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GROWTH AND ACCUMULATION OF MINERAL ELEMENTS IN THE AXIS OF YOUNG PEA (PISUM SATIVUM L.) SEEDLINGS

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SUMMARY

Changes in fresh and dry weight, total nitrogen, protein nitrogen, phosphorus, potassium, and sulphur, have been followed in the shoot and in the root of young pea seedlings grown under a variety of growth conditions. It is shown that light inhibited shoot elongation, transport of reserve materials from the cotyledons, and acropetal transport, but enhanced net protein synthesis both in the shoot and in the root, and accumulation of mineral elements in the root. Treatment of the seedlings with gibberellic acid (GA) partly lifted the growth inhibition caused by light and shifted the nitrogen metabolism close to that of dark-grown seedlings, but did not affect transport from the cotyledons and only slightly the internal distribution of minerals.

Competition between the shoot and the root from light-grown seedlings for the reserve minerals studied is not established until the end of the second week. The extent of secondary transport depends on the element considered. Potassium appears to be highly immobile once deposited, under the conditions of these experiments, while sulphur is the most mobile, nitrogen and phosphorus behaving in an intermediate way. Although the amount of acropetal transport depends on the growth conditions and age of the seedlings, the influence of these variables is non-specific, as indicated by the constant proportion in which the different elements are transported to the shoot.

1. INTRODUCTION

The transport of metabolites from the storage organs of the seed during germination, and their distribution in the different organs of the developing seedling, have been studied in a number of plants. This distribution depends on the age of the seedlings (RIGA & BUKOVAC 1961; AIBA 1968) and the growth conditions (HALEVY et al. 1964; RAI & LALORAYA 1965, 1967; MER 1969), but a definite pattern of distribution has not emerged from these works.

Gibberellins have been shown to affect both the pattern of growth and the export of reserves in a number of plants (HALEVY et al. 1964; RAI & LALORAYA 1965), although in some cases no effect on the transport of metabolites to the axis has been detected (RAI & LALORAYA 1967). In this paper, the effect of gibberellic acid (GA) on growth and distribution of mineral elements between the shoot and the root of young 'Alaska' pea seedlings, as compared with plants grown in the light and in the dark, is described. This plant regulator has been shown to affect the pattern of growth of this plant (LOCKHART & GOTTSCHALL 1959; MOORE 1967), while having no effect on the export of reserves from the cotyledons (GUARDIOLA & SUTCLIFFE 1972). In addition, the influence of the

different growth conditions on nitrogen metabolism in the shoot and in the root was investigated.

2. MATERIALS AND METHODS

Pea seeds, *Pisum sativum* L. 'Alaska' (Messrs. Suttons Seeds Ltd., Reading, Berks.), were surface-sterilized and soaked for 24 hours at room temperature in aerated distilled water or in a 10^{-3} M solution of gibberellic acid (B.D.H.). They were then germinated on 'Netlon' 0.25 in. (6.4 mm) grids suspended over a water bath maintained at 20 °C. Air was pumped through diffusers in the bath so that a current of water-saturated air passed the peas. Two or three days later, uniform seedlings were selected and placed in culture tanks filled with aerated solutions of 0.1 mM calcium chloride, the seedlings being kept for the rest of the experiment in a growth cabinet with either a light cycle of 16 hours illumination (17.2 Kluxes provided by a mixture of incandescent and fluorescent lights at 22 $\pm$ 0.5 °C and 75 per cent relative humidity) and 8 hours darkness (18 $\pm$ 0.5 °C and 90 per cent relative humidity), or in the dark with the same temperature and relative humidity regime.

At desired intervals a sufficient number of seedlings was sampled and the fresh and the dry weight of the shoot and the root measured. Analytical determinations on the dry, powdered material were carried out as described previously (GUARDIOLA & SUTCLIFFE 1972). Total nitrogen was determined by means of the microkjeldahl method as described by HUMPHRIES (1956), slightly modified. Protein nitrogen was determined after extracting the tissues exhaustively with cold 5 per cent trichloroacetic acid.

For the determination of the other elements the samples were digested in succession with nitric, perchloric and hydrochloric acids following the micromethod described by CHAPMAN & PRATT (1961). In the clear solution thus obtained, potassium was determined with an Eppendorf flame photometer; sulphur by the method of JOHNSON & NISHITA (1952), and phosphorus by the method of FISKE & SUBBAROW (1925).

