HOURS (in mg.)

	a						b					
	Per total ash of plant part					Average	Per 100 mg. ash					Average
μc.Na^{22} per 2 l. nutrient solution	1/3	1	3	9	27		1/3	1	3	9	27	
Part of the plant												
Upper half of leaf-blade	0.057	0.058	0.047	0.092	0.157	0.082	0.38	0.31	0.23	0.37	0.53	0.36
Lower half of leaf-blade	0.175	0.179	0.143	0.165	0.208	0.174	0.71	0.64	0.61	0.73	0.64	0.67
Upper half of stem	0.303	0.199	0.263	0.269	0.311	0.269	1.41	1.25	1.30	1.89	1.57	1.48
Lower half of stem	0.549	0.467	0.392	0.459	0.400	0.453	2.64	1.96	1.84	1.78	1.47	1.96
Rhizome	0.137	0.155	0.203	0.203	0.252	0.190	1.43	1.53	2.44	1.89	2.81	2.02
Upper half of root	0.413	0.521	0.409	0.601	0.714	0.532	2.49	2.81	2.48	2.57	3.55	2.78
Lower half of root	0.239	0.120	0.188	0.222	0.204	0.195	3.68	3.11	2.99	3.27	2.76	3.16

It appears from the tables that the amounts of total-sodium (Table 8a; Fig. 3) and of uptake-sodium (Table 9a; Fig. 4) differ in the various parts of the plant.

Total-sodium and uptake-sodium are present in greatest quantity in the lower half of the stem and the upper half of the root. In leaf, stem and root they become progressively less in amount with advance from the base towards the tip. The percentages of total-sodium and uptake-sodium of the upper and lower halves of stems and leaves exhibit trends similar to those of the contents of total-sodium and uptake-sodium.

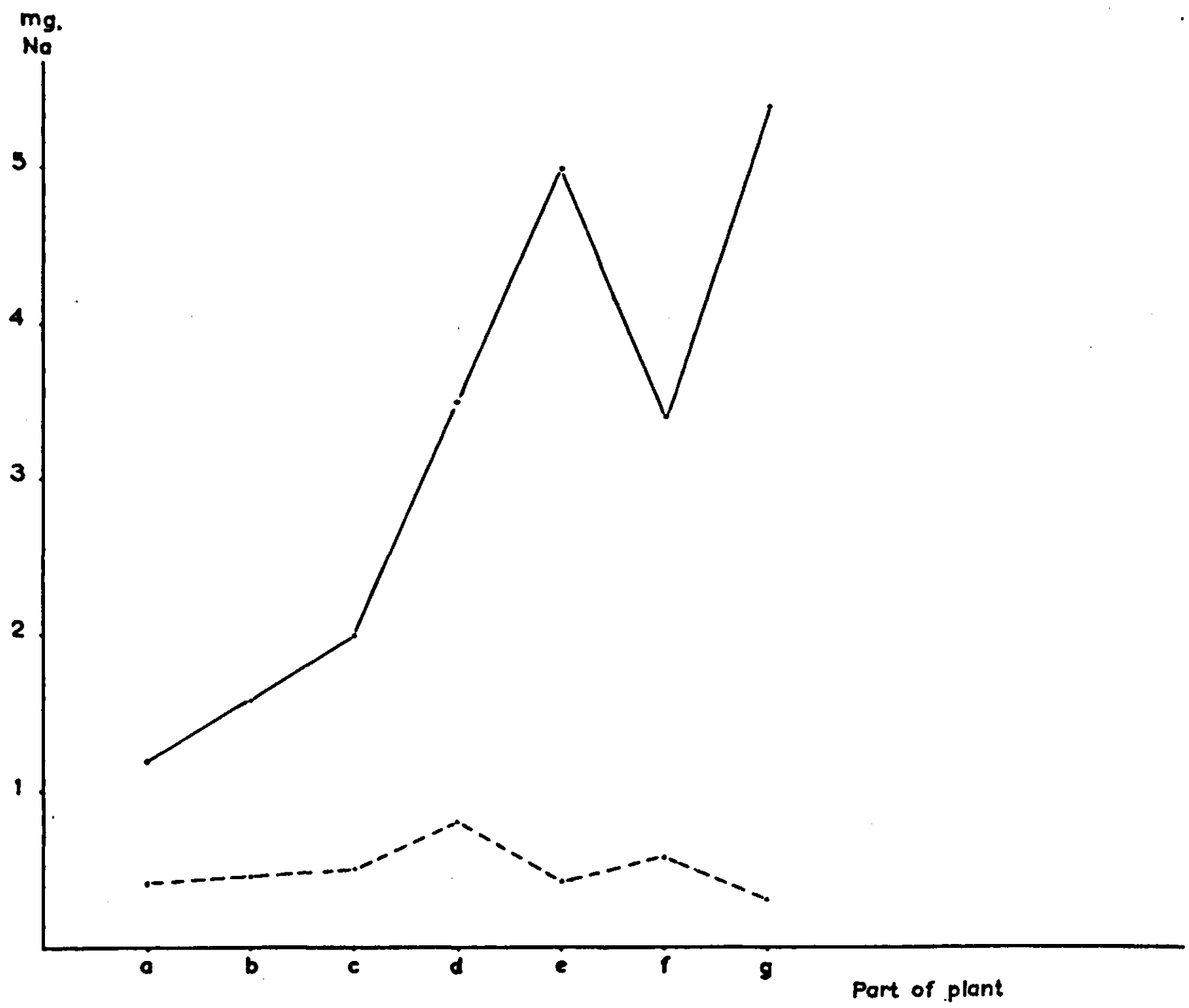


Fig. 3. Average contents of total-sodium in the various parts of the plant

——— Contents of total-sodium per 100 mg. ash
- - - Contents of total-sodium per part of plant

a. Upper half of leaf-blade
b. Lower half of leaf-blade
c. Upper half of stem
d. Lower half of stem
e. Rhizome
f. Upper half of root
g. Lower half of root

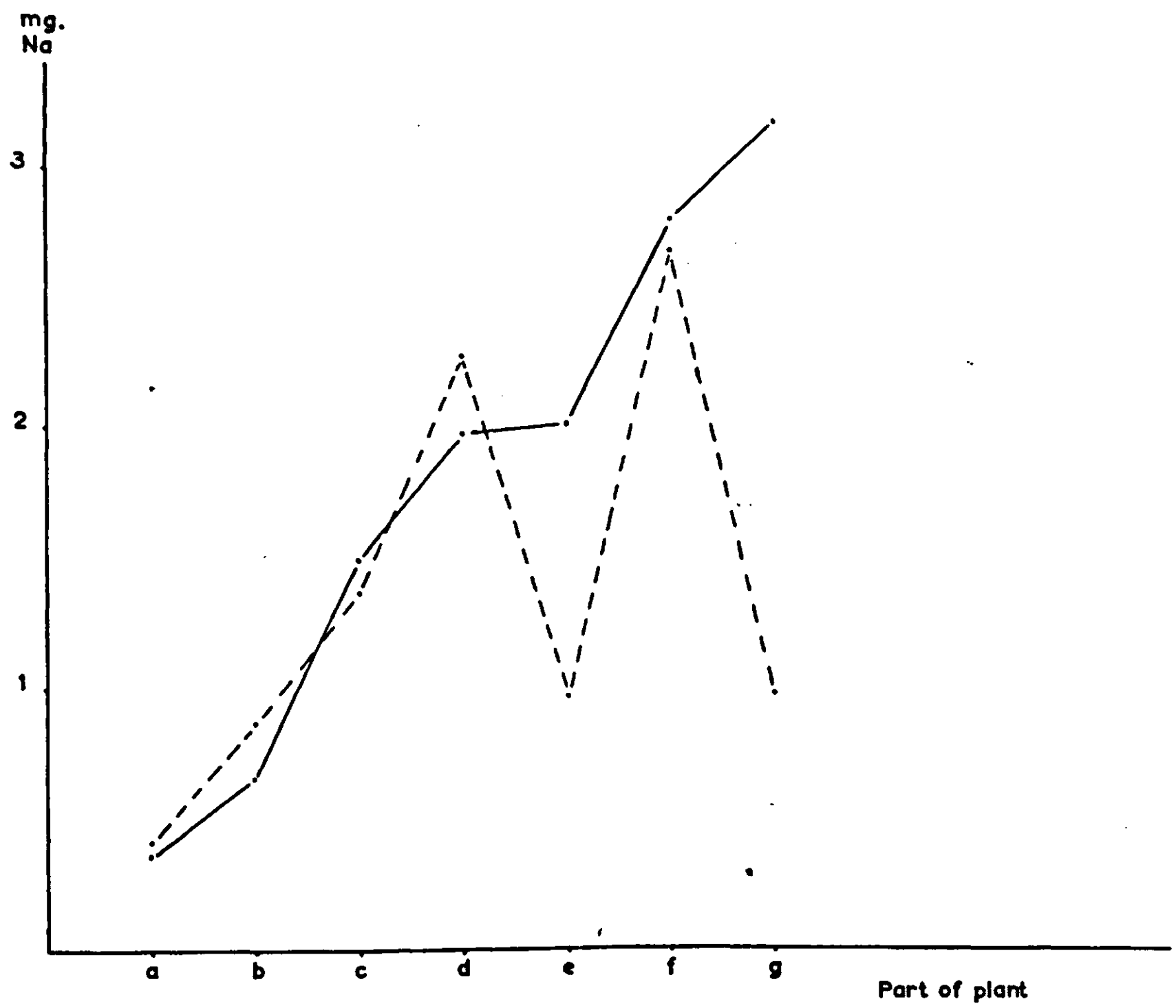


Fig. 4. Average contents of uptake-sodium in the various parts of the plant

—— Uptake-sodium per 20 mg. ash
- - - Uptake-sodium per part of plant

a. Upper half of leaf-blade
b. Lower half of leaf-blade
c. Upper half of stem
d. Lower half of stem
e. Rhizome
f. Upper half of root
g. Lower half of root

In the rhizome and in the lower half of the root, only very small amounts of total-sodium and uptake-sodium are found (Tables 8a, 9a; Figs. 3 and 4). These parts, however, appear to possess the highest percentages of total-sodium, (Table 8b; Fig. 3). They are the parts which grow most quickly and in which great cell activity has occurred.

This is in excellent agreement with the findings in Chapter III and IV, namely, that in parts in which great cell activity prevails, proportionally great amounts of sodium are accumulated.

Since, in contrast with the lower half of the root, the rapid development of the rhizome had already ceased before the commencement of the experimental period, and in view of the relationship between sodium accumulation and cell activity, it is to be expected that the percentages of uptake-sodium in the rhizome and in the stem will differ little and that the percentage of uptake-sodium in the lower half of the root will be greater than that in the upper half where, during the experimental period, less growth takes place. This assumption, based upon the difference in cell activity between rhizome and the lower half of the root, was, in fact, confirmed by the results (Table 9b; Fig. 4). Moreover, the data for uptake-sodium support the results presented in Chapter III and IV, from which it appeared that sodium is accumulated in tissues in which division of cells occurs.

The analyses of Tables 8 and 9 are to be found in Appendix 2: Tables XXI to XXIV. From these, it is apparent that the total contents and percentages of total-sodium and uptake-sodium present in a given plant part depend chiefly upon the plant part in question. It is further apparent that the concentration of radioactive sodium in the nutrient solution has no important influence upon the distribution of the sodium in the plant.

The differences between the contents of total-sodium and of uptake-sodium in the leaf, stem and root are considerable (Appendix 2: Tables XXV and XXVII). The contents of total-sodium and uptake-sodium in the lower half of the stem and in the upper half of the root are considerably greater than in the other parts of the plant.

The differences in the percentages of total-sodium and of uptake-sodium between the two halves of the different parts of the plant are, in general, considerable (Appendix 2: Tables XXVI and XXVIII). Only the difference in percentage of total-sodium between the lower and upper half of the leaf is unimportant. In general, it appears that the lower halves of stems and leaves have higher contents and higher percentages of total-sodium and uptake-sodium than do the upper halves. In the roots, the contents of total-sodium and uptake-sodium are higher in the upper halves and the percentages are higher in the lower halves.

IV. CONCLUSIONS

(1) The concentration of radioactive sodium in the nutrient solutions was found to have exercised no important influence upon either

the fresh weights, the dry-matter yields, the dry-matter percentages or the contents, the percentages and the distribution of total-sodium in the different parts of the plant. Otherwise expressed, no stimulating or suppressing effect from external or internal irradiation from radioactive sodium concentrations of 0 to 27 μc per two litres of nutrient solution were observed during optake periods ranging from 1/3 to 81 hours.

(2) The duration of the uptake period was found to have a considerable influence on the dry-matter percentages and the contents and percentages of total-sodium and uptake-sodium of the culm and root. Important differences were found between the contents and percentages of total-sodium and uptake-sodium of the various parts of the plant.
In general, the contents and percentages of total-sodium increase with the duration of uptake. The increase per unit of time is reduced as the uptake period is lengthened. The lower halves of the leaves or stems have greater contents and higher percentages of total-sodium and uptake-sodium than the upper halves. In case of the root more sodium and a lower sodium percentage being found in its upper half.

(3) Sodium is accumulated in tissues where great cell activity prevails.

(4) Sodium taken up by the root is translocated to the stem in an appreciable degree only after sodium which was already present in the root has entered the stem.

(5) In the case of low-salt plants, ion exchange plays a secondary role in the ion uptake and this enables the amount of sodium taken up during the experiment to be calculated directly from measurements of the radioactivity of the plant.

Although it appeared from this exploratory experiment that relatively large amounts of radioactive sodium in the nutrient solutions have no influence upon the development, production capacity or sodium uptake of the plant, it is advisable, in order to preclude every possibility of a stimulating or suppressing effect, to use no more radioactive sodium than is absolutely necessary. As the radioactivity of 20 mg. ash must be readily measurable (at least 100 c.p.m.) and as the uptake of Na^{22} is dependent upon the ratio of the radioactive to non-radioactive sodium in the nutrient solution, upon the ability of the plant to accumulate sodium and upon the duration of the uptake period, the concentration of radioactive sodium employed must, however, be large enough to meet these requirements. For these reasons a concentration of radioactive sodium of 3 μc. per two litres of nutrient solution was chosen in the experiment with oats described in Chapter VI. Since an increase in the uptake period results in greater radioactivity of the plant ash and since, moreover, the sodium accumulation per unit of time decreases as the uptake period is lengthened, (causing progressive flattening of the uptake curve) the uptake period chosen for the experiment described in the following chapter was extended from 81 to 144 hours.

CHAPTER VI

THE UPTAKE AND OUTGO OF SODIUM IONS IN OATS

(Avena sativa var. Marne)

I. INTRODUCTION

The degree to which a certain element is accumulated by a plant is measured by the difference between the amounts of the element contained in the plant before and after the period during which accumulation occurs. The accumulation, the extent of which is dependent upon the activity of the living organism, is the resultant of the uptake and of the outgo of the element or the nutrient ion.

Normal chemical methods cannot be used to determine the uptake and outgo, because no differentiation can be made chemically between the ions of an element present in the plant before the experiment and the ions of that same element taken up by the plant during the experiment. Nor can a chemical method of determination differentiate between the ions of the same element originally present in the nutrient solution and those which were transferred to the nutrient solution from the plant during the experiment. For these reasons, Na^{22} was used in this research on sodium.

II THE DESIGN AND EXECUTION OF THE EXPERIMENT

1. The design of the experiment

A member of the Gramineae known to be a moderate accumulator of sodium was chosen as the experimental plant, namely, oats (*Avena sativa* variety Marne).

The culture of the plants before the experiment and the general conditions of the experiment were described in Chapter III. This section is, therefore, limited as far as possible to details of the circumstances under which the experiment was carried out.

The experiment may be divided into three periods as follows:

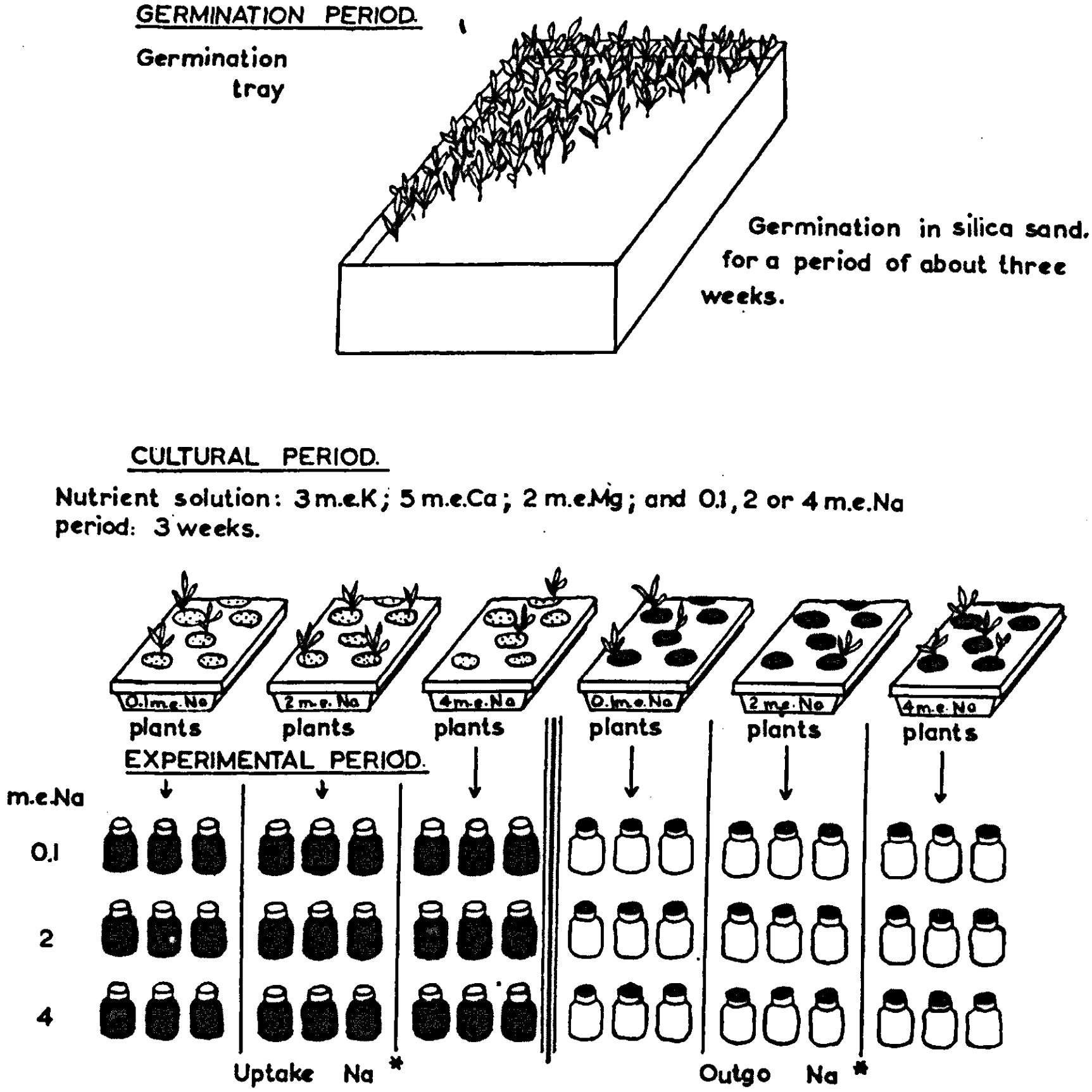


Fig. 5. Experimental design

(1) The germination period

The oats were sown in silica sand on 21st April 1953. The seedlings appeared above the ground on 1st May.

(2) The cultural period

On 7th May the plants, all 8 cm. in height and visually assessed as being in all respects comparable, were placed in corks and made secure with cotton-wool, six to a cork. The corks were then transferred to twelve culture trays, which were each filled with 1.050 cc. of a nutrient solution, the composition of which is given in Chapter III. In six of the trays 1.5 μc. Na^{22} as $NaNO_3$ was added per litre nutrient solution. In this way the nutrient solutions were divided into a radioactive group and a non-radioactive group. Each group was further divided into three sodium levels by the addition of 0.1, 2 or 4 m.e. Na^{23} as Na_2SO_4 per litre nutrient solution. Thus there were two culture trays per sodium level per group. Each tray contained 7 corks.

The plants in the non-radioactive group were used for the investigation on the uptake and those in the radioactive group for the investigation on the outgo of sodium. To ensure that plants with low salt content were obtained, the nutrient solutions were not renewed during the culture period and no aeration was given.

(3) The experimental period

After a cultural period of three weeks the experimental units, each consisting of one cork with six plants 28-30 cm. in height, were transferred to the experimental pots. These pots had a volume of approximately 200 cc. and contained 150 cc. of a nutrient solution which consisted of 0.05 m.e. $CaSO_4.2\ H_2O$ and 0.1, 2 or 4 m.e. Na_2SO_4 per litre.

The two experiments, the one relating to the uptake and the other to the outgo, which will be referred to hereafter as Experiment A and Experiment B respectively, were both carried out in triplicate. (See Figure 5 - Experimental design.)

The non-radioactive plants for Experiment A were transferred to the experimental pots containing the radioactive nutrient solutions with 1.5 μc. Na^{22} per litre; the radioactive plants for Experiment B were transferred to the experimental pots containing the non-radioactive nutrient solutions.

The plants were distributed among the pots in such a way that some from each sodium level of cultural solution were placed in each sodium level of experimental solution, namely 0.1, 2 and 4 m.e. per litre.

When all the pots were duly planted the remaining plant material was harvested. The roots were rinsed off with an excess of demineralized water, rinsed again with distilled water and squeezed out. These plants were divided into culm and root, the parts then being analysed for sodium.

The pots were regularly aerated with air filtered through cotton-wool and glass-wool in the manner described in Chapter III.

After an experimental period of six days the plants were harvested. Their roots were treated in the same way as were those of the plants previously harvested. Subsequently the culms were separated from the roots.

2. The treatment and analysis of the plant material

The fresh and dry weights of both the roots and culms were determined in groups of six. The material was then ashed and the ash content determined. The sodium content of the ash was measured by flame photometer. In determining the radioactivity of the plant material 20 mg. ash was consistently used. The radioactivity of the nutrient solutions was determined before and after the experiment. The methods employed for the determination of the radioactivity and for the analysis are described in Chapter III. The working-up of the values obtained was carried out in the manner described in Appendix 3.

Attention is here drawn to the fact that when reference is made to the plant, root or culm, an experimental unit of six plants is concerned.

III. THE EXPERIMENTAL RESULTS

The analytical results which, as has already been stated, were based partly on chemical and partly on physical determinations, were grouped as follows:

(1) The results of the chemical analysis of the plants of Experiments A and B.
(2) The results of the physical determinations carried out on the plants of Experiments A and B.
(3) The outgo of the sodium ions taken up during the germination and cultural periods (Experiment B).
(4) The vice-versa effect.
(5) The distribution of the sodium ions between the culms and roots of the plants after the cultural period.
(6) The distribution of the sodium ions between the culms and roots of the plants after Experiment A.
(7) The distribution between the culms and roots of the plants of the sodium ions taken up during the experimental period and of those present in the plants before the experiment.
(8) The influence of the experimental conditions upon the distribution and translocation of the sodium ions taken up during the cultural period.

1. The results of the chemical analysis of the plants of Experiments A and B

(1) Sodium contents of the plants before the experiments

Only very minute amounts of radioactive material were used. In the experiment described in Chapter V it was found that, even in

the presence of higher radiation intensity, the absorption of sodium was in no way influenced by radiation. In view of this, it may be assumed that in Experiments A and B radiation had no effect upon the amounts of sodium accumulated.

TABLE 10

AVERAGE RADIOACTIVE AND NON-RADIOACTIVE SODIUM CONTENTS OF THE PLANTS AFTER THE CULTURAL PERIOD

Sodium contents of cultural nutrient solutions (in m.e. per litre)	0,1		2		4	
	Radio-active	Non-radio-active	Radio-active	Non-radio-active	Radio-active	Non-radio-active
Sodium contents of the plants after the cultural period (in mg.)	1.21	1.22	4.93	4.99	7.53	7.03

From the average amounts of sodium determined in the plants cultured in radioactive and non-radioactive nutrient solutions (Table 10), it appears that this assumption is completely justified. Thus the average amount of sodium present in the plants before the experiment can be taken as the average of the amounts which were present in all plants in both the radioactive and the non-radioactive groups at that time. The averages for the plants cultured in the nutrient solutions containing 0.1, 2 and 4 m.e. sodium were 1.22 ± 0.02, 4.96 ± 0.08, and 7.28 ± 0.50 mg. sodium respectively. These amounts correspond with sodium concentrations of 191.5, 779.8 and 1090.1 mg. respectively per litre moisture in the fresh material. From this it appears that the sodium levels of the nutrient solutions considerably influenced the amounts of sodium taken up by the plants. The average amounts taken up by the plants cultured in the nutrient solutions containing 2 and 4 m.e. sodium are 306.5% and 496.7% respectively more than those taken up by the plants in the 0.1. m.e. solution.

2. *Changes in the sodium contents of the plants during the experimental period*

The amounts of sodium present in the plants of corresponding treatments in Experiment A and Experiment B (Table 11) differ by only a few per cent.

TABLE 11

AVERAGE SODIUM CONTENTS OF THE PLANTS AFTER EXPERIMENTS A AND B

Sodium contents of cultural nutrient solutions (in m.e. per litre)	Experiment	Sodium contents (in mg.) of the plants after treatment with experimental nutrient solutions having sodium contents (in m.e. per litre) of			Average sodium contents after Experiments A and B (in mg.)
		0.1	2	4	
0.1	A	1.07	2.41	2.79)	2.09
0.1	B	1.10	2.34	2.84)	
2	A	4.69	6.78	6.90)	6.17
2	B	4.90	6.80	6.95)	
4	A	7.15	8.19	9.27)	8.19
4	B	7.18	8.20	9.17)	
Average		4.35	5.79	6.32	

These figures appear further to confirm the assumption that the accumulation of sodium was in no way influenced by the different conditions under which Experiments A and B were carried out.

TABLE 12

AVERAGE SODIUM ACCUMULATION DURING THE EXPERIMENTS IN PLANTS WITH DIFFERENT INITIAL SODIUM CONTENTS

Sodium contents of cultural nutrient solution (in m.e. per litre)	Sodium contents of the plants (in mg.)		Average accumulation (in mg.)
	Average before the experiments	Average after the experiments	
0.1	1.22	2.09	0.87
2	4.96	6.17	1.26
4	7.28	8.19	0.91

TABLE 13

AVERAGE SODIUM ACCUMULATION DURING THE EXPERIMENTS IN PLANTS TREATED WITH DIFFERENT EXPERIMENTAL NUTRIENT SOLUTIONS

Sodium contents of experimental nutrient solutions (in m.e. per litre)	Sodium contents of the plants (in mg.)		Average accumulation (in mg.)
	Average before the experiments	Average after the experiments	
0.1	4.49	4.35	- 0.14
2	4.49	5.79	1.30
4	4.49	6.32	1.83

From comparison of the average accumulation by plants with different sodium contents (Table 12), it appears that those plants with the higher initial contents took up more sodium during the experiment than those with lower initial contents. Comparison of the average sodium accumulation by plants in the different experimental nutrient solutions (Table 13) shows that the sodium level of the experimental nutrient solution had a great effect upon the average accumulation of sodium. The average accumulation by the plants in the experimental nutrient solution containing 0.1 m.e. sodium is negative, that is to say, the uptake is less than the outgo.

The differential increases in the sodium contents of the plants during the experiment (Table 14) clearly demonstrate the influence of the sodium contents of the plants at the beginning of the experimental period and of the experimental nutrient solutions upon sodium accumulation.

TABLE 14

SODIUM CONTENTS AFTER EXPERIMENTS A AND B OF PLANTS TREATED WITH EXPERIMENTAL NUTRIENT SOLUTIONS CONTAINING 2 AND 4 M.E. SODIUM IN RELATION TO THAT OF PLANTS TREATED WITH AN EXPERIMENTAL NUTRIENT SOLUTION CONTAINING 0.1 M.E. SODIUM PER LITRE

Sodium contents (in m.e. per litre) of		Excess of sodium contents over those of plants treated with an experimental nutrient solution containing 0.1 m.e. sodium			
the cultural nutrient solutions	the experimental nutrient solutions	Experiment A (non-radioactive cultural solutions)		Experiment B (radioactive cultural solutions)	
		mg.	%	mg.	%
0.1	2	1.34	125	1.14	104
0.1	4	1.72	161	1.74	158
2	2	2.09	45	1.90	39
2	4	2.21	47	2.05	42
4	2	1.04	14.5	1.02	14.2
4	4	2.12	29.7	1.96	27.3

As the sodium content of the cultural nutrient solution increases,, so the sodium contents of the plants of all treatments of both Experiment A and B increase. Expressed as a percentage, the sodium content rises most sharply for the plants cultured in the nutrient solution with 0.1 m.e. sodium. The sodium contents of plants treatedd with experimental nutrient solutions containing 2 and 4 m.e. sodium per litre were 125 and 161% respectively greater in Experiment A and 104 and 158% respectively greater in Experiment B than those of plants treated with an experimental nutrient solution containing 0.1 m.e. sodium.

In the case of plants cultured in a nutrient solution containing 2 m.e. sodium per litre, the sodium contents of those treated with experimental nutrient solutions containing 2 and 4 m.e. sodium were 45 and 47% respectively greater in Experiment A and 39 and 42% respectively greater in Experiment B than the sodium contents of those treated with an experimental nutrient solution containing 0.1 m.e. sodium. The corresponding figures for plants cultured in a nutrient solution containing 4 m.e. sodium per litre were 14.5 and 29.7% in Experiment A and 14.2 and 27.3% in Experiment B.

The size of this increase appears to be dependent upon the sodium content of the experimental material and is thus dependent upon the amount of sodium available to the plant during the cultural period. In the experimental nutrient solution containing 4 m.e. sodium, the size of the sodium increases in the plants cultured in the nutrient solutions with 2 and 4 m.e. sodium are of the same order and as much greater than in the case of the plants cultured in the nutrient solution containing 0.1 m.e. sodium. In the experimental nutrient solution with 2 m.e. sodium, the increase in the amount of sodium is clearly dependent upon the sodium content of the plant. The connection between the size of the sodium increase occuring during the experiment and the original sodium content of the experimental plants is such that, above a certain minimum content of sodium in the experimental plant, the increase in sodium during the experimental period is independent of the sodium level of the experimental plant, always provided that sufficient sodium is supplied in the nutrient solution. When insufficient sodium is supplied (Table 14) the ratio of the concentration Na plant : Na nutrient solution becomes decisive for the size of the accumulation. Examples of this in Table 14 are the weight increases of only 1.04 mg. (14.5%) in Experiment A and 1.02 mg. (14.2%) in Experiment B shown when plants cultured in a nutrient solution containing 4 m.e. sodium per litre were supplied with only 2 m.e. sodium per litre in the experimental nutrient solution.

TABLE 15

SODIUM ACCUMULATION DURING EXPERIMENTS A AND B OF PLANTS GIVEN DIFFERENT CULTURAL AND EXPERIMENTAL TREATMENTS

Sodium contents (in m.e. per litre) of		Sodium accumulation (in mg.) in			
		Experiment A		Experiment B	
the cultural nutrient solutions	the experimental nutrient solutions	Treatment	Accumulation	Treatment	Accumulation
0.1	0.1	a	1.07–1.22=–0.15	j	1.10–1.22=–0.12
0.1	2	b	2.41–1.22=+1.19	k	2.34–1.22=+1.12
0.1	4	c	2.79–1.22=+1.57	l	2.84–1.22=+1.64
2	0.1	d	4.69–4.96=–0.27	m	4.90–4.96=–0.06
2	2	e	6.78–4.96=+1.82	n	6.80–4.96=+1.84
2	4	f	6.90–4.96=+1.94	o	6.95–4.96=+1.99
4	0.1	g	7.15–7.28=–0.13	p	7.18–7.28=–0.10
4	2	h	8.19–7.28=+0.91	q	8.20–7.28=+0.92
4	4	i	9.27–7.28=+1.99	r	9.14–7.28=+1.86

TABLE 16

SODIUM ACCUMULATION DURING EXPERIMENTS A AND B IN RELATION TO THE SODIUM CONTENTS OF THE PLANTS BEFORE THE EXPERIMENTS AND TO THOSE OF THE EXPERIMENTAL NUTRIENT SOLUTIONS

Sodium contents (in m.e. per litre) of		Sodium accumulation (in mg.) in the plants during the experiment in relation to the ratio of the sodium contents of the plants before the experiment and the sodium contents of experimental nutrient solutions				Plant sodium: solution sodium ratio before the experiment
		Experiment A		Experiment B		
the cultural nutrient solutions	the experimental nutrient solutions	Treatment	Accumulation	Treatment	Accumulation	
4	0.1	g	- 0.13	p	- 0.10	496.5
2	0.1	d	- 0.27	m	- 0.06	339.1
0.1	0.1	a	- 0.15	j	- 0.12	83.3
4	2	h	+ 0.91	q	+ 0.92	23.5
2	2	e	+ 1.82	n	+ 1.84	17.0
4	4	i	+ 1.99	r	+ 1.86	11.7
2	4	f	+ 1.94	o	+ 1.99	8.5
0.1	2	b	+ 1.19	k	+ 1.12	4.16
0.1	4	c	+ 1.57	l	+ 1.62	2.08

From Table 16 it appears that the ratio of the sodium content of the plant to that of the experimental nutrient solution determines whether the accumulation is positive or negative. With higher ratios the accumulation is negative. With a ratio lying somewhere between 83.3 and 23.5 it becomes positive. With ratios of 83.3 and progressively less, it increases at first, then remains virtually constant until a ratio of between 8.5 and 4.16 is reached, and finally decreases at still lower ratios.

This signifies that, provided sufficient sodium is supplied, plants with a high sodium level accumulate sodium more easily than plants with a low sodium level. It appears therefore that, by following a specifically directed cultivation method, it is possible deliberately to increase the sodium requirement of the plant.

In short, the plant's absorptive powers for sodium are not lessened but rather increased by its initially high sodium content. This is clearly shown in the present experiments by the fact that plants cultured in nutrient solutions containing 2 and 4 m.e. sodium contained much more sodium after the experiments than did those cultured in a nutrient solution containing 0.1 m.e. sodium per litre (Table 17).

TABLE 17

SODIUM ACCUMULATION DURING EXPERIMENTS A AND B IN PLANTS TREATED WITH EXPERIMENTAL NUTRIENT SOLUTIONS CONTAINING 2 AND 4 M.E. SODIUM IN RELATION TO THOSE OF PLANTS TREATED WITH AN EXPERIMENTAL NUTRIENT SOLUTION CONTAINING 0.1 M.E. SODIUM PER LITRE

Sodium contents (in m.e. per litre) of		Increases (in mg.) of sodium contents of plants					
		Experiment A			Experiment B		
the cultural nutrient solutions	the experimental nutrient solutions	After the cultural period	After the experimental period	Total	After the cultural period	After the experimental period	Total
0.1	2	0	1.34	1.34	0	1.14	1.14
0.1	4	0	1.72	1.72	0	1.74	1.74
2	2	3.74	2.09	5.83	3.74	1.90	5.64
2	4	3.74	2.21	5.95	3.74	2.05	5.79
4	2	6.06	1.04	7.10	6.06	1.02	7.08
4	4	6.06	2.12	8.18	6.06	1.96	8.02

On consideration of the facts that:

(a) the plant is growing during the experimental period so that more room becomes available for the ions taken up, but only sodium and 0.05 m.e. Ca are supplied in the nutrient solution, and

(b) in spite of (a) above, the sodium accumulates less readily in plants with a low sodium content than in plants with a high sodium content

the thought naturally occurs that when a cell with a definite ion-constellation divides, daughter cells try to maintain this same ion-constellation, by reason of the fact that their vital functions have adapted themselves before the division to a certain environment. In these circumstances, the factors which determine the environment of the cell apparently exercise an influence similar to that which, in genetics, is responsible for the habit of the plant.

2. *The results of the physical determinations carried out on the plants of Experiments A and B*

From the radioactivities of the plant material and the nutrient solutions before and after the experiment, it is possible to determine the sodium uptake in Experiment A and the outgo in Experiment B in the manner described in Appendix 3. Uptake and outgo determined in this way cannot possibly be completely accurate as the method does not allow for the vice-versa effect (see p. 96).

However, it will be seen later that the influence of the vice-versa effect is negligible under the experimental conditions.

TABLE 18

MINIMUM UPTAKE AND OUTGO OF SODIUM IN EXPERIMENTS A AND B
(in mg.)

Sodium contents (in m. e. per litre) of		Experiment A				Experiment B			
the cultural nutrient solutions	the experimental nutrient solutions	Treatment	Accumulation (measured)	Uptake (measured)	Outgo (calculated)	Treatment	Accumulation (measured)	Uptake (calculated)	Outgo (measured)
0.1	0.1	a	−0.15=0.33 − 0.47			j	−0.12=−0.10 − 0.02		
0.1	2	b	+1.19=2.17 − 0.98			k	+1.12= 1.44 − 0.32		
0.1	4	c	+1.57=2.54 − 0.97			l	+1.62= 1.96 − 0.34		
2	0.1	d	−0.27=0.33 − 0.60			m	−0.06=−0.04 − 0.02		
2	2	e	+1.82=2.35 − 0.53			n	+1.84= 2.41 − 0.57		
2	4	f	+1.94=2.95 − 1.01			o	+1.99= 3.00 − 1.01		
4	0.1	g	−0.13=0.30 − 0.43			p	−0.10=−0.03 − 0.07		
4	2	h	+0.91=2.20 − 1.29			q	+0.92= 1.96 − 1.04		
4	4	i	+1.99=2.82 − 0.83			r	+1.86= 2.99 − 1.13		

The uptake and outgo values determined are minimum values since they do not take the vice-versa effect into account. They are not always equal for the corresponding treatments of the two experiments, those for Experiment B being lower in part than those for Experiment A (Table 18).

It will be seen that the greatest differences between the results of Experiments A and B occur between plants cultured in a nutrient solution containing only 0.1 m. e. sodium and between those supplied with an experimental nutrient solution containing only 0.1 m. e. sodium per litre. The major differences thus relate either to a low sodium level in the plant material used in the experiment or to a low sodium level of the experimental nutrient solution.

Given equal accumulation as is the case in these two experiments, it is not acceptable that the uptake and outgo occurring in plants in corresponding treatments can be appreciably different. As such differences were established, however, it is clear that the results obtained from one or from both of the experiments were erroneous.

In explanation of the observed differences, the following three possibilities present themselves:

(1) The values calculated from Experiment A are too high. This would be the case if the radioactivity of the plant after the experiment is greater than can be reconciled with the ratio Na*:Na in the nutrient solution.

(2) The values calculated from Experiment B are too low. This would be the case if the radioactivity of the nutrient solution after the experiment is lower than can be reconciled with the ratio Na*:Na in the plant.

(3) The values calculated from both experiments are incorrect.

If the values calculated from Experiment A are too high, it may be inferred that:

(1) The plant is able to choose selectively between the Na* and Na in the nutrient solution and shows a definite preference for Na*

(2) After the uptake the plant fixes the Na* to a greater degree than the Na.

In view of the fact that Na* and Na are chemically identical, no convincing argument can be advanced as to why such a selective action should occur. This line of thought leads to the supposition that the values calculated from Experiment B do not reflect the true uptake and outgo.

The cause of the appreciable differences between the values as calculated from Experiments A and B must therefore be sought in differences in the design of the two experiments.

