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THE USE OF THE SHORT-LIVED RADIO-ISOTOPES ^{11}C and ^{13}N TO STUDY NITROGEN UPTAKE AND PHOTOSYNTHATE TRANSLOCATION IN FODDER BEET

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INTRODUCTION

Following discussions at the Nitrogen Balance Workshop held at Massey University, May 1980, on the use of the 10 min half-life isotope ^{13}N, it was decided to carry out collaborative experiments with Dr K M Goh from Lincoln College. These were concerned with the mechanism of the effect of sodium chloride on the uptake of nitrate and ammonium ions by beet (Beta vulgaris L) plants.

In this report we firstly summarise briefly some of the relevant literature then report on the experiments carried out to November 1982. The initial experiments used ^{13}N to investigate, with hydroponically grown plants, the effect of sodium chloride on the uptake by roots, and the transport to leaves, of ^{13}N applied to the roots as nitrate or as ammonium ions. After failing to find any response to NaCl in these experiments, it was decided to determine whether there was any effect of NaCl on the transport of ^{11}C labelled photosynthates from the leaves.

Production of this preliminary report is a first step to assessing the next phase, if any, of this investigation.

SOME EFFECTS OF NITROGEN AND CHLORIDE ON THE GROWTH OF BEET PLANTS

At the time this project began, proposals to produce liquid transport fuel from beet were being considered, the nitrogen required for continuous cropping possibly to be supplied by an expected overproduction from a urea fertiliser works. In soil, urea breaks down to give both nitrate and ammonium so there was a need to understand the mechanisms of nitrogen uptake and assimilation for production of sugar to be optimised. Alexander (1971) noted that nitrogen supply had a profound effect on beet quality. Too little nitrogen early in the season results in poor root yields which may reduce sugar content if top growth is severely reduced. Excessive nitrogen encourages continued root growth at the expense of sugar production. Sugar crystallisation is prevented by the presence in juice of non-sucrose substances, especially soluble nitrogenous ones. Rapid growth of beet decreases sugar content and Milford and Watson (1971) found that nitrogen did not alter the partition of total assimilate between root and shoots but increased the fraction of total assimilate entering the roots that was used in growth, at the expense of that stored as sugar.

Draycott and Cooke (1966) showed the application of nitrogen could either increase or reduce sucrose concentrations in fresh sugar beet roots. In later work Smith and Martin (1977) reported lower sucrose concentrations and lesser purity at higher levels of nitrogen application. On the other hand Stephen, Kemp and Todd (1980) on a New Zealand soil found a limitation of fermentable sugars by withholding nitrogen.

Vladimirov (1934), using a sand medium with drip cultures, investigated the effects of potassium, chloride and sulphate ions and pH on the yield, sugar content and nitrogen content of sugar beet plants. The inter-relationships were complex. In later Russian field trials Pakhomova, Balakhontsev and Girfanov (1978) successfully increased both the sugar content and also the total yields of sugar beet in field trials in which the preharvest

fertiliser treatments included catechol and chlorocholine chloride in addition to superphosphate and mineral salts such as NaCl, KCl and $ZnSO_4$. It is claimed that the treatments lower leaf invertase activities and increase CO_2 fixation and carbon outflow. James, Kidman, Weaver and Reeder (1970) commented on the known antagonism between chloride and nitrate in nutrient absorption with sugar beet and showed positive sugar responses to KCl fertilization. Greater sucrose yields may not however be obtained with KCl fertilization if background soil concentrations are high (Ludwick, Gilbert and Westfall 1980). In New Zealand, Goh (1981) found about 27% maximum sugar increases for NaCl fertilizer additions of about 400 $kg.ha^{-1}$. Subsequently further trials have been carried out using NaCl, KCl, Na_2SO_4 and K_2SO_4 fertilizer treatments and positive effects have been found for some conditions.

In addition to the above field trials, some pot and hydroponic experiments have been carried out to try to elucidate aspects of the chloride effect. Hurvitz-Lerman and Waisel (1971) found growth of sugar beet plants optimal at 25 mM NaCl but hypocotyl and root growth greatest at 10 mM NaCl. Smith and McComb (1981) showed a maximum in growth of beet at intermediate levels in the range 0.1-250 mM NaCl. Lassani and Marschner (1978) found beet to be tolerant to NaCl addition, there being less than 20% depression of dry matter production at 100 mM NaCl. Marschner, Kylin and Kuiper (1981) showed growth stimulation by 50 mM NaCl in three genotypes with different growth depressions up to 150 mM NaCl. Terry (1977) showed a 60% reduction in growth in Cl^- - deficient beet was not due to an effect on photosynthesis but due to lower cell multiplication rates in leaves which slowed their growth and ultimately drecreased their area. Heuer and Plaut (1981) showed RuBP carboxylase activity in beet leaves was stimulated by 180 mM NaCl in the nutrient medium and at rate limiting light intensities this medium stimulated CO_2 fixation.

Other ways in which chlorides may affect growth are by inhibiting nitrification of ammonium ions in acid soils (Golden, Sivasubramaniam, Sandanam and Wijedasa, 1980); by reducing germination especially at higher temperatures (Mahmoud and Hill, 1981). Protein synthesis may be inhibited by chloride (Peumans, Carlier and Delaey, 1982) although in potato it did not affect the total amount or concentration of protein-N under conditions in which total N and nitrate-N were reduced (Murarka, Jackson and Moore, 1973). Chloride can affect nitrate reductase activities and the effect may be different for different species (Billard and Boucaud, 1982). Evidence from experiments with other species show NaCl may affect other enzymes, i.e. the saccharogenic ones like amylase (Ahmed and Chughtai, 1971).

To conclude it seems clear that mineral salts and chloride in particular can affect sugar production in a variety of ways -

by affecting germination
by modifying the nitrogen source available to the roots
by altering the uptake and assimilation of nitrate and ammonium ions
by affecting enzyme systems controlling nitrogen assimilation, protein synthesis and sugar interconversions
by reducing nitrogen concentrations in the plant which prevent sugar crystallization

EXPERIMENTAL METHODS

Pelleted seeds of Beta vulgaris L. Fodder beet cv "TRESTEL" were obtained from Dr K.M. Goh, Soil Science Department, Lincoln College.

These were placed in a refrigerator for a week to promote germination then stored at room temperature. When required pellets were washed in running tap water for two hours which removes pelletizing material, then the seeds were germinated in a paper column at 25/18°C in a plant cabinet as shown in Figure 1. After 4 days shoots appear and very straight roots are obtained.

Seedlings can be removed as required and transferred to a hydroponic growth system. This may be a tank with partitions to prevent tangling of roots of different plants, or individual cylinders like that shown in Fig. 1. The containers must be covered with aluminium foil to keep out light, or algae will grow. The solution must be air bubbled and the bubbles are kept away from the roots lest they be carried to the surface. The use of split rubber bungs allows the easy removal of plants without damage to the roots.

Plant size is designated by the number of leaves (omitting the cotyledons), a leaf first being counted when it becomes about 10mm long. The growth rate of seedlings is shown in Fig. 2.

