Effect of limited supply of assimilates on the relationships between their sources and acceptors

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Abstract

Sink activity in young sunflower and bean plants was determined mainly by their growth rate. The organ with higher RGR (stem in sunflower and apical part with expanded trifoliolate leaf — in bean plant) was the dominant acceptor even in conditions of limited supply of assimilates.

Specific activity of root — donor of phosphorus, depends on the root's metabolic and physiological activity only in the case, when supply of P to the aerial parts is not a factor limiting photosynthesis. If the activity of the whole root system is relatively low (like in preshaded series of sunflower) the photosynthetic compensation observed in plants replaced into better conditions coincides with compensation of P-absorption (both calculated per g of dry matter). It may explain the existence of a functional balance between shoot and root activity in the case of a changed proportion between their sizes.

Following the period in which much of the research into yield physiology was focussed upon the productive capacity of the photosynthetic system, there has been a shift towards a greater awareness of the interrelations between:

photosynthesis $\rightleftharpoons$ translocation $\rightleftharpoons$ growth

(Bremner, 1972; Jenner, Rathjer, 1972 a, b; Khan, Sagar 1969 a, b).

In conditions optimal for growth, as well as in the case of limited supply of assimilates, distribution of dry matter is regulated by some unknown mechanism, controlling the priority of sinks receiving photosynthates. The problem of functional relationships between root and shoot, has been the subject of many recent papers (Brauer 1970; Hunt et. al. 1973; Throughton, 1974, Thornley 1972 and many others). The results of experiments reported indicate a functional balance existing between root and shoot activity.

The object of the present study is the continuation of research already published (Starck 1966, 1973) concerning further analysis of source-sink relationships in young,

sunflower and bean plants, with reference to Brauer's (1966), Davidson's (1969) and Hunt's (1973) hypothesis that more attention should be paid to the $\frac{\text{root}}{\text{shoot}}$ activity than to the mass ratio.

These relations between several processes in leaves and roots were examined in plants with a limited supply of assimilates owing to restriction of photosynthesis by shading (as in previous paper) (Starck 1969, 1973), and by partial defoliation or by both manipulations. Some parameters of growth analysis were calculated such as LAR, RGR and NAR on the blades dry matter basis, according to the following formula:

$$\begin{aligned} \text{RGR} &= \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}, \\ \text{NAR} &= \frac{W_2 - W_1}{t_2 - t_1} \cdot \frac{\log_e W_2 - \log_e W_1}{W_2 - W_1}, \\ \text{LAR} &= \frac{A}{W} \end{aligned}$$

where:

W — dry matter of total plant

A — surface area of leaves

Much attention was also devoted to the changes in the proportion of growth of the particular organs and their participation in current photosynthates exported from the blades and in ^{32}P absorbed by roots.

MATERIALS AND METHODS

The relationships between processes in particular organs were examined in plants grown in water culture, in nutrient solution as previously described, under natural light and air conditions. Seedlings with two (expt. IA, IIA) or three expanded pairs of leaves (expt. IIB) (sunflower) or only primary leaves (bean plant) were examined. Shading treatment (S) was done by the use of cheese-cloth, which transmitted about 50 percent of natural daylight (NL). In both series, NL and S plants, one primary leaf (bean) or one leaf of the first pair (sunflower) were cut off, a few days before exposure to $^{14}\text{CO}_2$, done in all experiments under natural light conditions, in a plexiglass chamber (Table 1).

In spite of the fact, that the plants used in experiment Ia and II a were of the same age, more comparable were plants from experiment Ia and IIB (Table 2). The dry matter of the apical part together with a very young leaf in control intact plants was on the average 190 mg (expt. Ia) and that of expt. IIB — about 315 mg, but in expt. IIA — only 40 mg (data not presented). This was the result of different weather conditions (smaller number of sunny and warm days — Table 1).

For each species two experiments were performed, both in spring (May and June). Experiment II included estimation of the dynamics of growth of particular

Table 1
Conditions during growth, ^{14}C - and ^{32}P -exposures

Species examined	No. of experiment	Age of plants (days)	Weather conditions ¹	Days of treatment	Conditions of ¹⁴ CO ₂ exposure				Conditions of ¹⁴ C-translocation		Conditions of ³² P-absorption	
					time and weather ¹	temp. C°	CO ₂ % v/v	spec. rad. ²	temp. °C	time	temp. °C	
Bean plant	Ia	20	11 s 5 d	4	7 ²⁵ —7 ⁵⁰ S	about 27	0.06	1.7	26—29	12 ²⁰ —17 ²⁰	28—40	
	II a	19	8 s 6 d 1 s-d	4	8 ¹⁰ —8 ³⁰ s—d	24—27	0.05	1.8	about 25	9 ¹⁵ —14 ¹⁵	22—25	
	II b	23	8 s 8 d 3 s-d	8	8 ³⁰ —8 ⁵⁰ d	22—24	0.05	1.8	about 19	9 ⁵⁰ —14 ⁵⁰	18—29	
Sunflower	I A	23	11 s 5 d 3 s-d	6	7 ¹⁰ —7 ³⁰ S	26—30	0.05	1.6	26—30	9 —14	32—36	
	II A	24	5 s 9 d 6 s-d	4	7 ³⁰ —7 ⁴⁵ S	26—32	0.05	4.3	28—30	9 —14	28—30	
	II B	27	6 s 10 d 7 s-d	7	10—10 ²⁰ d	22—26	0.07	2.0	20—22	8 ³⁰ —13 ³⁰	21—30	

