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Photosynthesis, translocation and accumulation of assimilates in cereals during grain development

II. Spring barley — photosynthesis and the daily accumulation of photosynthates in the grain

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INTRODUCTION

In our previous investigations on barley and wheat (Birecka, Skupińska, Wojcieska, Zinkiewicz, Part I, 1963) it was revealed that the application of shading or defoliation technique for a period of 30, 15 and even 8 days — in order to determine the role of particular parts of the plant after ear emergence in the total weight increase as well as in the accumulation of assimilates in the grain — led to very divergent and thus uncertain results. This was caused mainly: 1) by a partial compensation for removed or shaded organs, manifesting in an increased photosynthetic activity of parts exposed to light (first of all of the flag leaf and glumes and awns, which were increasing in size) and also 2) by a more intense translocation — under these conditions — of organic compounds to the grain.

A number of workers have often applied short exposures of particular leaves of intact plants to labelled CO_2 and have examined the translocation of ^{14}C — assimilates to other organs and also to the kernels. Among cereals, rye (Mayer, Porter 1960), wheat (Krawcowa 1957, Pietinow, Szan-Łuń 1962, Shen and others 1959, Zółkiewicz, Prusakowa 1957) and rice (Asada Kozi 1960, Murayama 1961) were investigated in such a way. In experiments with barley Buttrose and May (1959) — in contrast to others — exposed the ears to ^{14}C — labelled CO_2 and tested the radioactivity of the kernels at various intervals after exposure.

Such a technique, however, does not permit simultaneous examination of the contribution of photosynthesis in particular organs to the total CO_2 assimilation or to the accumulation of organic matter in the grain. Simultaneous examination of all green parts in such a way, that only one and every time a different organ of a particular plant is exposed to labelled CO_2, is from the practical point of view exceptionally difficult and would be burdened with very great errors through various causes. Therefore continuing experiments on cereals — already using $C^{14}O_2$ — it seemed impossible to give up the technique

of shading or defoliation completely. However we tried to diminish the eventual „artefacts" caused by these treatments by significantly reducing the duration of their effect on the plants.

Results of a part of the investigations, i. e. of experiments with barley var. Browarny PZHR are reported below.

METHODS

On April 15, 1961 seeds were sown in pots filled with a mixture of soil and sand (7 + 2 kg). Basal and top dressing was as in the experiment with barley carried out in the same year at Puławy (part I, 1963). Full sprouting was noted on April 20. The plants were thinned gradually to 12 per pot. The beginning of ear emergence was observed on June 8. At that time the plants had two ear — bearing shoots (very few plants, 1—2 per pot had a second small tiller — these plants vere removed); only three upper leaves on each shoot were green. The leaf lamina of the tiller were smaller than analogous lamina on the main shoot (mean area, main shoot: I — 15.7; II — 14.6; III — flag leaf — 7.8 cm^2; tiller: I — 12.0; II — 11.8; III — flag leaf — 4 cm^2). On the day of the first sampling, i. e. on June 12 the lower yellow leaves were removed; their average weight amounted to 320 mg per plant (from the main shoot — 172, from the tiller — 149 mg).

The plants were sampled (always early in the morning) seven times at five day intervals except for the last harvesting, which was accomplished 10 days after the preceding one (Tab. 1). They were killed at 105° and subsequently dried at 60° C.

In the middle of each five day period some of the plants were placed in a plexiglass chamber * (about 750 l in volume), into which ^{14}C — labelled CO_2 was introduced. Following treatments were investigated (in three replicates, 2 plants each): 1. control; 2. tiller removed; 3. leaf laminae removed; 4. awns removed; 5. ears removed; 6. ears shaded; 7. all vegetative parts shaded (ears only exposed to light). In the treatments 3—7 the tillers were treated similarly to the main shoots. The appropriate technical procedures were applied immediately before introduction of plants into the chamber. For shading a double sheet of white and black (on the inside) paper was used. The soil surface in pots was covered with cotton soaked in a weak solution of H_2SO_4. The plants were always placed in the chamber early in the morning. Immediately before CO_2 liberation two small rotation fans were set in motion and the chamber — placed out-of-doors — was covered with opaque material for 10—15 min. During this time the reaction between natrium carbonate and lactic acid ceased. The

* A more detailed description of the chamber used in these experiments is to be found in another publication (Birecka 1963).