Beets were grown on the "old" North Carolina State University complete nutrient solution (NCSU). Concentrations of the ions present have been given by Brooking (1976). When experiments were to be carried out at other concentrations the plants were changed to the required nutrient 3 days before use. Four nutrient types were used details of which are given in Table 1.

EXPERIMENTS WITH ^{13}N-LABELLED NUTRIENTS

The preparation of complete nutrient solutions contain ^{13}N-labelled nitrate or ammonium ions has been described by McNaughton and More (1979) and McNaughton and Presland (1982). Fig. 3 shows the experimental arrangement for the present experiments with fodder beet. A 6-8 leaf plant grown hydroponically for about 4 weeks was sealed through a neoprene cover into a 25 ml vial. Nutrient solution was air bubbled and passed through the root chamber (i.e. the vial) by gravity flow for at least 16 hours before the start of the uptake experiment. Then circulation through the vial was stopped, 5 ml of nutrient removed by syringe and 5 ml of labelled nutrient mixed into the chamber by syringe. After a load time of usually 15 min the activity was flushed to waste by a nutrient flow of about 40 ml min^{-1} (i.e. at least 1.5 chamber volumes per min). Nutrient was recycled after passing approximately 500 ml to waste.

The observed counts were corrected for background, half life, cross-talk from the load zone, detector efficiency, residual activity from the previous experiment and if necessary the attenuation factor of a lead block used to reduce the count rate at the load zone detector.

Fig. 4 shows activity/time profiles for a typical ^{13}N-nitrate uptake experiment. At the end of the load period activity at the root detector decreases rapidly for about 5 min as unabsorbed activity is flushed from the root chamber, and thereafter more slowly for at least another 30 min. The problem is to know what criterion to use to measure root uptake. Associated with each day's series of experiments was at least one in which a 1 min uptake was carried out. Root activities were calculated by subtacting the 1 min load time activity fraction from the 15 min load time activity fraction for the same time after the end of the load period. In a preliminary analysis root activities were calculated at two arbitrarily chosen times - 8 min and 25 min after the end of the load period (i.e. for times 23 and 40 min after the start of the experiment). The symbols used are $_{8}f_R$ and $_{25}f_R$.

The leaf activity/time profile is also shown in Fig. 4. The uptake parameter chosen was the activity fraction at the end of the load period (f_L).

Usually 6-8 experiments could be carried out each day and the same plant could be used for several days. Plant weights were found after the last experiment. Weights for the experiments described below are given in Table 2.

Results are summarised in Table 3 and Fig. 5. All the plants used were grown in NCSU nutrient with 1 mM NaCl but conditioned in different ways. The pH was 5.5.

Series 1: Plants were conditioned in 1x NCSU nutrient with 1 mM added NaCl. Aspect studied were the effect of increasing the NaCl concentration to 5.6 mM until the end of the load period of each experiment. The [NaCl] was increased in one day's experiments at the start of the load period, and on another day 15 min before the load period.

Series 2: Plants conditioned in 1/5x NCSU nutrient with 0.2 mM added NaCl. The effects of increasing [NaCl] to 5.6, 14 and 56 and 70 mM were studied on two plants. The effect of 56 mM NaCl was studied with labelled ammonium nutrient as well as labelled nitrate nutrient.

Series 3: Plants were grown on NCSU nutrient but conditioned on a PEL N-free nutrient. The effects of 2.8 and 56 mM NaCl added with 4 mM labelled nitrate, and of 5.6 mM NaCl added with 1.5 mM labelled ammonium were also studied.

Concerning ^{13}N-nitrate uptakes:

(i) It was thought that measurement of root uptakes at 8 and 25 min might give some indication of the sizes of the fixed and exchangeable nitrate pools proposed by Kresland and McNaughton (1983). The differences which should be indicative of the activity in the exchangeable pool were for the most sensitive experiments about 10% of the fixed root pool activity. In the discussions which follow only the activity fraction after 25 min ($_{25}f_R$) will be used and these with the leaf activity fraction (f_L) are plotted in Fig. 5 a-c.

(ii) The fractional uptakes by the root for three plants in series 1 and 2 were 10-30 x 10^{-3} for 15 min load times and the stem uptakes were 4-14 x 10^{-3}. The N-starved plants in series 3 however had higher root uptakes of up to 80 x 10^{-3} and very low leaf activities of no more than about 0.4 x 10^{-3}. It is clear that in the time scale of our experiments all the absorbed nitrate was used to fill depleted root pools with very little going to the leaves.

(iii) The occurrence of occasional anomolously higher or low values makes firm statement concerning NaCl effects difficult. However, there seems to be no evidence in Fig. 5 of any consistent effect of up to 70 mM NaCl on nitrate uptake for NaCl added from 0 to 160 min before the start of an experiment. This seems true for both root uptakes and leaf accumulation for plants conditioned on nutrients containing nitrate and ammonium ions.

(iv) The situation is less clear for N-free nutrient conditioned plants. Here only the root uptake is relevant as little N moves to leaves. If it were not for the first uptake point a pattern of uptake increasing during the day could be associated with a history of increasing contact with nitrate. The first point seems anomolously high. Whatever the true pattern there still is no reliable evidence of any NaCl effect even with N-free nutrient.

Fewer experiments were carried out with labelled ammonium.

From Table 3B:

(i) Although no 1 min uptake control was carried out there is no evidence from series 2 that there was any root uptake change due to an increase in [NaCl] from 14 to 56 mM. The increase in leaf uptake is no greater than the scatter shown in other series.

(ii) For N-free conditioning no significant activity was carried to the leaves and there is no evidence of any effect of 5.6 mM NaCl on the uptake from added 1.5 mM NH_4^+.

EXPERIMENTS WITH ^{11}C-LABELLED CARBON DIOXIDE

Experiments to investigate the movement of photosynthate from a load leaf to root and to other leaves were carried out as shown in Fig. 6. Air was flushed through the leaf chamber surrounding part of one leaf (usually the largest). Gamma-ray scintillation detectors were mounted to measure radioactivity in the load leaf, the root and probably most of the hypocotyl, and finally the rest of the leaves.

The plant was mounted with the roots coiled into a 50 ml glass jar with a cover which was not sealed from the atmosphere. During the experiment nutrient was pumped into the jar at about 40 ml min^{-1} and nutrient and air pumped out at about 50 ml min^{-1} using a peristaltic pump with two tubes of different diameters. The nutrient was recycled. At times other than during experiments in and out flow rates of about 3.0 and 3.6 ml min^{-1} were used.

The experiment was started by shutting of the load leaf chamber air circulation, injecting $^{11}CO_2$ in a small volume of gas, then flushing out after about 5 min. Counting of radioactivity was begun as the residual labelled CO_2 was removed when flushing the load leaf chamber with air was resumed.

It is possible to carry out three experiments in one day and the topics investigated were:

- reproducibility
- the effect of changing from 1 to 30 mM NaCl
  (i) at different pHs (4.3 and 5.5)
  (ii) with different nitrate/ammonium ion ratios (3:1 and 1:3).