¹) weather conditions in period from germination to exposure and during exposure: s — sunny days
d — dull

s-d — sunny and dull

²) spec rad = specific radioactivity $\mu\text{C}/\text{mg CO}_2$

plant organs, by collecting them and estimating their dry matter on the same day, when the plants were divided into experimental series (shading and defoliation), and two times more simultaneously with $^{14}\text{CO}_2$ -exposure, ^{23}P -absorption and dark respiration measurement. Parameters of growth were calculated. Translocation of ^{14}C -assimilates, after a 2-hr period (from the beginning of $^{14}\text{CO}_2$ -exposure) was estimated. The radioactivity of homogenized plant organs as well as of 80% percent ethanol-soluble fraction (supernatant) and sugars by ion exchangers was estimated by means of a thin end-window G-M counter, as previously described (Starck 1964, 1969). Sugars were determined by the anthron method.

Radioactivity of ^{32}P was measured by means of a liquid G—M counter (VA-Z 110) after digestion of the plant material in a mixture of perchloric, nitric and sulphuric acid; the rate of dark respiration (in terms of oxygen absorption) with a Warburg apparatus (see Starck, 1973).

The particular experiments were subjected to factor analysis of variance, Snedecor's test and Student's "t" test. Relative values of radioactivity were transformed according to the table of Bliss.

RESULTS

Dynamics of plant growth in shaded and partially defoliated plants

In spite of the fact that both experiments were started with even-aged plants (Table 1), the degree of the shading effect, measured on the basis of the blade's specific weight, is more comparable in experiments Ia (or IA) and IIb (or IIB) for both species examined (Table 3).

Bean plant experiments

Shading and partial defoliation treatment drastically reduced growth of all organs of bean plants, but in various degree. The dynamics of their growth in experimental conditions was estimated in detail only in experiment II, (Fig. 1; effects of defoliation and shading highly significant for all organs — Table 4). Root growth in the shaded and partially defoliated series was seriously reduced, especially after 8 days of treatment. The values of RGR for root (Table 2) were affected in a similar degree by partial defoliation in NL conditions and shading treatment. Growth of the stem was also reduced in conditions with limited supply of assimilates, especially in the first 4-day period; in the second one (expt. IIb) differences were lower, probably owing to the lower growth rate as compared with the first period (Table 2, Fig. 1). In plants with most serious reduction of photosynthesis, root growth was seriously retarded after 4 days and abolished almost completely after 8-days (interaction between $T \times D$ and $T \times L$ statistically significant — Table 4).

In contrast, growth of the intensively expanding trifoliate leaf, estimated together with apical part, was slightly reduced by shading and defoliation: the effect was significant only after 8 days treatment (data obtained on the basis of dry matter

Table 2
Effect of shading and partial defoliation on some growth parameters

Estimation	Experiment No.	Bean plant						Sunflower					
		NL			S			NL			S		
		I	D	I	I	D	I	I	D	I	I	D	I
dry matter of the whole plant (mg)	Ia (or A) IIa (or A) IIb (or B)	985 653 1037	505 453 788	630 534 840	420 345 521		1039 1222 1815	699 1020 1607	543 760 761		372 628 756		
blades roots (dry matter)	Ia (or A) IIa (or A) IIb (or B)	1.8 2.0 2.3	1.0 1.3 2.5	2.2 2.0 2.9	1.2 1.3 2.6		2.1 1.9 1.6	1.9 1.9 1.5	2.2 2.3 1.9		1.7 1.8 1.8		
RGR (whole plant)	IIa (or A) IIb (or B)	0.220 0.114	0.200 0.138	0.170 0.113	0.132 0.103		0.278 0.132	0.276 0.152	0.159 0.010		0.155 0.060		
LAR $\text{dm}^2 \cdot \text{g}^{-1}$	Ia (or A) IIa (or A)	1.8 1.5	1.5 1.2	2.3 2.3	2.1 2.0		1.2 1.4	1.3 1.4	1.7 2.1		1.7 2.1		
NAR g/g day	IIa (or A) IIb (or B)	0.40 0.19	0.46 0.24	0.31 0.16	0.31 0.19		0.68 0.28	0.65 0.33	0.36 0.15		0.42 0.15		
RGR (for apical part)	IIa (or A) IIb (or B)	0.584 0.485	0.621 0.449	0.588 0.455	0.559 0.395		0.223 0.281	0.196 0.281	—1.091 0.087		0.023 0.117		
RGR (for stem)	IIa (or A) IIb (or B)	0.173 0.067	0.105 0.041	0.114 0.062	0.056 0.046		0.415 0.140	0.366 0.175	0.313 0.023		0.259 0.093		
RGR (for roots)	IIa (or A) IIb (or B)	0.194 0.114	0.151 0.086	0.141 0.082	0.073 0.041		0.195 0.133	0.159 0.131	0.045 0.010		0.028 0.029		

NL — natural light

S — shading series

I — intact plants

D — partially defoliated

Experiments denoted as in table 1

Symbols in parentheses refers to experiment with sunflower: $\frac{\text{blades}}{\text{root}}$

dry matter ratio in expt. II b — blades included also expanded trifoliate leaf.