Through the medium of the experimental nutrient solutions, Na* and Na were supplied in a specific proportion to the non-radioactive plants used in Experiment A. Before the beginning of the experiment, the nutrient solution was well stirred to ensure a uniform distribution of the Na*.

The plants used in Experiment B took up Na* and Na in specific proportions from the radioactive nutrient solutions in which they were cultured. The specific activity** of this mixture was, however, reduced by the non-radioactive sodium which the plants al-

* radioactive

ready contained and which they had taken up during the germination period.

The greater the extent to which the sodium originally present in the plant is added to and replaced by the sodium mixture taken up during the cultural period, the greater the specific activity of the sodium in the plant becomes.

The amount of non-radioactive sodium originally present in the plants - the germination-sodium - is considerably reduced by the time that the plants enter the experimental period as a result of their uptake of Ca, K, Mg and the mixture of Na* and Na ions during the three weeks' cultural period.

The reduction may have been so complete that the plants enter the period entirely devoid of their original non-radioactive sodium content. In this case a complete exchange and replenishment of the non-radioactive sodium has been effected by the radioactive sodium mixture, which will then be regularly distributed throughout the plant in a way dependent upon the nature of the plant tissue.

In all cases in which the original non-radioactive sodium has not been entirely exchanged and replenished, the distribution of the radioactive mixture throughout the plant will probably be more or less irregular. The possibility that the mixture is regularly distributed throughout a part of the plant is not excluded. With a regular distribution throughout the whole plant, the specific activity of the plant will decrease during the experimental period as a result of the uptake of non-radioactive sodium from the nutrient solution.

With an irregular distribution of the radioactive sodium mixture, the specific activity of the plant may increase, decrease or remain the same during the experimental period. The change which it undergoes is dependent upon the amount of sodium taken up during the experimental period and the amount of germination-sodium which is still present in the plant.

If it is the case that germination-sodium is still present during the experimental period in the plants from all the different sodium treatments of the cultural period, it follows that some germination-sodium must still be present at the end of the cultural period, whatever the relationship between the outgo (z) during the cultural period and the amount of sodium present in the plant at the end of the germination period (x). The relationship can be either $x<z$, $x = z$ or $x>z$.

* radioactive
** specific activity - the radioactivity per mg. sodium.

TABLE 19

AVERAGE GERMINATION-SODIUM CONTENTS AFTER DIFFERENT CULTURAL TREATMENTS (in mg.)

Treatment	Sodium contents of cultural nutrient solutions (m.e. per litre)	Sodium contents of plants end of		Accumulation during cultural period	Uptake during cultural period	Outgo during cultural period	Relationship between z and x	Uptake percentage	Sodium remaining from germination period
		cultural period	germination period						
s	0.1	1.22 - x	= y_1	= 0.271 - z_1	$\longrightarrow z_1 <$	x		78.5	0.949
t	2	4.96 - x	= y_2	= 4.41 - z_2	$\longrightarrow z_2 <$	x		63.4	0.55
u	4	7.28 - x	= y_3	= 6.85 - z_3	$\longrightarrow z_3 <$	x		49.2	0.43

If the outgo, during the cultural period is less in amount than the contents of germination-sodium, some germination-sodium must still be present at the end of the period and the sodium taken up during the period will not necessarily have been involved in the outgo. If, on the other hand, the outgo during the cultural period is greater in amount than the contents of germination-sodium, the sodium taken up during the period must be involved in the outgo, if some of the germination-sodium is to remain in the plant at the end of the three weeks' cultural period in a nutrient solution containing 3 m.e. K, 5 m.e. Ca, 2 m.e. Mg and either 0.1, 2 or 4 m.e. Na (see Tables 19 and 20).

TABLE 20

RADIOACTIVITIES AND SPECIFIC RADIOACTIVITIES BEFORE AND AFTER EXPERIMENTS A AND B (in c.p.m.)

* total activity ** specific activity

Treatment	EXPERIMENT A Total and specific activity of the			Treatment	EXPERIMENT B Total and specific activity of the		
	plant after the experiment	nutrient solution before the experiment	nutrient solution after the experiment		plant before the experiment	plant after the experiment	solution after the experiment
a	77,517* 72,445**	81,060 234,957	3,340 6,747	j	73,040 59,869	71,600 65,090	1,440 3,200
b	26,283 10,906	84,300 12,112	57,500 9,965	k	64,800 53,114	48,050 20,534	16,750 2,868
c	14,671 5,258	80,400 5,776	64,700 55,240	l	75,160 61,606	54,430 19,165	20,730 1,685
d	72,933 15,551	77,700 225,217	4,770 7,694	m	64,840 13,072	64,600 13,084	240 593
e	26,260 3,873	77,700 11,164	51,870 10,091	n	63,677 12,838	56,400 8,294	7,277 1,421
f	17,618 2,553	83,100 5,970	65,482 5,512	o	68,950 13,901	54,950 7,906	14,000 1,173
g	66,100 9,244	75,850 219,855	9,750 20,547	p	37,120 5,099	36,770 5,120	350 786
h	25,040 3,186	79,200 11,379	54,260 8,969	q	47,600 6,538	40,800 4,976	6,800 1,126
i	16,050 1,739	79,270 5,695	63,220 5,299	r	48,590 6,674	41,050 4,491	7,535 625

From the data shown in Table 19, it appears that in the case of treatment s, germination-sodium has certainly remained behind in the plant. The values obtained from treatments t and u, however, do not allow for any certainty in this respect. The differences between the values for x and z in treatments t and u are in the range of 10% or less. Bearing the experimental error in mind, the possibility that the z value is in reality equal to or somewhat greater than the x value cannot be dismissed.

The possible influence of the germination-sodium will be most pronounced in those treatments of Experiment B in which the plants were cultured in the nutrient solutions with 0.1 m.e. sodium and also in those treatments in which 0.1 m.e. sodium was supplied during the experimental period, this being due, in the former case, to the fact that more germination-sodium has remained behind in the plants (Table 19) and in the latter case to the fact that only minute amounts of sodium were supplied during the experiment. The maximum amounts of germination-sodium which remained behind in the plants at the end of the cultural period were 0.949, 0.55 and 0.43 mg. respectively for the plants cultured in nutrient solutions with 0.1, 2 and 4 m.e. sodium per litre.

When the theoretical conclusions drawn from the hypothesis that germination-sodium is present during the experimental period in the plants from all the different cultural nutrient solutions were checked against the radioactivities and specific activities found applicable to Experiment B, further confirmation was obtained that germination-sodium must indeed have been present during the experimental period.

When the plant material cultured in nutrient solutions with 0.1, 2 and 4 m.e. sodium was placed in nutrient solutions containing 0.1 m.e. sodium during the experimental period (treatments j, m, p, Table 20), the specific activity either rose or remained the same. According to the foregoing consideration, this indicates that germination-sodium was present in these plants during the experimental period. In view of the fact that the same plant material was used for the treatments with higher sodium concentrations in the nutrient solutions, that which has been found applicable to treatments j, m and p must necessarily apply also to the other treatments. That this influence did not make itself apparent in the outgo from plant material from the cultural nutrient solutions with 2 and 4 m.e. sodium which was placed in nutrient solutions with 2 and 4 m.e. sodium during the experimental period may be attributed to the fact that in these plants only very little non radioactive germination-sodium is present and also to the fact that they took up considerable amounts of non-radioactive sodium during the experimental period.

It has thus been shown that the participation of the germination-sodium, wholly or in part, in the outgo must be held responsible for the low outgo values found in Experiment B. From this and the fact that no basic objections can be raised to the results obtained from Experiment A, it is evident that the third possibility, namely that the results of both Experiment A and Experiment B are incorrect, becomes void and the results from Experiment A should be given preference to those of Experiment B.

It may be assumed that the following occurred in Experiment B. During the experimental period part of the germination-sodium left the plant and this resulted in an increase in the specific activity. But at the same time part of the culture-sodium also left the plant in the outgo and this resulted in a decrease in the specific activity, as did also the uptake of non-radioactive sodium. The final specific activity of the plant is entirely dependent upon the amounts of sodium taken up and lost in the outgo.

It is surprising to establish, as one must from these experiments, that sodium, which is supposed to be an extremely mobile element and which has not yet been accorded general recognition in plant nutrition, was not completely exchanged or expelled by the cations during the three weeks that the plants were in the cultural nutrient solutions containing 3 m.e. K, 5 m.e. Ca, 2 m.e. Mg and 0.1 m.e., 2 m.e. or 4 m.e. sodium and that no isotope balance was reached during this period.

It appears from these results (Table 19) that the sodium in the plant is more easily exchanged by other sodium ions than by Ca, K or Mg. This strengthens the opinion that sodium can fulfil a specific function in the plant as it leads to the supposition that sodium is able to take up various positions in the plant and that it is present in stronger or weaker combinations with other substances. This is a property which sodium shares with other nutrient ions.

3. *The outgo of the sodium ions taken up during the germination and cultural periods of Experiment B.*

(1) Introduction

It cannot be assumed that all the sodium taken up during the germination period and present in the plants of the various treatments at the beginning of the experiment, is embraced by the sodium outgo. It is therefore pertinent to ask to what extent the germination-sodium participates under various conditions in the exchange and conversion reactions during the experimental period and to what extent the sodium outgo is provided by the culture-sodium. For plants cul-

tured in the nutrient solutions containing 0.1, 2 and 4 m.e. sodium, the maximum amounts of germination-sodium which were able to participate in these reactions were 0.949, 0.55 and 0.45 mg. respectively (Table 19).

At the end of the experiment, the following types of sodium can be present in the plants:

(a) A part of the sodium taken up during the germination period (germination-sodium) - Na_g - non-radioactive sodium;

(b) A part of the sodium taken up during the cultural period (culture-sodium - Na_c - a mixture of radioactive and non-radioactive sodium;

(c) Sodium taken up during the experimental period (experimental-sodium) - Na_e - non-radioactive sodium.

In the plants cultured in the nutrient solutions with 0.1 m.e. sodium, α (0.271 mg. Na in Table 19) mg. culture-sodium is present prior to the experiment. During the experiment the radioactivity of the plant (treatment j, Table 20) is reduced by β c.p.m. (1440 c.p.m.). Before the experiment the radioactivity of the plant, or more precisely the radioactivity of the sodium taken up during the cultural period, was γ c.p.m. (73,040 c.p.m.). During the experimental period, this sodium disappeared from the plant to the extent given by the following equation:

$$\frac{\beta}{\gamma} \times \text{mg.} = \delta \text{ mg.} \qquad (\frac{1,440}{73,040} \text{ x } 0.271 \text{ mg. Na} = 0.005 \text{ mg. Na}).$$

The amount of culture-sodium remaining in the plant after the experiment is therefore:

$$\alpha - \delta = Na_c \text{ mg.} \quad (0.271 - 0.005 = 0.266 \text{ mg. Na}).$$

The total amount of sodium Na_t present in the plant at the end of the experiment is:

$$Na_c + Na_e + Na_g = Na_t \text{ mg. Na} \ldots\ldots \ldots \ldots \quad (1)$$

Reasonably correct values for the uptake of sodium by plants subjected to the various treatments of Experiment A, the Na_e values, are known. The uptake values for treatments n, o, q and r (Table 18) of Experiment B, which agree fairly well with the uptake values for the corresponding treatments of Experiment A, may also be used for the calculation, actual values thus being employed in preference to those obtained for the corresponding treatments of Experiment A.

From (1) it follows that:

$$Na_t - Na_e - Na_c = Na_g \quad \ldots \quad \ldots \quad \ldots \quad (2)$$

From this, the only unknown value, namely, the maximum amount of germination-sodium which can be present in the plant at the end of the experiment, can be determined.

The results are given in Tables 21 and 22.

TABLE 21

AVERAGE CONTENTS OF DIFFERENT TYPES OF SODIUM IN THE PLANTS AFTER THE EXPERIMENTS

Treatment	Sodium contents (in m.e.per litre) of		Contents of different types of sodium in the plants after the experiments					
	the cultural nutrient solutions	the experimental nutrient solutions	Total sodium (mg.) (1)	Culture-sodium (mg.) (2)	Culture-sodium (%) (3)	Experiment sodium (mg.) (4)	Germination-sodium (mg.) (5)	Germination-sodium (%) (6)
j	0.1	0.1	1.10	0.27	98.1	0.33	0.50	53.1
k	0.1	2	2.34	0.21	77.1	2.17	-0.04	-4.1
l	0.1	4	2.84	0.19	69.0	2.54	0.11	11.9
m	2	0.1	4.90	4.41	100.0	0.33	0.16	30.1
n	2	2	6.80	3.99	90.6	2.41	0.39	74.2
o	2	4	6.95	3.52	79.7	3.00	0.44	82.1
p	4	0.1	7.18	6.84	100.0	0.30	0.04	9.3
q	4	2	8.20	5.88	85.9	1.96	0.36	84.7
r	4	4	9.14	5.79	84.6	2.99	0.36	83.7

TABLE 22

AMOUNTS OF SODIUM OF DIFFERENT TYPES INVOLVED IN THE OUTGO DURING THE EXPERIMENTS

Treatment	Sodium contents (in m.e.per litre) of		Germination-sodium in outgo		Culture-sodium in outgo		Total outgo	Outgo Experiment A	Outgo Experiment B	Ratio of sodium content in plant to sodium content in nutrient solution before the experiment
	the cultural nutrient solutions	the experimental nutrient solutions	(mg.)	(%)	(mg.)	(%)	(mg.)	(mg.)	(mg.)	
			(7)		(8)		(9)	(10)	(11)	(12)
j	0.1	0.1	0.445	46.9	0.005	1.9	0.45	0.47	0.02	83.3
k	0.1	2	0.989	104.1	0.062	22.9	1.05	0.98	0.32	4.16
l	0.1	4	0.846	88.1	0.084	31.0	0.93	0.97	0.34	2.08
m	2	0.1	0.39	69.9	16×10^{-6}	0	0.39	0.60	0.02	339.0
n	2	2	0.157	25.8	0.413	9.4	0.57	0.53	0.57	17
o	2	4	0.115	17.9	0.895	20.3	1.01	1.01	1.01	8.5
p	4	0.1	0.39	90.7	65×10^{-6}	0	0.39	0.43	0.07	469.5
q	4	2	0.066	15.3	0.974	14.1	1.04	1.29	1.04	23.5
r	4	4	0.07	16.3	1.06	15.4	1.13	0.83	1.13	11.7

The outgoes of sodium taken up during the cultural period and the germination period are not two separate and independent processes. They influence each other and must therefore be considered as being interdependent.

The outgo is influenced by:

(a) The amounts of culture-sodium and germination-sodium present in the plants prior to the experiment;

(b) The sodium concentration of the nutrient solution;

(c) The vice-versa effect (see p.101).

(2) The outgo from plants cultured in nutrient solutions containing 0.1, 2 and 4 m.e. sodium per litre in relation to increasing sodium concentrations in the experimental nutrient solutions

The outgo of culture-sodium and germination-sodium from plants cultured in nutrient solutions with 0.1, 2 and 4 m.e. sodium in relation to increasing sodium concentrations in the experimental nutrient solutions proceeds in accordance with the following general scheme:

Outgo of culture-sodium from plants cultured in nutrient solution with:	*Outgo of germination-sodium from plants cultured in nutrient solution with:*
0.1 m.e. Na: increases	0.1 m.e. Na: increases
2 m.e. Na: increases	2 m.e. Na: decreases
4 m.e. Na: increases	4 m.e. Na: decreases

As the sodium concentrations of the nutrient solutions increase, the outgo of culture-sodium *increases*, irrespective of the sodium contents of the plants and of the ratio of culture-sodium to germination-sodium in the plants. It would therefore appear that the outgo of culture-sodium is largely dependent upon the sodium concentration of the experimental nutrient solution.

With plants cultured in nutrient solutions with 0.1 m.e. sodium and thus containing little culture-sodium and much germination-sodium - plants with relatively low sodium contents - the outgo of germination-sodium *increases* as the sodium concentration of the experimental nutrient solution increases, and it is worthy of mention that in these circumstances, the uptake was twice as great as the amount of sodium which was found to be present in the plants before the experiment.

In the case of plants cultured in nutrient solutions with 2 and 4 m.e. sodium and thus containing much culture-sodium and little germination-sodium - plants with high sodium contents and a high ratio of sodium concentration in the plant to sodium concentration in the experimental nutrient solution - the outgo of germination-sodium *decreases* as the sodium concentrations of the experimental nutrient solutions increase. Here the uptake amounts to one-half to one-third of the amount of sodium present in the plants before the experiment.

The dependence upon the sodium concentration of the experimental nutrient solutions does not apply to the minute amounts of germination-sodium present in the plants cultured in the nutrient solutions with 2 and 4 m.e. sodium.

It may be concluded that, in general, the outgo of culture-sodium and germination-sodium is dependent upon the amounts of these types of sodium which are present in the plants before the experiment. The outgo of culture-sodium and germination-sodium from the plants with low sodium levels appears to be dependent upon the concentration of the experimental nutrient solution. In plants with high or medium sodium levels, only the outgo of culture-sodium is dependent upon the experimental nutrient solution. The outgo of germination-sodium from such plants is, on the contrary, dependent upon the extent of the uptake in relation to the amount of sodium present in the plant before the experiment. As this relative uptake decreases, so the outgo of germination-sodium also decreases. In other words, with a proportionately large uptake and with the presence in the plant of much germination-sodium, the outgo of germination-sodium is dependent upon the sodium concentration of the experimental nutrient solution. With a proportionately small uptake and little germination-sodium present in the plant, the outgo of the germination-sodium is *not* dependent upon the sodium concentration of the experimental nutrient solution. With a relatively large or small uptake in conjunction with much or little culture-sodium present in the plant before the experiment, the outgo of culture-sodium is always dependent upon the sodium concentration of the experimental nutrient solution.

This indicates that the distribution of all the culture-sodium and germination-sodium in the plant is not the same, as the germination-sodium is less ready to leave the plant than is the culture-sodium.

(3) The outgo from plants containing increasing amounts of sodium in the experimental nutrient solutions containing 0.1, 2 and 4 m.e. sodium per litre

The outgo of culture-sodium and germination-sodium from plants in relation to increasing sodium content occurs according to the following general scheme:

Outgo of culture-sodium from plants with increasing sodium levels in experimental nutrient solution containing:	*Outgo of germination-sodium from plants with increasing sodium levels in experimental nutrient solution containing:*
0.1 m.e. Na: decreases	0.1 m.e. Na: decreases
2 m.e. Na: increases	2 m.e. Na: decreases
4 m.e. Na: increases	4 m.e. Na: decreases

The outgo of culture-sodium is dependent upon the sodium concentration of the experimental nutrient solution. With high sodium concentrations it increases with the amount of culture-sodium present in the plant before the experiment. With low sodium concentrations it is more dependent upon the ratio of germination-sodium to culture-sodium in the plant prior to the experiment.

The outgo of germination-sodium is not dependent upon the concentration of the experimental nutrient solution but upon the amount of germination-sodium present in the plant prior to the experiment. The plants cultured in the nutrient solutions with the highest sodium contents contain the smallest amounts of germination-sodium. Thus the outgo of germination-sodium decreases as the sodium content of the plant increases, irrespective of the sodium concentration of the experimental nutrient solutions.

With an experimental nutrient solution containing 0.1 m.e. sodium, there is, however, a relative increase in the outgo of germination-sodium as the sodium contents of the plants increase.

The outgo values for plants cultured in solutions containing 0.1, 2 and 4 m.e. sodium are 46.9, 69.9, and 90.7% respectively, so that, given a uniform uptake, the outgo of germination-sodium is dependent upon the sodium concentration of the plant. The fact that the germination-sodium does not entirely leave the plants, even when the sodium concentrations in the plants are high, indicates with what difficulty it is replaced by sodium from other sources. Even in the case in which the outgo is greater than the uptake (treatment p), the culture-sodium present in the plant is not able to expel the germination-sodium completely.

From the data (Table 22, columns 7 and 8), it would seem that treatments m, n, in p, q and r, the outgo at first contains much germination-sodium and later an increased amount of culture-sodium.

In general, it has been observed that:

(a) The outgo of germination-sodium is dependent upon:

(i) The amount of germination-sodium in the plant;

(ii) The extent of the uptake in relation to the amount of sodium present in the plant before the experiment.

(b) The outgo of culture-sodium is dependent upon:

(i) The sodium concentration of the nutrient solution;

(ii) The ratio of germination-sodium to culture-sodium in the plant.

From this it appears that, as has previously been stated, the behaviour of the germination-sodium and the culture-sodium differs with regard to the outgo and that it may consequently be assumed that a part of the germination-sodium initially taken up by the plant sites itself in a position different from that of the sodium taken up later and, furthermore, that it is only with great difficulty that the sodium taken up later can expel part of the sodium already present in the plant.

From the results of these experiments it is safe to deduce that the sodium can be present in the plant in varying circumstances. From the generally applicable conception that, in given circumstances and within certain limits, cations are mutually exchangeable, it appears that sodium can be present in the plant in three different combination forms, namely:

(a) That in which it can easily be exchanged by all cations;

(b) That in which it can easily be exchanged by other Na, but only with difficulty by Ca, K and Mg (selective binding, see Table 19);

(c) That in which it can be exchanged only with difficulty by other Na (specific binding, see Table 19 and 22).

This means that three different functions must be attributed to the sodium.

In the three possibilities mentioned above, the bonds by which the sodium is combined become stronger in the order in which they are given. From a functional point of view, the significance which must be attributed to the sodium will change from one of a general nature to one of an essential nature with the increase in the combination strength.

The functional significance of the strength by which the sodium is combined may be interpreted as follows:

(a) A general function, e.g., the maintenance of the osmotic pressure;

(b) A specific function, e.g., the control of the hydration of the plasma;

(c) An essential function, e.g., participation in one of the metabolic processes.

4. The vice-versa effect

(1) The nature of the vice-versa effect

By vice-versa effect is understood the re-uptake by the plant of an element or compound which owes its presence in the nutrient solution solely to the outgo.

During the experiment the composition of the nutrient solution undergoes a change due to the influence of two factors, viz.

(a) The Uptake

The uptake of a particular element from the nutrient solution results in a corresponding impoverishment of the latter in respect of the element.

(b) The Outgo

The outgo of a particular element from the plant results in the enrichment of the nutrient solution in respect of the element.

In theory, the nature of an accumulation of any particular element can be either positive, negative or zero. In the investigation under discussion, the accumulation was negative in one-third of the treatments and positive in the case of the other two-thirds.

(2) The theoretical conception of the vice-versa effect

(a) The vice-versa effect in the case of a negative accumulation

In the event of a negative accumulation the outgo has exceeded the uptake. Thus the nutrient solution finally receives a greater amount of sodium from the plant than it has surrendered to it.

In the present investigation a negative accumulation is attributable to the fact that the sodium concentration of the plant is very much higher than that of the nutrient solution (see Table 22, column 12).

In the case of these particular treatments a pronounced change in the concentration of the nutrient solution is possible and, as a result, the uptake in Experiment A as calculated from the radioactivity and, therefore, the outgo, might lie considerably below the actual value.

(b) The vice-versa effect in the case of a positive accumulation

In the event of a positive accumulation the uptake exceeds the outgo and the sodium concentration is higher in the plant than in the nutrient solution. With a positive accumulation the sodium concentration in the plant is at the most 23 times as high as in the nutrient solution whilst with a negative accumulation, it is at the most 469.5 times and at the least 83.5 times as high in the plant as in the nutrient solution.

Thus the differences in concentration between the nutrient solution and the plant are appreciably smaller in those treatments in which a positive accumulation occurs than in those which result in a negative accumulation. It is, however, clear that the vice-versa effect will be less pronounced in the case of a positive sodium accumulation than in the case of a negative sodium accumulation. However, should the stream of outgoing ions only begin to flow strongly after most of the uptake has taken place, the vice-versa effect - i.e., the pollution of the nutrient solution - cannot contribute very much to the final uptake.

(c) The extent of the vice-versa effect

The equation $F - Na_t - Na_c = Na_g$, in which F = the amount of sodium in the plant after the experiment,

Na_t = the minimum amount of sodium taken up in Experiment A,

Na_c = the maximum amount of the minimum uptake of culture-sodium which has remained behind the plant after the experiment.

Na_g = the maximum amount of germination-sodium which has remained behind in the plant after the experiment,

represents the relationship between Na_g and the sodium of the cultural and experimental periods.

Irrespective of the extent of the pollution, it is certain that, when the vice-versa effect occurs, the values found for Na_t and Na_c are too low and that, as a result, too high a value is found for Na_g.

Theoretically, the treatment in which the vice-versa effect must have exercised the greatest influence upon the uptake is that in which the plants were cultured with 4 m.e. sodium and in which the experimental nutrient solution contained 0.1 m.e. sodium (treatment p, Table 21). In this case it appears that with an uptake of 0.30 mg. sodium the Na_g value is 0.04 mg. It may therefore be concluded with certainty that in no case can the vice-versa effect have been greater than 0.04 mg. The lowest value that Na_g can possibly have is nil. It is clear, therefore, that the influence of the vice-versa effect upon uptake must be very small and it may safely be assumed that, in the case of low-salt plants, the uptake occurs in a very short time and is largely completed before the outgo reaches its highest value per unit of time.

Here also the uptake reveals itself as an active process which is stimulated by the living plant, whilst the outgo is a passive process resulting from the uptake and limited in magnitude by the differences in sodium concentration in the plant and the nutrient solution.

5. *The distribution of the sodium ions between the culms and the roots of the plants*

(1) Introduction

It is readily acceptable that when uptake of a nutrient element - in this particular case sodium - occurs, it begins as soon as the root of the plant comes into contact with the nutrient solution.

Germination-sodium and culture-sodium are carried to the culm simultaneously. Provided that the experimental period is sufficiently

long, sodium taken up during this period finds its way into the culm, in addition to the germination-sodium and the culture-sodium and, in the event of an even longer experimental period, the sodium from these three sources will tend to leave the culm and again enter the root. As a result the nutrient solution will become enriched by this sodium.

The amount of originally non-radioactive sodium which is present in the culm after the experimental period can, in fact, be composed entirely of the sodium from the germination and cultural periods which was available in the culm and root before the experiment. As there are no means of determining the sources of the sodium found in the culm and the root the calculation of the intake* and the outgo of the culm and of the uptake, intake and outgo of the root from the radioactivity of the culm and root cannot produce true values. To illustrate this point consideration can be given to the relationship applicable to the culm, viz.

accumulation = intake - outgo

In Experiment A (non-radioactive plants in radioactive experimental nutrient solutions) the intake comprises:

(a) non-radioactive sodium from the root;

(b) a mixture of radioactive and non-radioactive sodium taken up during the experimental period and conveyed to the culm.

Only the sodium mentioned under (b) and the *total* amount of non-radioactive sodium (non-radioactive sodium from the root and non-radioactive sodium which has remained behind in the culm) which is present in the culm at the end of the experiment are measurable.

The question presents itself whether the amounts of non-radioactive sodium of these two different categories could be determined with the aid of data from Experiment B (radioactive plants in non-radioactive nutrient solution). In this connection, however, there are various impeding factors, viz.

(a) in addition to a mixture of radioactive sodium from the cultural period and non-radioactive sodium from the experimental period, the plants contain non-radioactive sodium from the germination period.

(b) A possible increase in the radioactivity of the culm during the experiment is the resultant of intake and outgo of radioactive sodium;

* Where a nutrient element is not taken up by the root or culm directly from the nutrient solution, this is known as 'intake'.

(c) A possible decrease in the radioactivity of the root during the experiment is the resultant of outgo of radioactive sodium to the culm and to the nutrient solution and the intake of radioactive sodium from the culm.

It will be seen from consideration of these factors that even if use be made of data from both experiments the resultants of the interaction between culm and root are the only available factors upon which further conclusions can be based.

As has been mentioned previously, the culms and roots are severed at the end of the experiment and analysed separately. The data show the distribution between culm and root of the total amount of sodium and of the sodium taken up during the experiment.

(2) The distribution of the sodium ions between the culms and roots of the plants after the cultural period

The distribution of the total amount of sodium and of the culture-sodium between the culm and root is not uniform for all treatments, being dependent upon the amount of sodium supplied in the nutrient solution (see Table 23).

TABLE 23

DISTRIBUTION OF SODIUM BETWEEN THE CULMS AND ROOTS OF THE PLANTS AFTER THE CULTURAL PERIOD

Treatment	Sodium contents of cultural nutrient solutions (in m.e. per litre)	Total-sodium contents of the plants after the cultural period (in mg.)		Culture-sodium contents of the plants after the cultural period (in mg.)		Germination-sodium contents of the plants after the cultural period (in mg.)	
		culm	root	culm	root	culm	root
s	0.1	0.587	0.633	0.064	0.207	0.523	0.426
t	2	2.73	2.23	2.43	1.98	0.30	0.25
u	4	4.66	2.62	4.32	2.53	0.34	0.09

When only a small amount of sodium is available the element is accumulated preponderantly in the organ through which uptake occurs, namely, the root. When a large amount of sodium is available, however, accumulation occurs mainly in the culm, but only after the root has acquired a certain content. In brief, therefore, as the amount of available sodium increases, so the main accumulation of this element tends to shift from the root to the culm.

TABLE 24

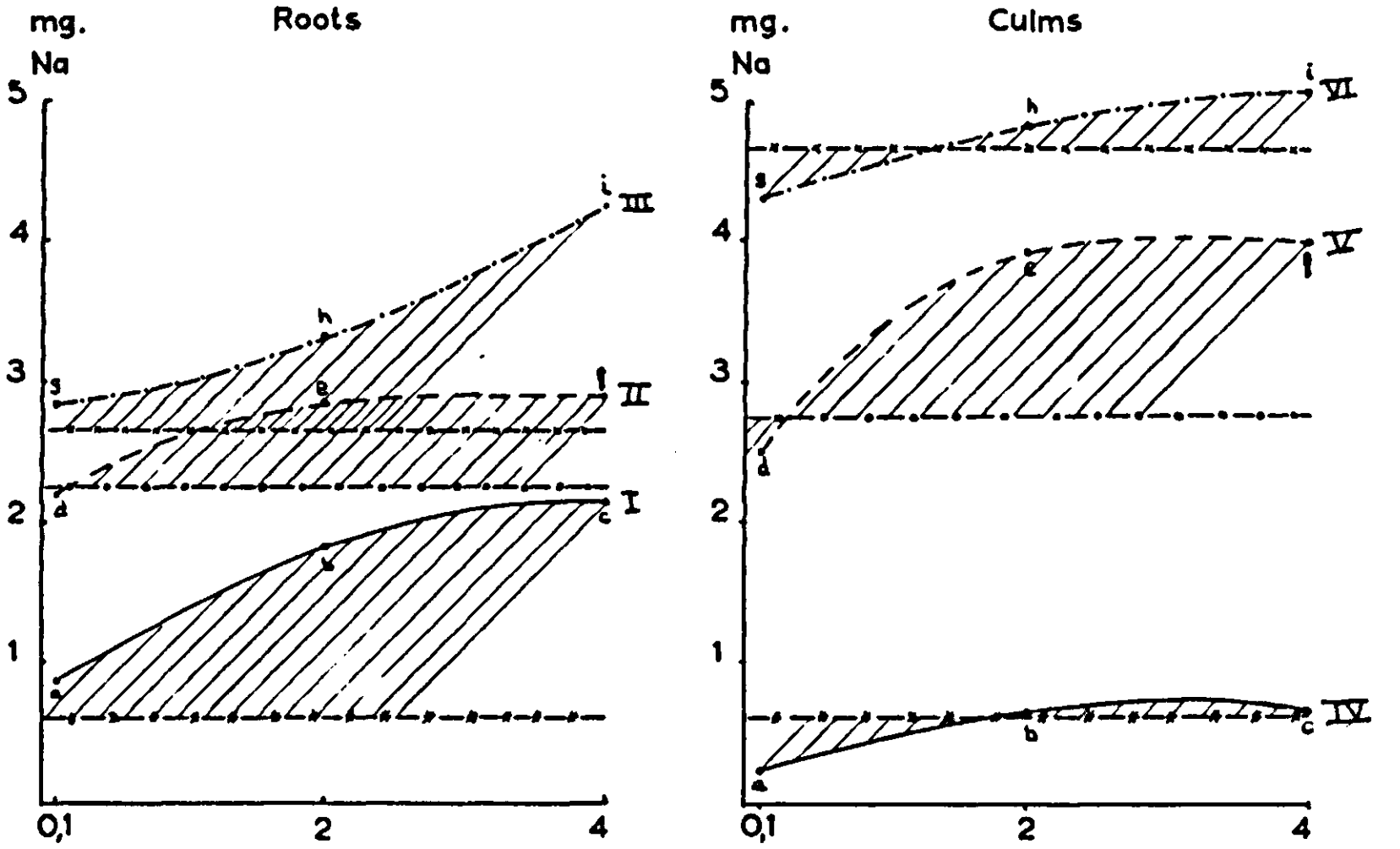
DISTRIBUTION OF SODIUM BETWEEN THE CULMS AND ROOTS OF THE PLANTS AFTER EXPERIMENT A

Sodium contents of cultural nutrient solutions (in m.e. per litre)	Average non-radioactive sodium contents of the plants before the experiment (in mg.)		Treatment	Sodium contents of experimental nutrient solutions (in m.e. per litre)	Average sodium contents of the plants after the experiment (in mg.)		Average amount of sodium taken up by the plants during the experiment (in mg.)		Average non-radioactive sodium contents of the plants after the experiment (in mg.)		Sodium accumulation (in mg.)	
	culm	root			culm	root	culm	root	culm	root	culm	root
0.1	0.587	0.633	a	0.1	0.229	0.839	0.0165	0.328	0.213	0.511	-0.358	0.206
0.1	0.587	0.633	b	2	0.607	1.805	0.56	1.61	0.047	0.195	0.020	1.172
0.1	0.587	0.633	c	4	0.632	2.158	0.68	1.85	0.048	0.308	0.045	1.525
2	2.73	2.23	d	0.1	2.487	2.201	0.075	0.255	2.412	1.946	-0.243	-0.029
2	2.73	2.23	e	2	3.905	2.871	0.77	1.55	3.195	1.325	1.175	0.641
2	2.73	2.23	f	4	4.004	2.888	1.10	1.85	2.904	1.038	1.274	0.638
4	4.66	2.62	g	0.1	4.295	2.850	0.08	0.221	4.215	2.629	-0.361	0.230
4	4.66	2.62	h	2	4.830	3.361	0.68	1.52	4.15	1.84	0.170	0.741
4	4.66	2.62	i	4	5.039	4.230	0.94	1.88	3.10	2.35	0.379	1.670

The culm not only receives a larger share of the sodium taken up by the root during the cultural period than does the root itself, but also contains the larger portion of the sodium taken up during the germination period. If it is accepted that, as a result of the larger sodium uptake in plants of treatment u, more germination-sodium has transferred from the roots to the culms than is the case in plants of treatment t it follows that, as the amounts of germination-sodium found in the culms of plants of the two treatments were equal, the roots of plants of treatment u have received more germination-sodium from the culms than have those of plants of treatment t. Nevertheless, the amounts of germination-sodium found in the roots of plants of treatment t after the experiment were greater than those found in the roots of plants of treatment u. Thus, the outgo of germination-sodium from plants of treatment u is greater than that from plants of treatment t. From this it may be concluded that, if the sodium once reaches the channels through which outgo occurs, it is readily surrendered to the nutrient solution.

(3) The distribution of the sodium ions between the culms and roots of the plants after Experiment A.

In the plants of Experiment A - non-radioactive plants in radioactive experimental nutrient solutions - it is possible to ascertain the distribution between the culm and root, not only of the total amount of sodium present in the plant, but also of the sodium taken up during the experiment. By comparing the amounts of sodium found in the culm and in the root before and after the experiment and taking the radioactivities and specific activities of these parts into account, it is possible to form an approximate estimation of the movement of the sodium during the experimental period.



me. sodium per litre in the experimental nutrient solution.

me. sodium per litre in the experimental nutrient solution.

*Fig.6. Sodium contents of the roots and culms after Experiment A.**

Sodium contents before the experiment of the roots and culms of plants cultured in nutrient solutions containing

0.1 m.e. Na per litre - * - * - * -

2 m.e. Na per litre - o - o - o -

4 m.e. Na per litre - x - x - x -

Sodium contents after the experiment of the roots and culms of plants cultured in nutrient solutions containing

0.1 m.e. Na per litre ——————

2 m.e. Na per litre - - - - - - - -

4 m.e. Na per litre - · - · - · - ·

Uptake of sodium during the experiment

* When reference is made to the plant, root or culm in this and subsequent figures, an experimental unit of 6 plants is concerned.

Although the absolute contents of sodium in the culms and roots change as a result of uptake during the experimental period the nature of the differences remains unaltered.

The sodium contents of the culms and roots of plants grown in the cultural nutrient solutions containing the three different sodium levels increase with, but not in proportion to, increases in the sodium concentration of the experimental nutrient solution (Fig.6).

A comparison of the curves representing the sodium contents at the end of the experiment of the culms and roots of plants to which different concentrations of sodium were supplied shows that a certain relationship exists between the accumulations of sodium in the culms and roots. In plants initially containing the smallest amount of sodium in the culm and root (those cultured in a solution containing 0.1 m.e. sodium per litre), the amount of sodium accumulating in the root during the experimental period increases considerably (curve I in Fig.6), not only with increases in the amount of sodium supplied during the experimental period, but also in comparison with the original sodium level.

The increase in the amount of sodium accumulating in the culms of such plants during the experiment is, on the other hand, very moderate (curve IV), the influence of the experimental nutrient solution containing 4 m.e. sodium per litre being virtually no greater than that of the solution containing only 2 m.e.

Once the sodium level of the roots has equalled that found in the roots of plants cultured in a nutrient solution containing 2 m.e. sodium (treatments c and d), it appears that the increase in the amount of sodium accumulating in the roots of such plants during the experiment is very moderate (curve II), the influence of the experimental nutrient solution containing 4 m.e. sodium per litre being virtually no greater than that of the solution containing only 2 m.e. On the other hand, a considerable amount of sodium has accumulated in the culms of these plants (curve V), but in this case also the experimental nutrient solution containing 4 m.e. sodium has had practically no more effect than that containing 2 m.e.

Once the sodium level of the roots has equalled that found in the roots of plants cultured in a nutrient solution containing 4 m.e. sodium (treatments e, f and g) and the culms have also acquired a high sodium level, it appears that the root is again capable of accumulating a considerable amount of sodium (curve III). Once again this strong sodium accumulation in the root is accompanied by a moderate sodium accumulation in the culm (curve VI).

It is apparent, therefore, that the extent to which sodium is accumulated in the root or culm is dependent upon their sodium level at the moment at which uptake begins. The regularity with which the preponderance of the accumulation shifts from root to culm and then again to root with increase in the sodium level of the nutrient solution in which the plant was cultured cannot be denied. The principle governing this trend is, however, still an open question.

It appears, moreover, that the sodium contents of the roots of the plants cultured in nutrient solutions containing 0.1, 2 and 4 m.e. sodium are not reduced when these plants are then placed in an environment having a sodium concentration of 0.1 m.e. The sodium content of the culms of the plants does diminish, however, and the roots surrender sodium to the nutrient solution. This signifies that when, for one reason or another, the sodium content of the root is reduced, the sodium so lost is replenished by sodium from the culm.

In view of the fact that the amount of sodium thus withdrawn from the culms (treatments a, d and g in Fig. 6) is approximately constant for the plants cultured at each of the three sodium levels, whilst a considerable difference exists between the sodium concentration of the experimental nutrient solution (0.1 m.e. Na) and the sodium concentration of the roots of these plants in all cases, it is apparent that the amounts of sodium withdrawn are almost entirely independent of the sodium level of the root and culm.