The usual daily experimental pattern was

1st Expt - NaCl 1 mM

2nd Expt - change to 30 mM when the uptake rate seemed constant, i.e. after about 40 min.

3rd Expt - NaCl left at 30 mM after 2nd expt. When experiment completed return to 1mM NaCl to condition for the next day's experiments.

Fig. 7 shows activity-time profiles from a typical experiment. Some features are:

- the loss of about 60% of the initial load leaf activity from the load leaf after 150 min;
- an increasing rate of arrival of activity in the other leaves attaining a constant rate after about 30 min. The arrival rate soon begins to fall off but activity is still arriving after 150 min;
- a similar arrival pattern in the root but the root activity reaches a maximum after about 100 min after which it decreases slowly.

The problem is to decide how best to compare the results of different treatments. This was done in 4 ways by measuring

(i) the times to reach the maximum root activity and

(ii) the ratio (R) of the root activity to the root plus other leaf activities measured at a fixed time (140 min); at the time of maximum root activity; and at the time of maximum uptake rates (about 40 min).

The results have been summarised in Table 4, the values having been obtained by visual inspection. These data and the individual activity plots indicate:

(a) the time to reach the root activity peak increases during the day but returns to its original value the next day. Inspection of the data indicates that is probably a diurnal effect unrelated to the NaCl concentration changes;

(b) there is no clear cut evidence for any significant effect due to Cl^- in the experiments described;

Other experiments carried out in this laboratory with wheat indicate that the final decrease in root activity may be due to a remobilisation of activity from root to shoot. Alternatively there may be loss of activity into the root bathing solution. The processes by which this may occur include respiration in the root to yield $^{11}CO_2$ which is easily lost to solution, and also efflux of labelled photosynthate.

CONCLUSIONS

It was concluded at this stage that the lack of any firm evidence for and NaCl effect over a wide range of [NaCl] plus the uncertainties shown by the scatter of the data points makes further experimentation seem unprofitable. However, if some hypotheses concerning possible nitrogen/chloride interaction can be proposed which suggest more specific experiments which could show some response with the time scale of ^{13}N and/or ^{11}C usefulness then the question could be reopened. It is recommended that the job be now closed, but reopened if any hypotheses can be proposed which are testable using the 13_N or "C techniques.

TABLE 1 - Nutrient formulations showing elemental concentrations (M)

	NCSU	PEL - N free	PEL - 1:3	PEL - 3:1
Total N	7960	-	15000	15000
$N(NO_3^-)$	5960	-	3750	11250
$N(NH_4^+)$	2000	-	11250	3750
K	1560	1000	6000	6000
Na	1000	1000	-	-
Ca	1350	2000	4000	4000
Mg	255	2000	2000	2000
Fe	107	66	66	66
S	750	4500	12189	4800
P	245	1000	1000	1000
Cl	5.4	18	18	18
B	12	46	46	46
Cu	0.08	0.30	0.30	0.30
Mn	2.64	9.2	9.2	9.2
Zn	0.18	0.76	0.76	0.76
Mo	0.02	0.50	0.50	0.50

Experiments were carried out at the following concentrations:

NCSU	1x	and	1/5x
PEL N-free	1x		
PEL 1:3	1/3x		
PEL 3:1	1/3x		

TABLE 2 - Plant sizes after the last experiment with each series

Plant	A	B	C	D	E	F
No. of Leaves	6	6-7	6-7	7	4-5	8
Weight-root/mg	804	220	360	-	600	-
-hypocotyl/mg		520	680	-	400	-
-leaves/mg		4760	4600	-	3700	-
-total/mg	1876	5550	5640	-	4700	-

TABLE 3A Fodder Beet - Root and leaf activities from $^{13}NO_3^-$ and $^{13}NH_4^+$ uptake experiments

LABELLED ION : nitrate

EXPERIMENT			PLANT CONDITIONING					EXPT NUTRIENT				UPTAKE FRACTION /10^{-3}		
				Nutrient				Increase					Roots	Leaves
Series	Date	No	Plant	Type Diln X	Concentration NO_3^- mM	NH_4^+ mM	NaCl mM	in NaCl mM	NO_3^- mM	NH_4^+ mM	at time min	at t=40 min control	expt less control	
1	30.10.81	1	A	NCSU 1	6.0	2.0	1.0	-	-	-	-	13	-	-
		2						-	-	-	-		22	5.0
		4						5.6	-	-	0		11	5.0
		5						-	-	-	-		10	5.7
		6						5.6	-	-	0		8	7.0
		7						-	-	-	-		8	5.3
		8						-	-	-	-		29	6.0
1	30.10.81	1	A	NCSU 1	6.0	2.0	1.0	-	-	-	-	12	-	-
		2						-	-	-	-		13	7.9
		3						5.6	-	-	-15		14	5.6
		4						-	-	-	-		16	5.3
		5						5.6	-	-	-15		13	3.9
		6						-	-	-	-		12	4.2
2	09.11.81	1	B	NCSU 1/5	1.2	0.4	0.2	-	-	-	-	5	-	-
		2						-	-	-	-		8	2.3
		3						-	-	-	-		7	4.4
		4						-	-	-	-		12	7.2
		5						-	-	-	-		13	7.4
		6						-	-	-	-		14	8.6

TABLE 3A (ctd)

2	10.11.81	1	B	NCSU 1/5	1.2	0.4	0.2	-	-	-	-	8	-	-
		2						-	-	-	-		15	9.6
		3						5.6	-	-	0		19	9.0
		4						-	-	-	-		15	9.4
		5						5.6	-	-	0		17	11
		6						-	-	-	-		17	12
2	11.11.81	1	B	NCSU 1/5	1.2	0.4	0.2	-	-	-	-	7	-	-
		2						-	-	-	-		22	13
		3						-	-	-	-		23	11
		4						14	-	-	0		20	13
		5						14	-	-	-80		20	12
		6						14	-	-	-160		22	13
2	12.11.81	1	B	NCSU 1/5	1.2	0.4	14	-	-	-	-	10	-	-
		3						-	-	-	-		26	12.8
		4						56	-	-	0		24	13.8
		5						56	-	-	-72		23	11.7
2	13.11.81	2	C	NCSU 1/5	1.2	0.4	0	-	-	-	-	11	-	-
		1						-	-	-	-		31	7.9
		3						-	-	-	-		25	9.8
		4						-	-	-	-		31	6.8
		6						70	-	-	-70		24	9.7
3	19.01.82	1	D	PEL 1	0	0	0	-	4	-	0	25	-	-
		2		N-				-	4	-	0	29	-	-
		3		free				-	4	-	0		85	0.0
		4						56	4	-	0		33	0.6
		5						-	4	-	0		67	0.6
		6						56	4	-	0		80	0.0

TABLE 3A (ctd)

3	20.01.82	1	D	PEL	1	0	0	0	-	4	-	0	48	-	-
		2		N-					-	4	-	0		34	0.4
		3		free					2.8	4	-	0		48	0.4
		4							-	4	-	0		53	0.6
		5							2.8	4	-	0		70	0.4
		6							-	4	-	0		76	0.3