The influence of exogenous phosphorus on the distribution of the endogenous fraction of this element was determined by growing one week-old seedlings in a solution 0.1 mM of calcium chloride supplemented with an equimolar mixture of monosodium and disodium orthophosphates, ^{32}P labelled (final activity in the culture medium 32,000 c.p.m. $\mu mole^{-1}$) at a final concentration 0.1 mM. Periodically samples of these seedlings were analyzed for their total phosphorus and exogenously applied absorbed phosphorus, the endogenous fraction being calculated as a difference. The amount of phosphorus absorbed from the medium was determined by measuring the radioactivity of the different organs and comparing it with that of the original culture medium corrected for decay as necessary. To do this, the samples were digested with a mixture of nitric, perchloric and hydrochloric acids, and an aliquot of the final solution, with an activity less than 7,500 c.p.m., was dried evenly onto a planchette and counted to a minimum of 5,000 counts or for 5 minutes in a proportional counter

(Panax Instruments Co.). The results were corrected for decay and background counts as necessary; corrections for self-absorption, geometry and coincidence proved to be negligible.

All experiments were repeated at least twice, and the results given are the mean values found together with the range of variation.

3. RESULTS

3.1. Growth and nitrogen changes in the axis of light-grown and dark-grown pea seedlings

Changes in fresh weight, dry weight, total nitrogen, and protein nitrogen in the root and in the shoot from seedlings grown in a 0.1 mM calcium chloride solution in the light and in the dark are presented in *figs. 1* to *4*.

In light-grown seedlings there was a preferential accumulation of metabolites in the root during the first week. Transport of nitrogen to this organ took place until the end of the second week, with no change afterwards, whilst accumulation in the shoot was maximal during the second and the third weeks (*fig. 3*). Dry matter accumulated in the root during the four weeks, although at a decreasing rate, whilst in the shoot it was maximal during the third week, mainly because of photosynthesis (*fig. 2*).

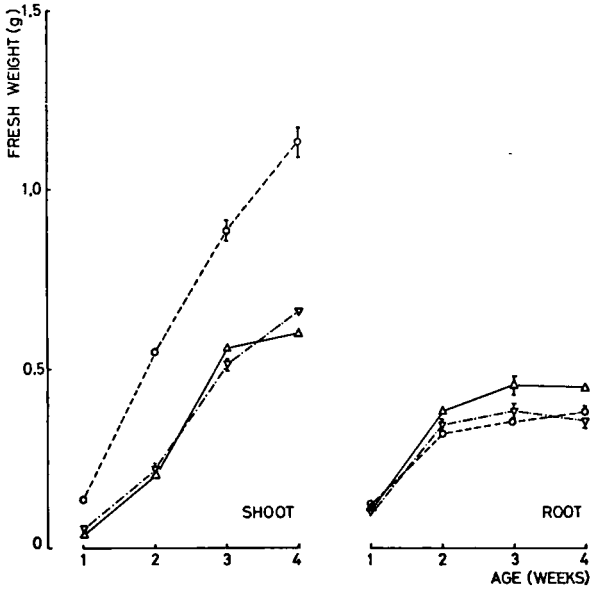

Fig. 1. Changes in fresh weight in the shoot and in the root of pea seedlings grown in a 0.1 mM calcium chloride solution in the light (△), in the dark (○) and GA-treated grown in the light (▽).

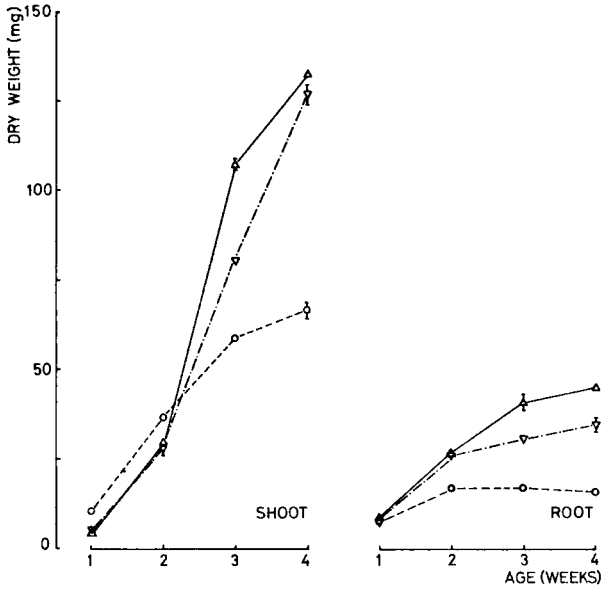

Fig. 2. Changes in dry weight in the shoot and in the root of pea seedlings grown in a 0.1 mM calcium chloride solution in the light (△), in the dark (○) and GA-treated grown in the light (▽).