Table 3
General characteristic of blades labelled with ^{14}C

Experi- ment No.	Estimations	Bean plant				Sunflower			
		NL		S		NL		S	
		I	D	I	D	I	D	I	D
I a or I A	sp. weight $\frac{\text{mg d}\cdot\text{m}}{\text{dm}^2}$	256	218	161	150	264	236	164	149
	respiration ml $\text{O}_2/\text{g d.m.}$	4.4 ^a	4.0 ^a	2.7 ^b	3.0 ^b	3.7 ^a	3.2 ^b	3.3 ^b	2.5 ^c
	photosynthesis $\frac{10^6 \text{ cpm/g d.m.}}{10^3 \text{ cpm/plant}}$	12.1 ^a 3317	12.8 ^a 1424	13.7 ^a 2633	19.7 ^b 1903	4.3 ^a 1775	4.6 ^a 1358	7.2 ^b 1733	8.3 ^b 1051
	^{14}C - exported (%)	65	70	56	62	37 ^a	39 ^a	37 ^a	30 ^b
II a or II A	RGR	0.277	0.245	0.173	0.175	0.301	0.433	0.202	0.297
	sp. weight $\frac{\text{mg d}\cdot\text{m}}{\text{cm}^2}$	281	275	218	193	260	261	206	184
	respiration ml $\text{O}_2/\text{g d. m.}$	4.4 ^a	5.0 ^a	3.9 ^a	3.4 ^a	3.9 ^a	3.7 ^a	4.0 ^a	4.4 ^a
	photosynthesis $\frac{10^6 \text{ cpm/g d.m.}}{10^3 \text{ cpm/plant}}$	2.21 ^a 575 ^a	2.47 ^a 370 ^b	2.84 ^b 683 ^a	2.65 ^b 315 ^b	1.10 ^a 430	1.20 ^a 377	1.44 ^b 386	1.48 ^b 255
II b or II B	^{14}C - exported (%)	47	48	46	51	50	51	44	43
	RGR	0.005	0.028	0.012	—1.15	0.082	0.064	—1.493	0.035
	sp. weight $\frac{\text{mg d}\cdot\text{m}}{\text{cm}^2}$	256	257	185	173	271	255	171	182
	respiration ml $\text{O}_2/\text{g d.m.}$	3.6 ^a	3.7 ^a	2.9 ^a	3.1 ^a	3.2 ^a	3.3 ^a	3.1 ^a	3.3 ^a
	photosynthesis $\frac{10^6 \text{ cpm/g d.m.}}{10^3 \text{ cpm/plant}}$	2.10 615 ^a	2.21 439 ^a	2.29 492 ^a	2.04 194 ^b	2.05 1144	1.92 730	1.95 658	2.26 491
	^{14}C - exported (%)	53	51	48	51	55	55	49	55

For explanation of treatment labels see Table 1 and 2.

Means designated by the same letter do not differ significantly at least at $P=0.05$.
sp. weight — specific weight of primary leaves (bean) or all the blades (sunflower).

analysis, $T \times D$ and $T \times L$ statistically significant, Fig. 1 Tab. 4). Experimental treatments affected much less RGR value (Table 2); which remained unchanged in all series examined.

Primary leaves in the control series completed their growth in the first experimental period (table 3). Defoliation of one leaf enhanced and prolonged growth of the other one.

Fig. 1. Changes in dry matter of particular organs (in mg) during experimental period. Means of 6 replications — sunflower and 9 replications — bean plant, two plants in each

Harvesting periods correspond to particular experiments: 4 days — expt. IIA or IIA; 7 days — expt. IIB; 8 days expt. IIB
Results of statistical analysis of dry matter presented in table 4

Different effects of defoliation on the RGR of particular organs caused that RGR of the whole partially defoliated plants, grown under NL conditions was almost the same as in the NL intact series. Also NAR (calculated on blades dry matter basis) was in most cases slightly higher in defoliated than in intact plants for both periods examined. The relative indicator of the leaf area, calculated per plant dry matter (LAR) was estimated only for expt. Ia and IIA. In both experiments shading treatment increased and defoliation decreased LAR in similar proportion.

Table 4
Analysis of significances of the responses to defoliation and shading

Growth (as dry matter increase)		^{14}C -translocation (as percentage of total radioactivity)									
$F_{\text{emp.}}$	Bean plant			$F_{\text{theoret.}}$		$F_{\text{emp.}}$	Bean plant			Sunflower	
	apical part	stem	roots	apical part	stem		blades	apical part	roots	blades	stem
F_T	524	62	79	32	45	F_L	6.54	1.00	30.86	6.41	1.12
F_L	15	63	77	89	135	F_D	5.58	2.21	<1	<1	<1
F_D	4	118	55	<1	5	$F_L \times D$	1.82	1.64	4.52	1	5.62
$F_T \times L$	11	<1	11	21	20	$F_{\text{Exp.}} \times L$	46.24	43.72	8.32	4.08	14.85
$F_T \times D$	4	8	8	<1	<1	$F_{\text{Exp.}} \times D$	5.05	1.96	1.82	<1	<1
$F_L \times D$	6	5	<1	<1	<1	$F_{\text{Exp.}} \times L \times D$	1.00	3.56	<1	<1	1.39
$F_T \times L \times D$	3	<1	<1	<1	<1	$F_{\text{Exp.}} \times L \times D$	<1	<1	2.07	2.10	1.10
S^2	6024	566	2838	13648	19327	S^2	1.93	3.05	1.81	2.89	1.39
degree of freedom	66	66	66	42	42	degree of freedom	24	24	24	24	24
$F_{\text{theoret.}}$	0.05 = 3.99			4.07							
	0.01 = 7.04			7.27							
9 replications (two plants in each)				6 replications (two plants in each)							
3 replications (two plants in each) for sunflower and bean plant											