Table 1

The state of barley plants during the period from ear emergence to maturity
Experiment 1961

No	Date of sampling and observations	The state of plants *
1	12.VI	Three leaves ** green, stems (including leaf sheaths) and ears green
2	17.VI	The lowest leaf partially yellow
3	22.VI	The lowest leaf fully yellow, the stem green above the first internode
4	27.VI	Flag leaf green only, the ends of awns turning brown
5	2.VII	Flag leaf completely yellow, only the upper part of the stem green
6	7.VII	All leaves and stems yellow, glumes and awns at their base only green
7	17.VII	Plants at full maturity

* The state of the tiller was similar to the state of the main shoot.
** Strictly speaking leaf laminae; the word leaf will be used subsequently with this meaning.

Table 2

Conditions, under which barley plants were kept in the plexiglass chamber

No	Date of experiment	CO_2 content*		Total radioactivity mc	^{14}C content found in plants** per cent of the total activity applied	Fluctuation of temperature in the chamber*** during the day — °C	Weather conditions
		g	%				
I	14-15.VI	4.4	0.3	1.5	90	14 – 23	clouded
II	19-20.VI	4.4	0.3	1.5	90	18 – 25	clouded
III	24-25.VI	4.4	0.3	1.5	80	23 – 30	sunny
IV	29-30.VI	1.3	0.12	1.5	90	19 – 28	varying cloudiness
V	4-5.VII	1.1	0.08	0.75	15	20 – 25	clouded

* Including the normal CO_2 content in the air volume in the chamber.
** In their aerial parts.
*** The chamber had been cooled with water several times during the day while it was hot. The temperature in the chamber did not differ markedly from the temperature under the net of the greenhouse, where the plants were placed during the daytime.

plants were removed from the chamber after 24 hours and immediately killed at —60°C.

Table 1 shows the state of plants sampled at particular periods in the greenhouse. Taking into account that 15 days after ear emergence only the flag leaf — among all leaves — was green, and after the following 5 days only the ear and peduncle were capable of photosynthesizing, the amount of labelled CO_2 in the two last experiments was markedly diminished (Tab. 2).

Radioactive plant material was ground in a suitable mill (in a frozen state) or in a M. S. E. homogeniser. Afterwards it was additionally homogenised in a glass homogeniser. The radioactivity was determined by means of a G. M. counter with a mica window 1.1 mg per cm^2 in thickness and 25 mm in diameter. Its efficiency at the geometry applied was about 4.7%. The amount of plant material on the planchette did not exceed 0.5 mg/cm^2.

RESULTS

The dry weight of the green parts of the main shoot immediately after heading was about 45% higher than the total weight of analogous parts of the tiller (Tab. 3). These shoots differed also with regard to their weight increase in the later period. The relatively highest total incre-

Table 3

Weight of barley — g d. m. per plant

Experiment 1961

Date of sampling	Main shoot			Tiller			Aerial parts total	Roots
	shoot	grain*	total	shoot	grain*	total		
12.VI	1.14	0.11	1.25	0.79	0.07	0.86	2.11	0.73
17.VI	1.20	0.25	1.45	0.86	0.18	1.04	2.49	0.65
22.VI	1.26	0.50	1.76	0.89	0.36	1.25	3.01	0.69
27.VI	1 12	0.72	1.84	0.80	0.52	1.32	3.16	0.65
2.VII	1.09	0.93	2.02	0.77	0.72	1.49	3.51	0.48
7.VII	1.08	1.03	2.11	0.79	0.81	1.60	3.71	0.47
17.VII	0.99	0.95	1.94	0.74	0.69	1.43	3.37	0.39
L.S.D. (p=0.05)	0.091	0.065	0.152	0.065	0.080	0.131		