If plants cultured at the same sodium levels are placed in an experimental nutrient solution with a higher sodium concentration, the accumulation in the culm becomes dependent upon the sodium level of the plant. It follows that only under conditions that give rise to a negative sodium accumulation in the culm does the sodium level of the plant fail to exercise an influence upon the extent of the accumulation. Therefore in those cases in which the outgo from the culm is greater than the intake by the culm from the root, the difference between intake and outgo is independent of the sodium level of the plant.

If it is assumed that the intake by the culm was not equal for all three treatments (a, d and g in Fig. 6) – as was the case with the uptake – this would signify that with plants of different sodium levels the amount of sodium that is able to migrate to the root without having been exchanged for other sodium is practically constant in all cases, and that any other amount of sodium which migrates from the culm to the root is induced to do so only as a result of its exchange with other sodium.

This is further evidence that not all the sodium in the plant is present there in the same circumstances. Since it has now appeared that the accumulation in the root is so extremely dependent upon the

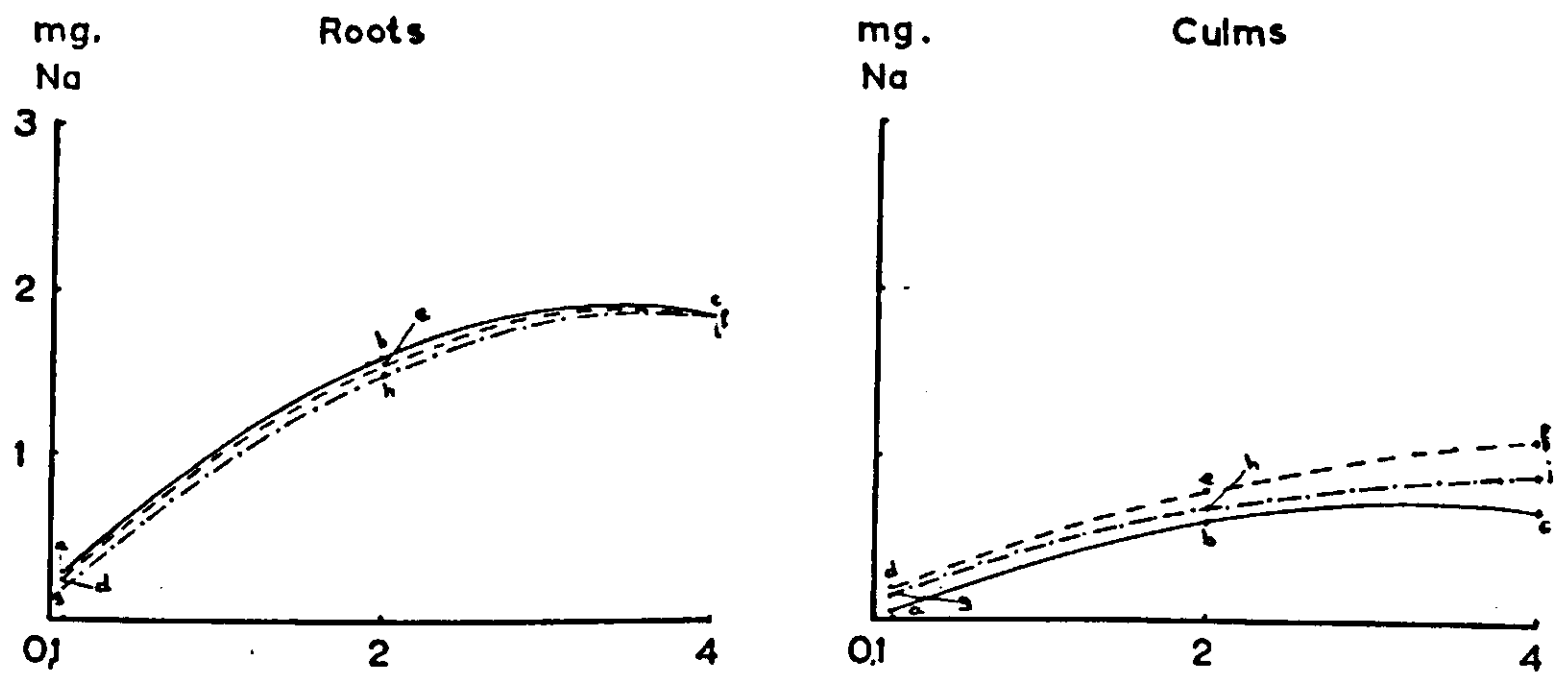


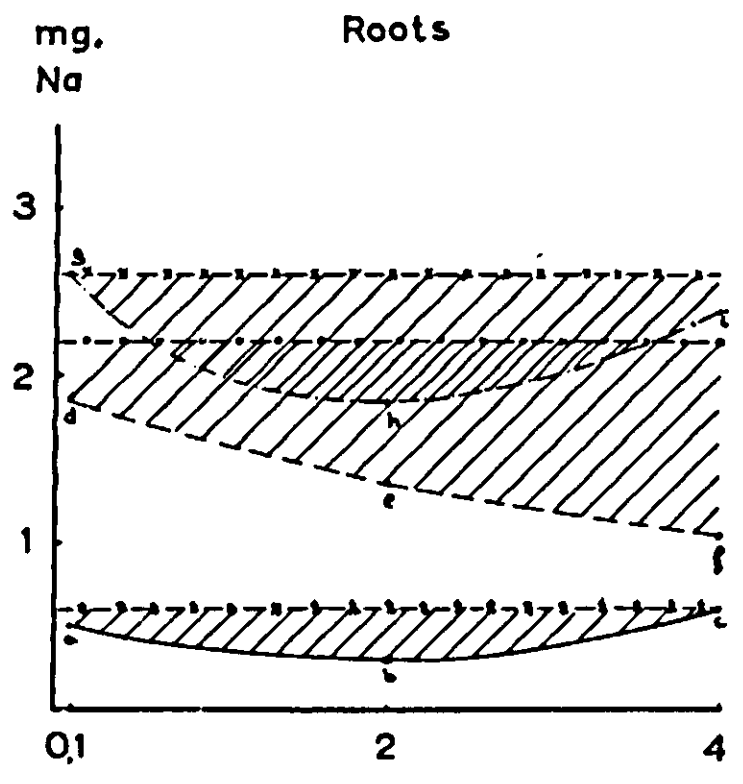
Fig. 7 Uptake-sodium contents of the roots and culms after Experiment A

Uptake-sodium contents after the experiment of roots and culms cultured in nutrient solutions containing:

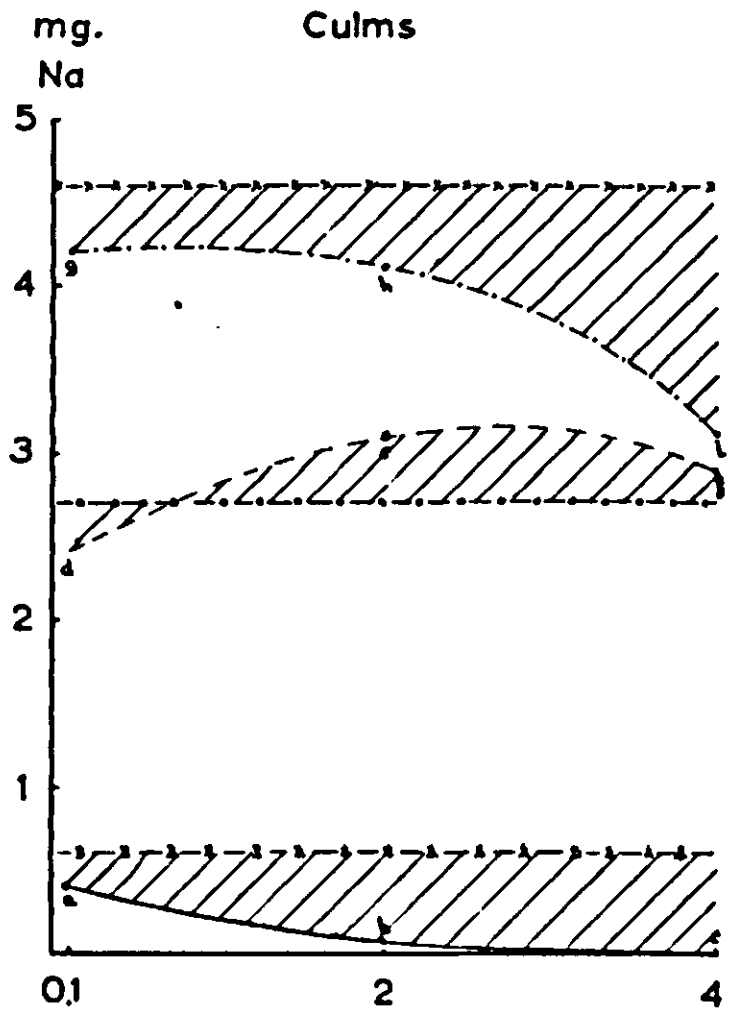
0.1 m.e. Na per litre ——————

2 m.e. Na per litre - - - - - - - -

4 m.e. Na per litre - · - · - · - ·



m.e. sodium per litre in the experimental nutrient solution.



m.e. sodium per litre in the experimental nutrient sclution.

Fig. 8. Non-radioactive sodium contents of the roots and culms after Experiment A

Sodium contents before the experiment of the roots and culms of plants cultured in nutrient solutions containing

0.1 m.e. Na per litre * - * - * - * - *

2 m.e. Na per litre - o - o - o - o -

4 m.e. Na per litre x - x - x - x - x

Sodium contents after the experiment of the roots and culms of lants cultured in nutrient solutions containing

0.1 m.e. Na per litre ——————

2 m.e. Na per litre - - - - - - - - -

4 m.e. Na per litre - . - . - . - . -

Outgo of non-radioactive sodium from the roots (left-hand figure), and intake of non-radioactive sodium by the roots from the culm(right-hand figure).

sodium level of the rest of the plant, it would be imprudent, to say the least, to assess the results of experiments carried out with excised roots on their true values on the basis of the values for the accumulation found in these roots.

6. *The distribution between the culm and root of the sodium ions taken up during the experimental period and of the sodium present in the plants before the experiment*

The amounts of sodium taken up during the experimental period and found in the roots and culms after the experiment increase with, but not in direct proportion to, the sodium concentration of the nutrient solutions.

It is noteworthy that the amount of sodium taken up during the experimental period and found in the roots of the plants with different initial contents of sodium is practically the same in each of the three experimental treatments. (This is further evidence that the exchange of isotopes is of negligible importance in this respect.) The amount is therefore independent of the sodium level of the plant before uptake begins (Fig. 7).

Since the accumulation in the root (Fig. 6) does exhibit this dependence (accumulation=uptake - outgo), the difference between the intake of sodium from the culm and the *total* outgo of sodium from the root must depend upon the sodium level of the root and culm.

The amounts of sodium taken up during the experiment and found in the culms of plants with different initial levels of sodium were, in contrast with that which was observed in the case of the roots, not the same in each of the three experimental treatments (Fig. 7).

Accepting the undeniably reasonable assumption that the plants initially containing the smallest amount of sodium should be found to have taken up the greatest amount of sodium during the experiment, the actual result is somewhat surprising. The ascending order of sodium uptake was: plants cultured with 0.1 m.e., those cultured with 4 m.e. and those cultured with 2 m.e.

If, however, this is related to the previously described differences in sodium accumulation in root and culm by plants with different sodium levels (Fig. 6) it then appears that the largest intake occurs in the culms of plants cultured in a nutrient solution containing 2 m.e. sodium. And it is with these plants that the accumulation in the roots is relatively smaller (Fig. 6) when the amount of uptake-sodium in their roots is equal to that in the roots of plants of the other sodium levels (Fig. 7).

A similar relationship holds for plants cultured in nutrient solutions with the other two sodium levels. Therefore, the reason for the above-mentioned order for the amounts of uptake-sodium in the culms must be attributed to the alternation in the extent to which sodium accumulates in the culm and root, dependent upon the original sodium level of the experimental plant. At the same time it appears that that amount of sodium taken up during the experimental period which migrates to the culm is dependent upon the sodium level of the root.

If the sodium level of the root is such that only a very small amount of sodium is accumulated in it, a relatively strong enrichment of the uptake-sodium in the culm results. If, on the other hand, it is such that the accumulation of sodium is considerable, relatively little enrichment of the uptake-sodium in the culm occurs.

In comparing the amounts of non-radioactive sodium which are found in the culms and roots after the experiment it is essential that consideration be given to the facts that:

(1) The amount of non-radioactive sodium found in the root is the resultant of the intake of non-radioactive sodium from the culm and the outgo of non-radioactive sodium to the culm and to the nutrient solution.

(2) The amount of non-radioactive sodium found in the culm is the resultant of the intake of non-radioactive sodium from the root and the outgo of non-radioactive sodium from the culm.

With plants cultured in nutrient solutions containing 0.1 and 4 m.e. sodium more non-radioactive sodium leaves the culm during the experimental period than that which migrates from the root to the culm (Fig.8).

As previously mentioned, in the case of these experimental plants, the accumulation of sodium in the culm is minute in comparison with that in the root (Fig.6). The amount of non-radioactive sodium in the root is, in the first instance, increased at the expense of the non-radioactive sodium in the culm. It is for this reason that, on the whole, the roots of plants having one of these two sodium levels relinquish little non-radioactive sodium. In the case of plants cultured in the nutrient solution containing 2 m.e. sodium more non-radioactive sodium is, generally speaking, conveyed from the root to the culm than from the culm to the root during the experimental period. Thus, the total outgo of non-radioactive sodium from the root in the latter plants is appreciably greater than in those originating from the other two sodium levels.

The cause of this difference in retention of non-radioactive sodium by plants with different sodium levels can again be found in the previously mentioned phenomenon of the unequal accumulation which occurs in the roots and culms of such plants.

In the experimental treatments employing similar culture material (treatments a, b, c, d, e, f, etc.), the amounts of non-radioactive sodium found in the roots and the culms of the plants do not differ to any appreciable extent.

In treatments a, b, c, d, g, h and i (Fig. 8), the amounts of non-radioactive sodium which migrate from the roots to the culms are smaller than the amounts which migrate from the culms to the roots. In these cases, therefore, the culms become poorer in non-radioactive sodium as a result of the experimental conditions. The reverse is applicable, however, in treatments e and f. No causal connection can be found between the enrichment or impoverishment of the culm in respect of this sodium, on the one hand, and the sodium concentration of the nutrient solution and the uptake, on the other. It thus appears that the size of the resultant of the gain and loss by the culm of this sodium is dependent solely upon the sodium level of the plant.

In treatments a, c, g and i, the amount of non-radioactive sodium found in a given root after the experiment is practically equal to that which was present in it before the experiment, despite the outgo to the culm and to the nutrient solution which has meanwhile occurred (Fig. 8). In these cases, therefore, the total outgo of non-radioactive sodium from the plants has been balanced by the amounts of this type of sodium which have migrated from the culm to the root.

The considerable loss of non-radioactive sodium from the root which was found to have occurred in treatments e and f (Fig. 8) is attributable to the fact that in these cases the outgo to the culm is greater than the intake from the culm.

With the root, as with the culm, the sodium level of the plant thus appears to play a decisive role in the migration of non-radioactive sodium from the root.

7. *The influence of the experimental conditions upon the translocation and distribution of the sodium ions taken up during the cultural period of Experiment B.*

Because of the heterogeneous mixture of radioactive and non-radioactive sodium present in the culture-plants, true values for the uptake and the outgo cannot be obtained from Experiment B (radioactive plants in non-radioactive experimental nutrient solution).

The changes occurring in the amounts of culture-sodium present in the roots and culms as a result of the uptake of non-radioactive sodium during the experimental period can, however, be deduced in terms of true values from the changes in the radioactivity of the roots and culms. For this purpose, however, the radioactivity of the plants before and after the experiment must not be related to the total amount of sodium present in the roots and culms, but to the amount of sodium taken up during the cultural period.

TABLE 25

DISTRIBUTION OF CULTURE-SODIUM BETWEEN THE CULMS AND ROOTS OF THE PLANTS AFTER EXPERIMENT B

Sodium contents of the cultural nutrient solutions (in m.e. per litre)	Average amounts of sodium taken up by the plants during the cultural period (in mg.)			Treatment	Sodium contents of the experimental nutrient solutions (in m.e. per litre)	Average culture-sodium contents of the plants after the experiment (in mg.)		
	culm	root	plant			culm	root	plant
0.1	0.064	0.207	0.271	j	0.1	0.049	0.219	0.268
0.1	0.064	0.207	0.271	k	2	0.060	0.149	0.209
0.1	0.064	0.207	0.271	l	4	0.051	0.135	0.186
2	2.43	1.98	4.41	m	0.1	2.756	1.654	4.410
2	2.43	1.98	4.41	n	2	2.485	1.507	3.993
2	2.43	1.98	4.41	o	4	2.015	1.495	3.510
4	4.32	2.53	6.85	p	0.1	4.085	2.752	6.837
4	4.32	2.53	6.85	q	2	3.779	2.098	5.877
4	4.32	2.53	6.85	r	4	4.007	1.769	5.781

In comparison with the differences between the amounts of culture-sodium present before the experiment in the plants cultured at the three sodium levels, the differences between the total outgo of this type of sodium from plants of corresponding treatments in the experiment (j, m, p; k, n, q; l, o, r) are not large (Table 25, Fig. 9). As the amounts of uptake during the experimental period by the plants of the corresponding treatments are of the same order, the original sodium levels of the experimental plants can exercise only a slight influence upon the total outgo of culture-sodium.

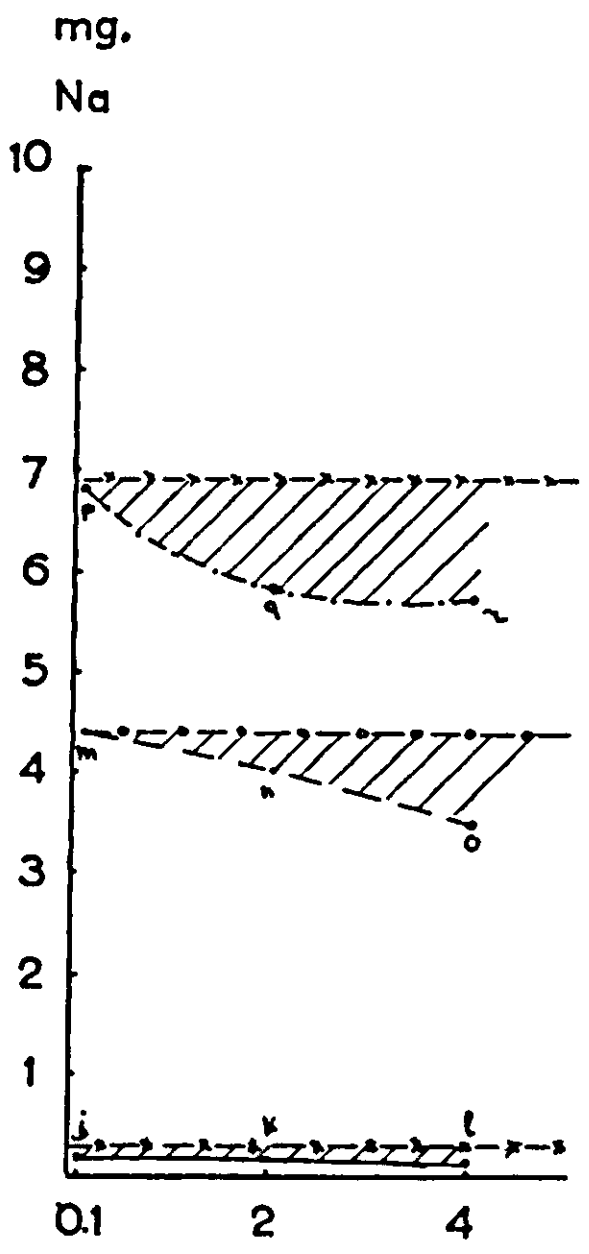


Fig. 9. Culture-sodium contents of the plants after Experiment B

Sodium contents before the experiment of the plants cultured in nutrient solutions containing

0.1 m.e. Na per litre – * – * – * – *

2 m.e. Na per litre o – o – o – o –

4 m.e. Na per litre – x – x – x – x

Culture-sodium contents after the experiment of plants cultured in nutrient solutions containing

0.1 m.e. Na per litre ————————

2 m.e. Na per litre – – – – – – – –

4 m.e. Na per litre – . – . – . – .

Outgo of culture-sodium

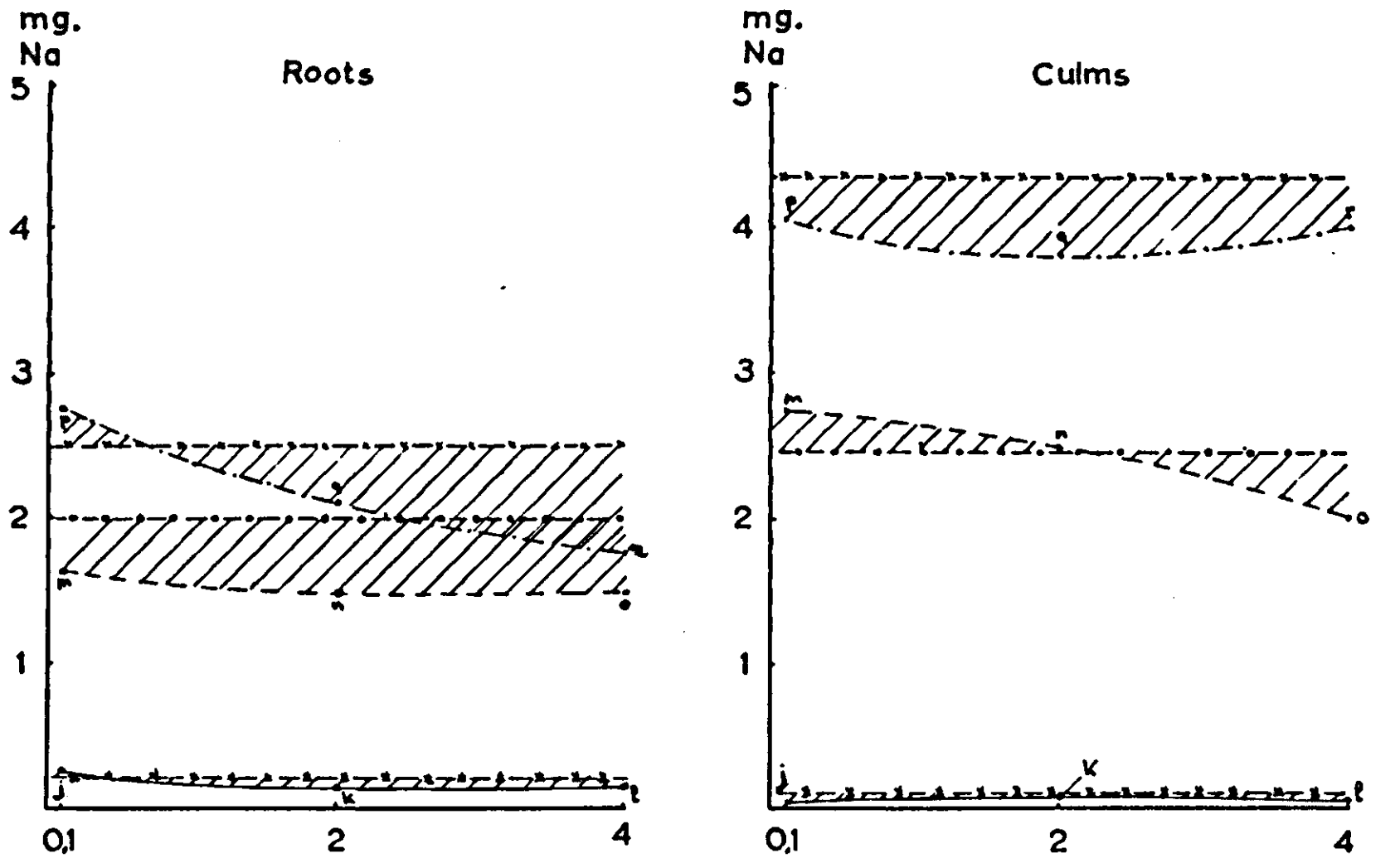


Fig. 10. Culture-sodium contents of the roots and culms after Experiment B.

Sodium contents before the experiment of roots and culms cultured in nutrient solutions containing

0.1 m.e. Na per litre - * - * - * -

2 m.e. Na per litre o - o - o - o

4 m.e. Na per litre - x - x - x -

Culture-sodium contents after the experiment of roots and culms cultured in nutrient solutions containing

0.1 m.e. Na per litre ————————

2 m.e. Na per litre - - - - - - -

4 m.e, Na per litre - . - . - . -

Intake or outgo of culture-sodium

In the case of the plants cultured in nutrient solutions containing 0.1 and 2 m.e. sodium (treatments j,k, l; m, n, o), the outgo increases approximately in proportion with the sodium concentration in the nutrient solution (Fig.9). This proportional increase in outgo suggests that part of the culture-sodium is exchanged by a part of the experimental-sodium. The fact that this linear relationship is not found in the case of the plants cultured in the nutrient solutions with 4 m.e. sodium is attributable to the phenomenon that in treatment r (Fig. 10) the difference between the amount of culture-sodium which has migrated from the root to the culm and from the culm to the root is smaller than in treatment q.

In the case of plants cultured in nutrient solutions with 0.1 and 2 m.e. sodium the outgo of culture-sodium from the culms and roots is more or less proportional to the increase in sodium concentration of the nutrient solution (Fig 10).

The outgo from plants with higher initial sodium levels (those cultured in nutrient solutions with 2 and 4 m.e. sodium) is larger than that from plants with the lowest sodium level, whilst the uptake by plants of corresponding treatments during the experimental period is of the same order. This is explainable by the fact that plants containing less culture-sodium have more germination-sodium. Thus, with these plants, more germination-sodium is exchanged by uptake-sodium than is the case with plants containing much culture-sodium and little germination-sodium.

In the case of treatments j, k and l (Fig. 10) the resultant of the migration of culture-sodium is such that only the roots of the plant exhibit an appreciable depletion of this type of sodium. It appears, therefore, that the amounts of sodium migrating from the root to the culm and from the culm to the root are equal. That migration from the root to the culm had indeed occurred was deducible from measurements of the specific activity of the root made before and after the experiment (Table 26).

The plants of treatments j,k, l; m, n, o; and p, q, r were cultured in nutrient solutions containing 0.1, 2 and 4 m.e. sodium respectively, all these solutions containing, in addition, the same amount of radioactive sodium. The change in specific activity exhibited by the culm and the root occurred through the uptake during the experiment of non-radioactive sodium from nutrient solutions containing 0.1, 2 and 4 m.e. sodium. During this uptake part of the sodium which was present in the plant before the experiment has migrated from the root to the culm, from the culm to the root and from the root to the nutrient solution. In the case of treatment j the total specific activity after the experiment has increased and it is clear that whilst non-radioactive sodium has been surrendered to the nutrient solution, little or no radioactive culture-sodium has thus been lost by the plant. In all other cases, however, radioactive culture-sodium has been conveyed to the nutrient solution to a greater or lesser degree.

TABLE 26

SPECIFIC ACTIVITY OF GERMINATION-SODIUM AND CULTURE-SODIUM IN THE PLANTS (in c.p.m.)

Sodium contents (in m.e. per litre) of		Treat-ment	Specific activity			
			before the experiment		after the experiment	
the cultural nutrient solutions	the experi-mental nutrient solutions		culm	root	culm	root
0.1	0.1	j	28,654	85,545	66,332	64,944
0.1	2	k	28,654	85,545	27,733	18,580
0.1	4	l	28,654	85,545	19,473	19,050
2	0.1	m	265,500	264,140	265,920	260,700
2	2	n	265,500	264,140	204,300	125,840
2	4	o	265,500	264,140	189,040	137,320
4	0.1	p	212,440	300,600	207,680	200,720
4	2	q	212,440	300,600	227,160	162,720
4	4	r	212,440	300,600	220,920	126,040

The influence of the various sodium concentrations of the experimental nutrient solutions upon the specific activity of the culm decreases as the sodium level of the plants themselves increases. As regards the root, this relationship is not so clearly indicated, this being apparently attributable to the fact that here, apart from a certain outgo to and intake from the culm, there is also outgo to the nutrient solution.

It is clearly apparent from these changes in specific activity that migration of sodium from the root to the culm and from the culm to the root and to the nutrient solution has taken place. However, the difficulties attached to measuring the extent to which this migration occurs become obvious when it is considered that, for instance, a change in specific activity can be occasioned not only by an increase in radioactive sodium but also by the surrender by the plant of non-radioactive germination-sodium.

In treatments k, l, m, o and p more radioactive sodium has migrated from the culm than has been compensated for by migration of this sodium from the root. This radioactive sodium, further increased by other radioactive sodium from the root, has migrated from the root to the nutrient solution. In treatments m, q and r, on the other hand more radioactive sodium has migrated to the culm from the root than to the root from the culm.

Although this last-named factor has also contributed to a reduction in the specific activity of the root the chief cause is the outgo of radioactive sodium from the root to the nutrient solution. Thus it can be stated that the outgo of culture-sodium to the nutrient solution is influenced by but not quantitatively correlated with the migration of sodium from the root to the culm and from the culm to the root.

IV. CONCLUSIONS

(1) The radioactivity of the plant and of the nutrient solution has no influence upon sodium accumulation.

(2) Sodium is taken up more readily during the experiment by plants having a considerable sodium content before the experiment than by plants having a low sodium content.

(3) The role played by the exchange of isotopes is only of secondary importance.

(4) The vice-versa effect is of very little importance.

(5) Uptake reveals itself as an active process, and outgo as a passive process.

(6) The accumulation of sodium ions occurs alternately in root and culm.

(7) The sodium level of the culm does not increase until the roots had acquired a certain sodium level.

(8) During the experimental period the behaviour of the sodium taken up during the germination period is different from that of the sodium taken up during the cultural period.

(9) The outgo and the translocation of the sodium taken up during the cultural period are not related quantitatively.

(10) The sodium in the plant is more readily exchanged by other sodium ions than by ions of Ca, K or Mg.

(11) Sodium is present in the plant in three different forms of binding, namely:

(a) A form in which it can easily be exchanged by Na, Ca, K or Mg ions;

(b) A form in which it can easily be exchanged by other Na ions but only with difficulty by ions of Ca, K or Mg (selective binding);

(c) A form in which it can be exchanged only with difficulty by other Na ions (specific binding).

(12) On the basis of b and c it must be assumed that, apart from its general function in the plant (see a) sodium must also fulfil a specific and an essential function. Whether or not these functions are of vital importance to the plant is still an open question.

CHAPTER VII

THE INFLUENCE OF TOP-DRESSING WITH SODIUM NITRATE AT DIFFERENT STAGES OF DEVELOPMENT UPON THE UPTAKE AND DISTRIBUTION OF SODIUM IN OATS (Avena sativa var. Marne)

I. INTRODUCTION

Sodium accumulation at different stages of plant development and the influence thereon of the time of application of a top-dressing of sodium nitrate were investigated in a pot experiment on oats carried out in triplicate in 2-litre glass cylinders containing a mixture of dusarite and silica sand.

The plants were harvested in groups on five different dates, the date of harvesting of each group except the last coinciding with the date on which the top-dressing was applied to the next group for harvesting. In the case of the final group both sodium accumulation and sodium distribution in the plants top-dressed at different times were investigated. In order that the sodium taken up from the basal dressing could be differentiated at the end of a development period from that taken up from the top-dressing the latter was applied as sodium nitrate labelled with Na^{22}.

At each harvesting, plants which had received no top-dressing were harvested simultaneously with the plants which had. It was thus possible to determine by means of the Na^{22} not only the uptake of sodium from the top-dressing but also the contribution of the top-dressing to the total accumulation of sodium.

A dusarite-silica sand mixture was used as the culture medium in order to preclude the uptake of sodium from any source other than the applied fertilizer.

The harvesting times were chosen in such a way that they coincided as nearly as possible with the beginning of the successive stages of development of the plants.

II. THE DESIGN AND EXECUTION OF THE EXPERIMENT

1. Fertilizer dressings

Full details of the design and execution of the experiment are given in Appendix 4. The basal dressing which contained 200 mg. N in the form of $NaNO_3$ was applied in two equal portions, the one half when the pots were filled, the other immediately following the thinning out.

The dates of top-dressing with 100 mg. N as $NaNO_3$ labelled with radioactive sodium and of harvesting the treatments are as follows:

Treatment:	A. F. J. M. O.	B. C. D. E.	G. H. I.	K. L.	N
Date of top-dressing:	no top-dressing	19th May	27th May	11th June	18th June

Treatment:	A.	B. F.	C. G. J.	D. H. K. M.	E. I. L. N. O.
Date of harvesting:	19th May 10 days before the rapid height-growth stage	27th May 2 days before the rapid height-growth stage	11th June the beginning of the escape of the panicle	18th June panicle fully developed	23rd July: fully ripened crop

Seed from oat plants which had received no sodium fertilization was used. This seed contained very little sodium, viz. 0.46 mg. per 100 g. dry matter. The experimental error was 7.3%.

2. Radioactive sodium

The radioactive sodium used was obtained from 60 μc. Na^{22} which was prepared on 21st May 1952, a year before it was used in the experiment. In calculating the amount of Na^{22} required for the experiment (1.5 μc. per top-dressing per pot) its reduced radioactivity was taken into account. At the time of application its radioactivity was 79.38% of its original strength.

III. THE DEVELOPMENT OF THE CROP

1. Height growth

At the beginning of the experiment the plants of all treatments were equally developed.

TABLE 27

HEIGHTS, FRESH WEIGHTS AND DRY-MATTER YIELDS OF THE PLANTS AT DIFFERENT HARVESTING DATES

Treatment	Height (in cm.)	Fresh weight (in g.)	Dry matter (in g.)	Percentage dry matter	Dry matter (in g.)				Weight of 1000 grains (in g.)	Date of harvesting
					Grain	Chaff	Endosperm	Stem		
	1	2	3	4	5	6	7	8	9	
A_o	26	10.15	0.95	9.35						19th May
B_a	43	34.35	3.80	11.06						27th May
C_a	64	80.00	14.15	17.69						11th June
D_a	70	86.45	16.18	19.43						18th June
E_a	77	31.00	17.60	56.80	6.39	1.55	4.84	11.21	24	23rd July
F_o	38	30.20	3.80	12.58						27th May
G_b	64	61.75	10.90	17.65						11th June
H_b	73	90.60	19.20	21.19						18th June
I_b	77	29.00	15.18	52.30	5.04	1.22	3.82	10.15	26	23rd July
J_o	60	58.40	10.25	17.55						11th June
K_c	70	81.30	16.20	19.92						18th June
L_c	78	35.00	16.04	45.50	6.42	1.64	4.78	9.62	25	23rd July
M_o	73	74.95	15.85	21.14						18th June
N_d	77	37.00	16.56	44.80	6.16	1.56	4.60	10.40	30	23rd July
O_o	78	40.00	16.39	41.00	6.24	1.98	4.26	10.15	27	23rd July

Legend:
- o no top-dressing
- a top-dressed with 100 mg.N on 19th May
- b top-dressed with 100 mg.N on 27th May
- c top-dressed with 100 mg.N on 11th June
- d top-dressed with 100 mg.N on 18th June

Up to the escape of the panicle and during the ripening, the time of application of the top-dressing had no effect on the rate of height-growth (Table 28). During the development of the panicle, on the contrary, growth was somewhat suppressed in cases in which the top-dressing had been applied 10 days before the rapid height-growth stage or at the beginning of the escape of the panicle. Such arrears in height-growth were, however, made good completely after the panicle had developed fully. Top-dressing and its time of application had, therefore, no effect upon the total growth.

TABLE 28

HEIGHTS OF THE PLANTS (in cm)

Treatment	Not top-dressed	Top-dressed on				Development stage at time of harvesting
		19 May	27 May	11 June	18 July	
Harvested on:						
19 May	26	–	–	–	–	10 days before the rapid height-growth stage
27 May	38	43	–	–	–	2 days before the rapid height-growth stage
11 June	60	64	64	–	–	At the beginning of the escape of the panicle
18 June	73	70	73	70	–	Panicle fully developed
23 July	78	77	77	78	77	Fully ripened crop

2. Colour of the leaf

The difference in colour of the leaf between plants which had and had not received nitrogen as top-dressing was clearly observable even at the time of the first harvest (27th May). It became

more pronounced as the plants developed further. A considerable difference in colour was also seen between plants which were top-dressed after 19th May and those which received no top-dressing. The intensity of greenness appeared to be dependent upon the time of application of the top-dressing. The earlier the top-dressing with nitrogen was applied, the darker was the green colour of the leaves.

3. *Withering of the culms*

The time at which the leaves began to yellow and wither was influenced by the application or withholding of the top-dressing and the time of application. The earlier top-dressing was applied, the later yellowing of the leaves occurred. The plants which were top-dressed at an early stage of development (treatment E) withered more slowly than those top-dressed at a later stage.

IV. THE EXPERIMENTAL RESULTS

1. *The yields obtained at different stages of development as influenced by the time of application of the top-dressing.*

The average fresh weights and dry-matter yields and percentages arranged in accordance with date of harvesting and time of application of top-dressing are shown in Table 29.

The yields increase progressively through the different stages of development up to and including that in which complete development of the panicle occurs (19th May to 18th June). Thereafter (23rd July) the fresh weights decline sharply as a result of the ripening process, the dry-matter percentages increase sharply and the dry-matter yields remain practically unaffected.

The yields from the crop are influenced by:
(1) The stage of development reached at the time of harvesting;
(2) The time of application of the top-dressing.

As the times of harvesting coincided approxymately with the beginning of new stages of development, the average yields of plants top-dressed with sodium nitrate 10 days before the beginning of the rapid height-growth stage (treatments B, C, D, E) and those of plants which received no top-dressing (treatments A, F, J, M, O) reflect the increases in fresh weight and dry-matter production of the plants at each stage of development.

Up to and including the stage of the beginning of the escape of the panicle (11th June) both the top-dressed and the non-top-dressed plants exhibited pronounced yield increases in the order mention-

TABLE 29

FRESH WEIGHTS, DRY-MATTER YIELDS AND DRY-MATTER PERCENTAGES

Date of harvesting	19th May	27th May	11th June	18th June	23rd July
Development stage	10 days before the rapid height-growth stage	2 days before the rapid height-growth stage	begin-ning of escape of panicle	panicle fully devel-oped	crop fully ripe
Treatment	A	B	C	D	E
Fresh weight (in g.)	10.15	34.35	80.00	86.45	31.00
Dry-matter yield (in g.)	0.95	3.80	14.15	16.80	17.60
Dry-matter percentage	9.35	11.06	17.69	19.43	56.80
Treatment		F	G	H	I
Fresh weight (in g.)		30.20	61.75	90.60	29.00
Dry-matter yield (in g.)		3.80	10.90	19.20	15.18
Dry-matter percentage		12.58	17.65	21.19	52.30
Treatment			J	K	L
Fresh weight (in g.)			58.50	81.30	35.00
Dry-matter yield (in g.)			10.25	16.20	16.04
Dry-matter percentage			17.55	19.92	45.50
Treatment				M	N
Fresh weight (in g.)				74.95	37.06
Dry-matter yield (in g.)				15.85	16.56
Dry-matter percentage				21.14	44.80
Treatment					O
Fresh weight (in g.)					40.00
Dry-matter yield (in g.)					16.39
Dry-matter percentage					41.00

ed above. Some increase was also observable during the period of the escape of the panicle but it was appreciably less than in the previous stage of development.