T — changes with prolonged treatment (4 and 8 days — for bean plants or 4 and 7 days for sunflower).

L — light conditions (natural light — NL or shading — S).

D — partial defoliation

Exp. — comparison of 3 experiments: Ia, IIa, IIb — for bean plant and Ia, IIa, IIb for sunflower.

Sunflower experiments

In young sunflower (expt. IIA) the stem exhibits the highest rate of growth (Table 2 and Fig. 1), diminishing in the second period (see changes in RGR, expt. IIB, Table 2 and Fig. 1). Shading treatment affected gradually stem growth much more than did defoliation (effect of L and D significant as well as $T \times L$, Table 4). Growth of apical part with young leaves was also seriously and gradually reduced by shading, but not by defoliation (effect of L and $T \times L$ highly significant in contrast to D and other interactions — Table 4). In the shaded series growth of the apical part was completely abolished already after 4 days (RGR very low or no dry matter increment — Table 2). Unfavourable conditions affect also growth of roots, especially in the shaded series; retardation of root growth progresses gradually with time (effect of L and $T \times L$ highly significant in contrast to D, Table 4). Defoliation diminished RGR of roots in plants from NL conditions (expt. IIA). Root dry matter in both shaded plants did not increase with time; (interaction $L \times D$ highly significant) their growth was completely invalidated (Table 2, Fig. 1). Defoliation increased RGR of leaves in expt. IIA independently of light conditions (Table 3). In the second period, where leaves grew with lower intensity, defoliation depressed but shading completely abolished their growth.

Generally speaking, the effect of defoliation on growth parameters in sunflower was much lower than in bean plants, in contrast to the shading treatment reducing drastically NAR and RGR of the total plant. It may be a consequence of the fact, that removal of one primary leaf in bean plant reduced the leaf surface area to about one half, and in sunflower defoliation stimulated expansion of new leaves of the second pair. Therefore, at the time of exposure to $^{14}\text{CO}_2$ and other measurements, intact and defoliated sunflower plants had almost the same LAR in experiments IIA and IIB (Table 2) and recovered much faster the $\frac{\text{blades}}{\text{roots}}$ dry matter ratio after experimental treatments, than the bean plants did.

Blades — their physiological activity

Leaves of plants of both species shaded for a few days were much thinner (their specific weight decreased, Table 3) this changing among other things diffusion resistance to CO_2 . Shading reduced the blades respiration rate, in spite of the same or even slightly higher sugar content on dry matter basis (data not illustrated). Photosynthetic activity estimated for all series under NL conditions, calculated as assimilation of $^{14}\text{CO}_2$ per plant was diminished by defoliation in all experiments with bean and sunflower. The rate of photosynthesis, calculated per blade's dry matter in plants grown all the time under natural light conditions, and in most cases in the preshaded series, was similar in intact and partially defoliated plants (Table 3).

Preshading caused marked stimulation of photosynthesis in experiments Ia, IA and Ia, IIA, with younger plants, in contrast to experiments IIB and IIB, where

leaves exposed to $^{14}\text{CO}_2$ were older and had finished their growth (Table 2) and their respiration rate decreased (Table 3). In those experiments compensation effects might have been expected after defoliation in the NL series, in young, trifoliate leaves of bean plants and expanded leaves with apical part of sunflower but they were darkened during $^{14}\text{CO}_2$ -exposure. This supposition is based on the observation that in expt. IIB and IIB both NAR and RGR of the whole plants of the NL-D series exceeded that in the intact NL-series of both species.

In all experiments, within a 2-hr period, a great proportion of labelled assimilates were exported out of the blades (Table 3). The lowest value in expt. IA with sunflower, where the leaves and apical part were exposed to light and $^{14}\text{CO}_2$, seems to be the result of calculation of all ^{14}C -substances, estimated in the apical part as photosynthesis "in situ". Nevertheless the facts observed in expt. IIB and reported already (Starck, 1973) indicate, that the apical part with young, expanded leaves is a very strong acceptor of assimilates.

Defoliation of bean plant, especially of preshaded plants slightly stimulated ^{14}C -export out of the blades (response to defoliation, calculated by statistical factor analysis for all bean experiments together was significant) (Table 4).

Shading treatment reduced slightly export out of the blades in expt. Ia and IIB (effect of L as well as interaction between Expt. $\times$ L significant, Table 4).

The differences in sunflower were more irregular and insignificant. Only if calculation was done together for all experiments, retardation of ^{14}C -export in preshaded plants was statistically significant.