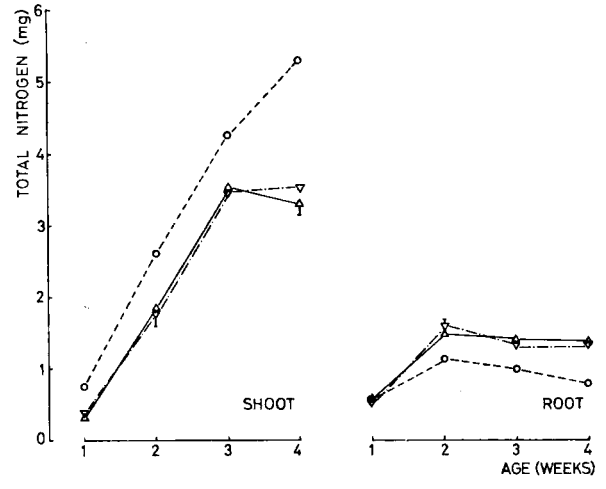

Fig. 3. Changes in total nitrogen in the shoot and in the root of pea seedlings grown in a 0.1 mM calcium chloride solution in the light (△), in the dark (○) and GA-treated grown in the light (▽).

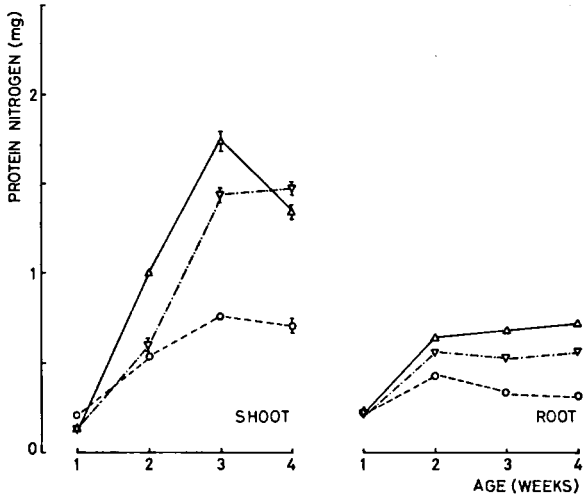

Fig. 4. Changes in protein nitrogen in the shoot and in the root of pea seedlings grown in a 0.1 mM calcium chloride solution in the light (△), in the dark (○) and GA-treated grown in the light (▽).

Changes in protein nitrogen (*fig. 4*) closely followed those for total nitrogen, but for a small but significant net synthesis of protein in the root during the last two weeks and a decrease in the shoot during the fourth week. This decrease was not present in all experiments and appears to be related to the senescence of the older leaves.

Changes in fresh weight closely followed those presented for dry weight (*fig. 1*). However, it is noteworthy that the root had always a higher water content per unit of dry weight than the shoot. Thus, whereas dry weight, total nitrogen, and protein nitrogen were higher in the shoot than in the root from the middle of the second week onwards, the fresh weight was lower until the end of the third week.

The pattern of growth was somewhat different for seedlings grown in the dark. There was a faster depletion of materials from the cotyledons than in the seedlings grown in the light, and it lasted for a longer period of time (GUARDIOLA & SUTCLIFFE 1972). It was accompanied by an increase in the accumulation of metabolites in the shoot, which at the end of the first week showed a higher fresh weight, dry weight, and total nitrogen than the root (*table 1*), this preferential accumulation of metabolites in the shoot being accentuated as the seedlings grew. The shoot in dark-grown seedlings had a higher nitrogen content, and the root a lower one, than in light-grown seedlings. After the second week there was a net loss of nitrogen from the roots, which during the last two weeks of the experiment lost some 30% of their nitrogen content by the end of the second week (*fig. 3*).