From this it appears that the period of optimal dry-matter production ends with the conclusion of the period of rapid height-growth. During the ripening period the plant loses considerable amounts of moisture. The amounts of dry matter scarcely change during this period, remaining at the level found at the end of the panicle development.

The effect of the extra application of nitrogen also reveals itself in the fresh-weight and dry-matter yields when top-dressing is applied at the beginning of the rapid height-growth stage (treatments G, H, I) or at the time when the panicle begins to escape (treatments K, L). When early application of top-dressing is made 10 days before the stage of rapid height-growth its effect appears to cease at the escape of the panicle.

The influence of the top-dressing applied on 27th May at the beginning of the rapid height-growth stage reveals itself during that stage and during the stage of the escape of the panicle. Top-dressing applied at a still later stage of development (treatments K, L, M) appears to have only a very small effect.

In the case of plants which received no top-dressing the dry-matter production appears to occur uniformly at all stages of development.

Top-dressing with sodium nitrate appears to have favoured dry-matter production at all stages of development up to and including that in which panicle development was complete. After this stage, it appears from the final harvest that the dry-matter yield was effectively stimulated only by the first top-dressing (Table 29) given on 19th May, 10 days before the rapid height-growth stage. The top-dressings applied on 27th May and 11th June depressed the dry-matter yield while that given on 18th June was apparently too late in the development period to influence dry-matter production.

It is apparent from the final harvests that the top-dressings, irrespective of their date of application, all had a depressing effect upon the fresh weights. The later in the development of the crop the nitrogen is applied, the less pronounced is its depressing effect. This signifies that the nitrogen dressings given during the later stages of development were unable to assert themselves to the full.

The fact that this trend in fresh weights was observed only with fully ripened and not with still developing plants implies that the plants given an early top-dressing of sodium nitrate must have had a higher moisture content than those plants top-dressed at a later stage of development of not at all.

The dry-matter yield from treatment I is exceptional because of the fact that the dry-matter yield of the grain happened to be low in this treatment.

In general, with the exception of that applied very late in the development period (18th June), top-dressing with nitrogen resulted in a reduction in the weight of 1000 grains (Table 27, column 9).

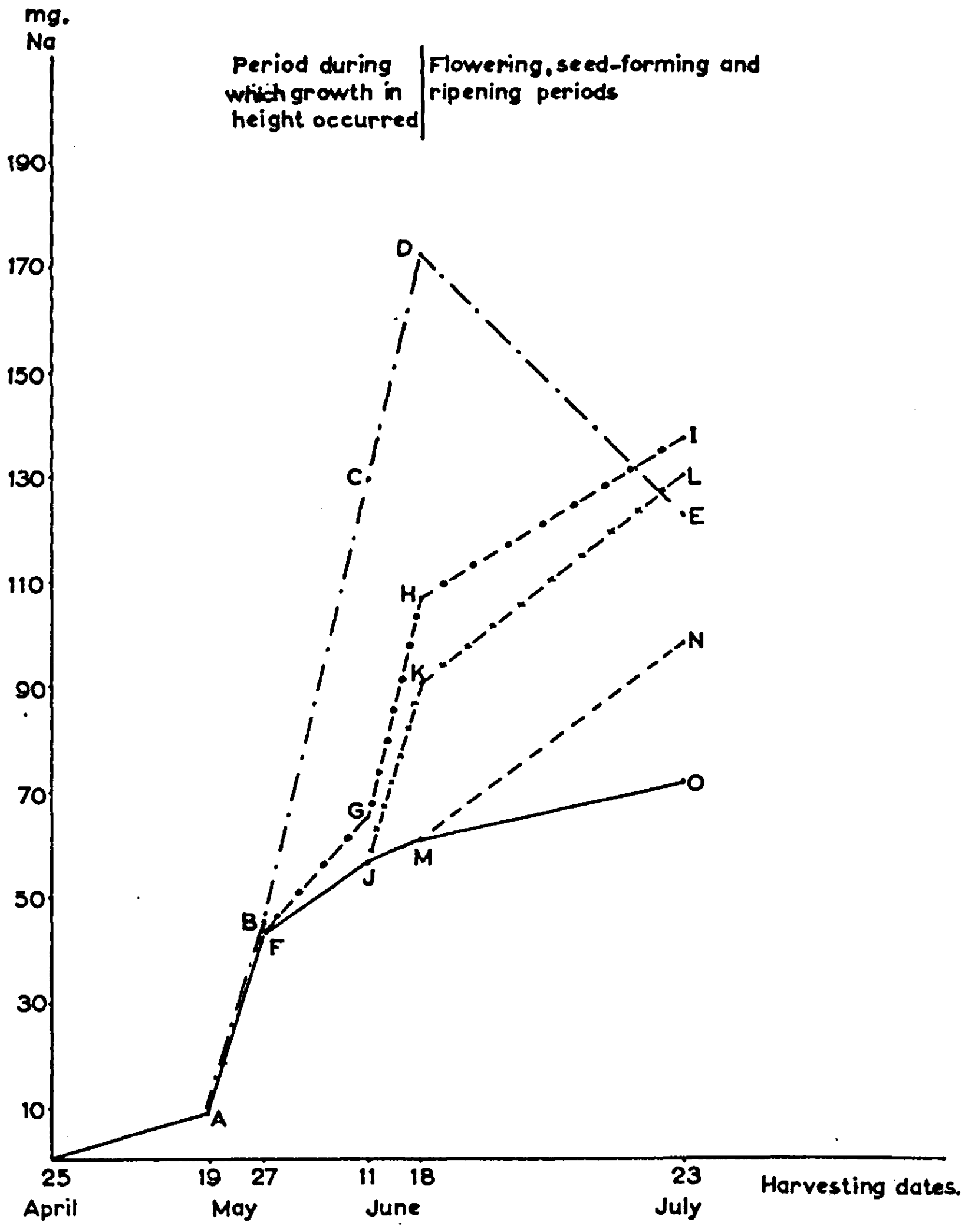


Fig.11. Total sodium accumulation in oat plants at different stages of development as influenced by the date of top-dressing.*

Top-dressed with sodium nitrate on:
- · - · 19th May (10 days before the rapid height-growth stage)
- o - o 27th May (2 days before the rapid height-growth stage)
- x - x 11th June (at the escape of the panicle)
——— 18th June(full panicle development)
——— No top-dressing

* For details of treatments A to O in this and subsequent figures see Chapter VII, II Design and Execution of the Experiment.

2. *The accumulation of sodium ions at different stages of development as influenced by the time of application of the top-dressing*

The accumulation of sodium in the aerial parts of the plant was determined at various stages of development of the crop. Using the chemical method, the total sodium accumulation from the basal dressing and the top-dressing, the sodium accumulation from the basal dressing before and after the application of the top-dressing and the sodium accumulation from the top-dressing were determined.

Since sodium accumulation from the basal dressing and the top-dressing can only be determined indirectly by the chemical method, determinations were also made by means of the tracer technique.

(1) Total sodium accumulation

The total sodium accumulation from the basal dressing and the top-dressing (Table 30, columns 1 and 2) by the plants of the different treatments is dependent upon the time of application of the top-dressing and upon the stage of development reached by the crop when harvested (Fig. 11).

The sodium accumulation found in plants of the treatments which received no sodium nitrate top-dressing, viz. treatments A, F, J, M, and O, is taken as the basis for comparison with the sodium accumulation of top-dressed plants.

During the period from 19th to 27th May, top-dressing with 100 mg. nitrogen in the form of sodium nitrate had practically no stimulating effect upon the sodium uptake as will be seen on comparison of treatment B with treatment F.

(a) Accumulation during the period of height development

During the rapid height-growth stage from 27th May to 11th June and the succeeding stage of the escape of the panicle from 11th to 18th June, the sodium accumulated per unit of time by the plants of the treatments top-dressed on 19th May showed a marked increase.

If the top-dressing is applied two days before the beginning of the rapid height-growth stage, the sodium accumulated by the plant during this stage of development is considerably less, while the rate of accumulation during the succeeding stages of development (the escape and development of the panicle) is equal to that found in the earliest top-dressed plants.

TABLE 30

SODIUM ACCUMULATION BY THE PLANTS OF THE DIFFERENT TREATMENTS FROM THE BASAL-DRESSING AND THE TOP-DRESSING AS DETERMINED BY THE CHEMICAL AND BY THE RADIOACTIVE METHOD

Treatment	Total sodium accumulation			Determination by the chemical method							Determination by the radioactive method				Top-dressed on	Harvested on
				Sodium accumulation from the basal dressing					Sodium accumulation from top-dressing		Basal dressing		Top-dressing			
				Total		Before top-dressing	After top-dressing									
	in mg.	in %	Sodium per 100 mg. dry matter in mg.	in mg.	in %	in mg.	in mg.	in %	in mg.	in %	in mg.	in %	in mg.	in %		
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)
A	8.68	2.64	0.913	8.68	2.64	8.68	–	–	–	–	–	–	–	–	–	19th May
B	44.96	9.12	1.183	43.61	13.26	8.68	34.93	10.61	1.35	0.82	26.18	7.96	18.78	11.43	19th May	27th May
C	129.26	26.22	0.914	56.34	17.13	8.68	47.66	14.49	72.92	44.46	64.02	19.46	65.24	39.71	19th May	11th June
D	173.04	35.10	1.030	60.88	18.5	8.68	52.20	15.87	112.16	68.39	87.08	26.47	85.96	52.32	19th May	18th June
E	123.39	25.03	0.704	71.74	21.8	8.68	63.06	19.18	51.65	31.49	70.76	21.51	52.63	32.03	19th May	23rd July
F	43.61	13.26	1.148	43.61	13.26	43.61	–	–	–	–	–	–	–	–	–	27th May
G	65.75	13.34	0.603	56.34	17.13	43.61	12.73	3.87	9.41	5.74	41.99	12.76	23.76	14.46	27th May	11th June
H	107.52	21.81	0.560	60.88	18.5	43.61	17.27	5.25	46.64	28.43	57.13	17.37	50.39	30.67	27th May	18th June
I	137.60	27.91	0.906	71.74	21.8	43.61	28.13	8.55	65.86	40.15	74.97	22.79	62.63	38.12	27th May	23rd July
J	56.34	17.13	0.550	56.34	17.13	56.34	–	–	–	–	–	–	–	–	–	11th June
K	90.88	18.43	0.561	60.88	18.5	56.34	4.54	1.38	30.00	18.29	75.70	23.01	15.18	9.24	11th June	18th June
L	131.34	26.64	0.819	71.74	21.8	56.34	15.40	4.70	59.60	36.28	87.52	26.60	43.82	26.67	11th June	23rd July
M	60.88	18.50	0.384	60.88	18.5	60.88	–	–	–	–	–	–	–	–	–	18th June
N	98.41	19.96	0.594	71.74	21.8	60.88	10.86	3.30	26.67	16.26	61.49	18.69	36.92	22.47	18th June	23rd July
O	71.74	21.81	0.438	71.74	21.8	71.74	–	–	–	–	–	–	–	–	–	23rd July
	determined		determined	determined		determined	calculated (7)=(4)-(6)		calculated (9)=(1)-(4)		calculated (11)=(1)-(13)		determined			

(2) As percentages of the sodium contained in the dressings.
(5), (8), (12) As percentages of the sodium contained in the basal dressing.
(10), (14) As percentages of the sodium contained in the top dressing.

In the plants of treatments B, C, D and E, the rate of sodium accumulation first increases at the beginning of the rapid height-growth stage, that is to say, at the time that sodium from top-dressing is first made available to the plants of treatments G, H and I. The fact that the plants of the latter treatments do not, however, exhibit accelerated sodium accumulation until some time after the plants of treatments B, C, D and E, must apparently be ascribed to the circumstance that their root systems require a certain period in order to adjust themselves to the sudden change in concentration of ions in the nutritive medium resulting from the top-dressing.

The top-dressing applied to the plants at the beginning of the escape of the panicle (treatment K) raises the rate of accumulation during this stage of development to practically the same value as that found in plants which were top-dressed 10 days before the rapid height-growth stage (19th May).

It therefore appears that, during the whole period of height-growth, the rate of accumulation is only dependent upon the time of application of the top-dressing during the stage of rapid height-growth. In view of the fact that the rate of accumulation during height-growth ultimately attains the same value irrespective of the time of application of the top-dressing, the plant would appear to aspire under these circumstances to a very definite maximal rate of accumulation (ca. 4.5 mg. sodium per day) during the period of height-growth. In the case of the plants of treatments which received no top-dressing, the accumulation is considerably less.

(b) Accumulation during the period of flowering, grain formation and ripening

A depletion of sodium during the later stages of development was observed only in those plants which were top-dressed 10 days before the beginning of the rapid height-growth stage. It may be that at the beginning of the period - during grain formation - sodium is still accumulated but that, as soon as the crop begins to wither, the amount of accumulated sodium decreases rapidly to the level reached by the plants top-dressed on 27th May and 11th June. This leads to the supposition that during the ripening and withering process, provided sufficient sodium is supplied, there is room in the plant for only a limited amount of sodium - for a definite sodium level - and that this is appreciably lower than that which the plant can easily acquire during its period of height-growth.

The plants of treatments top-dressed after 19th May exhibit a still considerable sodium accumulation during this period.

This supports the interpretation that, after considerable sodium has been taken up during the period of height-growth, the plant not only arrives at a definite sodium level during the ripening stage but, when sufficient sodium is available, strives to attain this level even after the period of height-growth is concluded.

In view of the fact that the plants top-dressed on 19th May, which clearly exhibited a depletion in sodium during the period of grain formation and ripening (Fig. 11), produced the highest yields (Table 27), the surplus sodium taken up during the period of height-growth should certainly not be regarded as a luxury consumption.

There is no reason for assuming that a depletion, such as was found in plants of treatment E, has not also occurred - even though to a lesser extent - in plants of other, corresponding treatments. The strong depletion which occurred in the case of treatment E may probably be ascribed in part to the fact that the withering process progressed more slowly in these plants than in those of the other treatments.

(2) Percentage sodium contents

The percentage sodium contents of the plants (Table 30, column 3) of the various treatments differ considerably. The observed differences are influenced both by the time of harvesting and the time of application of the top-dressing (Fig. 12), as was also the case with the sodium accumulation (Fig. 11).

After germination of the seed the percentage sodium content increases rapidly and reaches its highest value for the entire development period at the moment when the plant enters the rapid height-growth stage. During this period the sodium accumulation predominates over the dry-matter production. In the succeeding period of height-growth, this state of affairs is reversed; the sodium accumulation, which maintains the same value per unit of time, is then so completely overshadowed by production of dry matter that a sharp decline in sodium content is observable (Fig. 12).

The rate of this decline is influenced by the time of application of the top-dressing. In the case of early top-dressing on 19th June it is less pronounced than when top-dressing is omitted or applied late, owing to the strong sodium accumulation during the initial development.

At the time of transition from the rapid height-growth stage to the development of the panicle, the sharp decline in percentage sodium content is checked. At this time, the plants which were top-dressed on 19th May have already formed 80.4% of the total dry matter to be produced (Table 29). During the development of the panicle, the rate of dry-matter production decreases in the plants of these treatments whilst the sodium accumulation continues unabated, thus causing an increase in percentage sodium content. It appears from this that the sodium accumulation is dependent, not upon dry-matter production, but upon the stage of development in which the plant happens to be.

In the case of plants top-dressed at a later stage the production of dry matter is still in full swing during the period of panicle development. Moreover, because of the application of top-dressing

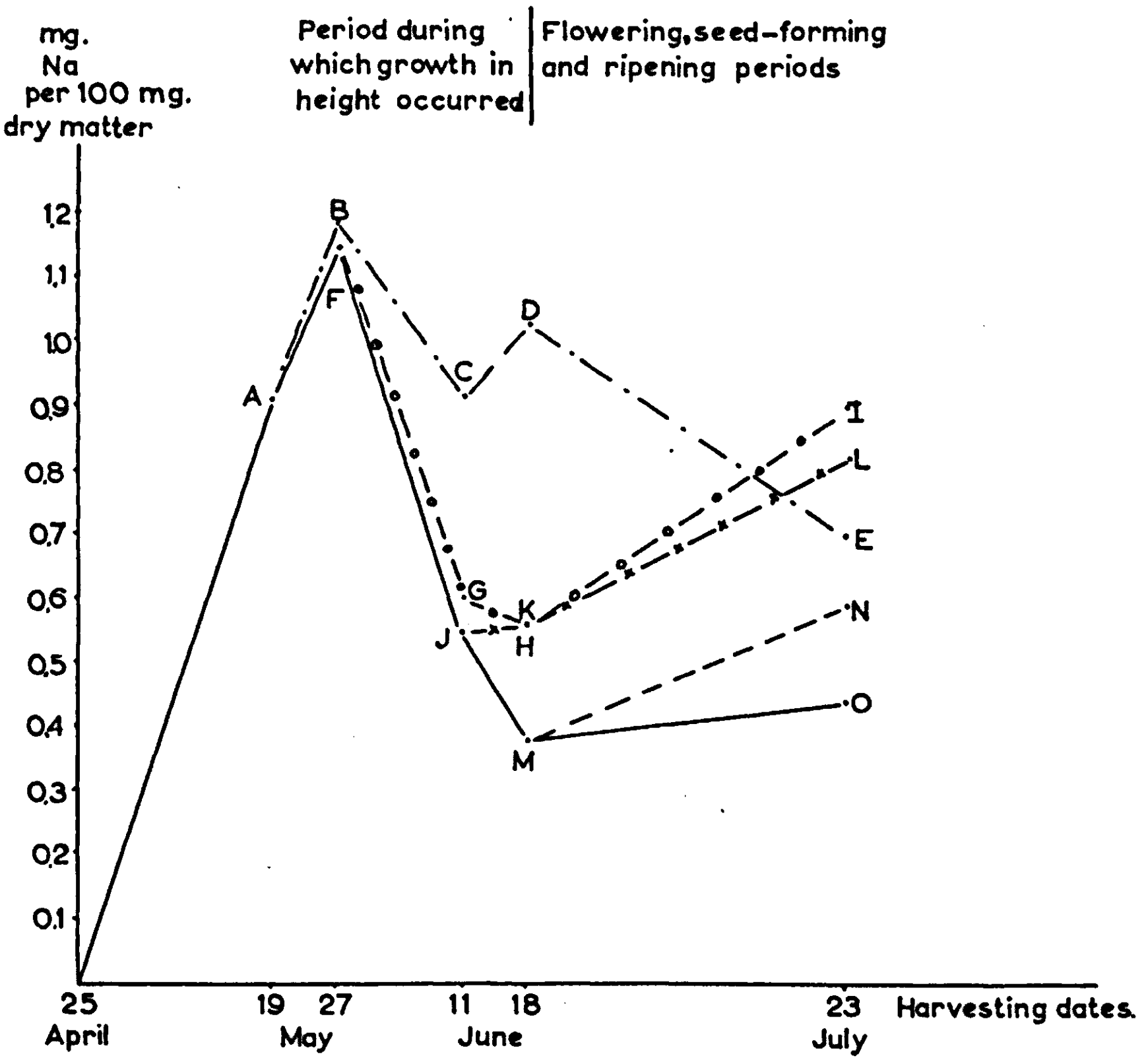


Fig.12. Sodium contents of the plants at different stages of development as influenced by the date of top-dressing.

Top-dressed with sodium nitrate on:

- . - . 19th May (10 days before the rapid height-growth stage)
- o - o 27th May (2 days before the rapid height-growth stage)
- x - x 11th June (at the escape of the panicle)
------- 18th June (full panicle development)
——— No top-dressing.

at a more advanced stage of development of the plant, the sodium accumulation lags behind that found during the same period of development in plants top-dressed on 19th May. As a result, the decline in percentage sodium content is less pronounced than in the preceding period but not completely arrested.

During the period of grain formation and ripening, in which only a very slight increase in dry matter is generally found (Table 29), an increase occurs in the percentage sodium content of the plants of all treatments. The one exception to this is formed by the plants which were top-dressed on 19th May (Fig. 12). This must be ascribed to the depletion in sodium which has occurred in this instance (Fig. 11).

(3) Sodium accumulation from the basal dressing and the top-dressing

The chemical determination of sodium accumulation from the basal dressing and the top-dressing by top-dressed plants is necessarily based upon sodium accumulation by non-top-dressed plants. The difference between the amounts of sodium in top-dressed plants and non-top-dressed plants harvested at the same time is normally regarded as the amount of sodium taken up from the top-dressing and thus represents the yield of top-dressing.

With the chemical method, however, it is not possible to take into account the influence which the top-dressing may have had upon the accumulation from the basal dressing, an influence which, in theory, can be either positive, negative or indifferent, Moreover, the chemical method allows of no conclusion in respect of the influence of the time of application of the top-dressing upon the accumulation from the basal dressing.

These shortcomings are due to the fact that two dissimilar treatments have to be compared, the determination of the accumulation from the basal dressing in top-dressed plants being based on the accumulation from the basal dressing in non-top-dressed plants.

For the determination of sodium accumulation from the basal dressing by the radioactive method, comparison with treatments which received no top-dressing is not necessary and the objections raised against the chemical method do not apply. By the tracer technique the accumulation from the basal dressing and from the top-dressing can be determined in one and the same specimen. It has been found that isotope exchange can safely be ignored (see Chapters V and VI).

In view of the fact that, but for the availability of radioactive isotopes, reliance would have to be placed upon the results obtained with the chemical method of determination, it is interesting to compare the results and conclusions from the methods (Tables 30 and 31).

TABLE 31

SODIUM ACCUMULATION FROM THE BASAL DRESSING AND THE TOP-DRESSED AFTER THE APPLICATION OF THE TOP-DRESSING
(in percentages of the dressing)

Treatment	Accumulation from basal dressing		Accumulation from top-dressing	
	Determined by the chemical method	Determined by the radioactive method	Determined by the chemical method	Determined by the radioactive method
B	10.6	5.3	0.8	11.4
C	14.5	16.8	44.5	39.7
D	15.9	23.8	68.4	52.3
E	19.2	18.8	31.5	18.9
G	3.9	-0.5	5.7	14.5
H	5.2	4.1	28.4	30.7
I	8.5	9.5	40.2	38.1
K	1.4	5.9	18.3	9.2
L	4.7	9.6	36.3	26.7
N	3.3	0.2	16.3	22.5
	Table 30 (8)	Table 30(12)-(2)	Table 30(10)	Table 30 (14)

In two-thirds of the treatments (B, D, G, K, L and N), the differences between sodium accumulations from top-dressing found by the radioactive and by the chemical method differ by more than twice the mean error * . The values determined by indirect chemical means therefore give a false impression of the respective contributions made by the basal dressing and the top-dressing to sodium accumulation. They differ from those determined by the radioactive method sometimes in a positive and sometimes in a negative sense. It is not possible to discern a definite trend in the differences. In the chemical method they appear to depend entirely upon the experimental conditions - in this case, upon the stage in the development of the plant at which top-dressing was applied. When the top-dressing is applied in the initial stage of development, it is practically immaterial whether the chemical method or the radioactive method is used for the determination of the accumulation from the basal dressing and from the top-dressing at maturity. When the accumulation is determined before maturity, however, the method employed makes a very definite difference, even in plants which received early top-dressing.

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*) In this experiment the error of the analyses was not greater than 5%.

TABLE 32

SODIUM ACCUMULATION FROM THE BASAL DRESSING DURING DIFFERENT STAGES OF DEVELOPMENT
(in percentages of the dressing)

Development stage	Chemically determined	Radioactively determined Top-dressed on 19th May	27th May	11th June	18th June	Harvested on
	Treatment	Treatment	Treatment	Treatment	Treatment	
30th April - 19th May: from germination to 10 days before rapid height-growth stage	A 2.64					19th May
19th-27th May: from 10 days to 2 days before rapid height-growth stage	B.F 10.6	B 5.32				27th May
27th May - 11th June: from 2 days before rapid height-growth stage to escape of panicle	C.E.J.3.87	C 11.50	G -0.5			11th June
11th-18th June: from escape of panicle to complete panicle development	D.H.K.M. 1.37	D 7.0	H 4.6	K 5.9		18th June
18th June - 23rd July: from complete panicle development to maturity	E.I.L.N, O 3.3	E 5.0	I 5.4	L 3.6	N 0.2	23rd July

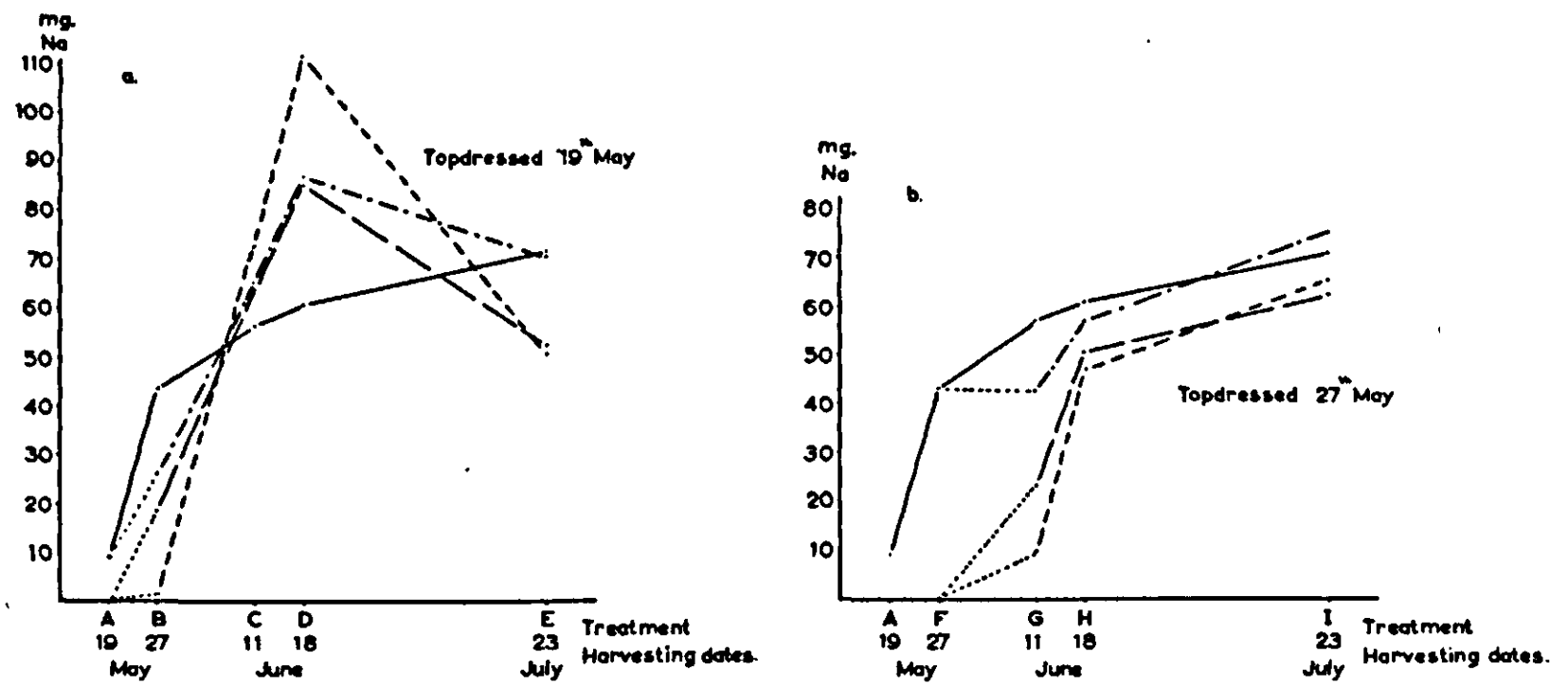

Fig.13. Sodium accumulation from the basal dressing and the top-dressing in plants at different stages of development as influenced by the date of top-dressing.

Chemically determined:

——— Sodium accumulation from the basal dressing

------- Sodium accumulation from the top-dressing

Physically determined (radioactive measurements):

– . – . – Sodium accumulation from the basal dressing

—— —— Sodium accumulation from the top-dressing

Measurements of the radioactivity of the plants show that the sodium accumulation from the basal dressing (and also from the top-dressing) was in no two cases equal. This signifies that, apart from a dependence upon the development stage at which the plant is harvested (and this can be found also by means of the chemical method) accumulation from the basal dressing and the top-dressing is also dependent upon the top-dressing and the time at which this is applied.

Using the chemical method, it was found that during the period from 19th to 27th May, the plants accumulated practically the same amount of sodium as in all the other periods of development put together. The plants of the different treatments accumulated less so-

dium during the period embracing the escape and development of the panicle than in any other single period of development. That this, however, is applicable only to plants of the treatments which received no top-dressing can be seen from comparison of the values with those obtained by means of the radioactive method (Table 32).

(4) The course of sodium accumulation from the basal dressing and the top-dressing determined by radioactive measurements in relation to that determined chemically

Since the course of accumulation from the basal dressing, determined chemically, is the same in top-dressed and non-top-dressed plants, the following effects of top-dressing on the course of accumulation from basal dressing can only be ascertained by radioactive determination. (Fig. 13):

(a) Plants top-dressed on 19th May (10 days before the rapid height-growth stage; treatments B, C, D, E; Fig. 13a)
  (i) Top-dressing promotes the uptake of sodium ions from the basal dressing.
  (ii) In the period of development preceding the rapid height-growth stage,, top-dressing suppresses accumulation from the basal dressing.
  (iii) In the case of the ripened crop, accumulation from the basal dressing is no longer influenced by the top-dressing.
  (iv) The rate of accumulation from the top-dressing during the rapid height-growth stage is identical with that obtaining during the period of escape and development of the panicle, but less rapid than would appear from the results of the chemical determinations.
  (v) The depletion of sodium taken up from the basal dressing during the periods of grain formation and ripening proceeds less rapidly than does the depletion of sodium taken up from the top-dressing during the same periods.
  (vi) According to the chemically determined values, depletion proceeds more rapidly than is, in fact, the case.
  (vii) Accumulation from the basal dressing is generally greater than - and only very rarely equal to - that from the top-dressing.
  (viii) Sodium from the basal dressing is less readily taken up than sodium from the top-dressing.

(b) Plants top-dressed on 27th May (2 days before the rapid height-growth stage; treatments G, H, I; Fig. 13b)
  (i) No accumulation of sodium from the basal dressing occurs during the rapid height-growth stage.

(ii) During the periods of escape and development of the panicle, grain formation and ripening, top-dressing stimulates uptake from the basal dressing.
(iii) The influence of the top-dressing upon uptake from the basal dressing is also positive in the case of the ripened crop.
(iv) The rate of accumulation from the top-dressing attains its highest value during the period of escape and development of the panicle.
(v) Accumulation from the basal dressing is always greater than that from the top-dressing.

(c) Plants top-dressed on 11th June (escape of the panicle; treatments K, L; Fig. 13c)
(i) The top-dressing promotes accumulation from the basal dressing during the period of escape and development of the panicle to a much greater extent than during the period of grain formation and ripening.
(ii) The rate of accumulation from the top-dressing is greater during the period of escape and formation of the panicle than during the period of grain formation and ripening, but less rapid than would appear from the chemically determined values.
(iii) Accumulation from the basal dressing is always greater than that from the top-dressing.

(d) Plants top-dressed on 18th June (at the beginning of the escape of the panicle; (Fig. 13d).
(i) As a result of the top-dressing, practically no accumulation of sodium from the basal dressing occurs during the period of grain formation and ripening.
(ii) Sodium accumulated during the period of grain formation and ripening originates solely from the top-dressing.

It is reasonable to assume that the more advanced the development of the plant when top-dressing is applied - that is, the longer the plant has had to depend upon the basal dressing as its source of sodium - the more sodium will be taken up from the basal dressing by the plant. This was in fact found to be the case in all plants (Table 30) except those of treatment N, which were the last to which top-dressing was applied and which did not receive it until after the escape and development of the panicle. In this last case it may be accepted that the sodium in the basal dressing was far less accessible to the plant than the sodium in the top-dressing and that, as a result, the plant took up sodium solely from the latter source during the period in question. Moreover, the top-dressing was presumably unable to work sufficiently into the soil in the short time available to allow a reasonable amount of its sodium to be exchanged. Apart from the more or less rapid growth dependent upon the stage of development, this exchange is one reason why the uptake from the basal dressing is stimulated by the top-dressing.

3. Total sodium accumulation in the organs of the plant

Since less exact information is obtained from the chemical determination and conclusions can be drawn which are at variance with the truth, the data given below were determined by the radioactive method.

TABLE 33

DISTRIBUTION OF THE ACCUMULATED SODIUM AMONG THE LEAF, THE STEM AND THE FRUIT IN PLANTS TOP-DRESSED AT DIFFERENT STAGES OF DEVELOPMENT

Treatment	Date of top-dressing	Part of the plant	Total accumulation in mg.	Total accumulation in %	Sodium content in mg. per 100 mg. dry matter	Accumulation from basal dressing in mg.	Accumulation from basal dressing in %	Accumulation from top-dressing in mg.	Accumulation from top-dressing in %
			(1)	(2)	(3)	(4)	(5)	(6)	(7)
E	19th May	leaf	29.19	23.7	1.76	20.72	29.3	8.47	16.1
		stem	89.32	72.6	1.03	46.69	66.0	42.63	81.0
		fruit	4.87	4.0	0.07	3.35	4.3	1.52	2.9
I	27th May	leaf	39.15	28.4	2.05	24.79	33.0	14.36	22.9
		stem	93.85	68.0	1.25	46.83	62.5	47.02	75.1
		fruit	4.60	3.3	0.08	3.35	4.5	1.25	2.0
L	11th June	leaf	24.05	18.4	1.42	19.72	22.5	4.33	9.9
		stem	104.40	77.4	1.41	63.06	72.0	38.34	87.5
		fruit	5.89	4.5	0.08	4.75	5.4	1.14	2.6
N	18th June	leaf	16.14	16.5	0.92	13.79	22.7	2.17	5.9
		stem	77.84	79.4	0.97	44.21	71.9	33.63	91.1
		fruit	4.44	4.5	0.07	3.31	5.4	1.13	3.1
0	not top-dressed	leaf	14.92	20.7	0.94	-	-	-	-
		stem	55.07	76.5	0.70	-	-	-	-
		fruit	1.75	2.4	0.03	-	-	-	-

(2) Sodium content expressed as a percentage of that of the total dressing.
(5) Sodium content expressed as a percentage of that of the basal dressing.
(7) Sodium content expressed as a percentage of that of the top-dressing.

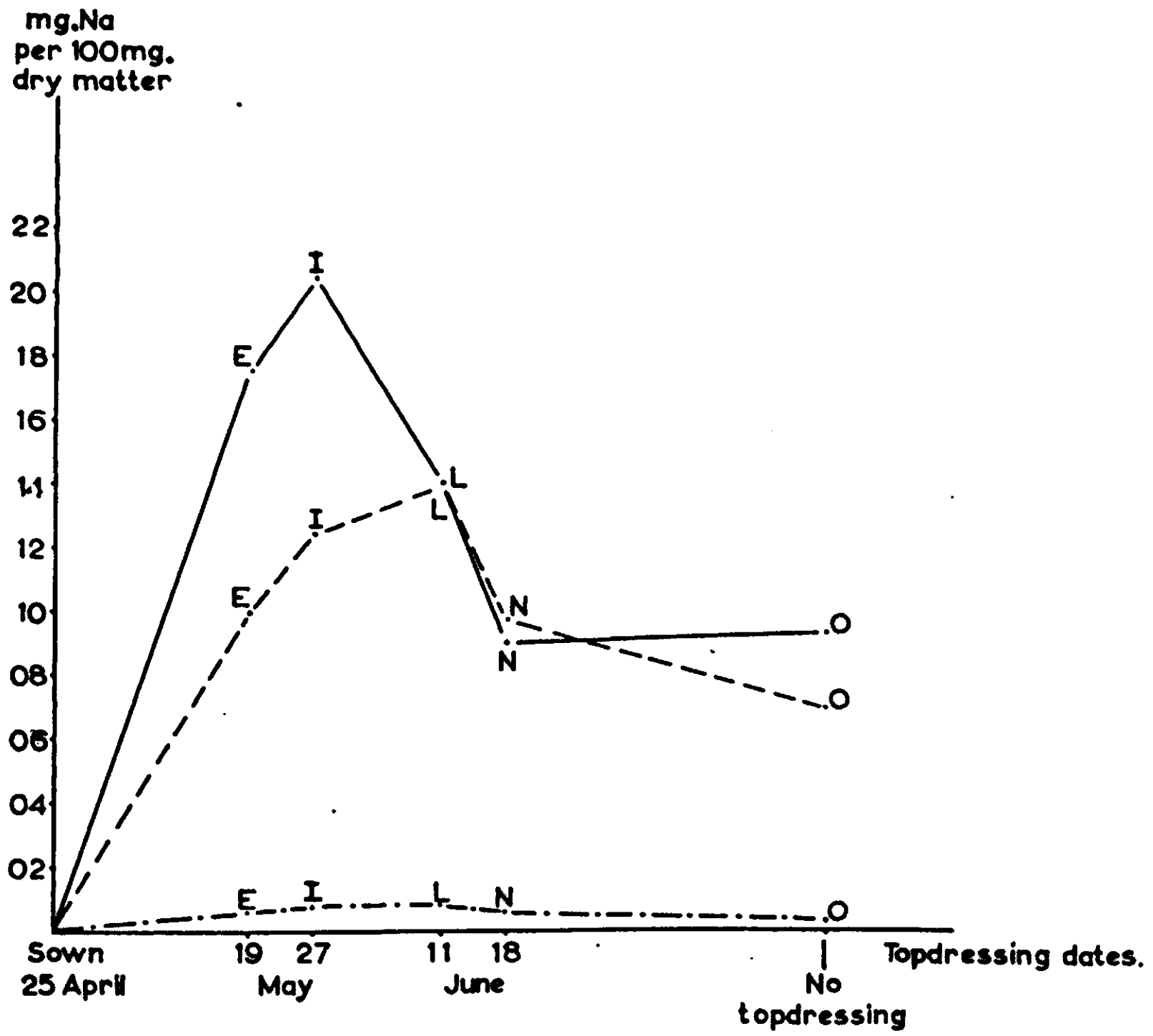

Fig.14. Total sodium accumulation in the leaf, the stem and the fruit at maturity as influenced by the date of top-dressing.