Distribution of ^{14}C -assimilates

Much more pronounced differences were observed in ^{14}C -distribution among the particular plant organs (Fig. 2).

In bean plant, the actively growing apical part with expanded leaf, attracted a great deal of ^{14}C -assimilates exported from the blades (Fig. 2), especially in expt. Ia. Their specific activity was very high and in the NL intact series surpassed that of roots up to 9 times (expt. Ia, IIa), but only about 2 times — in expt. IIB, where demand for assimilates of that organ, at least partially, was supplied by photosynthesis "in situ". In the preshaded series, the apical part had also priority over the other sinks, therefore, light conditions did not affect the share of the apical part in ^{14}C -assimilates distributed among particular acceptors (Table 4 — all effects insignificant); defoliation even increased this share owing to the exploitation of ^{14}C -substances from the petioles (expt. IIa). The dominance of the attractive power of the apical part, over the other organs, appears also in the rather stable sugar content in most experimental series of particular experiments, in contrast to their reduction in the petioles (Table 5).

In the preshaded series translocation of ^{14}C -substances to the roots with drastically restricted growth, was limited in all experiments, but in various proportions (fig. 2, effect of L — highly significant — Table 4). In plants deprived of one primary leaf and grown under NL conditions, the proportion of ^{14}C transported to the roots

Fig. 2. Distribution of ^{14}C -assimilates exported by labelled leaves during 2 hrs, expressed as percentage of radioactivity of whole plant.

Figures under bars — contribution of particular organs dry matter to total dry matter of plant (in percentage)

either increased (expt. Ia and IIa) or was the same as in NL control plants (expt. IIb), where already transport from the expanded trifoliate leaf may take place (interactions between $L \times D$ calculated for all experiments were slightly below the limit of error). This coincided with an increasing contribution of roots dry matter to the total plant mass (see values in Fig. 2) as well as with the relatively lower $\frac{\text{blades}}{\text{roots}}$ dry matter ratio (expt. Ia and IIa — Table 2). Sugar content in roots of bean plant in some experiments (Table 5) decreased in the preshaded series. Differences in the participation of the stem in total radioactivity fluctuated irregularly in the particular experiments, but in unfavourable conditions a great depression of sugar content was observed (expt. IIa and IIb).

In sunflower (fig. 2) the stem had priority over the other sinks, probably owing to its high growth rate; effect of light conditions and defoliation was insignificant — Table 4. In the last experiment, in contrast to the others, in both series of partially defoliated plants, stimulation of ^{14}C -transport to the stem was observed (interaction $L \times D$ calculated for all experiments significant, Table 4). Nevertheless, in plants with limited supply of assimilates, sugar content in the stem drastically decreased, (expt. IA and IIA — Table 5).

The highest relative radioactivity of the apical part in expt. IA is the consequence of its exposure to $^{14}\text{CO}_2$ and light, in contrast to darkening in the other experiments, as mentioned before (Fig. 2). Specific radioactivity of the apical part slightly exceeded that of roots in expt. IIA but was lower in expt. IIB. In all the cases, sugar content (on dry matter basis) was rather stable or even higher in preshaded series, (Table 5).

In contrast to the stem, root possessed a relatively lower mobilizing power in plants treated temporarily with suboptimal light conditions (L effect highly significant — Table 4). Nevertheless the reduction of ^{14}C migrating to the roots is relatively lower than the growth retardation (see Fig. 1, 2 and Table 2).

Absorption and distribution of ^{32}P

In analysis of the relationships between shoot and root, changes in roots activity as donor of ^{32}P in plants with limited supply of assimilates were observed.

In expt. Ia and IIa with bean plants, specific absorption of ^{32}P (calculated on roots dry matter basis) decreased in both preshaded series, but most drastically in defoliated plants (Table 6). The relative rates of ^{32}P -absorption in those experiments roughly coincided with the protein content in the root and its respiration rate, as well as with supply of current assimilates (Table 5). In the last experiment (IIb), with higher $\frac{\text{blades}}{\text{root}}$ ratio, especially in the defoliated series (Table 2), specific ^{32}P -absorption was stable and a much greater part of ^{32}P was transported to the shoot in both preshaded series, than in the first experiment, where the transport index (expressed as percentage of ^{32}P exported from the root) was lower in defoliated plants.

Relatively high ^{32}P -absorption and, in consequence, translocation to the shoot in both preshaded series, measured after replacing plants into natural light conditions, seems to be correlated both with some compensation of photosynthesis and a high