* The number of kernels: main shoot — 25, tiller — 21.

ment occurred during the first 10 days after ear emergence; during the subsequent 10 days it was less and just the same for both shoots. The increase in the total plant weight within the period between the 20th and 25th day is not statistically proved. At this time a rapid

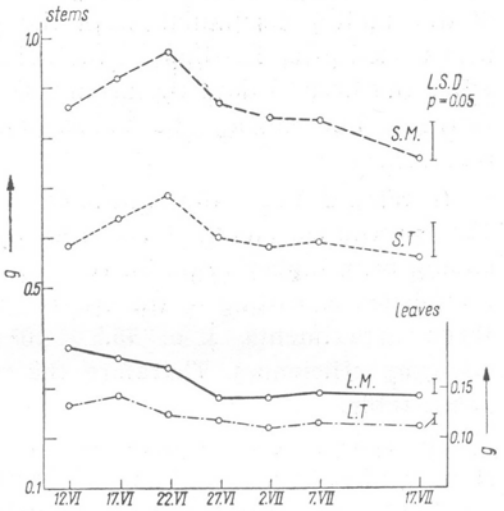

Fig. 1. Weight of leaves and stems of barley plants, g dm per plant

S. M. — stem of the main shoot; *L. M.* — leaves of the main shoot; *S. T.* — stem of the tiller; *L. T.* — leaves of the tiller.

decomposition of roots was noted. The grain increment after 25 days corresponded to the total plant increment. It should be added that during the last 10 days of maturation a decrease of dry weight in the main as well as in the side shoot occurred, especially in their grain.

Changes in the weight of particular plant organs after heading were analogous to those observed in the experiment carried out at Puławy

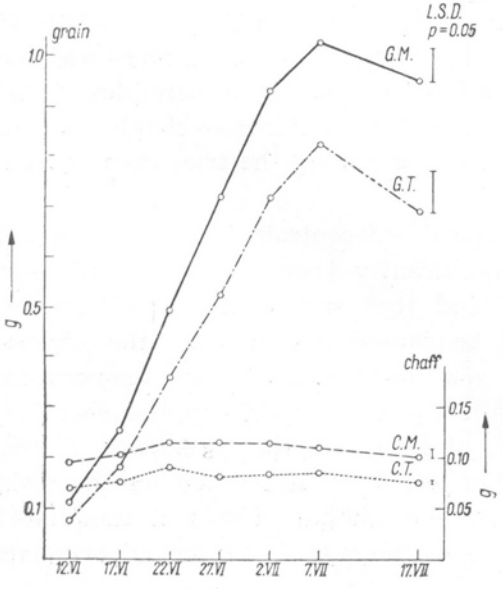

Fig. 2. Weight of grain and glumes & awns of barley plants, g d. m per plant

G. M. — grain of the ear of the main shoot; *G. T.* — grain of the tiller ear; *C. M.* — glumes & awns of the ear of the main shoot; *C. T.* — glumes & awns of the tiller ear.

(part I, 1963), i. e. 1. the weight of the laminae with ageing was diminishing (Fig. 1); 2. the stems showed a transient increase in their dry weight in the first period of grain filling (the differences in weight between sampling II and III is not statistically proved); 3. at the same time the weight of awns and glumes increased (Fig. 2), 4. the degree of dry matter accumulation in the grain was relatively small in the first period after heading, in the subsequent period considerably higher. After the first 10 days the grain increase was lower than the total plant increase, but during the subsequent 15 days this relationship was reversed.

In table 4 and 5 the results of experiments with ^{14}C are presented. The specific activity of $^{14}C - CO_2$ applied in the two last experiments having been higher (Tab. 2), the data obtained were converted and thus diminished according to the specific activity of CO_2 applied in the first three experiments, i. e. 35.5×10^3 cpm per mg CO_2 (at 4.7% of counting efficiency). Therefore the results of all five experiments are comparable.