——— leaf

----- stem

-·-·- fruit

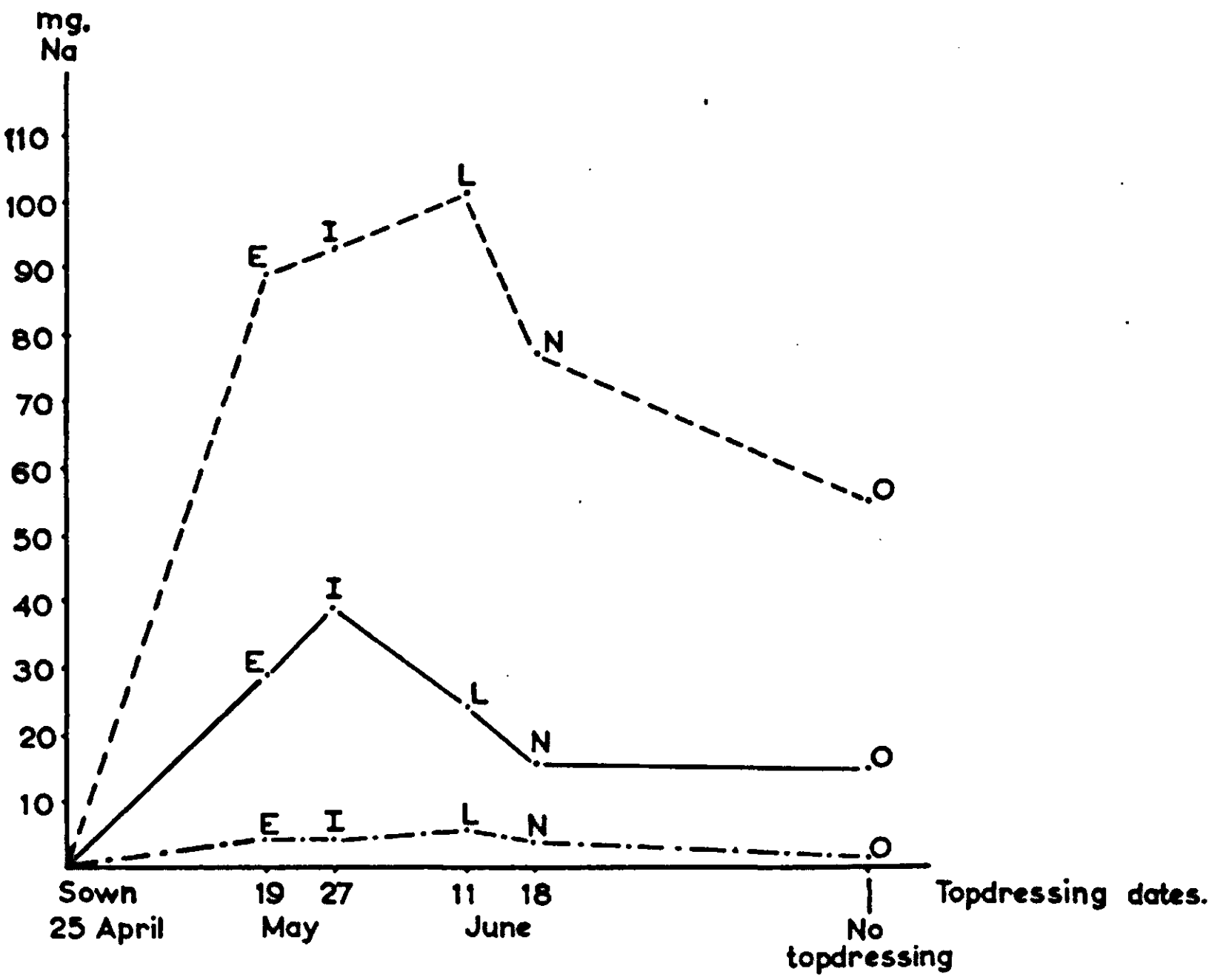

Fig. 15. Percentage sodium contents of the leaf, the stem and the fruit at maturity as influenced by the date of top-dressing.

——— leaf

----- stem

-·-·- fruit

(1) Total sodium accumulation

The total and percentage sodium contents of the experimental seed are so small (percentage only 0.0005 mg. per 100 mg. dry-matter) that they can be regarded as zero compared with those of the leaf, the stem and the fruit. Irrespective of the stage of development of the plant at the time it is applied, top-dressing with sodium nitrate increases the sodium accumulation in the leaf, the stem and the fruit. The greater part of the total sodium accumulated is found in the stem (Fig. 14).

The approximate ratio between the amounts of accumulated sodium in the leaf, the stem and the fruit is invariably 6½ : 18¼ : 1, irrespective of the time of application of the top-dressing.

The largest accumulation of sodium in the leaf occurs when top-dressing is applied a few days before the plant reaches the rapid height-growth stage. Top-dressing applied at a later stage in the development of the plant has only a very slight effect upon sodium accumulation in the leaf.

Ir In the case of the stem and fruit the largest accumulations of sodium occur when top-dressing is applied at the beginning of the escape of the panicle.

It appears from the foregoing that the size of the sodium accumulation is dependent upon the stage of development reached by the leaf, the stem and the panicle at the time of application of the top-dressing.

(2) Percentage sodium contents

The sodium percentages of leaf and stem form a quite different picture from that seen in (1) above. Those of the leaf are either higher than or equal to those of the stems (Fig. 15).

The leaf possesses a higher percentage of sodium than does the stem when top-dressing is not applied and when it is applied before the escape of the panicle (11th June).

From the beginning of the escape of the panicle onwards, the accumulation of sodium per unit of dry-matter in the leaf is practically identical with that occurring in the stem.

During the rapid height-growth stage, the leaf is more sensitive and therefore quicker to react to the sodium supplied, than is the stem.

Sodium is most readily accumulated in the stem in the period before the escape of the panicle - that is, in the period in which all leaves are fully grown and the inflorescence is in the process of developing.

As the plant ages, reduction in the sodium accumulation occurs earlier in the leaf than in the stem.

The sodium percentages of the fruit of plants of top-dressed treatments exhibit differences up to ca. 14%, and are low compared with those in the leaf and stem.

The highest sodium percentages of the fruit are obtained when top-dressing is applied to the plants during the rapid height-growth stage or at the beginning of the escape of the panicle.

Comparison of the sodium percentage of the seed from which the plants were cultivated (0.0005 mg. per 100 mg. dry matter) with that of the fruit after top-dressing the plants with sodium nitrate (0.07 mg. per 100 mg. dry matter) leads immediately to the conclusion that the composition of the nitrogenous fertilizer has a considerable influence on the mineral composition of the fruit (Tables 33 and 36).

4. Sodium accumulation in the organs of the plant from the basal dressing and the top-dressing

With regard to their respective accumulations of sodium, the various parts of the plant such as the leaf, the stem and the fruit which, together with the root, form an organic entity, may be distinguished between but not separated from each other.

Since twice as much sodium was given with the basal dressing as with the top-dressing and, moreover, the plants of all treatments were able to profit from the former for a longer period than from the latter, it is permissible to assume that the accumulation from the basal dressing will be more than twice as great as that from the top-dressing.

(1) Accumulation in the leaf

In the leaf (Table 33), the accumulation from the basal dressing is consistently more than twice as great as that from the top-dressing, the one exception being in the case of plants of treatment I which were top-dressed at the beginning of the rapid height-growth stage. The later the top-dressing is applied, the greater is the degree to which accumulation from the basal dressing exceeds that from the top-dressing.

Moreover, the later in the development of the plant the top-dressing is applied the less is the accumulation from the basal dressing and the top-dressing. It is evident that little accumulation occurs in the leaf from the top-dressing when it is applied at an advanced stage of development at which the period of leaf formation and development can be regarded as concluded (treatments L and N). In this connection, the fact that accumulation from the basal dressing shows a decrease corresponding to that from a late top-dressing strongly suggests that accumulation from the basal dressing is stimulated by the top-dressing.

In contrast with this general tendency, when top-dressing is given two days before the beginning of the rapid height-growth stage (treatment I), the plants accumulate more sodium from the basal dressing and the top-dressing than do the plants top-dressed eight days previously (treatment E). Furthermore, the amount of so-

dium taken up from the top-dressing is more than half the amount taken up from the basal dressing. The accumulation in treatment I differs from those in the other treatments in this respect also. The reason for this different behaviour of the plants of treatment I can lie only in the particular time at which they were top-dressed. Immediately following the application of top-dressing, the plants reach the stages (the rapid height-growth stage and the succeeding stage of the escape of the panicle) in which the greatest sodium accumulation per unit of time occurs (Fig.11). The strong sodium accumulation from the top-dressing can be attributed to the circumstances which allowed of rapid uptake immediately following the application of the top-dressing together with the fact that the sodium contained in the top-dressing had practically no opportunity to exchange with the sodium in the basal dressing.

As a result of the considerable sodium accumulation from the top-dressing, more sodium from the basal dressing, which was already contained in the root and the stem, was transported to the leaf which thus also acquired a greater accumulation of sodium from the basal dressing. The plants of treatment E, which were top-dressed 10 days before the rapid height-growth stage, should have accumulated more sodium than the plants of treatment I in view of the very rapid sodium accumulation during the period of height-growth (Fig. 11). Due to a strong depletion of sodium in the plants of treatment E during the period of grain formation and ripening, the amounts of sodium actually accumulated were smaller than might have been expected from the amount of sodium accumulated before the period of grain formation.

(2) Accumulation in the stem and the fruit

The greater part of the total sodium accumulated from the basal dressing and the top-dressing is found in the stem (Fig.14). As was also the case with the leaf, the shorter the period during which the sodium in the top-dressing has been available to the plant, the less is the accumulation from the top-dressing in the stem and the fruit.

The amount of sodium from the basal dressing accumulated in the stem and the fruit of plants of the different treatments is surprisingly constant. The plants of treatment L, which were top-dressed at the beginning of the escape of the panicle, were able to accumulate considerably more sodium from the basal dressing in their stem and fruit than were the plants of the other treatments (Table 33).

The conveyance of sodium from the basal dressing to the stem in plants of treatment L is greater than that in plants of treatment I due to the fact that, at the time of application of the top-dressing, the former contained more sodium from the basal dressing than did the latter when they were top-dressed. Moreover, when top-dressing was applied to the plants of treatment L, the period of maximal

leaf growth was past while the stem and panicle were still developing. It is, therefore, acceptable that the leaf of the plants of treatment L was able to take up less sodium while, as a result of the exchange in the root of sodium from the basal dressing by sodium freshly taken up, the stem and the fruit were provided with sodium from the basal dressing.

5. *The distribution of sodium among the leaves, the stem and the fruit*

In order to determine the distribution of sodium among successive leaves along the stem and in the stem and the fruit, the different parts of the plant were subdivided as follows:

(a) The leaves
Subdivided into:

(i) The leaf arising at the first or lowest node;
(ii) The leaf arising at the second node;
(iii) The leaves arising at the third and fourth nodes.

(b) The stem
Subdivided into sections of 15 cm. to give:

(iv) The first or lowest section;
(v) The second section;
(vi) The third section;
(vii) The top of the stem (peduncle of the inflorescence);
(viii) The stalks of the flower clusters.

(c) The fruit
Subdivided into:

(ix) The chaff of grain and flower clusters;
(x) The pericarp;
(xi) The endosperm and germ.

The total content, the percentage content and the amounts of sodium taken up from the basal dressing and the top-dressing were determined in the above-mentioned parts of the plants of treatments E, I, L, N and O.

(1) The distribution of sodium among successive leaves along the stem

(a) Percentage sodium contents

In general, the higher the point of origin of a leaf on the stem the lower the sodium percentage of that leaf. An exception to this

is found in the percentages of the leaves of plants which were top-dressed at the beginning of the escape of the panicle (Table 34; treatment L). The reason for this difference must be sought in the fact that the plants of treatment L were top-dressed at a time when the lowest leaf had already attained the physiological age at which it was no longer able to accumulate any further appreciable amount of sodium. Thus it is found that the sodium percentage of this leaf is only slightly higher than that of the corresponding leaf in plants of treatment O, which received no top-dressing, and is considerably lower than those of the corresponding leaf of plants of treatments E and I.

The influence of the top-dressing upon the sodium percentages of the leaves is related to the position of the leaves on the stems and to the stage of development* reached by the plants at the time of application of the top-dressing (Fig. 16). Expressed as percentages, this influence varies from -16 to +81% for the lowest leaf, from -8 to +121% for the leaf arising at the second node and from +34 to +180% for the leaves arising at the third and fourth nodes. The negative influence upon the sodium percentage is found to apply in cases where the top-dressing was given at a late stage, after the development of the panicle (treatment N). In this case, it is seen that the sodium percentages of the leaves arising at the first and second nodes are lower than those of the corresponding leaves of the plants of treatment O in which no top-dressing was applied. The total amounts of sodium accumulated by the corresponding leaves of plants of treatments O and N are, however, equal; the differences in the sodium percentage are due to the differences in production of dry matter. The first- and second-node leaves of the late top-dressed plants of treatment N produced more dry matter as a result of the top-dressing although their sodium accumulation did not increase. The highest sodium percentages are found in the leaves of plants of treatment I which were top-dressed two days before the rapid height-growth stage.

Despite the fact that the plants of treatment I had no more sodium at their disposal after the application of top-dressing than had the plants of treatment E, which were top-dressed eight days earlier, more sodium was accumulated by the former plants than by the latter.

*) The top-dressing exercises relatively the greatest influence upon the sodium percentage of the youngest leaf.

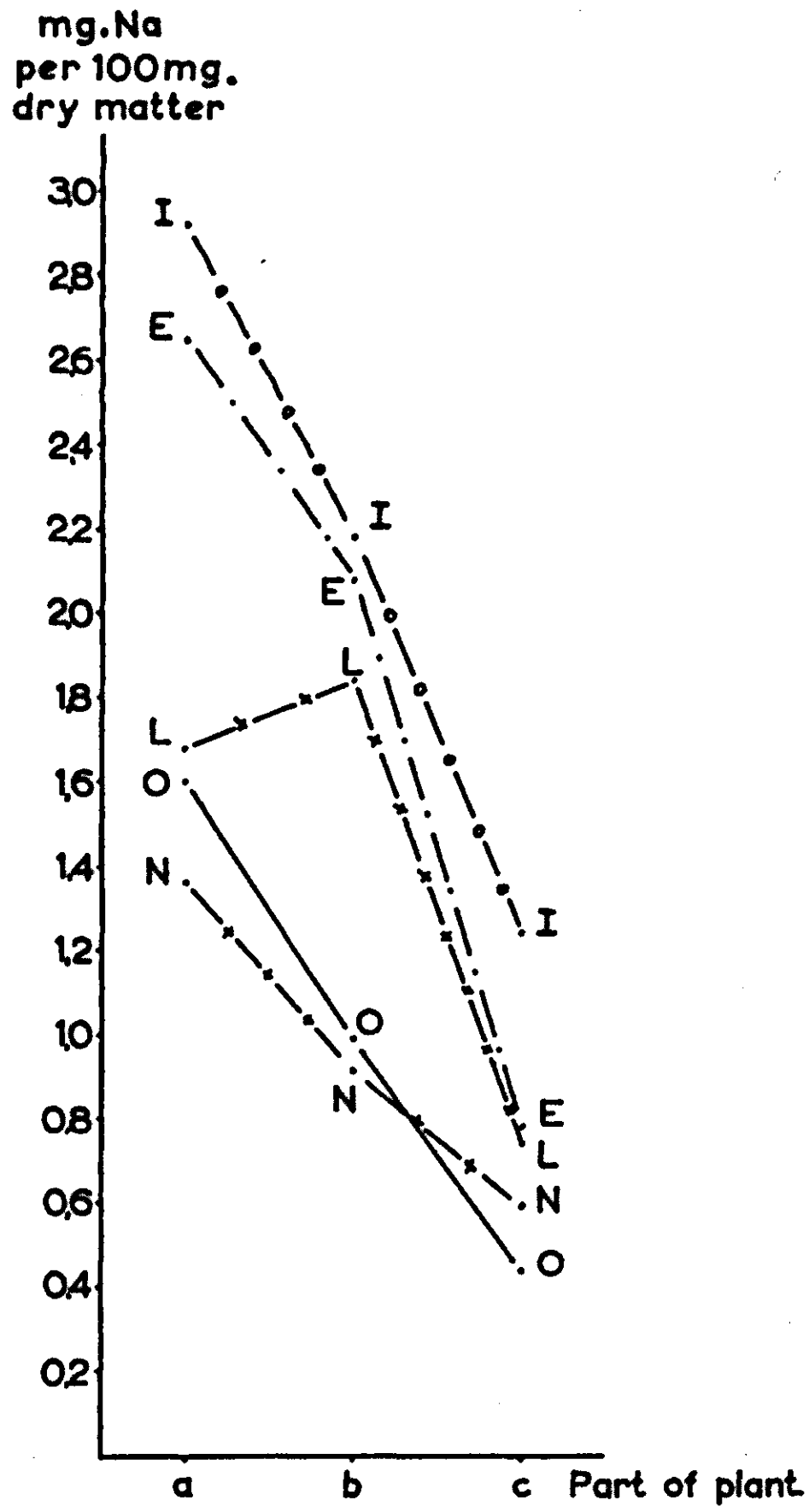

Fig.16. Percentage sodium contents of successive leaves at maturity as influenced by the date of top-dressing

Top-dressed with sodium nitrate on:
-·-·- 19th May (10 days before the rapid height-growth stage)
-o-o- 27th May (2 days before the rapid height-growth stage)
-x-x- 11th June (at the escape of the panicle)
-+-+- 18th June (full panicle development)
——— No top-dressing

a. leaf arising at first or lowest node
b. leaf arising at second node
c. leaves arising at third and fourth node

TABLE 34

DISTRIBUTION OF THE ACCUMULATED SODIUM AMONG THE LEAVES OF PLANTS TOP-DRESSED AT DIFFERENT STAGES OF DEVELOPMENT

Treatment	Date of top-dressing	Part of the plant	Total sodium		Sodium per 100 mg. dry matter		Sodium accumulation from			
							basal dressing		top-dressing	
			in mg. (1)	in % (2)	in mg. (3)	in % (4)	in mg. (5)	in % (6)	in mg. (7)	in % (8)
E	19th May	a	10.14	2.06	2.65	165	6.34	1.93	3.80	2.32
		b	14.53	2.95	2.08	210	11.13	3.38	3.40	2.07
		c	4.53	0.92	0.78	177	3.25	0.99	1.28	0.78
I	27th May	a	14.89	3.02	2.92	181	11.52	3.50	3.37	2.05
		b	16.31	3.30	2.19	221	9.46	2.88	6.85	4.18
		c	7.90	1.10	1.23	280	4.76	1.45	3.14	1.91
L	11th June	a	7.33	1.49	1.68	104	6.43	1.95	0.90	0.55
		b	12.59	2.55	1.82	184	10.27	3.12	2.32	1.41
		c	4.13	0.84	0.74	168	3.02	0.92	1.11	0.68
N	18th June	a	6.65	1.35	1.36	84	6.37	1.94	0.28	0.17
		b	5.62	1.14	0.92	93	4.90	1.49	0.72	0.44
		c	3.86	0.78	0.59	134	2.69	0.82	1.17	0.71
O	not top-dressed	a	6.60	1.34	1.61	100	-	-	-	-
		b	5.58	1.13	0.99	100	-	-	-	-
		c	2.75	0.56	0.44	100	-	-	-	-

a) Leaf arising at first or lowest node
b) Leaf arising at second node
c) Leaves arising at third and fourth nodes

(2) Sodium content expressed as a percentage of that of the total dressing
(4) Sodium content expressed as a percentage of that of the non-top-dressed plants
(6) Sodium content expressed as a percentage of that of the basal dressing
(8) Sodium content expressed as a percentage of that of the top-dressing

Since the plants of the series to which treatment E belongs (Fig. 11) had accumulated just as much sodium as the plants of that to which treatment I belongs at the time when the latter were top-

dressed the fact that the final sodium percentage of the leaf of plants of treatment I is higher than that of the leaf of plants of treatment E must be attributed to the depletion of sodium which occurred in treatment E.

(b) Total sodium accumulation

A top-dressing applied to plants in an early stage of development stimulates sodium accumulation by the leaf to a considerable extent (Fig.17).

In the case of the plants of treatment O, which received no top-dressing, and of treatment N, which received the latest top-dressing,

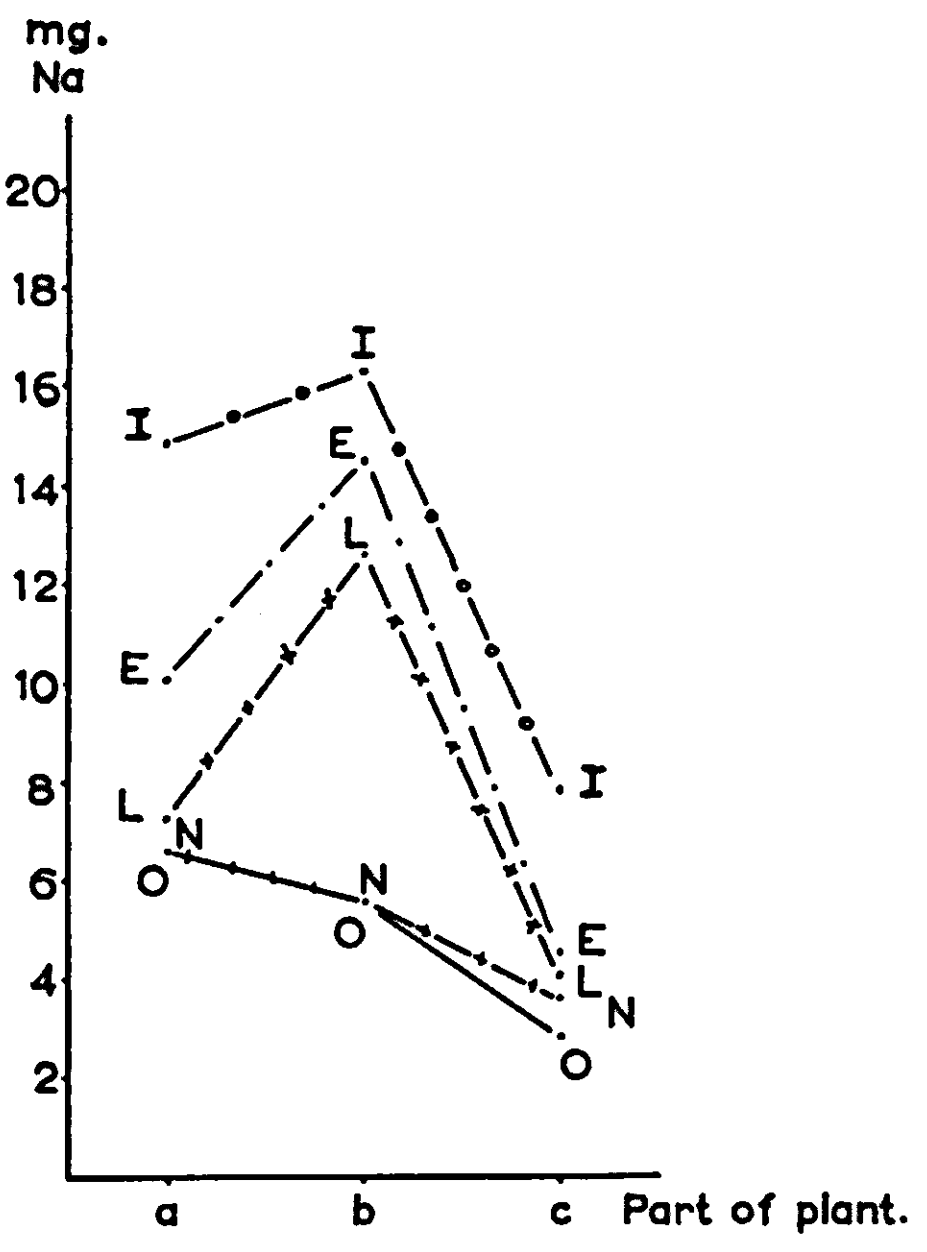

Fig.17. Total sodium accumulation in successive leaves at maturity as influenced by the date of top-dressing

Top-dressed with sodium nitrate on:

-.-.- 19th May (10 days before the rapid height-growth stage)
-o-o- 27th May (2 days before the rapid height-growth stage)
-x-x- 11th June (at the escape of the panicle)
-+-+- 18th June (full panicle development)
——— No top-dressing

a. Leaf arising at first of lowest node
b. Leaf arising at second node
c. Leaves arising at third and fourth node

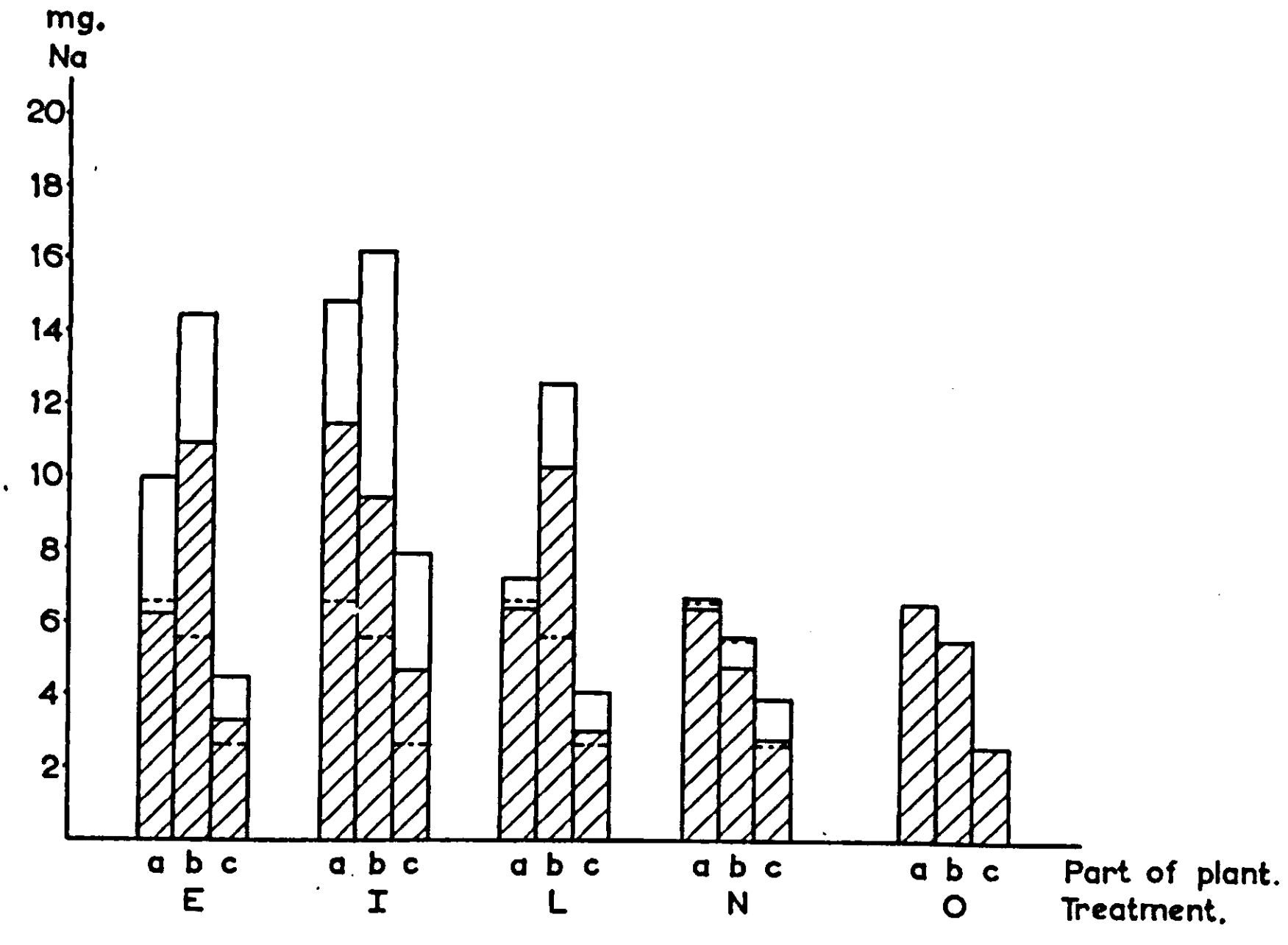

Fig.18. Sodium accumulation from the basal dressing and the top-dressing in successive leaves at maturity as influenced by the date of top-dressing

Sodium accumulation from the top-dressing (physically determined)
Sodium accumulation from the basal dressing

a. Leaf arising at first or lowest node
b. Leaf arising at second node
c. Leaves arising at third and fourth node.

the smaller the total amount of sodium in the leaves, the higher their point of origin (Table 34). When, however, the plants are top-dressed at an earlier stage of their development, the accumulation in the leaf is considerably greater than that which obtains in the plants of treatment N and, moreover, a regular decrease in the amounts of sodium in successive leaves is no longer found and the accumulation in the leaf at the second node far exceeds the accumulations in the other leaves (Fig. 18).

From the values for the total accumulation, it appears that the leaves of the plants of treatment I accumulated the greatest amounts of sodium and that the accumulation by the older leaves was less

when top-dressing was applied to plants in an advanced stage of development. This is further support for the view that the degree to which sodium can accumulate is dependent upon the age of the leaf.

(c) Accumulation from the basal dressing and the top-dressing

The accumulation from the basal dressing and the top-dressing decreases when the latter is applied at a late stage of development of the plant.

When top-dressing is given before the plant reaches the stage of the escape and development of the panicle, it greatly promotes sodium accumulation from the basal dressing (Fig.18). In the cases mentioned above, namely, in the oldest leaf of plants of treatments E, L and N, and also in the successive leaves of plants of treatment N, accumulation from the basal dressing is not stimulated by the top-dressing.

With the exception of the plants of treatment E in which a depletion of sodium occurs during ripening, these are the very cases in which sodium accumulation is very small because of the age of the leaf at the time of top-dressing. The leaf has in fact taken up sodium from the basal dressing (Fig.18; treatment L, leaf 'a'; N, leaf 'a' and 'b') but not to the same extent to which uptake from this source had occurred in other leaves.

This indicates that, as a result of the physico-chemical and structural changes which occur as the leaf ages the flow of sodium ions to the leaf largely stops. The fact that the total sodium accumulation is greater in these cases than the total accumulation in the corresponding leaf of the non-top-dressed treatment is due to the supplementary contribution from the top-dressing.

This supplementary contribution is very small - a further indication that it is not so much that the affinity of the older leaf for sodium decreases, as that the uptake of nutrient ions stops to a greater or lesser degree.

On the basis of the course of the accumulation in the plants of treatment E (Fig.11) it must be accepted that the oldest leaf of the plants of this treatment had also accumulated a considerable amount of sodium during the period of development. Since it may also be regarded as certain (compare treatment I) that a depletion in the sodium contents of leaf 'a' and 'c' of the plants of treatment E has occurred during the ripening period, it may be deduced that leaf 'b' had to relinquish sodium during this period. As has been remarked earlier, it is also probable that a certain depletion occurred in the plants of the other corresponding treatments.

The depletion occurring in the plants of treatment E assumed greater proportions than that in the plants of the corresponding treatments I, L and N, because the withering process proceeded more slowly in the former plants. This fact will also explain why leaf 'a' of the plants of treatment E possesses a considerable amount of sodium from the top-dressing but only a relatively small amount from the basal dressing.

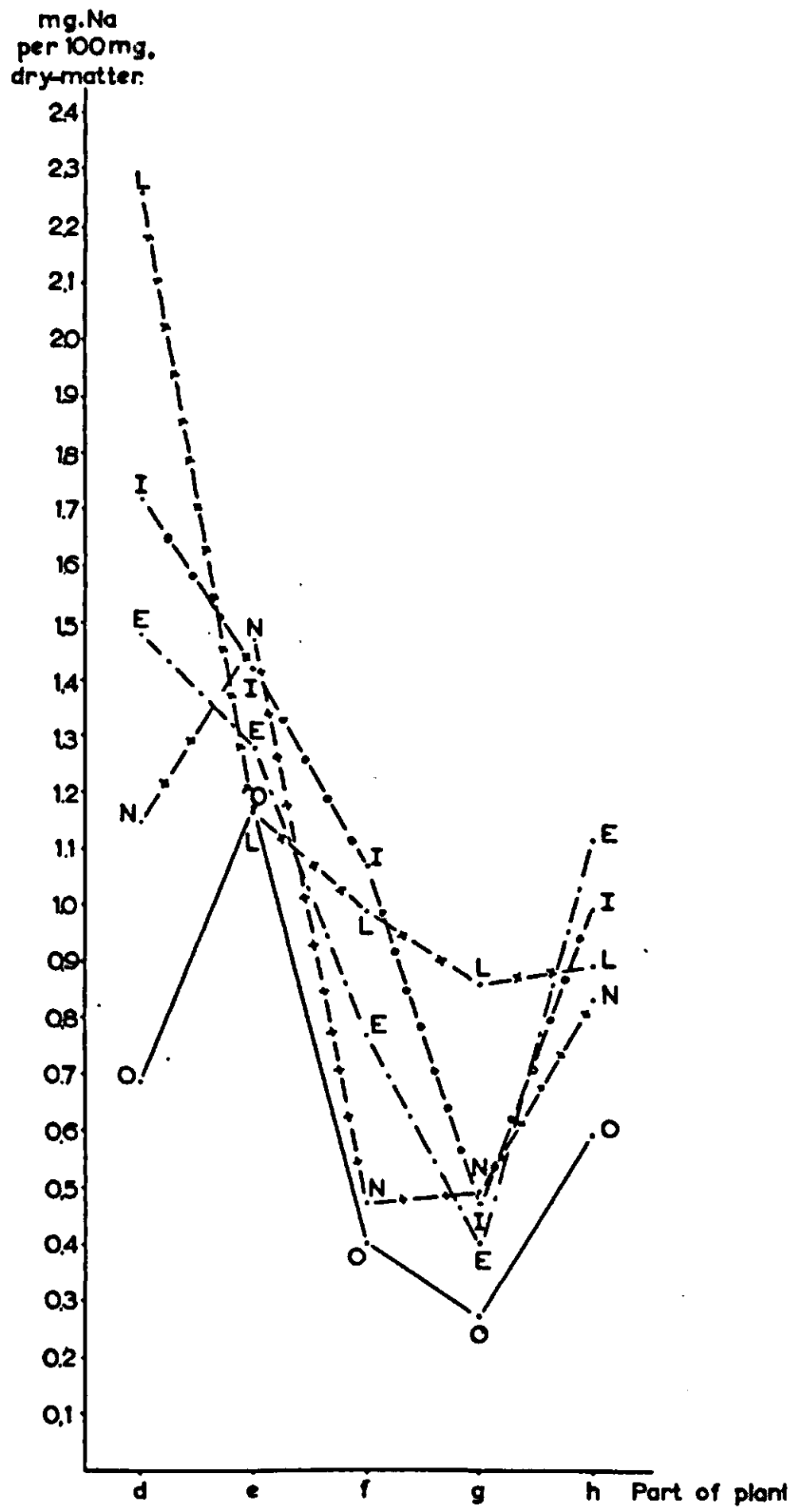

Fig.19. Percentage sodium contents of successive sections of the stem at maturity as influenced by the date of top-dressing

Top-dressed with sodium nitrate on:
-·-·- 19th May (10 days before the rapid height-growth stage)
-o-o- 27th May (2 days before the rapid height-growth stage)
-x-x- 11th June (at the escape of the panicle)
-+-+- 18th June (full panicle development)
——— No top-dressing

d) lowest section of stem (0-15 cm)
e) second section of stem (15-30 cm)
f) third section of stem (30-45 cm)
g) peduncle of panicle
h) stalks of flower clusters

When top-dressing is given during the period of rapid growth (treatment I and L) the leaf arising at the second node reacts the most readily. When top-dressing is applied at a later stage after the escape and development of the panicle, it is the youngest leaf that takes up the greatest amount of sodium from the top-dressing.

The main course of accumulation from the top-dressing changes later when sodium contained in the top-dressing becomes available to the younger leaf. In the majority of cases, accumulation from the basal dressing is stimulated by the top-dressing. Generally, it appears that sodium tends to collect in those parts of the plant where the greatest cell activity prevails.

(2) The distribution of the sodium among the different sections of the stem

(a) Percentage sodium contents

As was the case with the leaves, the sodium percentages are highest in the lower sections of the stem (Table 35; Fig. 19) and generally decrease rapidly from the base to the top. The peduncle of the panicle - the apex of the stem - has the lowest sodium percentage. It is noteworthy, however, that the stalks of the flower clusters of plants of all treatments have relatively high sodium percentages.

Top-dressing has a definite influence upon the course of the sodium percentages. Not only are those of the sections of the stem of top-dressed plants higher than those of the non-top-dressed plants but there also exist considerable variations between the treatments in the percentages of corresponding sections of the stem.

The time of application of the top-dressing, therefore, had also a very real influence upon the sodium percentages. The stems of plants which were top-dressed 10 and 2 days before the rapid height-growth stage (treatments E and I) exhibit a pronounced decrease in sodium percentage from the bases towards the tops. In the plants of treatment L, which were top-dressed at the beginning of the escape of the panicle, the sodium percentage in the second 15-cm. section of stem shows a pronounced decrease compared with the lowest; in the upper sections, this decrease is much less pronounced. The sodium percentages in the sections of the stem of plants of treatment N, which were top-dressed after the development of the panicle, and of treatment O, which received no top-dressing, exhibit an entirely different course. In these plants the sodium percentage of the second section is higher than that of the first or lowest section. In the third section, the sodium percentage again falls whilst the percentages of the peduncle of the inflorescence in treatments N and O show a slight increase and a slight decrease respectively. The course of the sodium percentages of treatment L occupies an intermediate position between that of treatments E and I top-dressed at an early stage and that of treatments N and O top-dressed at a late stage or not at all.