Table 5
Some physiological parameters of assimilates acceptors

Experiment No.	Estimation	Bean plant						Sunflower					
		NL			S			NL			S		
		I	D	I	I	D	D	I	D	I	I	D	D
Ia (or IA)	apical part	61	57	67	72	72	23	23	23	—	—	22	22
	petioles	50	56	60	77	77	85	64	64	51	51	32	32
	stem	64	54	70	62	62	155	133	133	102	102	48	48
	roots	34	28	41	33	33	57	67	67	71	71	52	52
IIa (or IIA)	sugars (mg/g d.m)	7.1 ^a	5.3 ^b	4.4 ^b	3.5 ^{bc}	3.5 ^{bc}	6.0 ^a	5.7 ^a	5.7 ^a	4.4 ^b	4.4 ^b	3.8 ^c	3.8 ^c
	respiration ml O ₂ /g d.m	162	164	152	137	137	264	236	236	164	164	149	149
	proteins (mg/g d.m)	104	87	119	73	73	28	28	28	35	35	35	35
	apical part	171	114	138	82	82	57	62	62	45	45	56	56
IIb (or IIB)	petioles	157	102	118	75	75	106	115	115	70	70	61	61
	stem	71	67	40	29	29	42	49	49	39	39	45	45
	roots	7.3 ^a	6.0 ^b	6.0 ^b	4.1 ^c	4.1 ^c	5.8 ^a	6.0 ^a	6.0 ^a	5.6 ^a	5.6 ^a	5.2 ^a	5.2 ^a
	respiration (ml O ₂ /g d.m)	178	184	169	156	156	227	233	233	226	226	212	212
IIb (or IIB)	apical part	101	112	102	108	108	—	—	—	—	—	—	—
	petioles	128	82	71	91	91	—	—	—	—	—	—	—
	stem	120	93	68	65	65	—	—	—	—	—	—	—
	roots	52	48	35	39	39	4.3 ^a	4.7 ^a	4.7 ^a	5.0 ^a	5.0 ^a	4.4 ^a	4.4 ^a
IIb (or IIB)	sugars (mg/g d.m)	6.7 ^a	5.6 ^{ca}	4.0 ^b	4.5 ^{cb}	4.5 ^{cb}	204	202	202	195	195	202	202
	respiration (ml O ₂ /g d.m)	187	197	173	173	173	—	—	—	—	—	—	—
	protein (mg/g d.m)	—	—	—	—	—	—	—	—	—	—	—	—

For explanation of treatment labels see table 1 and 2.

Table 6
Absorption and distribution of ^{32}P

Experiment No.	Estimations		Bean plant				Sunflower			
			NL		S		NL		S	
			I	D	I	D	I	D	I	D
Ia (or IA)	specific absorption 10^6 cpm.g ⁻¹		2.31	2.54	2.11	1.66	1.56	1.65	2.69	2.88
	transport index (%)		30	20	28	24	32	33	39	40
	distribution of ³² P in aerial parts (%)	blades	61	41	56	51	40	47	52	52
		apical part	25	41	24	27	26	20	9	9
		stem	14	18	20	22	34	33	39	39
IIa (or IIA)	specific absorption 10^6 cpm.g ⁻¹		1.78	1.83	1.31	1.10	0.70	0.66	0.71	1.02
	transport index (%)		13	18	23	26	17	7	6	5
	distribution of ³² P in aerial parts (%)	blades and apical part	72	72	80	83	57	51	55	52
		stem	28	23	20	17	43	49	45	48
IIb (or IIB)	specific absorption 10^6 cpm.g ⁻¹		1.16	1.36	1.32	1.29	0.68	0.59	0.90	0.72
	transport index (%)		9	8	21	23	16	16	16	17
	distribution of ³² P in aerial parts (%)	blades	40	21	38	24				
		apical part	43	57	46	60	52	52	51	60
		stem	17	22	16	16	48	48	49	40

For explanation of treatment labels see Table 1 and 2.

Transport index (%) — all ^{32}P exported to the aerial part assumed as percent of total plant's radioactivity.

Distribution — expressed as percent of ^{32}P in the whole aerial part assumed as 100 percent.

rate of trifoliate leaf expansion creating an active sink for P compounds. This conclusion indirectly supports the fact that in both preshaded series radioactivity of P in the apical part was two times higher than that in blades, in contrast to the NL intact plants, where P-specific radioactivity in the apical part exceeded slightly that in blades (Tab. 7).

The rate of total absorption of phosphorus per unit of roots increase (mg P per increase of 1 g roots dry matter) was calculated for the whole 4-day period between expt. IIa and IIb, according to the formula (White, 1973):

$$AR = \frac{\log_e R_2 - \log_e R_1}{R_2 - R_1} \cdot \frac{M_2 - M_1}{t_2 - t_1}$$

where:

R — root dry matter (g)

AR — absorption rate

M — amount of P (mg)

$t_2 - t_1 = 4$ days

The data obtained were as follows in the respective series:

NL.I	NL.D	S.I	S.D
5.09	4.89	4.73	4.41

Table 7
Specific radioactivity of phosphorus in 10^3 cpm/mg P

	Experiment No.	Natural light						Shaded					
		intact				defoliated		intact			defoliated		
		blades	apical part	stem	blades	apical part	stem	blades	apical part	stem	blades	apical part	stem
Bean plant	Ia	17.8	9.9	38.1	9.9	6.5	43.3	9.6	8.7	21.3	8.0	6.5	15.3
	IIa	8.6		19.2	12.2		20.0	8.9		12.9	10.4		9.6
	IIb	3.3	4.2	7.7	1.7	3.7	7.0	5.2	7.8	12.6	4.1	9.5	11.8
Sunflower	IA	13.4	16.0	17.0	15.5	16.1	15.3	22.0	17.7	21.9	26.3	20.5	20.5
	IIA	2.3		4.3	0.9		1.8	0.7		1.1	0.8		1.0
	IIB	4.2		7.8	4.2		6.8	4.9		5.4	5.3		4.3

They indicate a successive decrease of P-absorption rate with the reduction of assimilates production under reduced light intensity and in partially defoliated plants.