The radioactivity of plants found after 24 hours — by the normal daily rhythm of light and darkness — characterises in particular experiments a value between the true and net assimilation, taking into account in the latter case the utilisation of the photosynthetic products in respiration at night. It should be added, that during the daytime the liberated — as respiration product — labelled CO_2 was in all probability reassimilated by the green plant parts, at night — similarly as in daytime — organic compounds previously accumulated could also have served as substrates for respiration (to a different degree in various plant organs). Taking into account that the average rate of respiration at the investigated stages of plant development, especially at night, was relatively not high (Porter and others 1950, Thorne 1959, Scheibe and others 1959, Müller 1960, Stalfelt 1960), the activities found in plants — interpreted as amounts of CO_2 assimilated — should perhaps be considered rather as values more approaching the true than the net assimilation.

The amounts of carbon assimilated by controls in the first three experiments were similar, but significantly lower in the fourth one. However it must be borne in mind that similarities or differences in the photosynthesis rate could be caused not only by the physiological state of the plant, but also by differences in temperature (e. g. exp. III) and CO_2 concentration (e. g. expt. IV) in the chamber. The average daily weight increase of barley in the greenhouse during 10—15 days after ear emergence accounted for 40—50 mg for the main shoot and 30—39 mg for the tiller. The amount of carbon assimilated by the controls in the chamber — as average for three experiments

Table 4

The radioactivity of barley plants after 24 hours exposure to $^{14}CO_2$ — 10^3 cpm per plant

Experiment I and II — 1961

No	Treatment	Shoots *	Date of experiment									
			I — June 14 - 15					II — June 19 - 20				
			leaf laminae	stem*	glumes awns	grain	total	leaf laminae	stem**	glumes awns	grain	total
1	Control	M.S.	221	1293	126	933	**2573**	290	779	174	1265	**2508**
		T.	162	914	110	726	**1912**	156	600	173	887	**1816**
2	Tiller removed	M.S.	228	1203	123	975	**2529**	257	769	189	1254	**2469**
		T.	—	—	—	—	—	—	—	—	—	—
3	Leaves removed	M.S.	—	595	123	666	**1384**	—	636	173	1195	**2004**
		T.	—	463	110	495	**1068**	—	460	132	859	**1451**
4	Awns removed	M.S.	324	1356	47	740	**2467**	237	927	80	1452	**2696**
		T.	240	1035	35	544	**1854**	146	752	57	940	**1895**
5	Ears removed	M.S.	300	1903	—	—	**2203**	298	1526	—	—	**1824**
		T.	198	1466	—	—	**1661**	149	1248	—	—	**1397**
6	Ears shaded	M.S.	248	1136	35	671	**2090**	276	732	71	1230	**2309**
		T.	186	995	28	474	**1683**	150	587	56	936	**1729**
7	Only ears exposed to light	M.S.	0	7	105	483	**595**	0	8	100	501	**609**
		T.	0	7	103	427	**537**	0	6	109	386	**501**
LS.D. (p — 0.05) for all treatments			22	160	13	71	196	74	200	44	209	352
for treatment nr 7					7	26	24			14	38	42

* M. S. — main shoot, T. — tiller.

** Including the rachis. In treatment nr 7 only the rachis was radioactive, the stems did not show any marked activity, their total activity including the leaf laminae being about $1{,}5 \times 10^3$ cpm (direct counting gave 2 cpm, which is within the limits of the background fluctuation).

Table 5

The radioactivity of barley plants after 24 hours exposure to $^{14}CO_2$ — 10^3 cpm per plant
Experiment III, IV and V — 1961