TABLE 3B Fodder Beet - Root and leaf activities from $^{13}NO_3^-$ and $^{13}NH_4^+$ uptake experiments

LABELLED ION : ammonium * control not measured

EXPERIMENT			PLANT CONDITIONING						EXPT NUTRIENT				UPTAKE FRACTION /10^{-3}		
				Nutrient					Increase in				Roots		Leaves
Series	Date	No	Plant	Type	Diln	Concentration NO_3^-	NH_4^+	NaCl	NaCl	NO_3^-	NH_4^+	at time	at t=40 min control	at t=40 min expt less control	
					X	mM	mM	mM	mM	mM	mM	min			
2	12.11.81	2	B	NCSU	1/5	1.2	0.4	14	-	-	-	-		170*	6.9
		6							56	-	-	-146		170*	9.7
3	21.01.82	1	D	PEL	1	0	0	0	-	-	1.5	0	14	-	-
		2		N-					-	-	1.5	0		29	0.0
		3		free					5.6	-	1.5	0		28	0.3
		4							-	-	1.5	0		31	0.2
		5							5.6	-	1.5	0		26	0.3
		6								-	1.5	0		38	0.0

TABLE 4 - Fodder Beet - Root/Leaf Partitioning with ^{11}C

Nutrient: PEL type, 1/3x plus 1 mM NaCl

Plants: about 4 weeks with 7-8 leaves

R is the ratio of the root activity to the sum of the root and leaf activities (excluding the load leaf)

Plant	Date 1982	Expt.	$\frac{NO_3^-}{NH_4^+}$	pH	[NaCl] mM		Time to root act. peak min	R at peak root act.	R at t = 140 min	activity from max. uptake rates
D	27 09	1144 /1	3:1	4.3	1		107	0.53	0.57	0.62
		/2			1	30	121	0.43	0.44	0.48
		/3			1		140	0.43	0.43	0.48
	28 09	1145	3:1	4.3	1		105	0.33	0.35	0.40
		1146			1	30	133	0.37	0.37	0.42
		1147			30		156	0.38	0.38	0.42
E	29 09	1148	1:3	5.5	1		116	0.55	0.59	0.68
		1149			1	30	121	0.57	0.59	0.66
		1150			30		134	0.61	0.61	0.71
	30 09	1151	3:1	5.5	1		93	0.46	0.53	0.61
		1152			1	30	103	0.47	0.52	0.61
		1153			30		123	0.50	0.51	0.63
	01 10	1154	3:1	5.5	1		95	0.46	0.52	0.59
		1155			1		101	0.46	0.55	0.57
		1156			1		-	-	-	0.53

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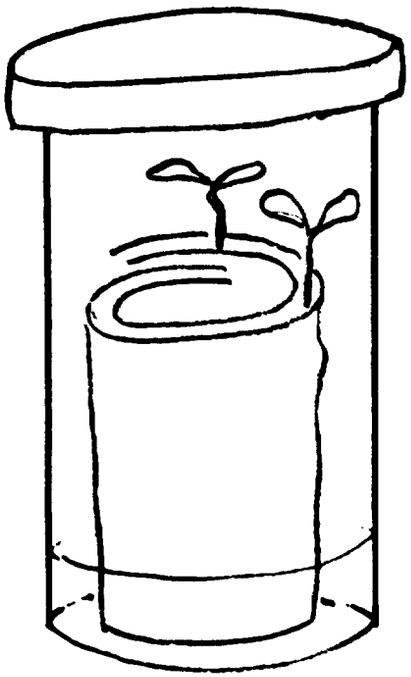
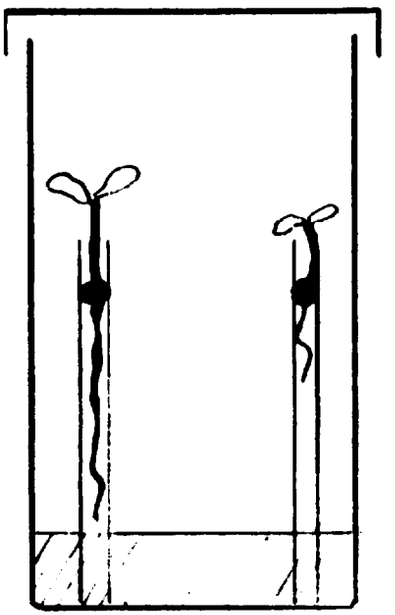
FIG 1. GERMINATION OF BEET SEEDS AND HYDROPONIC GROWTH.



Doubled paper in distilled water in 800 ml beaker



Cross-Section

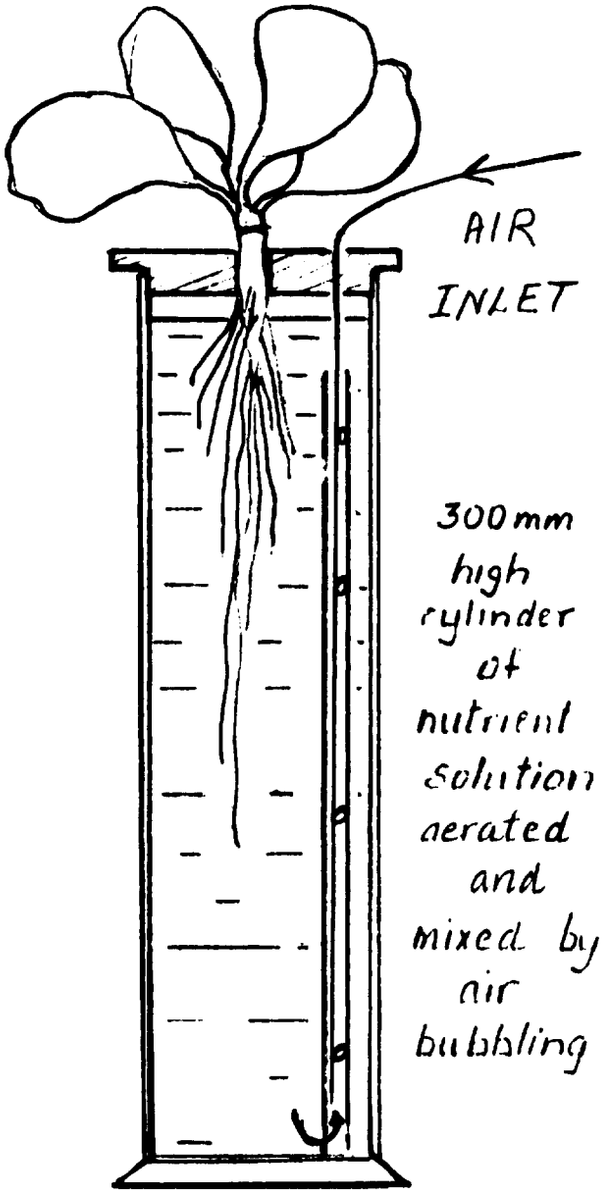


FIG. 2 GROWTH RATE OF FODDER BEET

SEEDLINGS IN HYDROPONIC SOLUTION

Day / Night Temperature 25°/18° C

Different symbols are used for different plants.