TABLE 35

DISTRIBUTION OF THE ACCUMULATED SODIUM IN THE STEM OF PLANTS TOP-DRESSED AT DIFFERENT STAGES OF DEVELOPMENT

Treatment	Date of top-dressing	Part of the plant	Total sodium		Sodium per 100 mg. dry matter		Sodium accumulation from			
							basal dressing		top-dressing	
			in mg. (1)	in % (2)*	in mg. (3)	in % (4)*	in mg. (5)	in % (6)*	in mg. (7)	in % (8)*
E	19th May	d	36.17	7.34	1.48	215	19.47	5.92	16.70	10.18
		e	25.72	5.22	1.28	109	13.56	4.12	12.16	7.41
		f	16.00	3.25	0.77	192	7.69	2.34	8.31	5.07
		g	6.70	1.36	0.40	148	3.63	1.10	3.07	1.87
		h	4.73	0.96	1.11	188	2.35	0.71	2.38	1.45
I	27th May	d	36.41	7.39	1.72	249	20.25	6.16	16.16	9.85
		e	31.58	6.41	1.42	124	15.12	4.60	16.46	10.04
		f	17.37	3.52	1.07	268	8.31	2.53	9.06	5.52
		g	6.16	1.25	0.47	175	1.91	0.58	4.25	2.59
		h	2.32	0.47	0.99	168	1.24	0.38	1.08	0.66
L	11th June	d	51.03	10.35	2.26	332	35.67	10.84	15.36	9.37
		e	21.63	4.39	1.17	99	10.49	3.19	11.14	6.79
		f	15.43	3.13	0.99	248	10.30	3.13	5.13	3.13
		g	10.18	2.07	0.86	319	5.00	1.52	5.18	3.16
		h	3.13	0.65	0.90	153	1.62	0.49	1.51	0.92
N	18th June	d	24.26	4.92	1.15	167	13.86	4.21	10.40	6.34
		e	36.21	7.34	1.47	125	23.37	7.10	12.84	7.83
		f	8.80	1.78	0.47	118	3.53	1.07	5.27	3.21
		g	6.16	1.25	0.49	182	2.51	0.76	3.65	2.23
		h	2.40	0.49	0.84	142	0.93	0.28	1.47	0.90
O	not top-dressed	d	14.14	4.30	0.69	100	-	-	-	-
		e	28.52	8.67	1.18	100	-	-	-	-
		f	6.93	2.11	0.40	100	-	-	-	-
		g	3.95	1.20	0.27	100	-	-	-	-
		h	1.54	0.47	0.59	100	-	-	-	-

d First or lowest 15-cm. section of stem
e Second 15-cm. section
f Third 15-cm. section
g Peduncle of the inflorescence
h Stalks of the flower clusters

*(2) Sodium content expressed as a percentage of that of the total dressing
(4) Sodium content expressed as a percentage of that of the non-top-dressed plants
(6) Sodium content expressed as a percentage of that of the basal dressing.
(8) Sodium content expressed as a percentage of that of the top-dressing

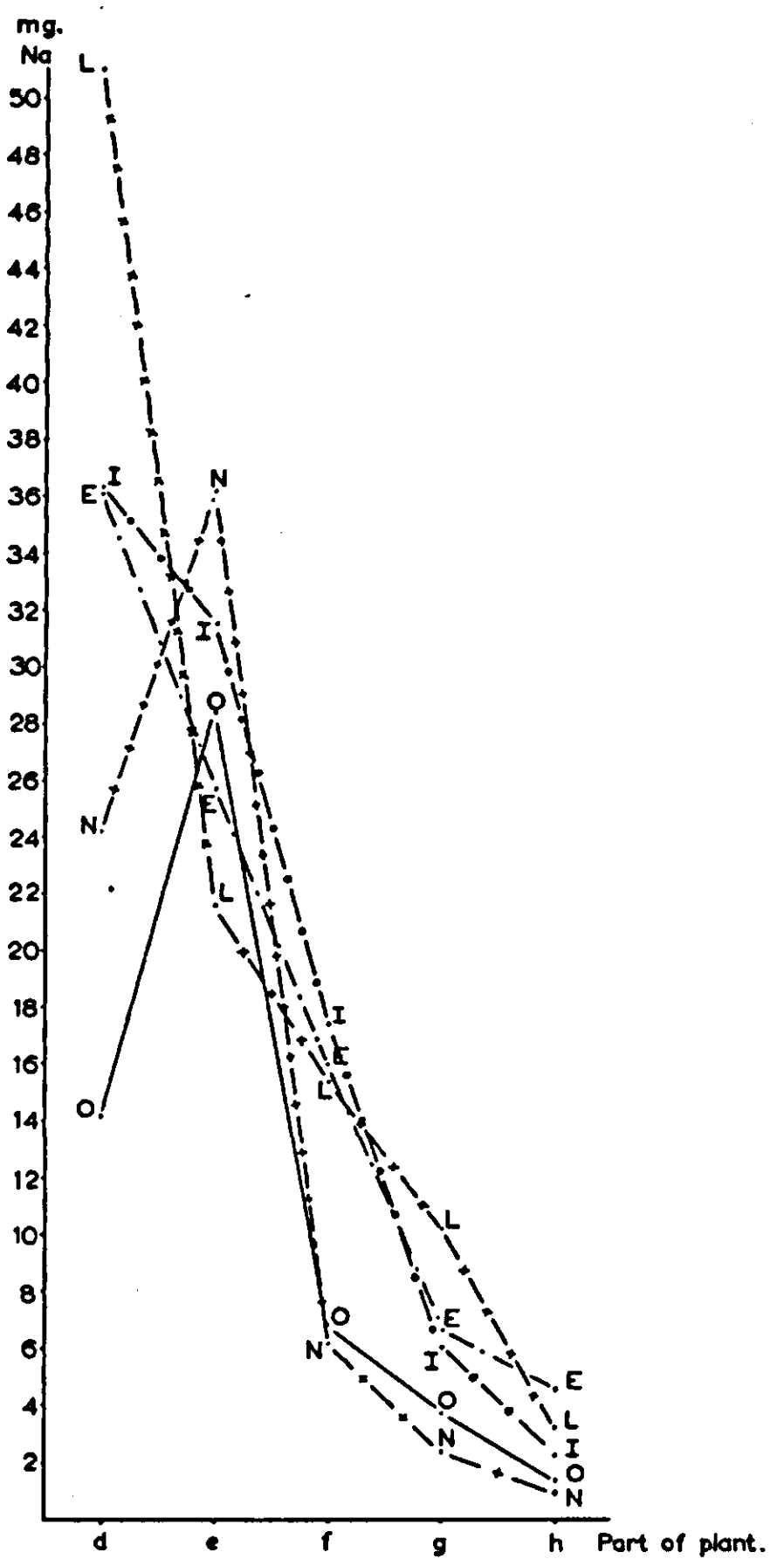

Fig. 20. Total sodium accumulation in successive sections of the stem at maturity as influenced by the date of top-dressing

Top-dressed with sodium nitrate on:

-·-·- 19th May (10 days before the rapid height-growth stage)
-o-o- 27th May (2 days before the rapid height-growth stage)
x-x-x 11th June (at the escape of the panicle)
-+-+- 18th June (full panicle development)
——— No top-dressing

d. lowest section of stem (0 - 15 cm.)
e. second section of stem (15 - 30 cm.)
f. third section of stem (30 - 45 cm.)
g. peduncle of panicle
h. stalks of flower clusters

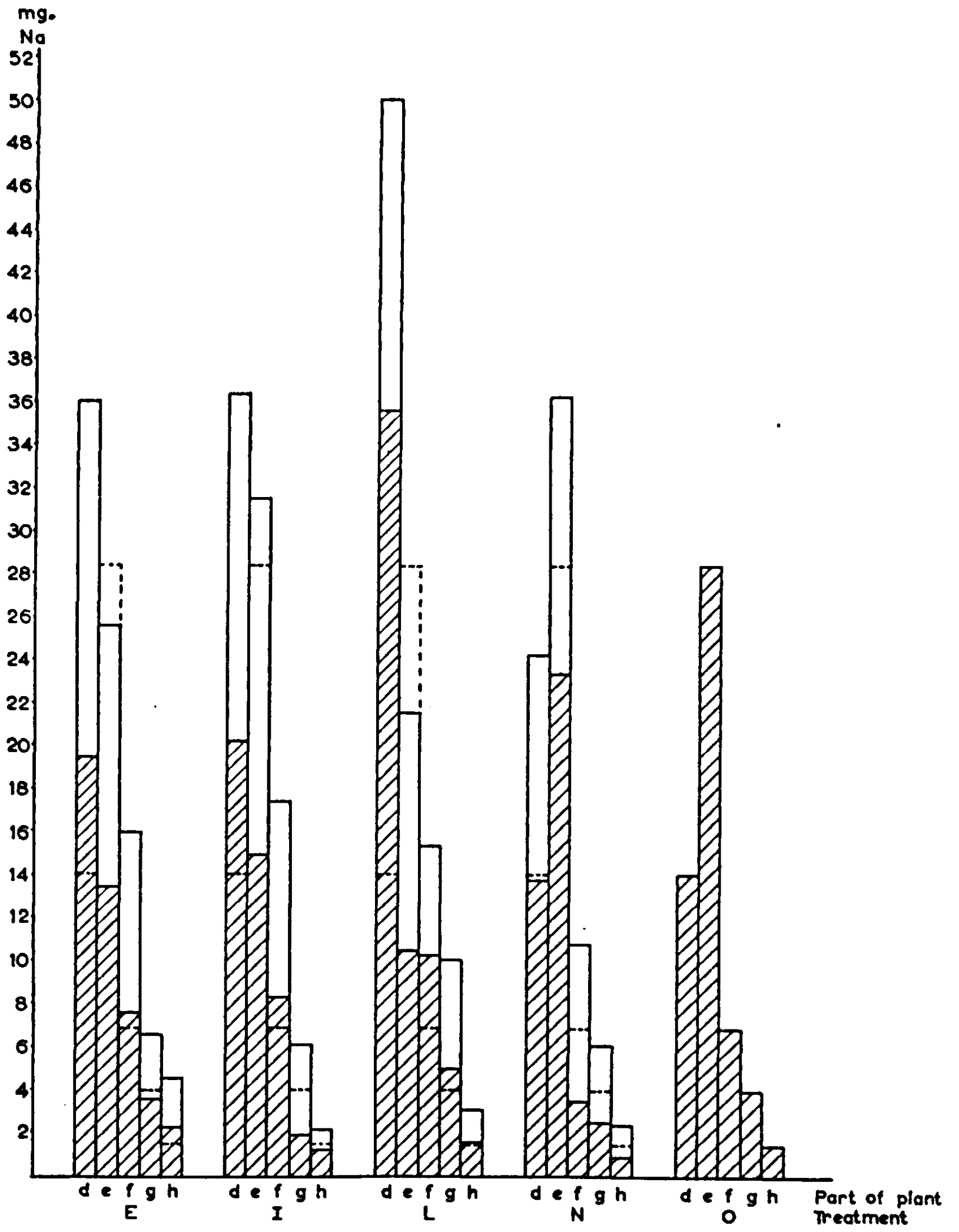

Fig. 21. Sodium accumulation from the basal dressing and the top-dressing in successive sections of the stem at maturity as influenced by the date of top-dressing

Sodium accumulation from top-dressing (physically determined)
Sodium accumulation from basal dressing
d. lowest section of stem (0 - 15 cm.)
e. second section of stem (15 - 30 cm.)
f. third section of stem (30 - 45 cm.)
g. peduncle of panicle
h. stalks of flower clusters

(b) Total sodium accumulation.

The distribution of sodium among the different parts of the plant as revealed by the total sodium accumulation by these parts exhibits practically the same general picture as that given by the course of the sodium percentages. In this case also, the course of the accumulations in the various sections of the stems of plants of treatment L occupies an intermediate position between that of the corresponding sections of the plants which received early top-dressing and that of those sections of plants which were top-dressed at a late stage or not at all (Fig. 20). The stalks of the flower clusters were found to have accumulated the smallest amounts of sodium, because of their very small amounts of dry matter, and despite the fact that their sodium percentages were high.

In considering sodium distribution in the leaves, it was seen that the strongest reaction to the top-dressing was exhibited by the leaves of plants which were top-dressed two days before the beginning of the rapid height-growth stage (treatment I). In comparing the distribution throughout the stem, however, it is the sections of the stem of plants which were top-dressed at the beginning of the escape of the panicle (treatment L) which are seen to have drawn the greatest profit from the top-dressing.

(c) Accumulation from the basal dressing and the top-dressing.

Accumulation from the basal dressing and the top-dressing decreases from the base to the apex of the stem (Table 35, Fig. 21). An exception to this is found in the plants of treatments N and O, whose second section (e) accumulated more sodium from the basal dressing than did the first section (d). Moreover, in treatment N, the second section accumulated more sodium from the top-dressing than did the first. This difference is found, therefore, in plants which either received no top-dressing or were top-dressed at a late stage of development.

Irrespective of its time of application, top-dressing suppresses accumulation from the basal dressing by the second section of the stem. In conformity with that which was found in the case of the leaf, top-dressing stimulated accumulation from the basal dressing in some sections of the stems of treatments E, I and L.

The accumulation from the basal dressing found in the stems of plants of treatments E, I, L and N are 25.98, 28.66, 23.37 and 20.51% respectively. When top-dressing is applied to the plants at the beginning of the escape of the panicle or at a later stage of development, the share of the total accumulation from the top-dressing acquired by parts f, g and h of the plant increases.

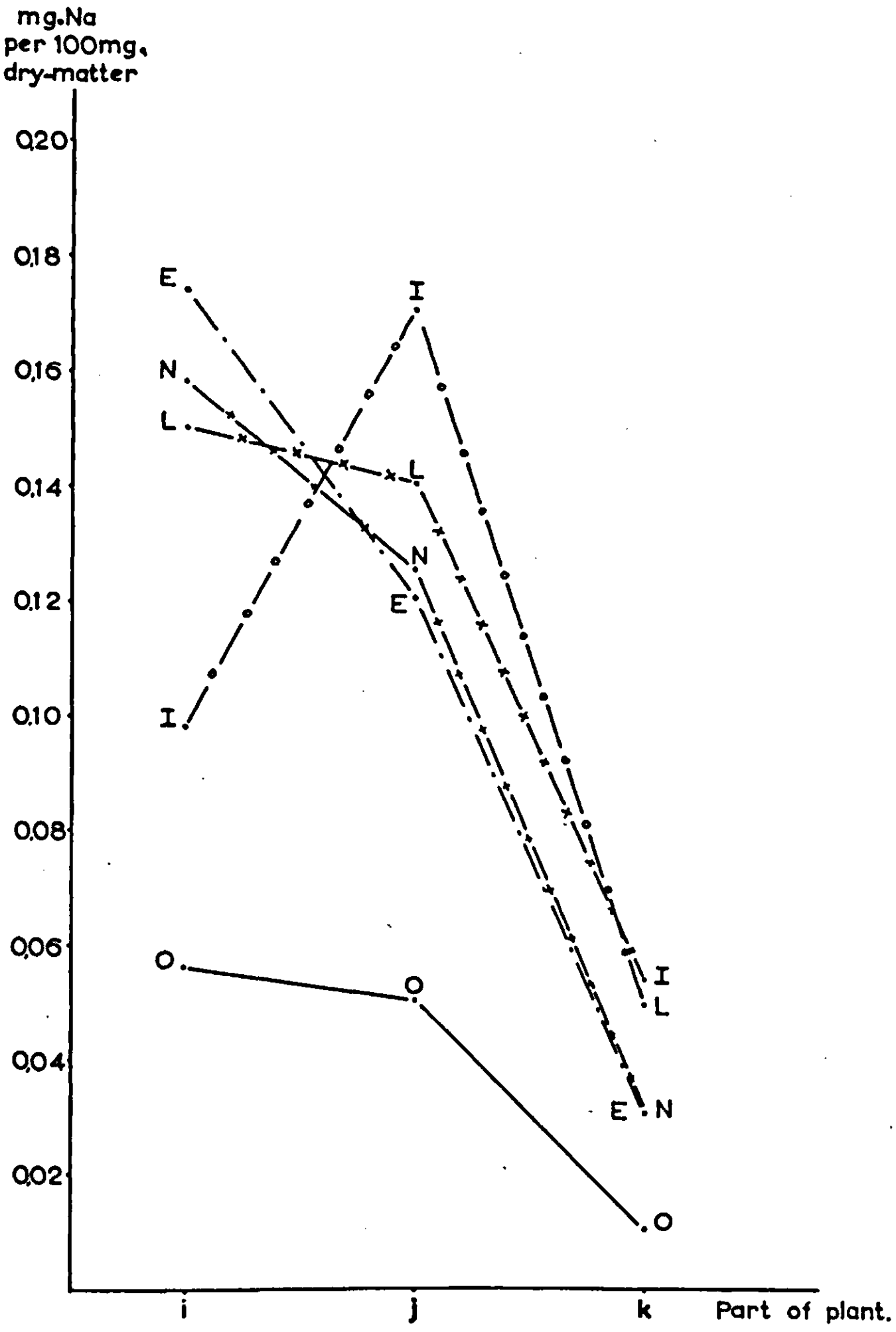

Fig. 22. Percentage sodium contents of the chaff, the pericarp and the endosperm at maturity as influenced by the date of top-dressing

Top-dressed with sodium nitrate on:

-·-·- 19th May (10 days before the rapid height-growth stage)
-o-o- 27th May (2 days before the rapid height-growth stage)
x-x-x 11th June (at the escape of the panicle)
-+-+- 18th June (full panicle development)
——— No top-dressing

i. chaff
j. pericarp
k. endosperm

In contrast with that which was found in the case of the leaf, considerable amounts of sodium are accumulated from the top-dressing by the various sections of the stem, even when the plants are top-dressed at an advanced stage of development.

Relatively more sodium is accumulated by the various sections from the top-dressing than from the basal dressing.

(3) The distribution of sodium among the chaff of fruit and flower clusters, the pericarp and the endosperm and germ

(a) Percentage sodium contents.

The sodium percentages decrease in the order: chaff, pericarp, endosperm (Table 36, Fig. 22). There is a sharp decline in the sodium percentages from the stalks of the flower clusters to the chaff and from the pericarp to the endosperm.

The sodium percentages of the chaff, pericarp and endosperm are appreciably increased by the top-dressing. In the pericarp and endosperm the greatest increases are found in the plants of treatments I and L; in the chaff they are found in treatments E and N.

(b) Total sodium accumulation

The total sodium accumulation in the chaff, the pericarp and the endosperm shows an entirely different course (Fig. 23) from that of the percentage sodium contents of these parts but exhibits some agreement with that of the total sodium accumulation in the leaf.

The accumulation in the endosperm is, in general, somewhat less than that in the pericarp. The influence of top-dressing upon accumulation is not inconsiderable as can be clearly seen from the differences between the amounts of sodium in corresponding parts of the plants of treatment O (Table 36, Fig. 23).

The greatest influence upon sodium accumulation in the pericarp and endosperm is exercised by the top-dressing applied at the time of the escape of the panicle, two days before the rapid height-growth stage.

(c) Accumulation from the basal dressing and the top-dressing.

The top-dressing has a highly stimulating effect upon sodium accumulation by the chaff, the pericarp and the endosperm from the basal dressing (Table 36, Fig. 24). The order in which the effect of the top-dressing upon accumulation from the basal dressing decreases, viz. endosperm, pericarp, chaff, is independent of the time of application of the top-dressing and independent, therefore, of the stage of development of the plant at the time of application.

TABLE 36

DISTRIBUTION OF THE ACCUMULATED SODIUM IN THE FRUIT OF PLANTS TOP-DRESSED AT DIFFERENT STAGES OF DEVELOPMENT

Treatment	Date of top-dressing	Part of the plant	Total sodium		Sodium per 100 mg. dry matter		Sodium accumulation from			
							basal dressing		top-dressing	
			in mg. (1)	in % (2)*	in mg. (3)	in % (4)*	in mg. (5)	in % (6)*	in mg. (7)	in % (8)*
E	19th May	i	1.51	0.31	0.17	283	0.70	0.21	0.81	0.49
		j	1.84	0.37	0.12	240	0.94	0.29	0.90	0.56
		k	1.52	0.31	0.03	300	1.31	0.40	0.21	0.31
I	27th May	i	0.71	0.14	0.10	167	0.26	0.08	0.45	0.27
		j	2.01	0.41	0.17	340	1.41	0.43	0.60	0.37
		k	1.88	0.38	0.05	500	1.67	0.51	0.21	0.13
L	11th June	i	1.07	0.22	0.15	250	0.62	0.19	0.45	0.27
		j	2.28	0.46	0.14	280	1.78	0.54	0.50	0.31
		k	2.53	0.51	0.05	500	2.34	0.71	0.19	0.12
N	18th June	i	1.05	0.21	0.16	266	0.62	0.09	0.43	0.26
		j	1.96	0.40	0.13	260	1.45	0.44	0.51	0.31
		k	1.48	0.30	0.03	300	1.29	0.39	0.19	0.12
O	not top-dressed	i	0.36	0.11	0.06	100	-	-	-	-
		j	1.00	0.33	0.05	100	-	-	--	-
		k	0.39	0.12	0.01	100	-	-	--	-

i) chaff of flower cluster and grain
j) pericarp
k) endosperm and germ

*(2) Sodium content expressed as a percentage of that of the total dressing
(4) Sodium content expressed as a percentage of that of the non-top-dressed plants
(6) Sodium content expressed as a percentage of that of the basal dressing
(8) Sodium content expressed as a percentage of that of the top-dressing

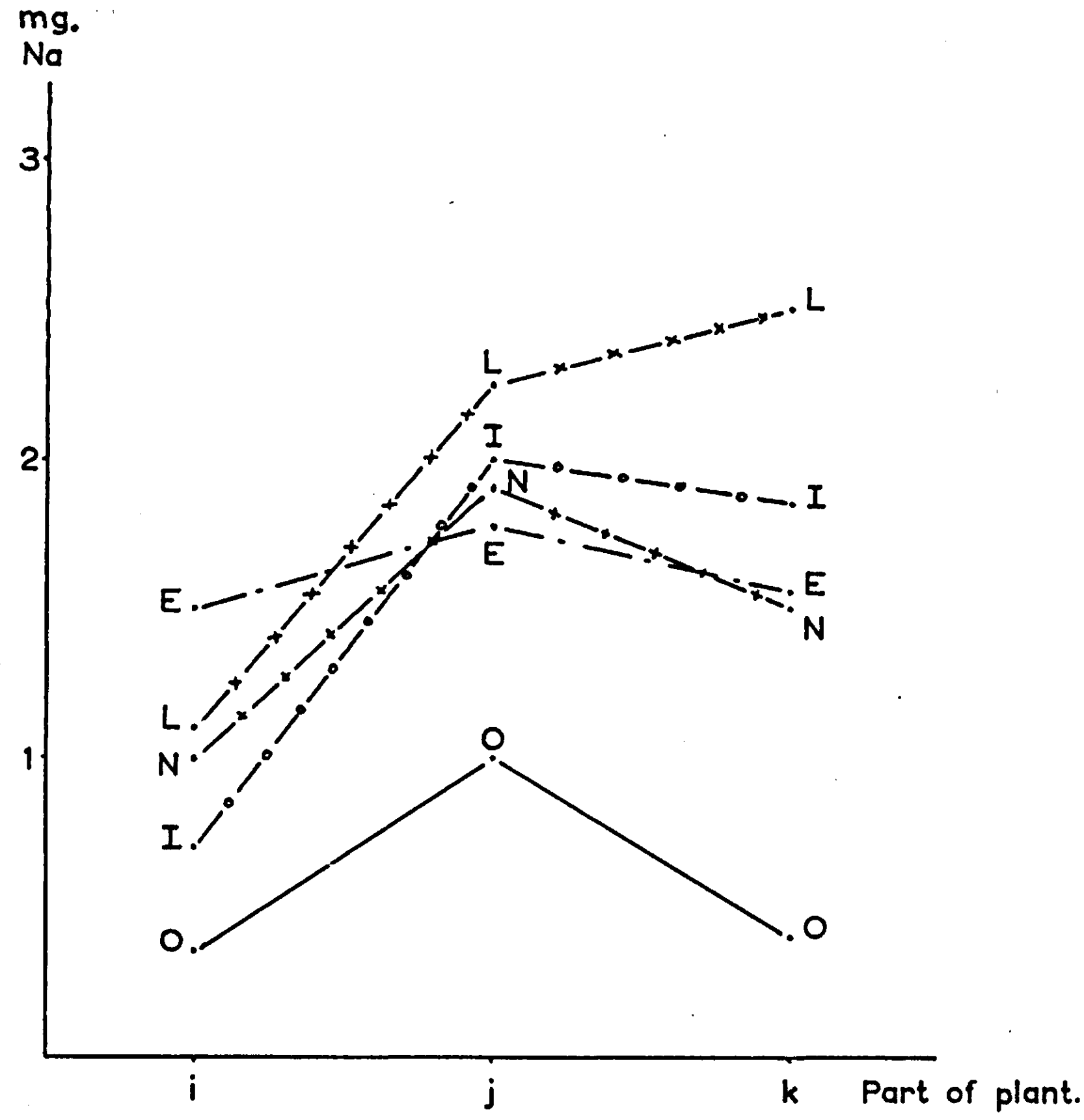

Fig. 23. Total sodium accumulation in the chaff, the pericarp and the endosperm at maturity as influenced by the date of top-dressing

Top-dressed with sodium nitrate on:

-·-·- 19th May (10 days before the rapid height-growth stage)
-o-o- 27th May (2 days before the rapid height-growth stage)
x-x-x 11th June (at the escape of the panicle)
-+-+- 18th June (full panicle development)
——— No top-dressing

i. chaff
j. pericarp
k. endosperm

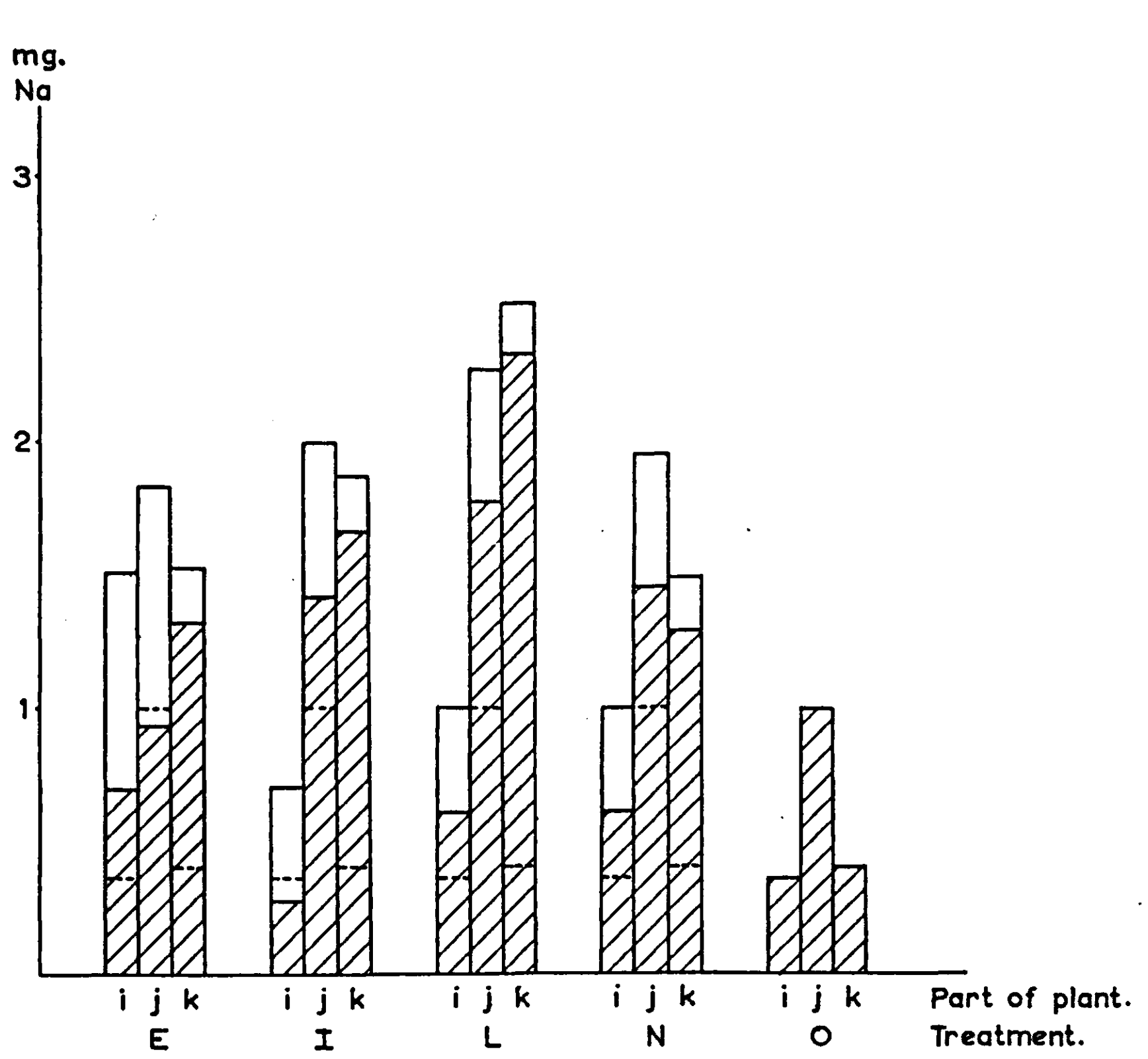

Fig. 24. Sodium accumulation from the basal dressing and the top-dressing in the chaff, the pericarp and the endosperm at maturity as influenced by the date of top-dressing

Sodium accumulation from top-dressing (physically determined)
Sodium accumulation from basal dressing

i. chaff
j. pericarp
k. endosperm

In the case of the plants of treatment O, which received no top-dressing, and those of treatment N, which were top-dressed after the escape of the panicle, the greatest accumulation from the basal dressing occurred in the pericarp. As was also the case with the leaf and the stem, the top-dressing applied to the crop after the escape of the panicle (treatment N) did not cause any change in the order of size of accumulation from the basal dressing in the various parts of the plant - in contrast with the top-dressings applied earlier. It is noteworthy that, irrespective of the time of application of the top-dressing, the amount of sodium accumulated in the endosperm from the top-dressing is practically constant. The chaff and the pericarp of plants of treatment E, which was the first to be top-dressed, accumulated larger amounts of sodium from the top-dressing than did those of the plants of the other top-dressed treatments.

In the case of plants of treatments I, L and N, practically equal amounts of sodium were accumulated from the top-dressing by the chaff and pericarp.

In spite of the varying accumulations from the basal dressing, very similar accumulations from the top-dressing are found in the corresponding parts of the fruits of the treatments I, L and N - top-dressed from the beginning of the rapid height-growth stage and onwards - while in the fruits of treatment E - top-dressed before this stage - larger amounts could be accumulated from the top-dressing (Fig. 24). At the moment at which the top-dressing was applied, the plants of treatments I, L and N contained more sodium than the plants of treatment E, which were top-dressed at an earlier date. As a result of this top-dressing during the period of rapid sodium uptake (i.e., the period of rapid height-growth), more sodium originating from the basal dressing could be transported to the fruits in the embryonic stage than when sodium from the top-dressing is made available during an earlier or later stage of development.

If the amount of sodium accumulated from the basal dressing by the non-top-dressed plants of treatment O is accepted as equal to that accumulated from the same source by the plants of top-dressed treatments - as is inevitable in the chemical method of determination - it appears that accumulation from the top-dressing (calculated by subtraction) differs considerably from the corresponding accumulations determined by the radioactive method (Figs. 18, 21 and 24).

It is seen, therefore, that no accurate picture of the actual accumulation can be obtained by means of the chemical method of determination and for this reason the conclusions based upon the results obtained by this method may justifiably be considered untrustworthy.

V. CONCLUSIONS

(1) The withering process of the plant is delayed by the top-dressing.
(2) Sodium accumulation per unit of time is increased by the top-dressing.
(3) The plant strives to acquire a certain sodium level irrespective of the time of application of the top-dressing.
(4) The percentage sodium content of the plant is dependent on its stage of development.
(5) The isotope method is indispensable for the determination of sodium accumulation from the basal dressing and the top-dressing when the crop is harvested before it has ripened.
(6) Sodium is more readily taken up from the top-dressing than from the basal dressing.
(7) The composition of the nitrogenous fertilizer has a considerable influence upon the mineral composition of the fruit.
(8) The percentage sodium content of the fruit is increased by the top-dressing.
(9) The sodium accumulation is dependent upon the time of application of the top-dressing.
(10) The influence of the top-dressing upon sodium accumulation in the leaf is dependent upon the physiological age of the leaf.
(11) Sodium accumulation by the leaf from the basal dressing is stimulated by the top-dressing.
(12) The percentage sodium content of the plant parts increases with increasing age.
(13) In contrast with the leaves the various parts of the stem accumulate considerable amounts of sodium from the top-dressing even when the latter is applied late in the growth cycle.
(14) Equal amounts of sodium were accumulated from the top-dressing by the endosperm of plants of all treatments.
(15) The sodium content of the endosperm is increased by the top-dressing.

SUMMARY AND CONCLUSIONS

CHAPTER I

INTRODUCTION

The uptake and outgo of sodium ions in the roots of oat plants *(Avena sativa var.Marne)* and the distribution of these ions throughout the plants were studied in an attempt to gain further insight into the significance of sodium as a nutrient ion for plant life.

CHAPTER II

THE IMPORTANCE OF THE SODIUM ION IN PLANT NUTRITION

The results of investigations carried out in the past on the effect of the sodium ion upon the plant were studied from the data available in the literature. These are summarized as follows:

The influence of sodium fertilization is only attributable in part to the liberation of potassium in the soil.

The sodium ion itself exercises a favourable influence upon the availability of phosphate.

The sodium ion has an influence upon the structure of the plant and, in particular, strengthens the vascular and supporting tissues.

Sodium also influences the permeability of the plant cell and the transpiration of plants.

In the case of plants which are capable of accumulating a considerable amount of sodium, evaporation is reduced less by potassium than by an equivalent amount of sodium.

Sodium ions reduce the transpiration coefficient.

In general, the significance of the sodium ion in the water economy of the plant is at least as great as that of the potassium ion.

In agricultural investigations considerable thought has been given to the possibility of reciprocal substitution of sodium and potassium ions in the plant.

Unlike the rubidium ion which also has the capacity to replace potassium, the sodium ion is selectively absorbed by the plant.

It appears that only limited significance can be accorded to the classification of crops in accordance with their sensitivity to sodium, as carried out by HARMER *et al.* (101).

Favourable influences of potassium and of sodium on the yield-capacity of plants are not always associated.

As a result of rather too one-sided consideration of the agreement which so often exists between the behaviour of the sodium and the potassium ions, the differences between them have tended to be overlooked. For instance, the sodium ion appears to form complexes better than the potassium ion does.

In certain investigations, specific sodium deficiency symptoms have been established.

Part of the sodium in the plant is present in a water-insoluble form.

Sodium is able to combine selectively with cell substances.

It has recently been established (4) that sodium is essential for the development of blue-green algae; for higher orders of plant life, the essentiality of this element has not yet found acceptance although in the course of research many facts have been revealed which strongly indicate that sodium has, indeed , an essential and a specific function in such plants.* The precise nature of these functions has not yet been elucidated.

CHAPTER III

THE METHOD OF INVESTIGATION

Water cultures and dusarite-silica sand cultures were employed.

The study of sodium uptake was facilitated by the application of radioactive sodium (Na^{22}). The total sodium content was determined by flame photometer; the amount of radioactive sodium was measured with a three-decade counting apparatus.

The technique employed for the preparation of the macroautoradiographs is described.

CHAPTER IV

THE DISTRIBUTION OF SODIUM IONS THROUGHOUT THE PLANT AS ESTABLISHED FROM AUTORADIOGRAPHS

In connection with the translocation of the sodium ion within the plant, classification of plants into the following three groups is possible:

(1) Plants in which the sodium ion is sluggishly translocated from the root to the stem (maize, bean, etc.).
(2) Plants in which an appreciable amount of sodium is translocated from the root to the stem and leaf (pea, oats, tomato, etc.).
(3) Plants in which large-scale translocation of sodium from the root to the stem and leaf occurs and in which a relatively large amount of sodium accumulates in the mesophyll (beet, spinach, chicory, etc.).

The greater the sensitivity of the plant to the sodium ion, the more uniform is the distribution of that ion throughout the plant. The sodium ion accumulates in the meristematic parts of the plant and at the points from which the side-roots develop.

All the sodium present in the oat seed appears to be translocated to the root at the time of germination.

* Since this was written Dr. Ray Specht of Adelaide, Australia, has informed our Laboratory that Dr. Brownell of the Botany Department, Adelaide University, has proved that sodium is an essential element for *Atriplex vesicaria* and that an account of his investigation has been submitted to *Nature*.

The distribution of the sodium ions is in no way influenced by the level of concentration of calcium or potassium in the plant. By application of the autoradiographic technique, it is possible to state, within six weeks of sowing, whether and to what degree sodium will increase the crop yield.

CHAPTER V

THE INFLUENCE OF CONCENTRATION OF RADIOACTIVE SODIUM AND OF DURATION OF UPTAKE UPON DRY-MATTER PRODUCTION AND UPON UPTAKE AND DISTRIBUTION OF SODIUM IN THE LEAF, STEM AND ROOT OF OATS

Concentrations from 0 to 27 μc. Na^{22} per 2 litres nutrient solution appear to exercise no significant radioactive influence upon the fresh weight, the dry-matter yield and percentage, the total and percentage contents of sodium, the amount of sodium taken up during the experiment, or the distribution of the total sodium and of the sodium taken up during the experiment.

The exchange of isotopes appears to be of only secondary importance.

CHAPTER VI

THE UPTAKE AND OUTGO OF SODIUM IONS IN OATS

The uptake and outgo of sodium in oats was investigated with the aid of radioactive sodium. To this end, distinction was made between the following three periods:

(1) The germination period, at the end of which the plants had attained a height of 8 cm.
(2) The cultural period of three weeks' duration, in which the plants were placed in nutrient solutions containing 0.1, 2 or 4 m.e. sodium - either radioactive or non-radioactive - per litre nutrient solution.
(3) The experimental period of 6 days, during which the plants from the non-radioactive nutrient solution of the cultural period were placed in a radioactive nutrient solution (Experiment A) and the plants from the radioactive nutrient solution of the cultural period were placed in a non-radioactive nutrient solution (Experiment B).

TOTAL SODIUM CONTENT

The radioactivity of the plant or nutrient solution had no effect upon the accumulation of sodium. Plants which possessed an appreciable sodium content before the experimental period accumulated sodium more easily during the experiment than did plants with a low initial sodium content.

It was demonstrated that non-radioactive sodium from the germination period is involved in the outgo of sodium during the experimental period. The sodium in the plant is more easily replaced by other sodium ions than by ions of calcium, potassium or magnesium.

THE OUTGO OF SODIUM TAKEN UP DURING THE GERMINATION PERIOD AND THE CULTURAL PERIOD

The factors governing the outgo of sodium from the germination period are different from those governing the outgo of sodium from the cultural period.

THE VICE-VERSA EFFECT

In the case of the low-salt plants the re-uptake of sodium from the nutrient solution is so small as to be negligible. Uptake reveals itself as an active process and outgo as a passive process.

THE DISTRIBUTION OF SODIUM BETWEEN THE CULM AND ROOT

The distribution between the culm and root of the sodium taken up by the plant is dependent upon the sodium level of the culm and the root.

A considerable amount of sodium is translocated from the root to the culm as soon as the root has attained a certain sodium level.

THE INFLUENCE OF THE EXPERIMENTAL CONDITIONS UPON THE DISTRIBUTION AND THE TRANSLOCATION OF THE SODIUM TAKEN UP DURING THE CULTURAL PERIOD

The outgo of the sodium taken up during the cultural period is influenced by, but not quantitatively related to, the translocation of sodium from the root to the culm and vice versa.

CONCLUSIONS

(1) The sodium contained in the plant is present in three different forms of binding, namely:
   (a) A form in which it can easily be exchanged by ions of Na, Ca, K or Mg.
   (b) A form in which it can easily be exchanged by other Na ions but only with difficulty by ions of Ca, K or Mg (selective binding).
   (c) A form in which it can be exchanged only with difficulty by other Na ions (specific binding).

(2) On this evidence sodium must have a specific and an essential function in the plant in addition to its general function. The vital importance of the functions has not yet been elucidated.

CHAPTER VII

THE INFLUENCE OF TOP-DRESSING WITH SODIUM NITRATE AT DIFFERENT STAGES OF DEVELOPMENT UPON THE UPTAKE AND DISTRIBUTION OF SODIUM IN OATS

The sodium nitrate used for the top-dressing was labelled with radioactive sodium.

THE DEVELOPMENT OF THE CROP, THE YIELDS, THE ACCUMULATION OF SODIUM, THE SODIUM CONTENT OF THE PLANTS AND THE ACCUMULATION OF SODIUM FROM THE BASAL DRESSING AND THE TOP-DRESSING

It was found that the later the top-dressing is applied, the darker green in colour is the foliage. Top-dressing resulted in an increase in the fresh weight and in the dry-matter yields of the crop in the interim harvest-periods. It appears that when sufficient sodium is supplied, the plant strives to attain a certain sodium level.

The plant possesses its highest sodium level at the time when it reaches the stage of rapid height-growth.

The chemical and the radioactive methods of determination gave identical results for the value of sodium accumulated from the basal dressing and the top-dressing provided that:

(1) the plants received early top-dressing, and
(2) the accumulation was measured after maturity.

In other cases, the radioactive method of determination is preferable.

In general, top-dressing promotes uptake from the basal dressing.

THE DISTRIBUTION OF THE SODIUM IONS THROUGHOUT THE VARIOUS ORGANS AND PARTS OF THE PLANT

The composition of the nitrogen fertilizer exercises considerable influence upon the mineral composition of the fruit. The contents of sodium in the leaf, the culm and the fruit are approximately in the ratio 6 : 18 : 1.

The influence of the top-dressing upon sodium accumulation in the leaf is determined by the physiological age of the leaf at the time of application of the top-dressing.

The sodium content of an organ of the plant is not uniform, more sodium being found in the lower portion than in the upper portion .

A constant amount of sodium is accumulated by the endosperm from the top-dressing, irrespective of the time of application.