No	Treatment	Shoots *	Date of experiment									
			III — June 24 - 25					IV — June 29 - 30				
			leaf laminae	stem**	glumes awns	grain	total	leaf laminae	stem**	glumes awns	grain	total
1	Control	M.S.	121	806	171	1540	**2638**	20	354	71	579	**1024**
		T.	75	409	128	1515	**2127**	15	226	49	540	**830**
2	Tiller removed	M.S.	121	616	148	1269	**2154**	26	370	87	337	**820**
		T.	—	—	—	—	—	—	—	—	—	—
3	Leaves removed	M.S.	—	399	138	1164	**1701**	—	181	71	603	**855**
		T.	—	326	124	1142	**1592**	—	143	42	534	**719**
4	Awns removed	M.S.	127	549	51	1176	**1903**	15	184	36	587	**822**
		T.	66	404	38	927	**1435**	10	223	21	267	**521**
5	Ears removed	M.S.	152	1619	—	—	**1771**	23	628	—	—	**651**
		T.	110	1330	—	—	**1440**	33	620	—	—	**653**
6	Ear shaded	M.S.	94	515	55	1010	**1674**	22	179	20	583	**804**
		T.	49	366	45	894	**1354**	19	168	20	495	**702**
7	Only ears exposed to light	M.S.	0	7	140	716	**863**	0	8	67	301	**376**
		T.	0	7	105	630	**742**	0	5	38	243	**286**
LS.D. (p — 0.05) for all treatments			44	147	33	125	260	4	43	12	103	150
for treatment nr 7					10	14	17			7	9	11
			V — July 4 - 5									
1	Control	M.S.	—	3	3	34	**40**					
		T.	—	2	5	36	**43**					
5	Ears removed	M.S.	—	5	—	—	5					
		T.	—	9	—	—	9					

* M. S. — main shoot, T. — tiller, in the third experiment the plants had two green leaf laminae one of which partially was yellow) on each shoot, in the fourth — only one, partially green leaf, in the fifth — no living leaf laminae.

** Including the rachis, in treat. nr 7 only the rachis was radioactive.

carried out at that period — accounted respectively for 43 and 32 mg, when the radioactivity is converted into amounts of organic compounds *.

The calculation of the organic matter increase on the basis of plant radioactivity is burdened with a certain error in plus and in minus for: 1) the activity does not correspond to the value of net assimilation, 2) the specific activity of assimilated $^{14}C - CO_2$ could have undergone changes, caused by the respired CO_2, which derived from organic compounds accumulated before the beginning of the experiment. In spite of these structures it can be assumed, that the average rate of photosynthesis in the chamber in the first two experiments was actually lower but not much as compared to the rate shown at that time by plants in the greenhouse. However it should be added that the rate of assimilation during the daytime in the chamber was undergoing marked changes not only because of changes in light intensity and temperature but also through changes in CO_2 concentration.

If in the fourth experiment a marked decrease in the amount of assimilated carbon could have resulted not only from a lower photosynthetic capacity of the plants, but also from the lower dose of CO_2 applied, then the minimal amount of photosynthates in exp. V — accounting for 2% of the amount found in the first period — resulted only from the physiological state of the investigated plants.

In order to determine to what degree the products of current photosynthesis were translocated during 24 hours to the roots, in exp. II the soil was washed carefully away from the roots of some plants, which then were put on a nutrient solution and placed in the chamber. The activity of their roots amounted to $10—12 \times 10^3$ cpm per plant, which constitutes hardly 0.3% of the radioactivity found in the aerial parts of control plants (in soil culture). If assumed that the true amount of photosynthates translocated **, to the roots of the latter plants was 4—5 times higher, then even this value would have been of little significance, when the total amount of assimilated carbon is under consideration.

In all experiments — except the last one — the total activity of the main shoot was higher than that of the tiller. During the first 10 days of investigations — assuming that each experiment with ^{14}C characterises the behaviour of plants for a 5-day period — there was no translocation of photosynthates from one shoot to another (at least during

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* Assuming that the carbon content in the organic matter accounts for 45%.

** In our experiments the transfer of plants from soil into water culture caused a diminishing of about 20—25% in the amount of carbon assimilated by the plant. Even by very careful washing of the roots a part of them could be damaged. Their radioactivity is lowered also because of the utilisation of assimilates in respiration.

24 hrs.). However in the following period — as the data obtained show — the main shoot was in all probability partially supplied with these compounds by the tiller. For the removal of the latter caused a decrease in the activity of the stem (exper. III) and especially of the grain in the main shoot (exp. III and IV). Thus, if in the first period, when each shoot had at least two green leaves, the photosynthetic capacity of the main shoot was higher than that of the tiller, then in the subsequent period this capacity in both shoots seems to be similar.