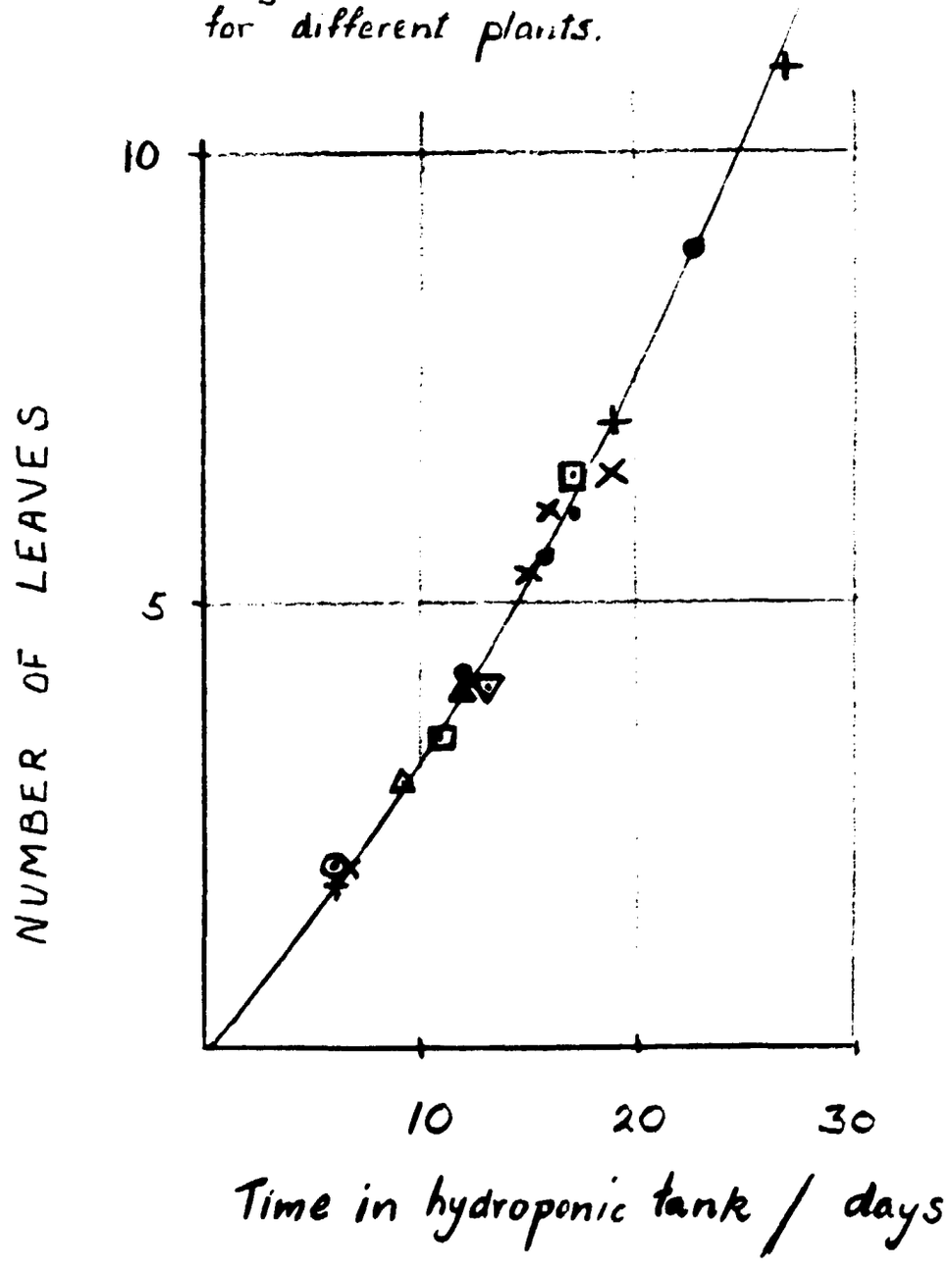


FIG 3. UPTAKE OF ^{13}N-LABELLED NITRATE OR AMMONIUM IONS BY BEET ROOTS

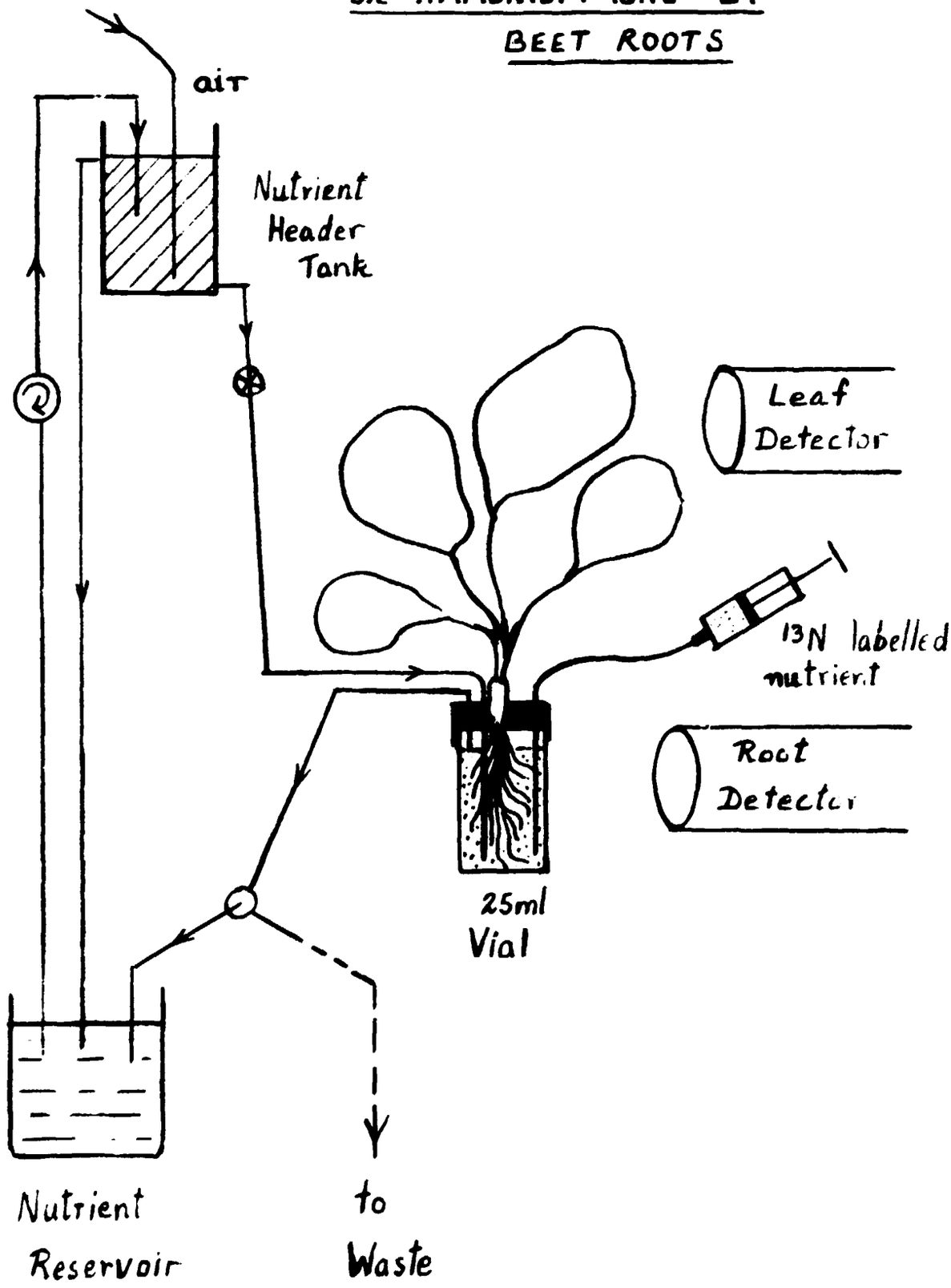


FIG 4. ACTIVITY - TIME PROFILE - ^{13}N-nitrate Uptake