Table 1. Growth parameters of one week-old seedlings grown in a 0.1 mM calcium chloride solution in the dark, in the light and GA-treated

Treatment	Organ	Length (mm)	Fresh weight (mg)	Dry weight (mg)	Total nitrogen (mg)	Protein nitrogen (mg)
Dark	Shoot	45.8 ± 1.6	135.3 ± 3.3	10.6 ± 0.2	0.76 ± 0.02	0.21 ± 0.01
	Root	102.1 ± 1.5	117.8 ± 2.7	8.3 ± 0.2	0.58 ± 0.01	0.21 ± 0.00$_5$
	Axis		253.1 ± 4.2	18.9 ± 0.3	1.34 ± 0.02	0.42 ± 0.01
GA-treated	Shoot	35.5 ± 2.0	59.8 ± 3.4	6.0 ± 0.3	0.40 ± 0.02	0.13 ± 0.01
	Root	83.4 ± 1.8	97.5 ± 2.2	8.6 ± 0.1	0.52 ± 0.01	0.20 ± 0.00
	Axis		156.5 ± 3.9	14.6 ± 0.3	0.92 ± 0.02	0.33 ± 0.01
Light	Shoot	11.5 ± 0.5	38.9 ± 2.0	4.6 ± 0.3	0.33 ± 0.03	0.13 ± 0.01
	Root	72.8 ± 1.1	105.0 ± 2.5	9.0 ± 0.1	0.57 ± 0.01	0.22 ± 0.00$_5$
	Axis		143.9 ± 2.9	13.6 ± 0.3	0.90 ± 0.03	0.35 ± 0.01

The same was true for dry weight (*fig. 2*). For two weeks, dry weight of shoots from dark-grown seedlings was higher than for light-grown ones. After that moment the reverse was true due to photosynthesis. Dry weight of the root was always lower in dark-grown seedlings, and no increase was noticed after the end of the second week, which contrasts with the pattern found for light-grown seedlings.

Light had a strong influence on the synthesis of proteins both in the shoot and in the root. In both organs the ratio of protein nitrogen to total nitrogen was lower in dark-grown than in light-grown seedlings, the total amount being lower as well after the end of the first week (*fig. 4*). In the root of dark-grown seedlings there was a net decrease in protein nitrogen after the end of the second week.

3.2. The influence of gibberellic acid on growth and nitrogen changes in the axis of light-grown seedlings

Despite its influence on the elongation of the shoot (LOCKHART & GOTTSCHALL 1959; MOORE 1967) that I have been able to reproduce at least partly, gibberellic acid failed to affect the export of metabolites from the cotyledons (GUARDIOLA & SUTCLIFFE 1972) and their distribution between the shoot and the root, but for a small preferential transport towards the shoot during the first week, which was not detectable afterwards (*table 1* and *fig. 3*). However, gibberellic acid-treated seedlings presented some features intermediate between light-grown and dark-grown seedlings. Their protein nitrogen content, both in the shoot and in the root, was intermediate to the values found for light-grown and dark-grown seedlings for most of the experiment. It follows then that the ratio of protein nitrogen to total nitrogen gives values intermediate to those for light-grown and dark-grown seedlings.

Differences in dry weight between GA-treated and untreated, light-grown seedlings appeared after the second week, due to a delayed photosynthesis in the treated ones. Despite this fact, fresh weight of the shoot was quite the same in both cases, whereas fresh weight of the root in treated seedlings was close to the values found for dark-grown seedlings.

Morphological changes in the root caused by GA were different from those caused by darkness. Thus, the roots from dark-grown seedlings were longer, thinner and showed a larger number of root laterals than roots from light-grown seedlings, whereas treatment with GA, although slightly increasing root length (*table 1*) reduced the number of laterals, which in many seedlings were nearly absent.

3.3. The distribution of mineral elements between the shoot and the root

The final distribution of cotyledonary reserves between the shoot and the root depended upon the age of the seedling and growth conditions. A higher percentage of the exported reserves accumulates in the shoot as the seedlings age, partly due to the cessation of accumulation in the root after the end of the

Table 2. Acropetal transport of mineral elements from the cotyledons after different periods of growth. Data expressed as percent of the total amount transported from the cotyledons recovered in the shoot.