CONCLUSIONS

(1) The withering process is delayed by top-dressing.
(2) For the determination of the sodium accumulation from the basal dressing and the top-dressing calculated on the yields produced by the crop in the interim harvest periods, the isotope technique is indispensable.
(3) The sodium content of the endosperm is increased by the application of top-dressing.

APPENDICES

1. DATA ON THE EXECUTION OF THE EXPERIMENT DESCRIBED IN CHAPTER V

Cultural Treatment and Sambling
1953

29th May – Oats (var. Marne) planted at a depth of 2 cm.* in silica-sand.

10th June – Corks were filled: 6 plants each about 9 cm. in height per cork.

10th June – The corks – with plants – were placed in the culture trays.

30th June – Plants were transferred to the experimental pots.

Harvesting – After accumulation periods of 1/3, 1, 3, 9, 27 and 81 hours.

(a) Nutrient Solutions
Culture Trays

0.0025 M. KNO_3
0.0025 M. $Ca(NO_3)_2$**
0.001 M. $MgSO_4$
0.0005 M. KH_2PO_4
7 p.p.m. Fe given as ferric potassium ethylene diamine tetra-acetate.

(b) Experimental Pots

2 m.e. Na given as Na_2SO_4
0.05 m.e. Ca given as $CaSO_4$
For each of the different accumulation periods 0, 1/3, 1, 3, 9 or 27 μc. Na^{22} per 2 l. nutrient solution were given.

Immediately after harvesting, the plants were divided into root and culm. The plants which were allowed an accumulation period of 27 hours from the pots receiving 0, 1/3, 1, 3, 9, and 27 μc. Na^{22} were divided as follows:

Upper half leaf-blade
Lower half leaf-blade
Upper half stem
Lower half stem
Rhizome
Upper half root
Lower half root

* By covering the seed with a 2 cm. layer of sand long rhizomes were obtained.
** According to Hoagland and Broyer (113).

2. ANALYSES TABLES - CHAPTER V

ANALYSIS OF THE FRESH WEIGHTS OF CULMS AND ROOTS

TABLE I

Analysis of the fresh Weight of the Culms

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	4.97	5	0.99	1.23	2.53	3.70	< 1	< 1
Error	24.33	30	0.80					
Uptake Period	6.18	5	1.23	1.70	2.60	3.86	< 1	< 1
Error	18.15	25	0.72					

Mean Error of the Experiment 2.8%

TABLE II

Analysis of the fresh Weight of the Roots

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	12.79	5	2.56	1.20	2.53	3.70	< 1	< 1
Error	63.89	30	2.13					
Uptake Period	13.84	5	2.77	1.38	2.60	3.86	< 1	< 1
Error	50.05	25	2.—					

Mean Error of the Experiment 11.02%

ANALYSIS OF THE DRY-MATTER YIELDS OF CULMS AND ROOTS

TABLE III

Analysis of the dry-matter Yields of the Culms

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	0.066	5	0.013	1.4	2.53	3.70	< 1	< 1
Error	0.282	30	0.009					
Uptake Period	0.028	5	0.006	0.5	4.53	9.49	< 1	< 1
Error	0.255	25	0.010					

Mean Error of the Experiment 2.2%

TABLE IV

Analysis of the dry-matter Yields of the Roots

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	0.006	5	0.0011	1.4	2.53	3.70	< 1	< 1
Error	0.023	30	0.0008					
Uptake Period	0.0019	5	0.0004	0.5	4.53	9.47	< 1	< 1
Error	0.021	25	0.0008					

Mean Error of the Experiment 1.64%

ANALYSIS OF THE PERCENTAGES OF DRY MATTER OF CULMS AND ROOTS

TABLE V

Analysis of the Percentages of dry Matter of the Culms

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	4.90	5	0.98	1.13	2.53	3.70	< 1	< 1
Error	26.08	30	0.87					
Uptake Period	8.70	5	3.74	12.46	2.60	3.86	4.79	3.23
Error	7.38	25	0.30					

Mean Error of the Experiment 0.7%

TABLE VI

Differences between the Percentages of dry Matter of the Culms totalled for the Replications

No.μc.Na^{22} per 2 l. nutrient solution						Sum	Uptake Period in Hours
3	9	1/3	27	1	81		
3	0	6.5 ++*	7.0 ++	7.4 ++	12.2 ++	82.4	3
	9	6.5 ++	7.0 ++	7.4 ++	12.2 ++	82.4	9
		1/3	0.5	0.9	5.7 +	75.9	1/3
			27	0.4	5.2 +	75.4	27
				1	4.8 +	75.-	1
					81	70.2	81

The minimum Value of a significant Difference 4.23 (P.0.05)
The minimum Value of a significant Difference 6.02 (P.0.01)

* The symbols + and ++ in Table VI and subsequent tables denote significant and highly significant differences respectively.

TABLE VII

Analysis of the Percentages of dry Matter of the Roots

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	10.56	5	2.11	0.59	4.50	9.38	< 1	< 1
Error	107.62	30	3.59					
Uptake Period	38.34	5	7.67	2.78	2.60	3.86	1.07	< 1
Error	69.28	25	2.77					

Mean Error of the Experiment 2.4%

TABLE VIII

Differences between the Percentages of dry Matter of the Roots totalled for the Replications

No. μc. Na^{22} per l. nutrient solution						Sum	Uptake Period in Hours
1	27	3	1/3	9	81		
1	4.6	6.5	9.4	10.3	20.1 +	77.4	1
	27	1.9	4.8	5.7	15.5 +	72.8	27
		3	2.9	3.8	13.6 +	70.9	3
			1/3	0.9	10.7	68.0	1/3
				9	9.8	67.1	9
					81	57.3	81

The minimum Value of a significant Difference 12.83 (P.0.05)
The minimum Value of a significant Difference 18.25 (P.0.01)

TABLE IX

Analysis of the sodium Percentages of the Culms

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	0.11	5	0.022	0.1	4.50	9.38	< 1	< 1
Error	6.64	30	0.221					
Uptake Period	4.80	5	0.96	12.97	2.60	3.86	4.92	3.36
Error	1.84	25	0.074					

Mean Error of the Experiment 2.7%

TABLE X

Differences between the sodium Percentages of the Culms totalled for the Replications

No. μc. Na^{22} per 2 l. nutrient solution						Sum	Uptake Period in Hours
81	27	9	1/3	1	3		
81	1.40	3.8 ++	4.7 ++	5.6 ++	6.0 ++	13.50	81
	27	2.4 +	3.3 ++	4.2 ++	4.6 ++	12.10	27
		9	0.9	1.8	2.2 +	9.7	9
			1/3	0.9	1.3	8.8	1/3
				1	0.4	7.9	1
					3	7.5	3

The minimum Value of a significant Difference 2.09 (P.0.05)
The minimum value of a significant Difference 2.98 (P.0.01)

TABLE XI

Analysis of the sodium Percentages of the Roots

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	2.29	5	0.46	0.22	4.50	9.38	< 1	< 1
Error	63.61	30	2.12					
Uptake Period	49.63	5	9.93	17.76	2.60	3.86	6.83	4.60
Error	13.98	25	0.56					

Mean Error of the Experiment 3.5%

TABLE XII

Differences between the sodium Percentages of the Roots totalled for the Replications

No. μc. Na^{22} per 2 l. nutrient solution						Sum	Uptake Period in Hours
81	27	9	1/3	1	3		
81	6.5 ++	12.9 ++	18.0 ++	18.0 ++	19.2 ++	33.9	81
	27	6.4 ++	11.5 ++	11.5 ++	12.7 ++	27.4	27
		9	5.1 +	5.1 +	6.3 ++	21.0	9
			1/3	0	1.2	15.9	1/3
				1	1.2	15.9	1
					3	14.7	3

The minimum Value of a significant Difference 3.80 (P.0.05)
The minimum Value of a significant Difference 5.79 (P.0.01)

TABLE XIII

Analysis of the Contents of Total-sodium in the Culms

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	0.55	5	0.11	0.39	4.50	9.38	< 1	< 1
Error	8.45	30	0.28					
Uptake Period	6.47	5	1.29	16.38	2.60	3.86	6.3	4.24
Error	1.98	25	0.08					

Mean Error of the Experiment 3.0%

TABLE XIV

Differences between the Contents of Total-sodium in the Culms totalled for the Replications

No. μc. Na^{22} per 2 l. nutrient solution						Sum	Uptake Period in Hours
81	27	9	1	1/3	3		
81	2.24 ++	5.36 ++	5.79 ++	6.04 ++	7.45 ++	13.73	81
	27	3.12 ++	3.55 ++	3.80 ++	5.21 ++	11.49	27
		9	0.43	0.68	2.09	8.37	9
			1	0.25	1.66	7.94	1
				1/3	0.20	7.69	1/3
					3	6.28	3

The minimum Value of a significant Difference 2.17 (P.0.05)
The minimum Value of a significant Difference 3.08 (P.0.01)

TABLE XV

Analysis of the Contents of Total-sodium in the Roots

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	0.48	5	0.096	0.508	4.50	9.38	< 1	< 1
Error	5.65	30	0.188					
Uptake Period	4.48	5	0.895	19.17	2.60	3.86	7.37	4.97
Error	1.17	25	0.047					

Mean Error of the Experiment 2.7%

TABLE XVI

Differences between the Contents of Total-sodium in the Roots totalled for the Replications

No. μc. Na^{22} per 2 l. nutrient solution						Sum	Uptake Period in Hours
81	27	1	9	3	1/3		
81	1.94 +	5.05 ++	5.28 ++	5.35 ++	5.48 ++	11.96	81
	27	3.17 ++	3.34 ++	3.41 ++	3.54 ++	10.02	27
		1	0.23	0.30	0.43	6.91	1
			9	0.07	0.20	6.68	9
				3	0.13	6.61	3
					1/3	6.48	1/3

The minimum Value of a significant Difference 1.66 (P.0.05)
The minimum Value of a significant Difference 2.37 (P.0.01)

TABLE XVII

Analysis of the Contents of Uptake-sodium in the Culms

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	0.014	4	0.004	0.03	5.76	13.92	< 1	< 1
Error	7.812	25	0.132					
Uptake Period	7.761	5	1.552	5.97	2.71	4.10	220	145.6
Error	0.052	20	0.003					

Mean Error of the Experiment 1.7%

TABLE XVIII

Differences between the Contents of Uptake-sodium in the Culms totalled for the Replications

No. μc. Na^{22} per 2 l. nutrient solution						Sum	Uptake Period in Hours
81	27	9	3	1	1/3		
81	2.24 ++	4.64 ++	6.33 ++	6.57 ++	6.91 ++	7.31	81
	27	2.40 ++	4.09 ++	4.33 ++	4.67 ++	4.89	27
		9	1.69 ++	1.93 ++	2.27 ++	2.49	9
			3	0.24	0.58 ++	0.80	3
				1	0.34	0.56	1
					1/3	0.22	1/3

The minimum Value of a significant Difference 0.36 (P.0.05)
The minimum Value of a significant Difference 0.54 (P.0.01)

TABLE XIX

Analysis of the Contents of Uptake - sodium in the Roots

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	0.05	4	0.012	0.083	5.76	13.92	< 1	< 1
Error	3.601	25	0.144					
Uptake Period	3.271	5	0.654	38.93	2.71	4.10	14.4	9.5
Error	0.335	20	0.017					

Mean Error of the Experiment 2.9%

TABLE XX

Differences between the Contents of Uptake - sodium in the Roots totalled for the Replications

No. μc. Na^{22} per 2l. nutrient solution						Sum	Uptake Period in Hours
81	27	9	3	1	1/3		
81	2.66 ++	3.24 ++	3.60 ++	4.28 ++	5.27 ++	7.27	81
27		0.58	9.4 +	1.62 ++	2.61 ++	4.61	27
9			0.36	1.04 +	2.03 ++	4.03	9
3				0.68	1.67 ++	3.67	3
1					0.99 +	2.99	1
1/3						2.00	1/3

The minimum Value of a significant Difference 0.94 (P.0.05)
The minimum Value of a significant Difference 1.37 (P.0.01)

TABLE XXI

Analysis of the Contents of Total-sodium in the various Parts of the Plant

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F.Theor.		F.Calc./F.Theor.	
					P.0.05	0.01	0.05	0.01
Replications	0.0534	5	0.0107	0.18	4.48	9.34	< 1	< 1
Error	2.0302	36	0.0564					
Plant Part	1.5998	6	0.2666	18.6	2.42	3.47	7.68	5.36
Error	0.4304	30	0.0143					

Mean Error of the Experiment 3.6%

TABLE XXII

Analysis of Percentages of Total - sodium in the various Parts of the Plant

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F. Theor.		F. Calc./F. Theor.	
					P.0.05	0.01	0.05	0.01
Replications	2.59	5	0.518	0.17	4.48	9.34	< 1	< 1
Error	109.02	36	3.03					
Plant Part	97.20	6	16.20	41.54	2.42	3.47	17.16	11.97
Error	11.82	30	0.39					

Mean Error of the Experiment 3%

TABLE XXIII

Analysis of the Contents of Uptake - sodium in the various Parts of the Plant

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F. Theor.		F. Calc./F. Theor.	
					P.0.05	0.01	0.05	0.01
Replications	0.034	4	0.009	0.019	5.80	14.02	< 1	< 1
Error	0.877	20	0.044					
Plant Part	0.739	6	0.132	37.72	2.51	3.67	15.00	10.03
Error	0.084	24	0.004					

Mean Error of the Experiment 3.7%

TABLE XXIV

Analysis of Percentages of Uptake-sodium in the various Parts of the Plant

Source of Variation	S.S.	D.F.	Variance	F.Calc.	F. Theor.		F. Calc./F. Theor.	
					P.0.05	0.01	0.05	0.01
Replications	0.30	4	0.07	0.04	5.80	14.02	< 1	< 1
Error	35.05	20	1.75					
Plant Part	31.66	6	5.28	37.43	2.51	3.67	14.91	10.20
Error	3.38	24	0.14					

Mean Error of the Experiment 3.5%

TABLE XXV

Differences between the Contents of Total-sodium in the various Parts of the Plant totalled for the Replications

L.h.s.	U.h.r.	R.	L.h.l.	U.h.s.	L.h.r.	U.h.l.	Sum	Plant Part
L.h.s.	0.72	2.3 ++	2.49++	2.81++	2.89++	3.50++	5.08	L.h.s.
	U.h.r.	1.59++	1.77++	2.09++	2.17++	2.78++	4.36	U.h.r.
		R.	0.18	0.50	0.58	1.19	2.77	R.
			L.h.l.	0.32	0.40	1.01+	2.59	L.h.l.
				U.h.s.	0.08	0.69	2.27	U.h.s.
					L.h.r.	0.61	2.19	L.h.r.
						U.h.l.	1.58	U.h.l.

The minimum Value of a significant Difference 0.92 (P.0.05)
The minimum Value of a significant Difference 1.31 (P.0.01)

Plant Part	Abbreviation
Upper half leaf-blade	U.h.l.
Lower half leaf-blade	L.h.l.
Upper half stem	U.h.s.
Lower half stem	L.h.s.
Rhizome	R.
Upper half root	U.h.r.
Lower half root	L.h.r.

TABLE XXVI

Differences between the Percentages of Total-sodium in the various Parts of the Plant totalled for the Replications

L.h.r.	R.	L.h.s.	U.h.r.	U.h.s.	L.h.l.	U.h.l.	Sum	Plant Part
L.h.r.	2.6	11.3++	11.9++	20.5++	22.8++	25.3++	32.5	L.h.r.
	R.	8.7++	9.3++	17.9++	20.2++	22.7++	29.9	R.
		L.h.s.	0.6	9.2++	11.5++	14.-++	21.2	L.h.s.
			U.h.r.	8.6++	10.9++	13.4++	20.6	U.h.r.
				U.h.s.	2.3	4.8+	12.-	U.h.s.
					L.h.l.	2.5	9.7	L.h.l.
						U.h.l.	7.2	U.h.l.

The minimum Value of a significant Difference 4.81 (P.0.05)
The minimum Value of a significant Difference 6.84 (P.0.01)

TABLE XXVII

Differences between the Contents of Uptake-sodium in the various Parts of the Plant totalled for the Replications

U.h.r.	L.h.s.	U.h.s.	L.h.r.	R.	L.h.l.	U.h.l.	Sum	Plant Part
U.h.r.	0.39	1.31++	1.69++	1.71++	1.79++	2.25++	2.66	U.h.r.
	L.h.s.	0.92++	1.29++	1.31++	1.40++	1.86++	2.27	L.h.s.
		U.h.s.	0.37	0.40	0.48+	0.93++	1.35	U.h.s.
			L.h.r.	0.02	0.10	0.56+	0.97	L.h.r.
				R.	0.08	0.54+	0.95	R.
					L.h.l.	0.46+	0.87	L.h.l.
						U.h.l.	0.41	U.h.l.

The minimum Value of a significant Difference 0.43 (P.0.05)
The minimum Value of a significant Difference 0.63 (P.0.01)

TABLE XXVIII

Differences between the Percentages of Uptake-sodium in the various Parts of the Plant totalled for the Replications

L.h.r.	U.h.r.	R.	L.h.s.	U.h.s.	L.h.l.	U.h.l.	Sum	Plant Part
L.h.r.	1.91	5.71++	6.02++	8.39++	12.48++	13.99++	15.81	L.h.r.
	U.h.r.	3.80+	4.11++	6.48++	10.57++	12.08++	13.90	U.h.r.
		R.	0.31	2.68	6.77++	8.28++	10.10	R.
			L.h.s.	2.37	6.46++	7.97++	9.79	L.h.s.
				U.h.s.	4.09++	5.60++	7.42	U.h.s.
					L.h.l.	1.51	3.33	L.h.l.
						U.h.l.	1.82	U.h.l.

The minimum Value of a significant Difference 2.74 (P.0.05)

The minimum Value of a significant Difference 3.99 (P.0.01)

3. METHOD OF CALCULATION OF THE AMOUNT OF SODIUM TAKEN UP DURING THE EXPERIMENTAL PERIOD BY THE PLANTS USED IN THE EXPERIMENT DESCRIBED IN CHAPTER VI

The experiment described in Chapter VI was carried out in triplicate. After harvesting, the plants were divided into culms and roots. The radioactivity of 20 mg. ash obtained from the separate ashing of culm and root was measured three times. The uptake of sodium by the plants during the experimental period was determined using these radioactivity measurements in the calculations.

Radioactivity of 20 mg. ash (measured on 16th December, 1953)

1st count : 3061.2 c.p.m.
2nd count : 2984.0 c.p.m. Average : 3037.7 c.p.m. ± 29.5
3rd count : 3068.0 c.p.m.

Correction for dead-time (D.T.) was made, using the following formula:

$$\frac{N_g}{1 - TN_g}$$, in which T = 300 μsec. and N_g = the c.p.m. measured.

After correcting for D.T. the sample strength was:

3,084.5 c.p.m. ± 29.9

The background rate was 45.7 c.p.m. ± 0.8. Thus, on the above-mentioned date the true sample strength was:

3,038.8 c.p.m. ± 29.9

In order to permit the comparison of ash samples of which the radioactivity was measured on different dates the results of all counts were reduced to values applicable to a single, common date. The date of the commencement of the experiment -26th May, 1953- was chosen.

For this purpose the results of the counts were corrected for disintegration of the isotope and loss of efficiency of the G.-M. tube. Both corrections could be made simultaneously by applying the radioactivity measurements of the standard Na^{22} preparation as made on 26th May (8,269 c.p.m.) and on 16th December (7084.3 c.p.m.).

4. DATA ON THE EXECUTION OF THE EXPERIMENT DESCRIBED IN CHAPTER VII

Composition of the Dusarite-Silica sand Culture Medium	Basal dressing	Top-dressing	Harvesting Dates	Development Stage on Harvesting	Na^{22}	Other Data
6 g. K dusarite 6 g. Mg dusarite 88 g. Ca dusarite 2.6 kg. silica sand 400 g. silica sand as germination layer pH = 6.2	1 g. $CaHPO_4$ 2 aq. 100 mg. $FeCl_3$ 80 mg. $MnSO_4$ 4 aq. 50 mg. $CuSO_4$ 5 aq. 5 mg. borax 5 mg. ammonium molybdate 200 mg. N given as $NaNO_3$	100 mg. N given as $NaNO_3$ to treatments B, C, D, E, G, H, I, K, L, N.	19th May 27th May 11th June 18th June 23rd July	10 days before rapid height-growth stage 2 days before rapid height-growth stage Moment of the escape of the panicle Full panicle development Crop fully ripened.	1.5 µc. per top-dressing per pot	25th April: pots filled and sown with 18 seeds each. Crop: Oats (var. Marne) 30th April: emergence of seedlings. 4th May: seedlings thinned out to leave 12 per pot.

Thus, the radioactivity of the sample, (20 mg. ash), corrected for 26th May, was:

$\frac{8269}{7084.3}$ x 3038.8 c.p.m. = 3546.9 c.p.m. ± 34.9

And the radioactivity of the whole of the ashed culms (58.6 mg. ash), was:

$\frac{58.6}{20}$ x 3546.9 c.p.m. = 10400 c.p.m. ± 102.2

In the same way the radioactivity of the roots was calculated : 15400 c.p.m. ± 304.4

And thus the total radioactivity of the plants was found : 25800 c.p.m. ± 321.0

The radioactivity of the plants of the 1st replication was : 27090 c.p.m. ± 540.8

The radioactivity of the plants of the 2nd replication was: 25880 c.p.m. ± 385.3

Thus the average radioactivity of the treatment was: 26260 c.p.m. ± 224

The radioactivity of the nutrient solution containing 6.96 mg. Na was: 77700 c.p.m.

Thus the uptake of Na was:

$\frac{26260}{77700}$ x 6.96 mg. Na = 2.35 mg. Na

Average amount of sodium in the plants after the experiment: 6.78 mg. ± 0.15

Average amount of sodium in the plants before the experiment: 4.96 mg. ± 0.08

Uptake - outgo = accumulation = 1.82 mg. ± 0.17

2.35 - 0.53 = accumulation = 1.82

LITERATURE

1. ACKER, W.
   Z. PflErnähr.Düng., 11 B, 313 (1932).

2. ACKER, W.
   Arch.f.Pfl.bau, 9, 104 (1932).

3. ALEXANDER, L.T.
   Agron.J.,42, 252 (1950).

4. ALLEN, M.B.,and ARNON, D.I.
   Physiol. Plant., 8, 653 (1955).

5. ALTEN, F.,and GOEZE, G.
   Ernähr.Pfl., 31, 181 (1935).

6. ANDREWS, W.B.
   The response of crops and soils to fertilisers and manures.
   Publ.author,State College, Mississippi, (1947).

7. ARISZ, W.H.
   Konink.Ned.Akad.Wetenschap, 53, 236 (1944).

8. ARISZ, W.H.
   Annu.Rev.Pl.Physiol., 3, 109 (1952).

9. ARISZ, W.H.
   Acta Bot.Neerl., 1, 506 (1953).

10. ARLAND, A.
    Ernähr.Pfl., 27, 445 (1931).

11. ARNOLD, B.L.
    Victory Farm Forum, 1949.

12. ARNON, D.I.
    Mineral Nutrition of Plants,(p.313) Ed.E.Truog, Univ. of Wisconsin Press, Madison, Wisconsin 1951 .

13. ARNON, D.I., and STOUT, P.R.
    Plant Physiol., 14, 371 (1939).

14. ARNON, D.I., FRATZKE, W.E.,and JOHNSON, C.M.
    Plant Physiol., 17, 515 (1942).

15. BAIRD, G.B., and MEHLICH, A.
    Proc.Soil Sci. Soc. Amer., 15, 201 (1950).

16. BARNETT, A.
    Physiol.Rev., 56, 963 (1939).

17. BASU, S.N.
    J.Gen.Microbiol., 5, 231 (1951).

18. BAYLISS, W.M.
Principles of Gen. Physiol. 4th Ed.Longmans, Green and Co. London, 1924.

19. BEQUEREL, P., and ROUSSEAU, J.
Compt.Rend.Heb.Séances Acad. Sci., 244, 773 (1947).

20. BERKNER, F., and SCHLIMM, W.
Landw.Jahrb., 73, 503 (1931).

21. BERTRAND, G.
Ann. Sc.Agron., 46, 1 (1929).

22. BERTRAND, G.
C.R. Ac.Sciences, 232, 1381 (1951).

23. BERTRAND, G., and PERIETZEANU, D.J.
Bull.Soc.Chim., 41,(4), 709 (1927).

24. BERTRAND, G., and PERIETZEANU, D.J.
Bull.Soc.Chim., 41,(4), 1378 (1927).

25. BERTRAND, G., and ROSENBLATT, M.
Bull.Soc.Chim., 43,(4), 368 (1928).

26. Bibliography of the Literature on the Minor Elements.
4th Edition, Vol. I, II, III. Publ. by the Chilean Nitrate Educational Bureau, New York.

27. BIRNER, H., and LUCANUS, B.
Landw.Versuchs-Stationen,VIII, 128 (1866).

28. BIZZELL, J.A.
Proc.Soil Sci. Soc.Amer., 2, 343 (1937).

29. BLUME, J.M.
Soil Sci., 73, 299 (1952).

30. BLUME, J.M., HAGEN, C.E., and MACKIE, R.W.
Soil Sci., 70, 415 (1950).

31. BOULD, C.
Nature, 167, 140 (1951).

32. BOULD, C., NICHOLAS, D.J.D., and THOMAS, W.D.E.
Plant and Soil, V, 1, 36 (1953).

33. BOUSSINGAULT, J.B.J.D.
Economie Rurale, 2, 73.

34. BOUYOUCOS, G.J.
J.Amer.Soc.Agron., 3, 130 (1911).

35. BOWER, C.A., and PIERRE, W.H.
J.Amer.Soc.Agron., 36, 608 (1944).

36. BOWER, C.A., and WADLEIGH, C.H.
Proc.Soil Sci.Soc.Amer., 13, 218 (1948).

37. BRAY, R.H.
J.Amer.Chem.Soc., 64, 954 (1942).

38. BREAZEALE, J.F.
J.Amer.Chem.Soc., 28, 1013 (1906).

39. BREAZEALE, J.F., and McGEORGE, W.T.
Ariz.Agr.Exp.Sta.Tech.Bull. 41, 113 (1932).

40. BRIGGS, L.J., and SHANTZ, H.L.
U.S.Dept.Agr.Bur.Plant Ind.Bull. 28, No.284-285, 1 (1913).
J.Agr.Res., 111, 1 (1914).

41. BROOKS, M.M.
Proc.Sci.Expt.Biol.Med., 42, 558 (1939).

42. BROOKS, S.C.
Advances in Enzymology, VII, 1 (1917).

43. BROUWER, R.
Konink.Ned.Akad.Wetenschap (C), 57, 68 (1954).

44. BROUWER, R.
Acta Bot.Neerl., 3, 264 (1954).

45. BROWN, L.A.
Soil Sci., 39, 277 (1935).

46. BROYER, T.C., CARLTON, A.B., JOHNSON, C.M., and STOUT, P.R.
Plant Physiol., 29, 526 (1954).

47. BURGERSTEIN, A.
Die Transpiration der Pfl., I, Jena, 141 (1904).

48. BURGERSTEIN, A.
Die Transpiration der Pfl., II, Jena, 95 (1920).

49. BUTKEVICH, V.S., and MARUASHVILI, L.V.
Compt.rend.Acad.Sci.USSR, 22, 127 (1939).

50. CARR, C.W., and TOPOL, L.
J.Physiol. and Colloid Chem., 54, 176 (1950).

51. COLBY, H.L.
Plant Physiol., 8, 357 (1933).

52. COLLANDER, R.
Plant Physiol., 16, 691 (1941).

53. COPE, J.T., BRADFIELD, R., and PEECH, M.
Soil Sci., 76, 65 (1953).

54. COOPER, H.P., and GARMAN, W.H.
Proc. Soil Sci. Soc. Amer., 7, 331 (1942).

55. COOPER, H.P., PADEN, W.R., and PHILLIPPE, M.M.
Soil Sci., 76, 19 (1953).

56. COWIE, D.B., ROBERTS, R.B., and ROBERTS, I.Z.
J.Cellular Comp. Physiol., 34, 243 (1949).

57. CRANE, H.R.
Physiol.Rev., 56, 1243 (1939).

58. CREPA, A.
Strahlentherapie, 16, 913 (1924).

59. DECOUX, L., VANDERWAEREN, J., and SIMON, M.
Inst.Belge Amélior.Better.Pub., 12, 663 (1944).

60. DION, G., BEDFORD, C.F., and ARNAUD, R.T.St.
Nature, 163, 906 (1949).

61. DOESBURG, J.J., and ZWEEDE, A.K.
Voeding, 9, 1, 12 (1948).

62. DOMONTOWITSCH, M.K.
Abh.des Inst. f. Düngerforsch. L.f.g., 12, (1924).

63. DORSEY, C.W.
Alkali soils of the United States. U.S.Dept.Agr.Bureau of Soils Bull. 35, 1 (1906).

64. DROBKOV, A.A.
C.R. Acad.Sci. (USSR), 17, 229 (1937).

65. DROBKOV, A.A.
Bull: Acad. Sci. (USSR) (Cl.Sci.Math.), 783 (1940).

66. DROBKOV, A.A.
C.R. Acad. Sci. (USSR), 49, 224 (1945).

67. DUHAMEL de MONCEAU.
Mém. Ac. Sci. 1736, p. 215 and 1767, p. 233 and 239.

68. DYER, B.
Phil. Trans. Roy. Soc. B., 194, 235 (1901).

69. EATON, F.M.
Plant Physiol., 16, 545 (1941).

70. EATON, F.M.
J.Agric. Res., 64, 357 (1942).

71. ECKSTEIN, O., BRUNO, A., and TURRENTINE, J.W.
Verlagsges. f. Ackerbau, M.B.H., Berlin, 1937.

72. EDDY, A.A., HINSHELWOOD, C., and DANLEY, C.J.
Proc.Roy.Soc. (London) (B), 136, 544 (1950).

73. EHRENBERG, L., GUSTAFSSON, A., LEVAN, A., and von WETTSTEIN, U.
Hereditas, 35, 469 (1949).

74. EMELEUS, H.J., and ANDERSON, J.S.
Modern Aspects of Inorganic Chemistry. 1948.
Van Nostrand, New York.

75. FEHER, D.
Erdész Kisérl. 45, 341, 362 (1945).

76. FLECKENSTEIN, A.
Arch. ges. Physiol. (Pflugers), 250, 643 (1948).

77. FLECKENSTEIN, A., and HERTEL, H.
Arch. ges. Physiol. (Pflugers), 250, 577, 643 (1948).

78. FLIEG, O.
Z. Pfl Ernähr. Düng., 38, 222 (1935).

79. FRANKLIN, F.J.
Ala. Agr. Exp. Sta. Res. Bull. 227, (1928).

80. FRENCH, C.D.
Canad. Chem., 33, 225 (1948).

81. GAGER, C.S.
Mem. N.Y. Bot. Garden, 6, 153 (1916).

82. GARDNER, R., and KELLEY, O.J.
Soil Sci., 50, 91 (1940).

83. GAUCH, H.G., and WADLEIGH, C.H.
Bot. Gaz., 105, 379 (1944).

84. GAUCH, H.G., and WADLEIGH, C.H.
Soil Sci., 59, 139 (1945).

85. GERICKE, S.
Z. Pfl Ernähr. Düng., 42, 39 (1948).

86. GIESEKING, J.E., and JENNY, H.
Soil Sci., 42, 273 (1936).

87. GINNEKEN, P.J.H., and BRUINSMA, J.R.
Meded.Inst.Ration.Suikerprod, 8, 227 (1938).

88. GLIEMEROTH, G.
Z. Pfl Ernähr.Düng., 52,(97),21 (1951).

89. GRACANIN, M.
Z. Pfl Ernähr.Düng., IX-B, 300 (1930).

90. GREAVES, J.E.
J.Biol.Chem., 7, 287 (1910).

91. GUTTENBERG, H., van, and BEYTHEIN, A.
Planta, 40, 36 (1951).

92. GUTTENBERG, H., van, and MEINL, G.
Planta, 40, 431 (1952).

93. HAAN, I. de
Protoplasma, 24, 186 (1935).

94. HAAS, A.R.C.
Citrus Leaves, 32, No.10, 10 - 11, 26 (1952).
(C.A., 47, 809 a).

95. HALE, J.B., WATSON, M.A., and HULL, R.
Ann. Appl.Biol., 33, 13 (1946).

96. HANKS, R.J., and TANNER, C.B.
J.Amer.Soc.Agron. 44, 98 (1952).

97. HAMSTEIN-CRANNER, B.
Jahrb. wiss. Bot., 53, 536 (1914).

98. HARMER, P.M.
Mich.Agr.Exp.Sta.Cir.Bull. 187, (1943).

99. HARMER, P.M., and BENNE, E.J.
J.Amer.Soc.Agron., 33, 952 (1941).

100. HARMER, P.M., and BENNE, E.J.
Soil Sci., 60, 137 (1945).

101. HARMER, P.M., BENNE, E.J., LAUGHLIN, W.M., and KEY, C.
Soil Sci., 76, 1 (1953).

102. HARTWELL, B.L.
J.Amer.Soc.Agron., 19, 479 (1927).

103. HARTWELL, B.L., and DAMON, S.C.
Rhode Island Agr.Exp.Sta.Bull. 177, 4 (1919).

104. HARTWELL, B.L., WHEELER, H.J., and PEMBER, F.R.
Rhode Island Agr.Exp.Sta.Rep. 1907, 299 (1904).

105. HAYWARD, H.E., and LONG, E.M.
Bot. Gaz., 102, 437 (1941).

106. HAYWARD, H.E., and LONG, E.M.
Plant Physiol., 18, 556 (1943).

107. HAYWARD, H.E., and SPURR, W.B.
Bot. Gaz., 105, 152 (1943).

108. HAYWARD, H.E., and SPURR, W.B.
J. Amer. Soc.Agron., 36, 287 (1944).

109. HEBERT, J.
Ann. Agron., 2, 334 (1951).

110. HENDRICKS, S.B., and DEAN, L.A.
Proc. Auburn Conf. Radioactive Isotopes Agr. Res., 76 (1948).

111. HEVESY, G.
Physiol. Rev., 57, 240 (1940).

112. HEVESY, G., and PANETH, F.
A Manual of Radioactivity. Oxford Univ. Press, London, 1938.

113. HOAGLAND, D.R., and BROYER, T.C.
Plant Physiol., 11, 471 (1936).

114. HOFLER, K.
Protoplasma, 33, 545 (1939).

115. HOLM-JENSEN, I., KROGH, A., and WARTIOVAARA, V.
Acta Botan. Fenn., 36, (1944).

116. HOLT, M.E., and VOLK, M.J.
J.Amer.Soc.Agron., 37, 821 (1945).

117. HONERT, I.H. van den
Meded.Proefst. Java - Suikerind., 23, 71 (1933).

117a. International Superphosphate Manufacturers' Association.
Rep.Gen.Meeting, Budapest, 1936.

118. ITALLIE, Th. B. van
Landbouwk. Tijdschr., 53, 53 (1941).

119. JACOBSON, L.
Plant Physiol., 26, 411 (1951).

120. JARUSOV, S.S.
Pedology (U.S.S.R.), 33, 799 (1938).

121. JENNY, H., and AYERS, A.D.
Soil Sci., 48, 443 (1939).

122. JOHAM, H.E.
Plant Physiol., 30, 4 (1955).

123. JONES, U.S., and HOOVER, C.D.
Amer.Fert., 110, (1949).

124. KEARNEY, T.H., and CAMERON, F.K.
U.S. Dept. Agr. Report, 71, 5 (1902).

125. KEISERLEHNER, E.
Protoplasma, 33, 579 (1939).

126. KELLEY, W.P.
Alkali Soils, their Formation, Properties and Reclamation.
Rheinhold Publishing Corporation, New York, 1951.

127. KISSER, J.
Planta, 3, 562 (1922).

128. KRAMER, P.J.
Annu.Rev. Pl. Physiol., 6, 253 (1955).

129. LAMM, O., and MALMGREN, H.
Z.Anorg.u.allgem.Chem., 245, 103 (1940).

130. LANCASTER, J.D., ANDREWS, W.B., and JONES, U.S.
Soil Sci., 76, 29 (1953).

131. LARSEN, S.
Bull. Doc., 8, 1 (1950).

132. LARSON, W.E., and PIERRE, W.H.
Soil Sci., 76, 51 (1953).

133. LAWTON, K., and COOK, R.L.
Adv.Agron., VI, 253 (1954).

134. LEHR, J.J.
Soil Sci., 52, 5, 373 (1941).

135. LEHR, J.J.
Plant and Soil, II, 37 (1949).

136. LEHR, J.J.
Soil Sci., 72, 157 (1951).

137. LEHR, J.J.
Plant and Soil, IV, 289 (1953).

138. LEHR, J.J.
J.Sci.Food Agric., 4, 460 (1953).

138a. LEHR, J.J.
Communication to the 2nd World Congress of Chemical Fertilizers, Rome (1951). J.Sci.Food Agric.4, 460 (1953).
Fertilizer colloquium, Wageningen University (1954).

139. LEHR, J.J., and HUDIG, J.
Een monografie over de oudste minerale meststof ter wereld. Uitgegeven door het Inlichtingenbureau voor Chilisalpeter te Den Haag, (1947)

140. LEHR, J.J., and van WESEMAEL, J.Ch.
J. Soil Sci., 3, 125 (1952).

141. LEHR, J.J., and WYBENGA, J.M.
Plant and Soil, VI, 3, 251 (1955).

142. LEMMERMAN, O., MICHAEL, G., and SCHMIDT, O.E.
Z. PflErnähr. Düng., 38, 185 (1947).

143. LEONARD, C.D., and BEAR, F.E.
New Jersey Agr. Exp. Sta. Bull. 752 (1950).

144. LEOPOLD, A.C., and THIMANN, K.V.
Amer. J. Bot., 36, 342 (1949).

145. LEWIS, G.C., JORDAN, J.V., and JAVE, R.L.
Soil Sci., 74, 227 (1952).

146. LIEBIG, J. von.
Walton and Marberly, London, 1863.

147. LINDSAY, F.K.
Ind. Eng. Chem., 30, 163 (1938).

148. LOEHWING, W.F.
Mineral Nutrition of Plants. Ed. E.Truog. Univ. Wisconsin Press, 1951.

149. LONG, E.M.
Amer. J. Bot., 30, 594 (1943).

150. LUNDEGARDH, H.
Lantbr. - Höggsk. Ann., 8, 233 (1940).

151. LUNDEGARDH, H.
Annu. Rev. Pl. Physiol., 6, 1 (1955).

152. LUNDEGARDH, H., BURSTROM, H., and RENNERFELT, E.
Svensk Bot. Tidskr., 26, 271 (1932).

153. MAGISTAD, O.C.
Bot. Rev., 11, 181 (1945).

154. MAGISTAD, O.C., AYERS, A.D., WADLEIGH, C.H., and GAUCH, H.G.
Plant Physiol., 18, 151 (1943).

155. MAGISTAD, O.C., and REITEMEYER, R.F.
Soil Sci., 55, 351 (1943).

156. MALMGREN.,H.
Acta Chem. Scand., 2, 147 (1948).

157. MARSHALL, J.G., and STURGIS, M.B.
Soil Sci., 76, 75 (1953).

158. MARSHALL, C.E.
Miss.Agr.Exp.Sta.Res.Bull. 385 (1944).

159. MAYER, W.
Z.Pfl Ernähr.Düng., 54, 210 (1951).

160. McGEORGE, W.T.
Ariz.Agr.Exp.Sta.Tech.Bull. 38 (1932).

161. McGEORGE, W.T.
Plant Physiol., 7, 119 (1932).

162. McGEORGE, W.T., and BREAZEALE, J.F.
Ariz. Agr. Exp.Sta.Tech.Bull. 35 (1931).

163. McGEORGE, W.T., and BREAZEALE, J.F.
Ariz.Agr.Exp.Sta.Tech.Bull. 36 (1931).

163a. McLEAN E.O.
Soil Sci., 82, 21 (1956).