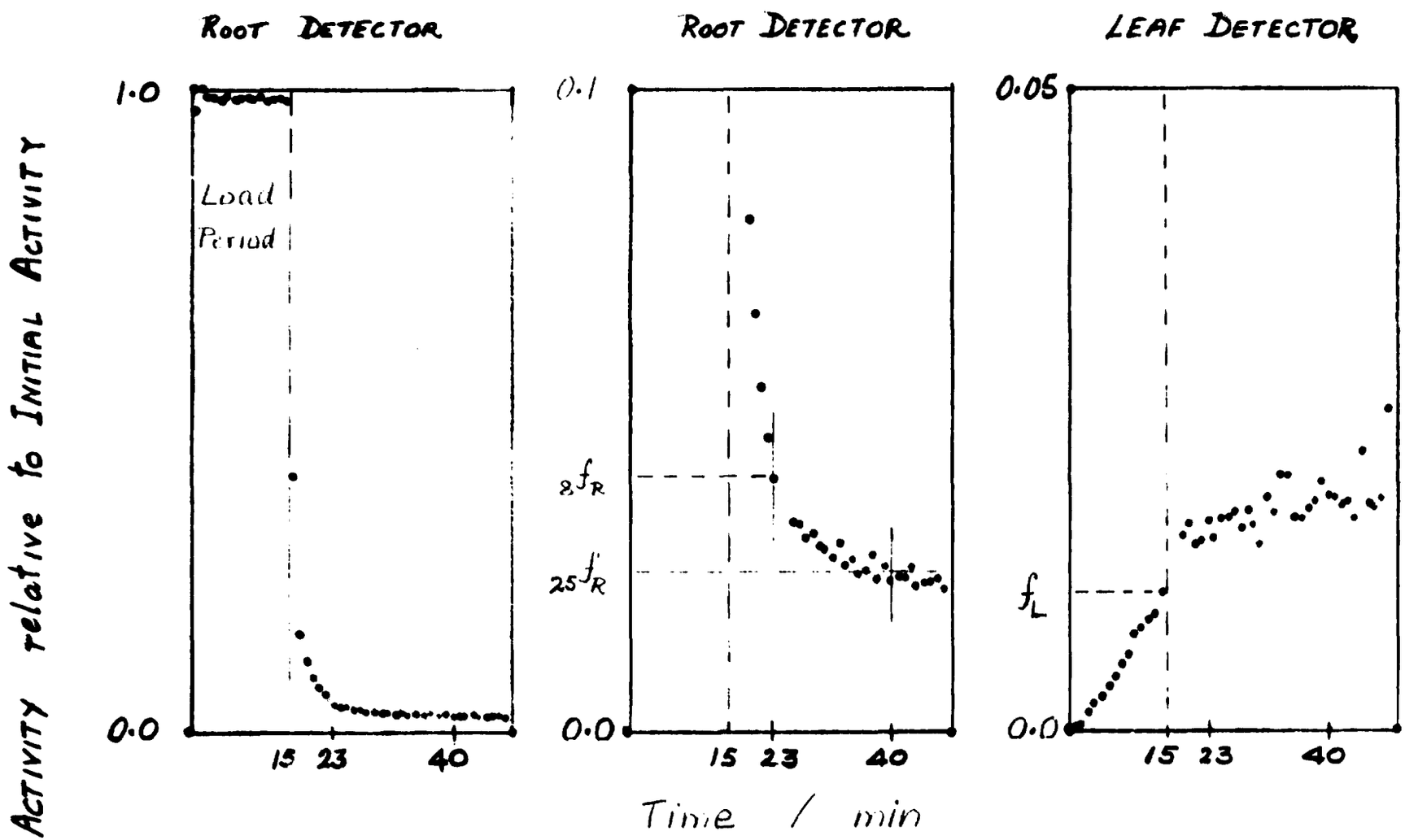


FIG 5(a) UPTAKE OF $^{13}NO_3^-$ TO ROOT AND LEAVES

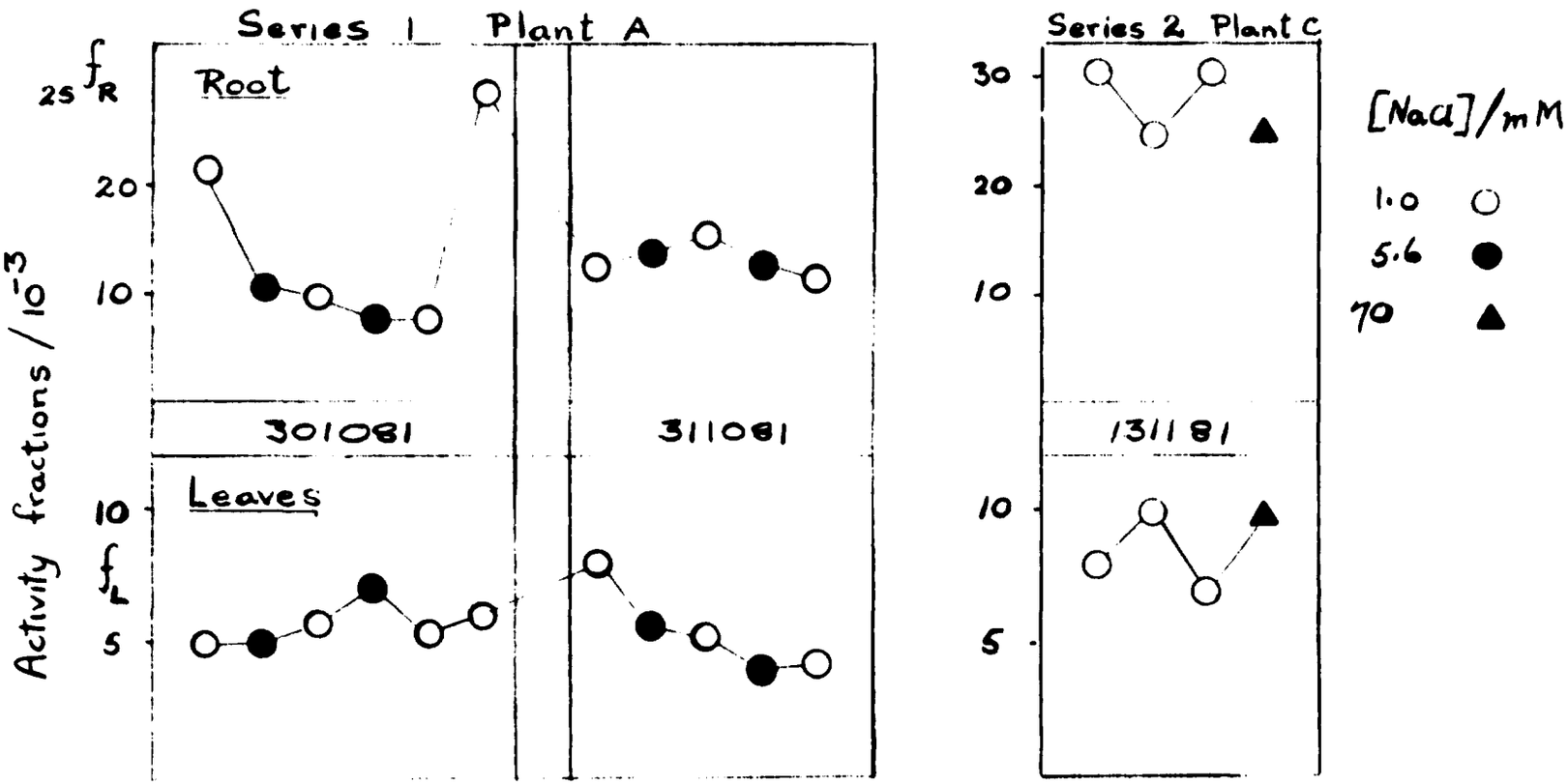


FIG 5(6) UPTAKE OF $^{13}NO_3^-$ TO ROOT AND LEAVES