	Element	Age of the seedlings (weeks)			
		1	2	3	4
Dark-grown seedlings	Nitrogen	63.3	72.6	83.3	88.8
	Phosphorus	62.2	71.9	84.1	88.6
	Potassium	56.1	69.5	77.7	81.4
	Sulphur	65.3	84.3	91.0	93.3
Light-grown seedlings	Nitrogen	43.4	57.8	73.9	73.1
	Phosphorus	44.2	54.6	73.6	78.4
	Potassium	31.3	45.8	62.3	62.6
	Sulphur	40.0	66.0	78.9	79.6

second week, partly to a net depletion of the root in some treatments (cf. *fig. 3*). On the other hand, some growth conditions stimulate this preferential accumulation in the shoot. Thus, dark-grown seedlings accumulated a higher proportion of the transported reserves in the shoot than did light-grown seedlings.

The effect of the age of the seedlings and the growth conditions on the distribution of materials between the shoot and root was non-specific. The relation between the content of the different mineral elements in the shoot and its nitrogen content is a straight line for different stages of the shoot development and with seedlings raised under a number of growth conditions, as shown in *fig. 5*. In this figure the points correspond to seedlings up to four weeks old grown in the conditions described above, plus seedlings grown in distilled water in the light. The position of the points corresponding to the mineral content of the roots, which have been plotted as a comparison, indicates that this organ is related to nitrogen richer in potassium and poorer in sulphur than the shoot, while the relative phosphorus content was about the same in both organs. Thus, the slope of the regression line for phosphorus over nitrogen was the same when the values for the shoot alone were considered than when both the shoot and the root values were taken into account, its value being 0.115, whereas the coefficient of correlation was not altered, 0.991 vs. 0.992, for the shoot values alone.

3.4. The influence of exogenously applied phosphorus on the distribution of endogenous phosphorus

The influence of exogenously applied phosphorus on the distribution of endogenous phosphorus was studied in one week old seedlings grown in the light in a 0.1 mM calcium chloride solution with and without the addition of sodium phosphate, ^{32}P labelled,at a final concentration 0.1 mM. The presence of this salt in the culture medium has been shown to increase slightly, in a non-specific way, the export of reserves from the cotyledons (GUARDIOLA & SUTCLIFFE 1972).

Table 3. The influence of exogenously applied phosphorus on the distribution of endogenous phosphorus. Seedlings grown in the light in a 0.1 mM calcium chloride solution. Sodium phosphate, ^{32}P labelled, at a final concentration 0.1 mM, was added to the phosphorus-grown seedlings (+ P) when one week old. Results expressed in milligrams of phosphorus per organ.

Treatment	Organ	Fraction	Age of the seedlings (weeks)		
			1	2	3
Control	Shoot	Total	0.036	0.212	0.386
Control	Root	Total	0.082	0.183	0.167
+ P	Shoot	Total	0.036	0.261 ±.007	0.585 ±.008
		Endogenous	0.036	0.242 ±.007	0.424 ±.009
		Exogenous	–	0.019 %.001	0.161 ±.005
+ P	Root	Total	0.082	0.311 ±.006	0.403 ±.018
		Endogenous	0.082	0.203 ±.007	0.203 ±.020
		Exogenous	–	0.108 ±.004	0.200 ±.009

The distribution of phosphorus between the shoot and the root in both control and phosphorus-grown seedlings is presented in *table 3*. During the first week most of the phosphorus absorbed was accumulated in the root, a very small proportion being transported to the shoot. Transport to this organ was significant only during the second week, when more than 60% of the phosphorus absorbed was transported to it.

The presence of exogenous phosphorus did not affect the distribution of endogenous phosphorus, as is shown in *fig. 6*, where the values for the content of endogenous phosphorus vs. content of nitrogen has been plotted for both, the shoot and the root, from control and phosphorus-grown seedlings, along with the regression line calculated from the values presented in *fig. 5*. Deviations from this line are well within the range of experimental error.

3.5. The competition between the shoot and the root

As has been shown above, no accumulation of mineral elements took place in the root after the end of the second week, whilst the shoot accumulated minerals until the end of the third week or longer, depending upon the growth conditions. The influence of the shoot on the pattern of growth of the root was investigated by comparing the growth of this organ in control, light-grown seedlings with