164. MERWE, A.J., van der.
Farming in South Africa, 243 (1949).

165. METZGER, W.H.
Soil Sci., 47, 15 (1939).

166. MEYER, B.S.
Amer.J.Bot., 18, 79 (1931).

167. MIDGLEY, A.R.
J.Amer.Soc.Agron., 23, 788 (1931).

168. MIDGLEY, A.R.
Proc.Soil Sci.Soc.Amer., 5, 24 (1940).

169. MIRTSCH, H.
Z. PflBau, 10, 209 (1934).

170. MITSCHERLICH, E.A.
P.Ges.Gel. in Königsberg, Schriften der Königsberger Gelehrten Gesellschaft, 12, (1935).

171. MONTGOMERY, E.G.
Ann.Rep.Neb.Agr.Exp.Sta. (1912).

172. MULDER, E.G.
Plant and Soil, 5, 246 (1954).

173. MULLINS, L.J.
Physiol. Rev., 56, 1244 (1939).

174. MULLISON, W.R.
Proc. Indiana Acad. Sci., 51, 94 (1942).

175. MULLISON, W.R., and MULLISON, E.
Plant Physiol., 17, 632 (1942).

176. NESZLER, J.
Cbl.Agr., 6, 39 (1874).

176a. NICKSON, J.J.
Symposium on Radiobiology. Chapman and Hall Ltd., London, 1952.

177. NIGHTINGALE, G.T., and FARNHAM, R.B.
Bot.Gaz., 97, 477 (1936).

178. NIGHTINGALE, G.T., SCHERMERHORN, L.G., and ROBBINS, W.R.
N.J.Agr.Exp.Sta.Bull. 499 (1930).

179. ODEBLAD, E.
Acta Radiologica Supplementum 93, 1952. Thesis.

180. OLSEN, C.
Physiol. Plant., 1, 136 (1948).

181. OLSEN, C.
Compt.rend.trav.lab.Carlsberg Sér.chim., 26, 197 (1948).

182. OPITZ, K., TAMM, E., EGGLHUBER, E., and KNIES, W.
Bodenk. PflErnähr. 12, 257 (1939).

183. OSTERHOUT, W.J., van.
Injury, Recovery and Death in Relation to Conductivity and Permeability. J.B. Lippencott and Co., Philadelphia, 1922.

184. OVERSTREET, R., and JACOBSON, L.
Annu.Rev.Pl.Physiol., 3, 189 (1952).

185. OVERSTREET, R., and JENNY, H.
Proc.Soil Sci.Soc.Amer., 4, 125 (1939).

186. PANNER, E.
Canad.J.agr.Sci., 34, 41 (1954).

187. PARKER, F.P., and THORNE, D.W.
Proc.Soil Sci.Soc.Amer., 13, 213 (1948).

188. PFEIFFER, Th., EINECKE, A., SCHNEIDER, W., and HEPNER, A.
Mitt.Landw.Inst.Breslau, 3, 567 (1905).

189. PIERRE, W.H., and BOWER, C.A.
Soil Sci., 55, 23 (1943).

190. PIRSON, A.
Annu.Rev.Pl.Physiol., 6, 71 (1955).

191. PIRSON, A., and SEIDEL, F.
Planta, 38, 431 (1950).

192. POWERS, W.L.
Oreg.Agric.Exp.Sta.Bull. 302 (1932).

193. POWERS, W.L., and LEWIS, M.R.
Oreg.Agric.Exp.Sta.Bull. 394 (1941).

194. PRJANISCHNIKOW, D.N.
Resultate der Gefäszversuch der Jahren 1899 - 1900. Moscou, 1901.

195. PRJANISCHNIKOW, D.N.
Agr.Chim., (1936).

196. RABER, O.L.
Bot.Gaz., 75, 298 (1923).

197. RAVIKOVITCH, S.
Soil Sci., 38, 279 (1934).

198. RAVIKOVITCH, S.
Soil Sci., 47, 357 (1939).

199. REED, H.S.
Ann.Bot., 49, 81 (1910).

200. REED, H.S., and HAAS, A.R.C.
J.Agr.Res., 28, 277 (1924).

201. RHODES, A., TEMPLEMAN, W.G., and THURSTON, M.N.
Ann.Bot., 14, 181 (1950).

202. RICHARDS, F.J.
Ann.Bot., 5, 263 (1941).

203. RICHARDS, F.J.
Ann.Bot., 8, 323 (1944).

204. RICHARDS, F.J.
Commun. 8th Intern.Bot.Congr.,Sect. 11, Rep., 101 - 2
(Paris, France, 1944).

205. RIETBERG, H.
Unpubl.Results of Pot Experiments with Sugarbeet, Inst.
Ration. Suikerprod., Bergen op Zoom, Holland.

206. ROBERTS, R.B., ROBERTS, I.L., and COWIE, D.B.
J.Cellular Comp Physiol., 34, 259 (1949).

207. ROSENE, H.F.
Amer.J.Bot., 28, 402 (1941).

208. ROSENE, H.F.
J.Gen.Physiol., 34, 65 (1950-1951).
J.Cellular Comp. Physiol., 35, 179 (1950).

209. ROSENE, H.F., and WALTHALL, A.M.J.
Physiol.Plant., 7, 190 (1954).

210. SAMOKHVALOV, G.K.
Chem.Soc.Agr. (U.S.S.R.), 7-8, 26 (1926).
(C.A., 31, 6284)

211. SAYRE, C.B., and SHAFER, J.I.
Farm for Victory, 1944.

212. SCHACHTSCHABEL, P.
Kolloid-Beihefte, 51, 199 (1940).

213. SCHARRER, K., and SCHREIBER, R.
Bodenk. PflErnähr., 34, 310 (1944).

214. SCHARRER, K., SCHREIBER, R., and KUHN, H.
Z. Pfl Ernähr. Düng.; 62, 128 (1953).

215. SCHARRER, K., and SCHROPP, W.
Ernahr. Pfl., 31, 301 (1935).

216. SCHEEL, R.
Ernähr. Pfl., 34, 302 (1938).

217. SCHEFFER, F., and WELTE, E.
Lehrb. der Agr. Chemie u. Bodenk., II Teil, PflErnähr., Ferdinand Enke, Verlag, Stuttgart, 1955.

218. SCHMALFUSS, K.
Ernähr. Pfl., 34, 100 (1938).

219. SCHOFIELD, C.S.
U.S. Dept. Agr. Circ. 735 (1945).

220. SCHREVEN, D.A. van.
Meded. Inst. Ration. Suikerprod., 7, 119 (1937).

221. SCHUFFELEN, A.C.
T.N.O.-Nieuws, 116, 493 (1955).

222. SCHUFFELEN, A.C., LEHR, J.J., and ROSANOW, M.
Trans. Int. Soc. Soil Sci., II, 263 (1952).

223. SCHULOW, Iw.
Izv. Moskov Selsk. Khoz. Inst. (Ann. Inst. Agron. Moscou), 8, 161 (1902).

224. SCHULZE, B.
Landw. Vers. Sta. 79/80, 431 (1913).

225. SCHULZE, B.
Landw. Vers. Sta. 86, 323 (1915).

226. SCHWEIGART, H.A.
Z. PflErnähr. Düng., 54, 36 (1951).

227. SCOTT, G.T.
J. Cellular Comp. Physiol., 23, 47 (1944).

228. SCOTT, G.T., and HAYWARD, H.R.
Science, 117, 719 (1953).

229. SCOTT, G.T., and HAYWARD, H.R.
J. Gen. Physiol., 37, 601 (1954). (C.A., 48, 8888e)

230. SCOTT RUSSELL, R., and MARTIN, R.P.
J. Expt. Bot., I, Pt, II, 133 (1951).

231. SCOTT RUSSELL, R., MARTIN, R.P., and ADAMS, S.M.
Trans.4th Int.Congr.Soil.Sci., Amsterdam, 1950. II. 138 (1950).

232. SEEMAN, F.
Protoplasma, 39, 147 (1950 a).

233. SEEMAN, F.
Protoplasma, 39, 535 (1950 b).

234. SEEMAN, F.
Protoplasma, 42, 109 (1953).

235. SEIFRIZ, W., and PLOWE, J.
J.Rheology, 2, 263 (1931).

236. SEMERGEI, K.I.
Doklady Akad. Nauk., U.S.S.R., 77, 867 (1951). (C.A., 45, 7736g).

237. SEMUSHKIN, V.V.
Izv.Moskov Selsk. Khoz.Inst. (Ann.Inst.Agron.Moscou) 22, 85 (1916).

238. SINCLAIR, W.K.
Nature, 167, 234 (1951).

239. SINGH, B.N., and MEHTA, B.K.
J.Amer.Soc.Agron., 30, 395 (1938).

240. SMITH, A.M.
Manures and Fertilizers,(p. 186) . Thomas Nelson and Sons Ltd. London, 1952.

241. SNOW, A.G.
Plant Physiol., 11, 583 (1936).

242. SODDY, F.
The Interpretation of the Atom.
John Murray, London, 1932.

243. Sodium Symposium.
Soil Sci., 76, 1 (1953).

244. SOKOLOW, A.W.
Die Phosphorsäure, 4, 65 (1934).

245. SPINKS, J.W.T., CUMMING, E., IRWIN, R.L.B., and ARNASON, T.J.
Canad.J.Res., 26, Sect. C, 249 (1948).

246. SPRAGUE, V.G., and GRABER, L.F.
J.Amer.Soc.Agron., 30, 986 (1938).

247. SPURWAY, C.H.
Soil Sci., 19, 399 (1925).

248. STAHL-SCHRODER, M.
J.f.Landw., 49 (1899).

249. STEINBACH, H.B.
Modern Trends in Physiology and Biochemistry. p.173 (1952).
Ed. E.S. B.Guzman, Academic Press, New York, 1951.

250. STEINBACH, H.B.
Annu.Rev.Pl. Physiol., 6, 323 (1955).

251. STEINBERG, R.A.
J.Agric.Res., 55, 891 (1937).

252. STEINBERG, R.A.
Amer.J.Bot., 33, 210 (1946).

253. STOKLASA, J., and MATOUSEK, A.
Beitrage zur Kenntnis der Ernährung der Zuckerrübe.
Finker, Jena, 1916.

254. STUCH, P.
. Z.PflErnähr. Düng., A 7, 257 (1926).

255. THOM, C.C., and HOLTZ, H.F.
Wash.Agr.Exp.Sta.Bull. 146 (1917).

256. THORNE, D.W.
Proc.Soil Sci.Soc.Amer., 9, 185 (1944).

257. THORNE, D.W.
Proc.Soil Sci.Soc.Amer., 11, 397 (1946).

258. THUN, R.
Bodenk.PflErnähr. 21/22, 723 (1940).

259. TIBAU, M.E.
Plant Physiol., 11, 731 (1936).

260. TIDMORE, J.W.
Soil Sci., 30, 13 (1930).

261. TOBLER, F.
Z.PflErnähr. Düng., A 13, 208 (1929).

262. TOBLER, F.
Jahrb. Wiss. Bot., 71, 26 (1929).

263. TOBLER, F.
Jahrb.Wiss.Bot., 78, 295 (1933).

264. TOLBERT, E., and PEARSON, P.B.
Adv.Agron., 4, 279 (1952).

265. TREGGI, G.C.
Ann.Sper.Agrar.Roma, 6, 1435 (1952).

266. TULLIN, V.
Physiol. Plant., 7, 810 (1954).

267. TRUOG, E., BERGER, K.C., and ATTOE, O.J.
Soil Sci., 76, 41 (1953).

268. ULBRICHT, H.
Ernähr. Pfl., 33, 28 (1937).

269. URL, W.
Protoplasma, 40, 475 (1951).

270. VERHOEVEN, B.
Maandbl.v.d.Land.Voorlichtingsdienst, 3, 162 (1946).

271. VERONA, O., and TREGGI, G.C.
Agrar.Ital.Roma, 51 (N.S. 6),153 (1951).

272. VIETS, F.G.
Plant Physiol., 19, 466 (1944).

273. VOLK, G.W.
J.Amer.Soc.Agron., 36, 46 (1944).

274. WADLEIGH, C.H., and AYERS, A.D.
Plant Physiol., 20, 106 (1945).

275. WADLEIGH, C.H., and GAUCH, H.G.
Soil Sci., 58, 399 (1944).

276. WADLEIGH, C.H., GAUCH, H.G., and MAGISTAD, O.C.
U.S.Dept.Agr.Tech.Bull. 925, (1946).

277. WADLEIGH, C.H., GAUCH, H.G., and STRONG, D.G.
Soil Sci., 63, 341 (1947).

278. WAGNER, E.C.
Dissertation Ph.D.,Ohio State Univ. (1936).

279. WAGNER, P.
Arb.dtsch.Landw.Ges., 96 (1904).

280. WALL, M.E.
Soil Sci., 47, 143 (1939).

281. WALLACE, A., TOTH, S.J., and BEAR, F.E.
Soil Sci., 65, 249 (1948).

282. WALLACE, A., TOTH, S.J., and BEAR, F.E.
Soil Sci., 65, 477 (1948).

283. WALLACE, T.
The Diagnosis of Mineral Deficiencies in Plants by Visual Symptoms. H.M.S.O., London, 1951.

284. WATSON, D.J., and RUSSELL, E.J.
Emp.J.Exp.Agric., 11, 49 (1943). (C.A., 37, 3548)

285. WAZER, J.R.,van, and CAMPANELLA, D.A.
J.Amer.Chem.Soc., 72, 655 (1950).

286. WEHUNT, R.L., and COLLINS, W.O.
Soil Sci., 76, 91 (1953).

287. WEISER, V.L.
Bull.Vt.Agr.Exp.Sta. 356 (1933).

288. WESEMAEL, J.Ch.,van, and LEHR, J.J.
Transactions of the Vth Intern. Congr. of Soil Sci., Leopoldville, II, 273 (1954).

289. WHEELER, H.J., *et al.*
Rhode Island Agr. Exp.Sta.Ann.Rpt. (1906).
(Bibliography of the Literature on the Minor Élements,Fourth Ed. 1, 1719, Publ.Chilean Nitrate Educational Bureau, New York,1948.)

290. WHEELER, H.J., and TUCKER, G.M.
Rhode Island Agr.Exp.Sta.Ann.Rpt. (1895).
(Bibliography of the Literature on the Minor Elements, Fourth Ed. 1, 1717 - 3). Publ.Chilean Nitrate Educational Bureau, New York 1948.

291. WIEDE, W.
Neue Mitteilungen Landw., 38, 752 (1949).

292. WIESMANN, H.
Z.PflErnähr.Düng., A 1, 1 (1923).

293. WILD, A.
J. Soil Sci., 1, 221 (1949-1950).

294. WILLIAMS, R.
J.Agric.Sci., 27, 259 (1937).

295. WOLFF, L.
Ebenda, 10, (1868).

296, WOLFF, L.
Landw.Versuchs-Stationen, 10, 349 (1868).

297. YORK, E.T.
Soil Sci., 76, 65 (1953).

SAMENVATTING EN CONCLUSIES

HOOFDSTUK I

INLEIDING

Door de bestudering van de opname en afgifte van natriumionen door de wortels van de plant en de verdeling van deze ionen over de plant *(Avena sativa, var.Marne)* werd getracht een beter inzicht te verkrijgen in de betekenis van het natrium als voedingsion voor de plant.

HOOFDSTUK II

DE BETEKENIS VAN NATRIUMIONEN VOOR DE PLANTENVOEDING

Aan de hand van de beschikbare literatuur gegevens werd nagegaan wat het in de loop der jaren uitgevoerde onderzoek, betreffende de werking van het natriumion, aan resultaten heeft opgeleverd. Het natriumion bleek een geringere invloed op de mobiliteit van de in de bodem geabsorbeerde kaliumionen te hebben dan de andere voedingsionen, zodat de invloed van een natriumbemesting slechts ten dele aan het vrijmaken van kaliumionen zal kunnen worden toegeschreven. De via de plant gemeten invloed van natriumionen op de fosfaatbeschikbaarheid heeft tegenstrijdige resultaten opgeleverd. De sterk uiteenlopende proefomstandigheden en de grote variatie in de proefgewassen moeten hiervoor verantwoordelijk worden gesteld. De aan het substraat gemeten veranderingen, door natriumionen teweeg gebracht in de oplosbaarheid van het fosfaation, hebben meer gelijkluidende resultaten opgeleverd. Het natriumion zelf oefent, naast een fosfaatoplossende werking die voortvloeit uit de soms met natriumzouten verkregen pH verhoging, een gunstige invloed uit op de beschikbaarheid van het fosfaat.

Via het metabolisme kunnen de natriumionen invloed uitoefenen op de inwendige struktuur en op de habitus van de plant. De invloed op de struktuur van de plant komt vooral tot uiting in de versteviging van vaat- en steunweefsels. De permeabiliteit van de plantencel, de imbibitie en de transpiratie van de planten worden eveneens door natriumionen beïnvloed. Na lithium is natrium het kation dat de permeabiliteit en imbibitie het sterkst bevordert. Bij planten, die een behoorlijke hoeveelheid natrium kunnen akkumuleren, wordt de verdamping door kalium minder sterk verlaagd dan door een equivalente hoeveelheid natrium. Bovendien wordt het ekonomisch verbruik van water, zoals dit in de transpiratie koëfficiënt tot uitdrukking wordt gebracht, door het natrium in gunstige zin beïnvloed. In het algemeen is de betekenis van het natriumion voor de waterhuishouding van de plant minstens zo groot als die van het kaliumion.

Bij het landbouwkundig onderzoek is aan de mogelijkheid van wederkerige substitutie van natrium- en kaliumionen in de plant veel aan-

dacht besteed. Het natriumion bekleedt in de plantenvoeding echter een andere plaats dan rubidium, dat ook het kaliumion gedeeltelijk kan vervangen. In tegenstelling met rubidium wordt het natriumion selektief geabsorbeerd.
De indeling van de gewassen in vier groepen volgens HARMER en BENNE (101) blijkt slechts een beperkte betekenis te hebben, omdat binnen de plantensoort aanmerkelijke verschillen in natriumgevoeligheid voorkomen.
Een gunstig effekt van kalium en natrium op het produktievermogen van de gewassen behoeft niet altijd samen te gaan. Door een te eenzijdige aandacht aan de overeenkomst tussen de natrium en kaliumionen te schenken, zijn de verschillen tussen deze ionen uit het oog verloren. Zo blijkt het natriumion een betere complexvormer te zijn dan het kaliumion. De opvatting van vele onderzoekers, dat natrium als een essentiëel element voor de planten moet worden beschouwd, wordt door het feit, dat specifieke natriumgebreksverschijnselen werden vastgesteld, gesteund. Hiermede wordt aan het tweede door ARNON en STOUT gestelde kriterium, ten aanzien van onontbeerlijkheid van een element voor de plant, voldaan. Ten aanzien van de andere twee, door hen gestelde, kriteria werd het natriumion niet of onvoldoende getest. Een element mag echter ook als essentiëel beschouwd worden, wanneer het deel uitmaakt van een essentiëel bestanddeel van de plantencel en betrokken is bij een, voor het leven van de plant beslissende, biochemische reaktie.
Uit onderzoekingen met radioaktieve isotopen is gebleken, dat het natriumion zich selektief met celsubstanties kan verbinden. Een deel van het natrium blijkt in een niet in water oplosbare vorm in de plant voor te komen. Recent werd aangetoond (4), dat het natrium een essentiëel element is voor blauw-groen wieren. Voor de hogere planten* werd dit nog niet gevonden. Uit het in de volgende hoofdstukken beschreven onderzoek komen echter verschillende feiten naar voren, die er sterk op wijzen dat het natrium inderdaad een essentiële en specifieke funktie bij deze planten vervult. De aard van deze funkties is evenwel nog niet opgehelderd.

HOOFDSTUK III

DE METODEN VAN ONDERZOEK

Als kultuurmedium werden waterkultures en dusariet-silica zand gebruikt. De natriumopname van de gewassen werd bestudeerd door toepassing van radioaktief natrium (22Na). De koncentratie van het radioaktieve natriumisotoop bedroeg in waterkultures 3 μc. per twee liter voedingsoplossing. Aan de dusariet-kultures werd met de overbemesting met natriumnitraat 1,5 μc ^{22}Na per pot gegeven.

* Door Dr. Brownell van het Botany Department, Adelaide University werd, naar een mededeling van Dr. Ray Specht uit Adelaide, onlangs aangetoond, dat het natrium een essentieel element is voor *Atriplex vesicaria*. De betreffende verhandeling werd aan *Nature* ter publicatie aangeboden.

De chemische en fysische bepalingen werden aan de plantenas verricht. Het totale natriumgehalte van de as werd vlamfotometrisch bepaald. Voor de bepaling van de hoeveelheid radioaktief natrium werd 20. mg. as op een 0.1 mm. dik alluminium schaaltje gebracht en gemeten met een drie dekaden teller. De teluitkomsten werden gekorrigeerd voor het nul-effekt, de dodetijd, de variërende efficiëntie van de telbuis, het tijdstip van meting. De metodiek voor het vervaardigen van makro-autoradiogrammen werd besproken. Het is gebleken, dat voor het verkrijgen van een betrouwbare weergave van de verdeling van natriumionen over de plant van snel gedroogd materiaal moet worden uitgegaan.

HOOFDSTUK IV

DE VERDELING VAN NATRIUMIONEN OVER DE PLANT, BEPAALD MET AUTORADIOGRAMMEN

Met behulp van autoradiogrammen werd de verdeling van natriumionen over een aantal verschillende planten met een normaal en een hoog calcium of kalium gehalte nagegaan. Ten aanzien van het transport van de natriumionen zijn de plantensoorten, aan de hand van de autoradiogrammen, in drie groepen te verdelen:

1. Plantensoorten, waarbij het natriumion traag van wortel naar stengel wordt getransporteerd. (Mais, boon) Dit blijken gewassen te zijn, die, ten aanzien van hun produktievermogen, weinig of niet op natrium reageren.
2. Plantensoorten, waarbij een aanzienlijk transport van natrium van wortel naar stengel en bladplaats heeft. (Erwt, haver, tomaat) Dit blijken gewassen te zijn, die, ten aanzien van hun produktievermogen, matig tot goed op natrium reageren.
3. Plantensoorten, waarbij veel natrium naar stengel en blad getransporteerd wordt en waarbij het natrium zich relatief sterk in het bladmoes ophoopt. (Biet, spinazie, witlof) Dit blijken gewassen te zijn, die, ten aanzien van hun produktievermogen, zeer goed op natrium reageren.

Naarmate de planten beter op het natriumion reageren, is de verdeling van de natriumionen gelijkmatiger. Ongelijkmatigheid in de verdeling uit zich in een meer of minder snelle afname van de hoeveelheid natrium van de basis naar de top van de bovengrondse organen van de plant.

Het natriumion akkumuleert in de meristematische delen. Bij alle plantensoorten wordt het natrium in de wortel opgehoopt waar zijwortels ontspringen. Het natrium in het haverzaad bleek bij ontkiemen vrijwel geheel naar de wortels te worden getransporteerd. De distributie van natriumionen wordt niet beïnvloed door hoge of lage calcium- of kalium koncentraties in de plant. Met gebruikmaking van de autoradiografische techniek is men is staat om binnen zes weken na het zaaien de vraag te beantwoorden of een gewas, ten aanzien van zijn produktievermogen, weinig of niet, matig, goed of zeer goed op natriumionen zal reageren.

HOOFDSTUK V

DE INVLOED VAN DE KONCENTRATIE VAN RADIOAKTIEF NATRIUM EN VAN DE DUUR VAN DE OPNAME OP DROGESTOFPRODUKTIE, NATRIUMOPNAME EN VERDELING VAN HET NATRIUM OVER BLAD, STENGEL EN WORTEL VAN DE HAVERPLANT

De mogelijkheid van een stimulerend of remmend effekt van het radioaktieve isotoop op de ontwikkeling en produktievermogen van de plant mag bij voorbaat niet uitgesloten geacht worden.
De invloed van het radioaktieve isotoop, bij verschillende koncentraties en opname perioden, op het produktievermogen, akkumulatie en verdeling van natriumionen, werd nagegaan. Koncentraties van 0 tot en met 27 μc. ^{22}Na per twee liter voedingsoplossing bleken geen signifikante invloed uit te kunnen oefenen op de versgewichten, drogestofopbrengsten, percentages drogestof, natriumgehalten, totale hoeveelheden natrium, tijdens de proef opgenomen hoeveelheden natrium en op de verdeling van totaal en tijdens de proef opgenomen hoeveelheid natrium over de plant. De isotopen omwisseling speelde bij deze proeven een ondergeschikte rol. De lengte van de opname-periode heeft nagenoeg op al de eerder genoemde grootheden wel een sinifikante invloed gehad. Op grond van de resultaten van deze oriënterende proef werd voor het volgende experiment een koncentratie van 1,5 μc. radioaktief natrium per liter voedingsoplossing en een opname periode van 144 uur gekozen.

HOOFDSTUK VI

DE OPNAME EN AFGIFTE VAN NATRIUMIONEN DOOR HAVER

Met gebruikmaking van radioaktief natrium werd de natriumopname en afgifte door haverplanten nagegaan. In het experiment worden drie perioden onderscheiden:

1. De kiemperiode; de periode waarin de plantjes na uitzaaien op silica-zand een lengte bereiken van ± 8 cm.
2. De kweekperiode; de periode van drie weken, waarin de planten geplaatst werden op voedingsoplossingen met 0,1; 2 of 4 m.e. natrium per liter voedingsoplossing, met of zonder radioaktief natrium.
3. De proefperiode; de periode van zes dagen, waarin de planten van de niet radioaktieve voedingsoplossingen uit de kweekperiode op radioaktieve voedingsoplossingen met 0,1; 2 of 4 m.e. natrium (Proef A) en de radioaktieve planten uit de kweekperiode op de overeenkomstige niet radioaktieve oplossingen werden geplaatst (Proef B).

HET TOTALE NATRIUMGEHALTE

In de kweekperiode en in de proefperiode heeft het al of niet radioaktief zijn van voedingsoplossing en/of planten geen invloed gehad op de natriumakkumulatie. De hoeveelheden natrium in de planten nemen toe met de natriumkoncentratie in de voedingsoplossing.

De grootte van de toename is afhankelijk van het natriumniveau van de planten. Planten, die bij de aanvang van de proef reeds een behoorlijk natriumniveau bezitten, akkumuleren de natriumionen gemakkelijker, dan planten met een laag natriumniveau.

HET RADIOAKTIEVE NATRIUM

De absorptie, het verschil tussen de voor en na de proef in de planten aanwezige totale hoeveelheden natrium, is gelijk aan de opname verminderd met de afgifte. Uit de metingen van de radioaktiviteit van de planten van proef A werd de opname en uit die van proef B de afgifte berekend. Hoewel de natriumakkumulatie in beide proeven dezelfde waarden opleverde, bleken de berekende opname en afgifte bij de objekten van proef A groter te zijn dan bij de overeenkomstige objekten van proef B.
Teoretisch werd aangetoond, dat de oorzaak van het verschil tussen de uit proef A en proef B verkregen uitkomsten te verklaren is, indien bij de proefplanten van proef B niet-radioaktief natrium uit de kiemperiode bij de afgifte in de proefperiode betrokken is geweest. Deze veronderstelling houdt in, dat ook tijdens de kweekperiode natrium uit de kiemperiode in de planten aanwezig geweest moet zijn. Door berekening werd dit aangetoond. Voorts werd de juistheid van de teoretisch afgeleide veronderstelling getoetst aan de specifieke aktiviteiten van de planten van proef B. De specifieke aktiviteiten van de kweekplanten van de natriumniveaux met 0,1; 2 en 4 m.e. natrium tijdens de proefperiode geplaatst op een voedingsoplossing met 0,1 m.e. natrium bleken na de proefperiode gestegen of gelijk gebleven te zijn. Dit is slechts mogelijk, indien er niet-radioaktief natrium uit de kiemperiode tijdens de proefperiode in de plant aanwezig is. Het natriumion, dat, zoals wordt aangenomen, zeer beweeglijk is, werd in de kweekperiode van drie weken door de kationen van voedingsoplossingen met 3 m.e. K; 5 m.e. Ca; 2 m.e. Mg en 0,1; 2 of 4 m.e. Na niet geheel verdreven of omgewisseld.
Het natrium werd in de plant gemakkelijker vervangen door andere natriumionen dan door calcium-, kalium-of magnesiumionen.

DE AFGIFTE VAN HET IN DE KIEM- EN KWEEKPERIODE OPGENOMEN NATRIUM

Ten aanzien van de afgifte gedraagt het natrium uit de kiemperiode zich anders, dan het natrium uit de kweekperiode. De afgifte van het natrium uit de kiemperiode is afhankelijk van:

1. De hoeveelheid kiemnatrium in de plant.
2. De relatieve opname (de verhouding van de opname en de voor de proef in de plant aanwezige hoeveelheid natrium).

De afgifte van natrium uit de kweekperiode is afhankelijk van:

1. De koncentratie van de voedingsoplossing.
2. De verhouding van kiem- en kweeknatrium in de plant.

HET VISA-VERSA EFFEKT

Bij lage zoutplanten is de heropname van natrium uit de voedings-

oplossing miniem. De natriumopname vindt in een korte tijd plaats en blijkt grotendeels beëindigd te zijn voordat de afgifte zijn hoogste waarde bereikt. De opname openbaart zich als een aktiefde afgifte als een passief proces.

DE VERDELING VAN HET NATRIUM OVER DE STENGEL EN DE WORTEL VAN DE PLANT

Bij de kweekplanten en bij de proefplanten blijkt de verdeling van het natrium afhankelijk te zijn van het natriumniveau van wortel en stengel. Naar de stengel worden pas aanzienlijke hoeveelheden natrium getransporteerd, nadat de wortel een bepaald natriumniveau heeft bereikt. Heeft de stengel eenmaal een zeker natriumniveau verkregen, dan vindt de akkumulatie van natriumionen weer hoofdzakelijk in de wortel plaats.

DE INVLOED VAN DE PROEFOMSTANDIGHEDEN OP DE VERDELING EN HET TRANSPORT VAN HET IN DE KWEEKPERIODE OPGENOMEN NATRIUM

Het natriumniveau van de proefplanten heeft slechts een geringe invloed op de afgifte van het in de kweekperiode opgenomen natrium. Bij de kweekplanten van de natriumniveaux met 0,1 en 2 m.e.natrium in de voedingsoplossing is de afgifte tijdens de proef afhankelijk van de natriumkoncentratie in de voedingsoplossing.
Tijdens de opname wordt natrium uit de kweekperiode van wortel naar stengel en van stengel naar wortel getransporteerd. De afgifte van dit natrium wordt wel beïnvloed door,maar is kwantitatief niet gebonden aan het transport van wortel naar stengel en omgekeerd.

KONKLUSIES:

1. Planten, (haver) die reeds een behoorlijk natriumniveau bezitten,nemen het natrium gemakkelijker op dan planten met een laag natriumniveau.
2. De opname openbaart zich als een aktief-,de afgifte als een passief proces.
3. Aanzienlijke hoeveelheden natrium worden eerst naar de stengel getransporteerd,nadat de wortel een bepaald natriumniveau heeft bereikt.
4. Het tijdens de proef in de plant aanwezige natrium uit de kiemperiode gedraagt zich bij de afgifte anders,dan het natrium opgenomen in de kweekperiode.
5. Het natrium komt in drie bindingsvormen in de plant voor:
   a. in een vorm waarin het vrij gemakkelijk tegen Na, Ca, K of Mg ionen wordt uitgewisseld.
   b. in een vorm waarin het vrij gemakkelijk tegen andere natriumionen,maar minder gemakkelijk tegen Ca, K of Mg ionen, wordt uitgewisseld. (selektieve binding).
   c. in een vorm waarin het niet gemakkelijk tegen andere natriumionen wordt uitgewisseld (specifieke binding).
6. Het natriumion moet naast een algemene-, een specifieke- en een essentiële funktie in de plant uitoefenen. Of de funkties van vitaal belang zijn, is nog een open vraag.

HOOFDSTUK VII

DE INVLOED VAN DE OVERBEMESTING MET NATRIUMNITRAAT, IN DIVERSE ONTWIKKELINGSSTADIA, OP DE OPNAME EN DE VERDELING VAN NATRIUM BIJ HAVER

In een potkultuur met dusariet-silica zand werd bij haver de invloed van een overbemesting met gemerkt natriumnitraat, toegediend in verschillende ontwikkelingsstadia, nagegaan.

DE ONTWIKKELING VAN HET GEWAS

De overbemesting en het moment van overbemesting hebben geen invloed op de totale lengtegroei. Naarmate het gewas vroeger in de ontwikkelingsperiode werd overbemest, was het blad donkerder groen van kleur en stierf het blad later af.

DE OPBRENGSTEN

De overbemesting verhoogt de tussentijdse versgewichten en drogestofopbrengsten. Enkel de 10 dagen voor het schietstadium gegeven overbemesting verhoogt de drogestofopbrengst van de planten bij de eindoogst.

DE NATRIUMAKKUMULATIE

Bij de niet overbemeste objekten is de akkumulatie-snelheid aanzienlijk kleiner dan bij de overbemeste objekten. Bij deze laatste objekten is de akkumulatie-snelheid tijdens de lengtegroei groter, naarmate de overbemesting eerder in de ontwikkelingsperiode van de plant werd gegeven. Tegen het einde van de lengtegroei is de akkumulatie-snelheid onafhankelijk van het tijdstip van overbemesting. Enkel bij de 10 dagen voor het schietstadium overbemeste objekten, die tijdens de ontwikkeling de grootste hoeveelheden natrium hebben geakkumuleerd, treedt er, in de periode van bloei, korrelzetting en afrijping, een depletie op. De totale natriumakkumulatie blijkt bij de eindoogst weinig of niet beïnvloed te worden door het tijdstip van overbemesting in de periode van lengtegroei. De plant streeft er blijkbaar naar om bij voldoende aanbod van natrium een bepaald natriumniveau te bereiken.

DE NATRIUMGEHALTEN

De plant bezit het hoogste natriumgehalte op het moment, waarop deze het schietstadium bereikt. In de periode van lengtegroei daalt het natriumgehalte wegens het feit, dat de natriumakkumulatie geen gelijke tred houdt met de drogestofproduktie. In de periode van korrelzetting neemt het natriumgehalte weer toe.

DE NATRIUMAKKUMULATIE UIT BASIS- EN OVERBEMESTING

De, via de chemische en radioaktieve metode, bepaalde akkumulatie loopt in vele gevallen uiteen. De chemische bepaling en de bepaling via de radioaktiviteiten geven bij vroeg overbemeste planten, wan-

neer de akkumulatie na de afrijping wordt bepaald, dezelfde resultaten voor de akkumulatie. In alle andere gevallen verdient de radioaktieve bepalingsmetodiek de voorkeur. De akkumulatie uit basis- en overbemesting is afhankelijk van de data van oogst en overbemesting.

HET VERLOOP VAN DE RADIOAKTIEF BEPAALDE NATRIUMAKKUMULATIE UIT BASIS- EN OVERBEMESTING TEN AANZIEN VAN DE CHEMISCH BEPAALDE AKKUMULATIE

In de ontwikkelingsperiode vlak na de overbemesting, drukt deze de natriumopname uit de basisbemesting.
In het algemeen verhoogt de overbemesting de opname uit de basisbemesting. Wordt de overbemesting na het in de pluim zijn van het gewas gegeven, dan wordt tijdens de korrelzetting en afrijping nagenoeg enkel natrium uit de overbemesting geakkumuleerd. Het natrium wordt uit de overbemesting naar verhouding gemakkelijker opgenomen dan uit de basisbemesting.

DE VERDELING VAN DE NATRIUMIONEN OVER DE ORGANEN VAN DE PLANT

Afhankelijk van het tijdstip van de overbemesting verhouden de hoeveelheden natrium in blad, stengel en zaad zich ongeveer als 6 : 18 : 1. De samenstelling van de stikstofmeststof heeft een aanzienlijke invloed op de minerale samenstelling van het zaad. De overbemestingen verhogen het natriumgehalte van het zaad.

DE NATRIUMAKKUMULATIE UIT DE BASIS- EN OVERBEMESTING IN DE ORGANEN VAN DE PLANT

Naar verhouding is in het blad de akkumulatie uit de basisbemesting groter, dan die uit de overbemesting. De akkumulatie uit de overbemesting neemt, naarmate deze bemesting op een later moment wordt gegeven, sterker af, dan die uit de basisbemesting. Bij het blad stimuleert de overbemesting de akkumulatie uit de basisbemesting. De bladeren akkumuleren de grootste hoeveelheden natrium uit basis- en overbemesting, wanneer de overbemesting even voor het schieten wordt gegeven. Het overgrote deel van het natrium wordt in de stengel geakkumuleerd. Wordt de overbemesting op het moment van het in de pluim komen gegeven, dan akkumuleren stengel en zaad de grootste hoeveelheden natrium uit basis- en overbemesting.

DE VERSPREIDING VAN DE NATRIUMIONEN OVER DE BLADEREN, DE STENGELDELEN EN DE VRUCHTEN

De invloed van de overbemesting op de natriumakkumulatie in de bladeren wordt bepaald door de fysiologische ouderdom van het blad ten tijde van de overbemesting. De natriumakkumulatie, door het op de tweede knoop ingeplante blad, wordt door de overbemesting het sterkst gestimuleerd. Het aksent van de akkumulatie uit de overbemesting verschuift met het later beschikbaarkomen van dit natrium naar het jongere, metabolistisch aktievere, blad. Bij de stengel nemen, evenals bij het blad, de natriumgehalten af van stengelbasis naar stengeltop. Bij de niet overbemeste- en bij de, na het in de

pluim zijn, overbemeste objecten, heeft het onderste deel van de stengel een lager natriumgehalte en hoeveelheid natrium, dan het hierop aansluitende stengeldeel. De vroeg aangewende overbemesting stimuleert de akkumulatie uit de basisbemesting in de stengeldelen, met uitzondering van de akkumulatie in de tweede 15 cm. van de stengel.

In tegenstelling met de bladeren akkumuleren de stengeldelen van de planten, overbemest na het in de pluim zijn, aanzienlijke hoeveelheden natrium uit de overbemesting. De overbemesting verhoogt het natriumgehalte en stimuleert de akkumulatie uit de basisbemesting door kaf, vruchtwand en endosperm in aanzienlijke mate. Door het endosperm wordt, onafhankelijk van het moment van overbemesting, steeds een zelfde hoeveelheid natrium uit de overbemesting geakkumuleerd.

KONKLUSIES:

1. De overbemesting vertraagt het afstervingsproces van de plant.
2. De plant streeft er naar om een bepaald natriumniveau te bereiken.
3. De toepassing van de isotopen metodiek is onmisbaar bij het vaststellen van de natriumakkumulatie uit basis- en overbemesting bij de tussentijdse oogst.
4. Het natrium wordt uit de overbemesting gemakkelijker opgenomen, dan uit de basisbemesting.
5. Uit de, laat in de ontwikkeling van de plant gegeven, overbemesting kunnen de stengeldelen nog aanzienlijke hoeveelheden natrium akkumuleren.
6. De overbemesting verhoogt het natriumgehalte van het endosperm.