Series 2 Plant B

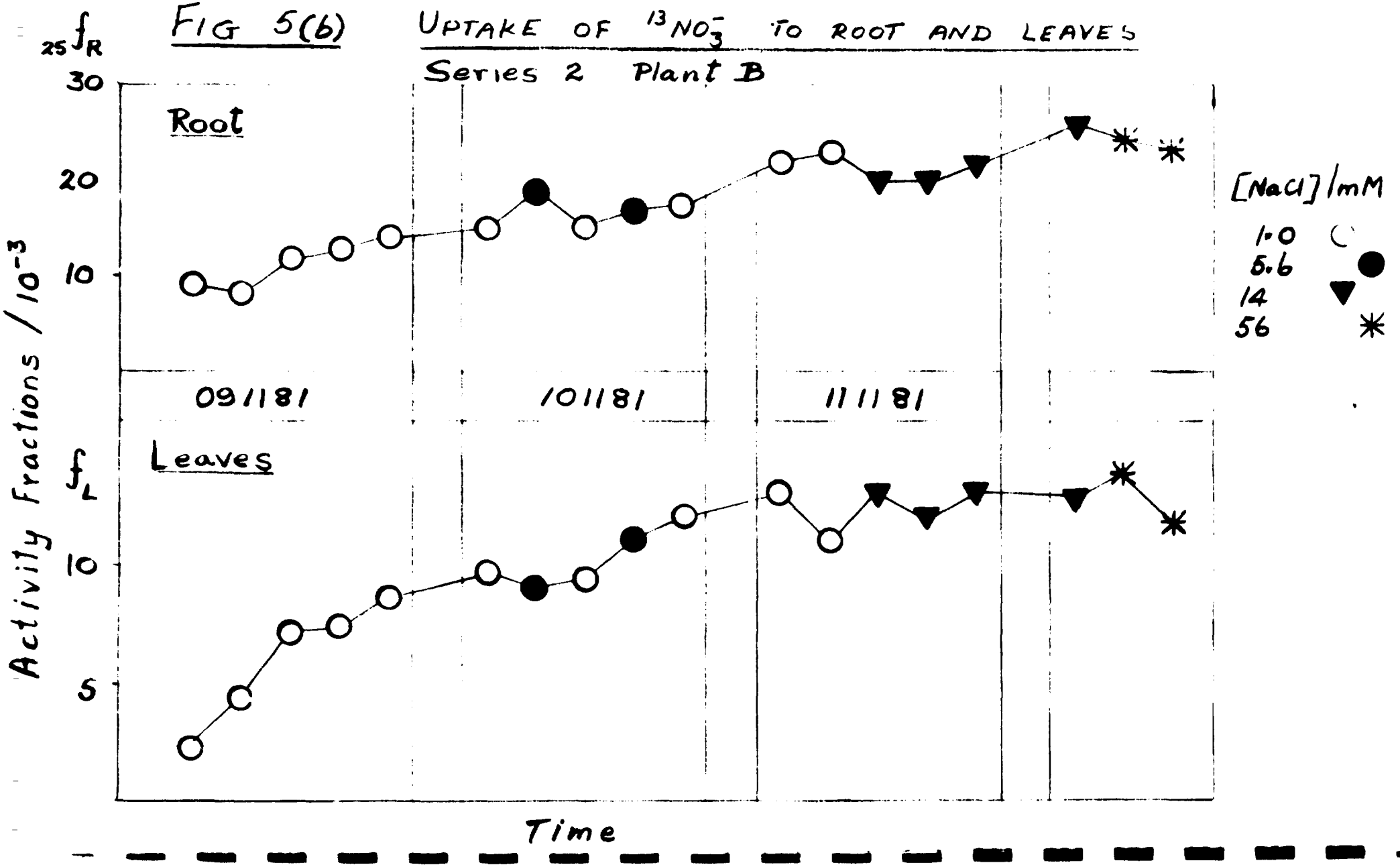


FIG 5(c) UPTAKE OF $^{13}NO_3^-$ TO ROOT AND LEAVES

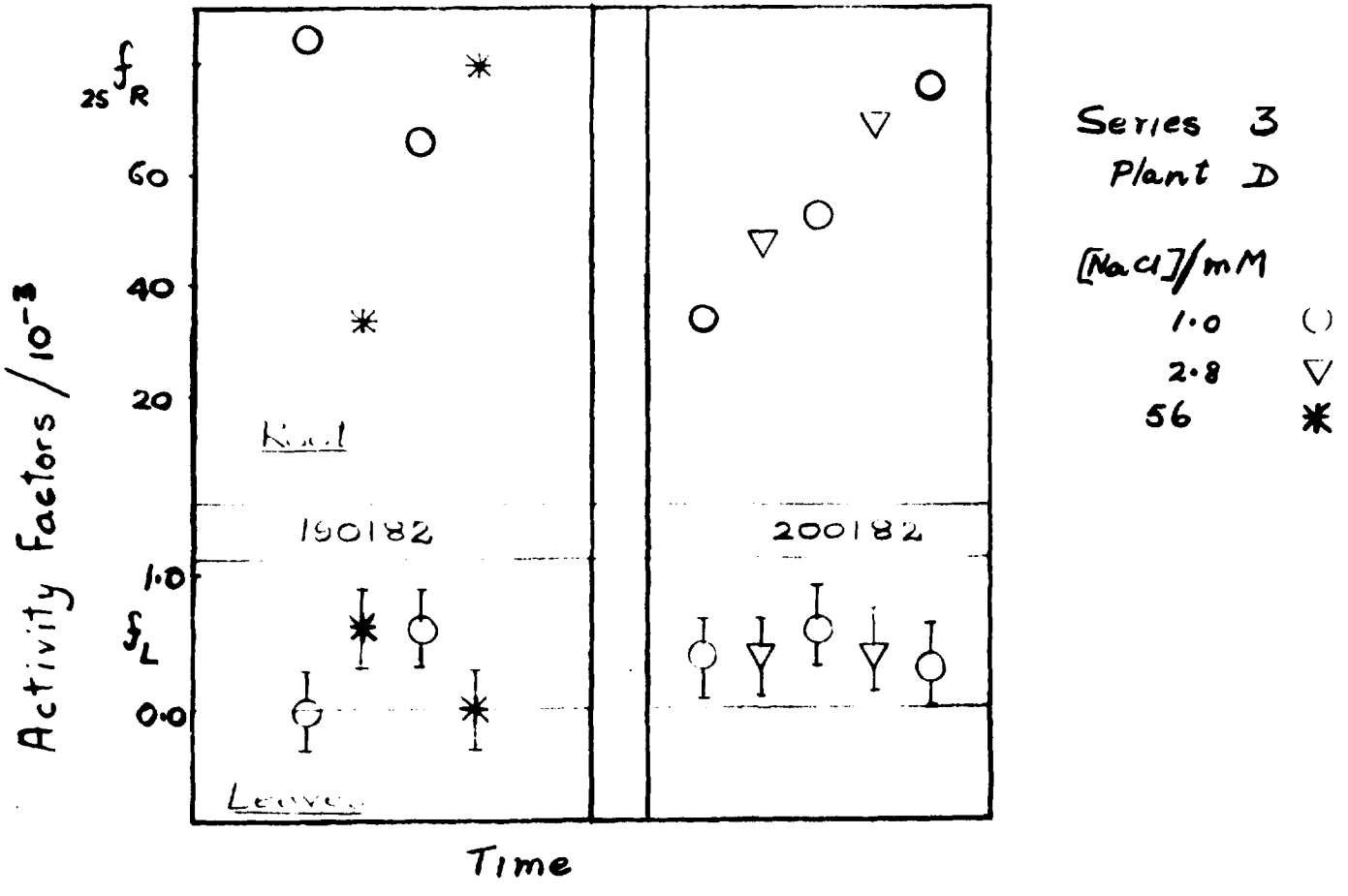