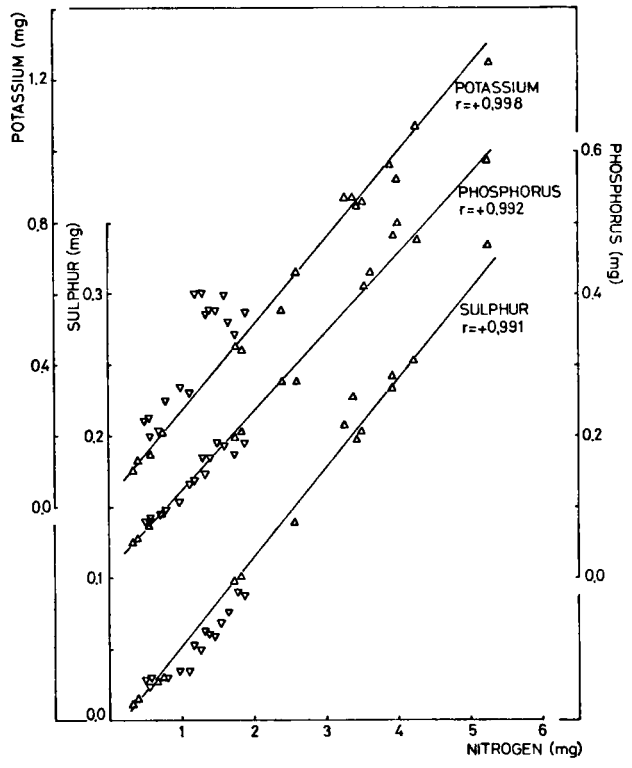

Fig. 5. Nitrogen vs. mineral elements content in the root (▽) and in the shoot (△) in pea seedlings grown under several conditions (see text). The drawn lines have been adjusted for the shoot results.

that of seedlings de-shooted when one week-old, just above the point of attachement of the cotyledons.

Results are presented in *table 4*. Roots from de-shooted seedlings had a lower fresh weight and dry weight throughout the experiment than roots from intact seedlings. No differences were present in the content of mineral elements for one week; after this period of time roots from de-shooted seedlings had a higher content of nitrogen, phosphorus and sulphur than roots from control seedlings. No differences were noticed for potassium nor for protein nitrogen content. Protein synthesis proceeded at the same rate in both control and de-shooted seedlings until the end of the experiment, despite the differences in total nitrogen content.

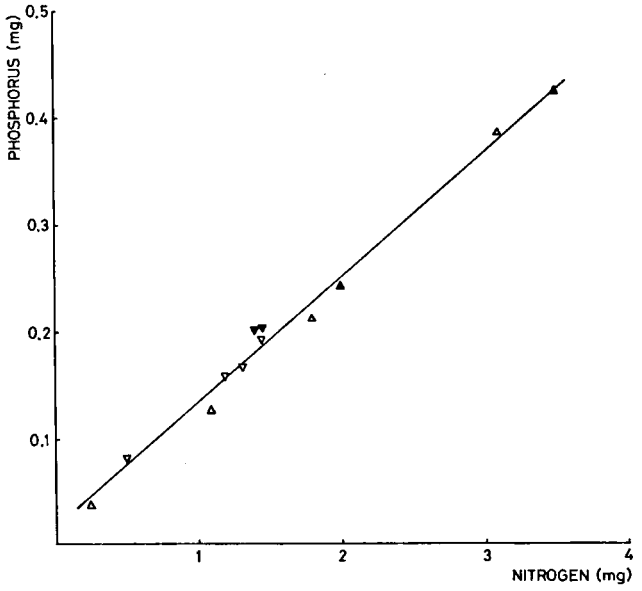

Fig. 6. Nitrogen content vs. endogenous phosphorus content in the shoot (△▲) and in the root (▽▼) of pea seedlings grown in the light in a 0.1 mM calcium chloride solution with (▲▼) and without (△▽) sodium phosphate (0.1 mM). The line drawn is the regression curve calculated from the values given in *fig. 5.*

Table 4. The influence of the shoot on growth and accumulation of mineral elements in the root. Plants de-shooted when one week old. Growth parameters of the root expressed as a percentage of those from intact plants. Values marked with an asterisk (*) differ significantly from the untreated control plants.

	Weeks after excision of the shoot		
	1	2	3
Fresh weight	77*	79*	77*
Dry weight	85*	76*	71*
Protein nitrogen	96	96	94
Total nitrogen	93	124*	126*
Phosphorus	97	133*	130*
Sulphur	101	112*	139*
Potassium	94	100	100

4. DISCUSSION AND CONCLUSIONS

Although gibberellic acid was capable to reverse, at least partly, the inhibition of shoot elongation caused by light and shifted nitrogen metabolism from both the shoot and the root close to that of dark-grown seedlings, giving protein nitrogen to total nitrogen ratios intermediate between dark-grown and light-grown seedlings, it failed to affect the export of metabolites from the cotyledons and their distribution between the shoot and the root, but for a small influence during the first week.