In sunflower treated in a similar way as bean plant the specific rate of ^{32}P -absorption and export out of the roots in the preshaded series surpassed significantly that of the NL-series, independently on the defoliation treatment (expt. IA) or was almost the same as in plants grown all the time under higher light intensity (Table 6). ^{32}P -specific absorption values did not coincide with the respiration rate, sugar content (Table 5) nor with root contribution to ^{14}C -assimilates migrating to particular acceptors. In the preshaded series of expt. IA, a higher proportion of ^{32}P migrated to the shoot, especially to the blades, (Table 6) where compensation of photosynthesis was observed. A further proof of enhanced ^{32}P -migration to the blades is the fact of higher P-specific activity of the blades in both preshaded series, but especially in the defoliated one (Tab. 7). In the other experiments a similar amount of ^{32}P was detected in the blades estimated together with the apical part and in the stem, but the stem's P-specific radioactivity was higher than that of blades.

DISCUSSION

The problem of functional relationships between the shoot and root systems have been the subject of many recent papers (Brauer 1966, 1970; Davidson 1969a, b; Hunt 1973; Thornely 1972; Throughton 1974).

Davidson (1969a, b) suggested, that a constant, functional balance may exist between the root and shoot systems. An externally induced decrease in the specific activity of root or shoot systems would tend to be compensated by an increase in the mass of the same component in order to maintain its total activity. Experimental manipulation of the $\frac{\text{root}}{\text{shoot}}$ dry matter ratio suggested to this authors the idea, that partitioning of photosynthates is controlled by the relative rate of photosynthesis and rate of root absorption of mineral elements in inverse proportion:

root mass·rate (absorption) α leaf mass·rate (photosynthesis), Brauer (1966, 1970) postulated, that the activity ratio would be more meaningful than the weight ratio.

In the studies reported, some simultaneous measurements of root and shoot activity were performed after experimental manipulations, causing changes in the supply of assimilates.

Some parameters of growth analysis calculated for plants, grown under natural light or shading conditions indicate a depression of NAR and an increase of LAR greater in sunflower than in bean plant as already reported by Èze (1973), Rajan et al. (1973) and others.

Replacement the plants under natural light conditions after shading treatment, caused complementary changes in photosynthesis, relative growth rate and absorption of mineral elements (Starck, 1973). Hunt (1973) reported strong reduction of specific absorption of K at lower light intensity in *Lolium*. Borzenkova (1970) postulated relationships between ^{32}P -absorption and photosynthesis.

In bean plant shading treatment decreased specific absorption of ^{32}P (calculated on roots dry matter basis) in some cases, but not in sunflower, where in some experiments the specific absorption rate distinctly exceeded that of control plants (in expt. IA and earlier paper — Starck 1973). This increment of roots activity coincided with compensation of photosynthesis, creating probably a higher demand for phosphate in blades. It seems to be in accordance with Davidson's concept. In sunflower, after a suboptimal growth period the smaller size of the root is compensated by its higher activity. In the sunflower plants examined, roots contributed in relatively low proportion to the total dry matter of the whole plant, therefore in the case of their growth retardation due to shading treatment, P-supply to the blades may limit photosynthesis and in turn shoot growth. This suggestion is supported by the facts that a relatively higher proportion of ^{32}P was transported to the shoot and P-specific activity increased in the blades, apical part and stem, a few hours after transfer of the plants to better light conditions as compared with control intact plants.

To the existence of functional relationships between shoot and root activity in sunflower points indirectly the high (and statistically significant) linear correlation between absorption of ^{32}P (on one plant basis) and blades area (expt. IA) as well as between dry matter of blades together with apical part and ^{32}P -absorption in particular series (calculated for expt's IA, IIA, IIB together). These last correlation coefficients were as follows:

Variability	Degree of freedom	r
between treatment	8	0.909**
within "	23	0.473*
total	32	0.767**

* — significant at $p=0.05$

** — " " " $p=0.01$

Similarly, in lucerne the demand for P associated with the rate of plant growth or the level of metabolic activity in the shoot seem to have a marked influence on the rate of P uptake (White, 1973).

On the other hand, in some preshaded sunflower series with completely retarded root growth, ^{32}P -absorption was not higher than in the NL plants (expt. IIB). Still another relation between roots and aerial parts after preshading treatment was observed in bean plant, where ^{32}P -absorption did not correlate, in particular series, with dry matter of aerial parts (correlation coefficient $r=0.162$ at 23 degree of freedom). In some cases, described in previous paper (Starck 1973) and in expt. Ia and IIa roots of preshaded plants absorbed ^{32}P at a lower rate — related roughly with some physiological root parameters like: growth, respiration, sugar and protein content. A similar observation was reported by Newman (1973), based on experiments done with winter wheat. Prolonged treatment of bean plant with lower light intensity (expt. IIB) results in stimulation of young trifoliate leaf growth and an increase of $\frac{\text{blades+apical part}}{\text{root}}$ mass ratio. It creates a great demand for P, transported from the roots owing to the fact that replacement of the plants in NL conditions accelerates probably the metabolic rate of P-compounds in the shoot. It is owing to all these facts that the specific rate of ^{32}P -absorption was similar in all treatments.