FIG 6 PARTITIONING OF ^{11}C-LABELLED PHOTOSYNTHATE

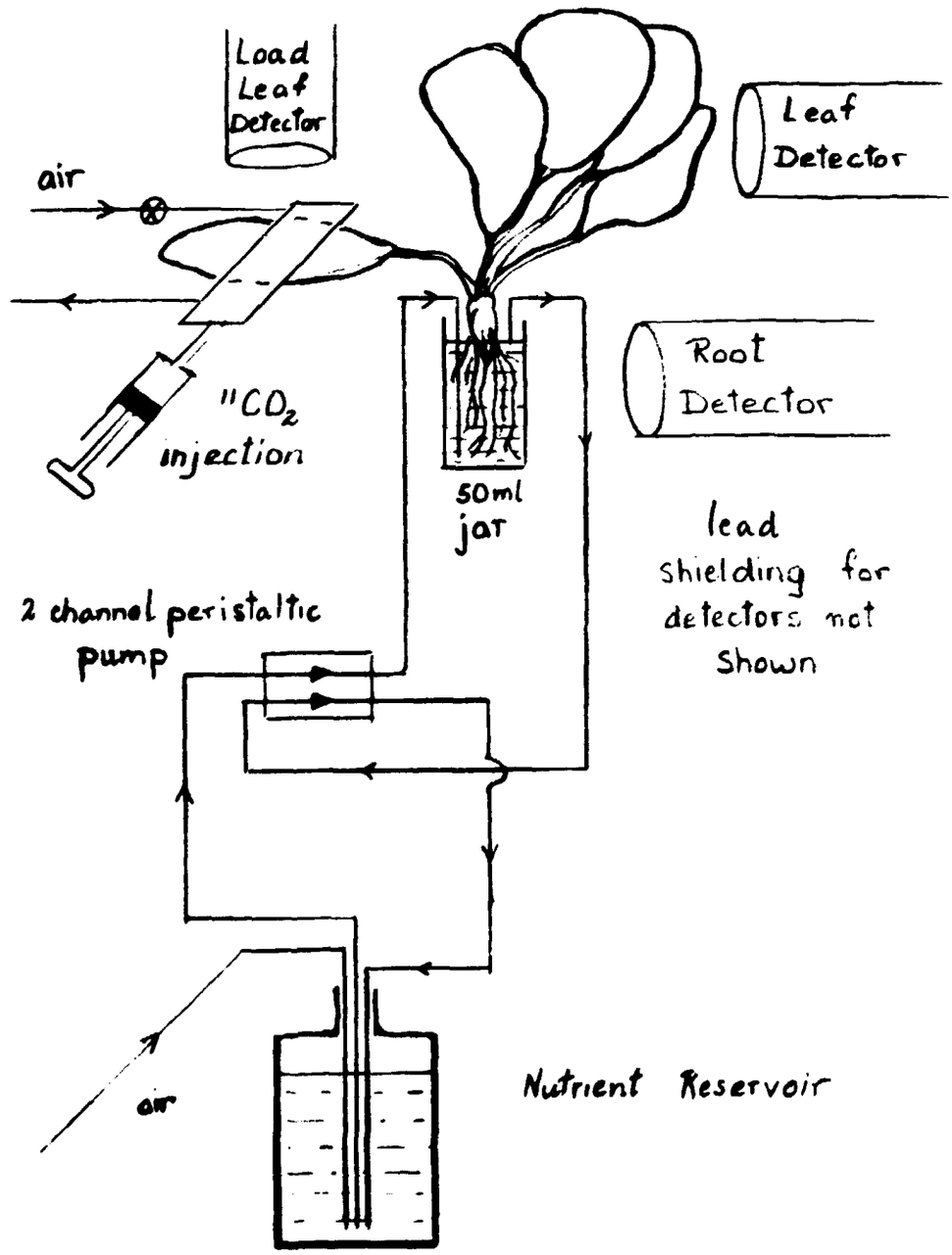


FIG 1 Activity - time profile for ^{11}C experiment # 1145

○ load leaf activity ● root activity

△ leaves other than load leaf