The lack of effect on the export of metabolites from the cotyledons is correlated with the inability of gibberellic acid to stimulate amylase activity in attached pea cotyledons (SPRENT 1968) and to affect protein hydrolysis both in detached (GUARDIOLA & SUTCLIFFE 1971) and in attached pea cotyledons. However, it does not mean that transport is controlled by mobilization of reserves, as has been discussed previously (GUARDIOLA & SUTCLIFFE 1971). Thus, RAI & LALORAYA (1965, 1967) have shown that gibberellic acid increased protein hydrolysis in the cotyledons of light-grown lettuce seedlings, with an increase in the level of soluble nitrogen compounds in these organs, but without an increased transport to the axis.

Enhanced distribution towards the shoot appears to be an almost general feature of response to gibberellic acid (BRIAN et al. 1954; HALEVY et al. 1964; RAI & LALORAYA 1965, 1967). The fact that such a preferential accumulation in the shoot did not take place in the experiments reported here after the first stages of germination, whereas internode length was increased until the late stages (LOCKHART & GOTTSCHALL 1959; MOORE 1967) indicates that increase in length is, at least partly, independent of the accumulation of metabolites. The lower dry weight of the root in GA-treated seedlings when compared with the root of untreated, light-grown seedlings (*fig. 2*) can not be attributed to a competition between the shoot and the root, since no difference was found in the content of any of the mineral elements studied (*fig. 3*). It is, no doubt, due to the delayed photosynthesis in GA-treated seedlings. Photosynthetically fixed CO_2 is readily translocated to the root from the first moment (*table 4*), and differences in root dry weight between GA-treated and untreated seedlings appear at the same time as do differences in the dry weight of the whole seedlings.

In light-grown seedlings, competition between the shoot and the root for the materials translocated from cotyledons does not appear to exist during the first two weeks, as indicated by the results presented in *table 4*. Competition for nutrients between the shoot and the root is apparent after the end of the second week. At this time roots from intact seedlings nearly ceased to grow and to accumulate nutrients (*fig. 3*; SUTCLIFFE 1962), whilst those from de-shooted seedlings continued to do so although at a decreasing rate, this accumulation being very small during the fourth week. However, the decreased nitrogen content in the roots of intact seedlings did not affect the rate of protein synthesis as compared with de-shooted seedlings, suggesting that either the pool of soluble

nitrogen is saturating from the point of view of protein synthesis or that the presence of the shoot is essential for maintained protein synthesis in the root.

Competition between the shoot and the root was apparent in dark-grown seedlings at the end of the second week, with a net loss of nitrogen from the root afterwards. There was a net hydrolysis of proteins in the roots of these seedlings as well, but there is no proof for it being directly caused by the shoot competition for nutrients. Differences in the distribution of the mineral elements between the shoot and the root may be due either to differences in the primary distribution or to a selective mobilization towards the shoot of nutrients previously transported to the root. Evidence for the second of these mechanisms comes from the fact that there is a net loss of nutrients from the root in some treatments, these amounts being recovered quantitatively in the shoot. However, there is some evidence that there is a preferential transport of some minerals towards the root. From the results presented in *table 4* it appears that potassium is not retranslocated from the root in the conditions of these experiments, with no cations other than calcium in the medium bathing the roots, and thus the amounts recovered both in the shoot and in the root are a measure of primary distribution of this mineral. In one experiment in which the seedlings were grown in distilled water, 56% of the potassium transported from the cotyledons was recovered in the shoot, against only 45% of the calcium, suggesting a preferential primary transport of calcium towards the root, since secondary transport of this element from the shoot is unlikely.

The inability of exogenous phosphorus to affect the distribution of the fraction exported from the cotyledons during the first week (*table 3*) is an indication that salt content does not control primary distribution. The accumulation of almost all the phosphorus absorbed in the root is a consequence of the low salt content of this organ (SUTCLIFFE 1962). The lack of influence on the final distribution of the endogenous phosphorus during the second week may be due to the cessation of transport to the root. The amount previously accumulated in this organ should be forming part of complex compounds with a low rate of turnover, and of a soluble pool behind a diffusion barrier which does not allow it to mix-up readily with the fraction absorbed and transported to the shoot.

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