All the above mentioned relations give some further evidence on the existence of dynamic equilibrium between photosynthesis, growth and absorption rate.

Partial defoliation as the second factor investigated also limited photosynthesis, but with much lower accessory effects as compared with shading treatments. Defoliation enhanced the growth of the leaves remaining on the plants especially in the first few days. Stimulation of leaves growth rate after defoliation was observed also by Brauer (1970) in bean plants, by Das Gupta (1972) and Fick (1971, 1973) in sugar beet. Defoliation increased photosynthesis in willow, corn and bean plant (Wareing 1968 and Neals et al., 1971) and in other species (Gej, 1971; Meidner, 1969; Mokronosov, 1971 and others). The compensation effect in photosynthesis and in net assimilation rate (NAR) was rather low in the experiments here reported, but it was observed in most cases. The highest stimulation was observed in the case of $^{14}\text{CO}_2$ -exposure done in sunny weather (Table 1 expt. Ia). It agrees with the results reported by Neals et al. (1971) that the effect of defoliation is more pronounced at relatively higher light intensity.

Diminished supply of assimilates after partial defoliation caused mobilization of reserve material from petioles and stem. Export of current ^{14}C -assimilates was slightly higher in defoliated plants, as also observed in peas by Lovell (1972). The proportion of ^{14}C migrating to the root increased, in contrast to that in preshaded plants, what may be connected with hormonal regulation and lower mass ratio of blades to roots in plants with one primary leaf cut off. In partially defoliated plants, blades are better supplied not only with mineral elements but also with growth regulators, produced in roots (Wareing, 1968).

All the above mentioned observations, concerning the effect of restriction of photosynthates supply (by defoliation or shading treatment), on the pattern of ^{14}C -distribution suggest that the priority in the share of photosynthate is determined among other things by the growth rate of acceptors, determining specific activity of sinks. The apical part with the expanding trifoliate leaf in bean plant continued

growth at an unchanged rate in all experimental conditions and it clearly correlated with its dominance as a ^{14}C -acceptor. It allowed for quicker recovery of the source area after defoliation. In the preshaded series, dominance of the apical part over the other acceptors appeared to be inversely correlated with the import of assimilates to the other sinks, mainly roots, with restricted growth.

In sunflower, after partial defoliation, stimulation of leaf RGR conditioned quick restoration of the predefoliation proportion of source to sink. In young sunflower, the stem as an organ with the highest growth rate (Starck, 1966) was the dominant acceptor even in the case of limited supply of assimilates. In slightly older plants, when RGR of the stem decreases, it was still the main acceptor but in that case owing to their dominant size creating a great capacity for accumulation of assimilates. In cases of relatively long treatment with conditions suboptimal for growth, some reserves from the stem were mobilized and transported to the apical part or other acceptors.

In conclusion the supposition may be advanced that photosynthesis of the sunflower and bean plant leaves controls in a relatively small extent the rate of assimilates export from the blades, the subsequent distribution pattern depending partly on the relative activity of particular sinks, is determined, among other things, by their growth rate; on the other hand, growth depends on assimilates supply. This indicates a very complex relationship between source and sink. Throughton (1974) and Jankiewicz (1972) suggested a feed-back regulation.

In further studies of the mechanism participating in regulation of the balance of the work done by roots and by blades, a more precise criterium of their physiological activity should be elaborated.

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Wpływ ograniczonego zaopatrzenia roślin w asymilaty na zależność pomiędzy akceptorami i donorami

Streszczenie

Badano zależności pomiędzy szeregiem procesów fizjologicznych zachodzących w donorach i akceptorach asymilatów w warunkach ograniczonego zaopatrzenia roślin w asymilaty (okresowe ocienienie i częściowa defoliacja), u 19—27-dniowych siewek fasoli i słonecznika.

Aktywność akceptorów była zdeterminowana głównie intensywnością wzrostu poszczególnych organów. Dominującym akceptorem, nawet w warunkach ograniczonej fotosyntezy, był organ o największej względnej intensywności wzrostu — RGR. U fasoli był to wierzchołek wzrostu z rozrastającym się liściem natomiast u słonecznika — łodyga.

Aktywność korzeni (w przeliczeniu na g s. m.) jako donorów fosforu, wydaje się być uzależniona od ich aktywności metabolicznej (intensywności oddychania, zawartości cukrów i białek), w przypadku gdy fosfor absorbowany i przemieszczany do części nadziemnej nie jest czynnikiem ograniczającym fotosyntezę. Jeśli jednak aktywność całego systemu korzeniowego jest stosunkowo mała (np. po zahamowaniu wzrostu spowodowanym okresowym ocienieniem), wówczas kompensacji fotosyntezy, obserwowanej po przeniesieniu roślin z warunków ocienienia do warunków naturalnego oświetlenia towarzyszyła kompensacja absorpcji fosforu, (w przeliczeniu na g s. m. korzeni), co szczególnie wyraźnie obserwowano u słonecznika. Może to warunkować utrzymanie funkcjonalnej równowagi pomiędzy częścią nadziemną i korzeniem przy zmienionych stosunkach masy poszczególnych organów.

Przedyskutowano przyczyny odmiennej reakcji roślin na ocienienie i defoliację.