Table 6

The contribution of leaf laminae, ears and stems to the total CO_2 assimilation — percent of the total radioactivity of control plants

No	Date of experiment *	Leaf laminae	Ears	Stems (calculated only)
I	14—15.VI	45	25	30
III	24—25.VI	31	34	35
IV	29—30.VI	15	36	49
V	4—5.VII	0	84	16

* The experiment carried out on the 19th—20th of June is omitted because of the great magnitude of the L.S.D., the contribution of ears in this experiment amounted to 25 per cent of the total CO_2 assimilation.

The contribution of photosynthesis in the leaf laminae (treat. 1 and 3) to the total CO_2 assimilation in the first period after heading in the main shoot as well as in the tiller amounted to about 45% (Tab. 6). In the later period it was gradually diminishing and 20 days after ear emergence it was nil. The contribution of ears can be estimated from the results of treat. 5, 6 and 7. In all experiments (except exp. II *, treat. 6) ear removal as well as ear shading brought about a decrease in the amount of assimilated carbon — in most cases to the same degree. It seems however that more reliable information can be obtained from plants, whose ears only were exposed to light (treat. 7). When the values of the standard errors for all treatments and for only treat. 7 are compared, it becomes clear that the differences between replicates were caused by differences in the rate of photosynthesis mainly in the vegetative organs. Therefore the values — presented in tab. 6 — of the contribution of ears to the total CO_2 assimilation were calculated from the results of treat. 7. It should be added that the magnitude of differences in radioactivity between

* The standard error of this experiment being relatively very high, its results will often be omitted in further consideration.

the control and the two aforementioned treatments (5 and 6) in most cases (within the limits of the standard error) were similar to these results.

The contribution of ears — as is shown by the data obtained — during the first 10 days, i. e. during the period of the greatest dry matter increase, accounted for about 25%, in the later period — with ageing of the leaves — it was increasing. At the end of plant development, when the photosynthetic capacity was minimal, almost all the carbon assimilated derived from the green parts of the ears. In all experiments, except the last one, the ear of the main shoot showed a higher radioactivity than that of the tiller in the treatment under consideration. However the differences were relatively small.

The attempt to determine the role of the awns themselves in the total CO_2 assimilation during the first ten days of investigations has not given any reliable results. This fact in all probability was due to the occurrence of recompensation processes *. On the other hand in exp. III and IV, when the assimilating area was decreasing rapidly the marked role of awns was distinctly revealed.

The approximate estimation ** of the role of stems *** shows that their contribution to the total CO_2 assimilation was changing from 30% in the first period to 49% in exp. IV. However in the latest period the role of the stems (strictly speaking of the peduncle only) was of little significance.

When the relative radioactivity of particular organs is compared with their contribution to the total amount of photosynthates, it becomes clear that during 24 hours new assimilates were intensely translocated. This process occurred at the highest rate in the leaf laminae, for in all experiments only 20% of carbon assimilated by these organs could be found in them. At the first stage of grain filling the main — although not the only — acceptor of photosynthates from leaf laminae were the stems. For their activity constituted about 50% of the total. activity, the contribution of these parts to the total CO_2 assimilation being only 30%. In the later period however the main acceptor of the leaf lamina photosynthates were the kernels.

The degree of accumulation of photosynthates in the grain during 24 hours was different in particular periods of investigations (tab. 7).

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* It is worth noting that in exp. I the grain of plants deprived of awns showed a lower activity, although their total activity was similar to that of the control.

** Total plant activity minus the activity due to photosynthesis in leaf laminae and ears.

*** Strictly speaking stems with leaf sheaths.

In experiment I it was the lowest constituting about 37% of their total amount; in the following period it was gradually increasing to 60—64% (per whole plant) reaching 85% at the advanced wax stage of kernels. Obviously the changes in absolute amounts of ^{14}C—assimilates daily transported to the grain in the investigated stages were of somewhat different character because of the differences in the photosynthetic capacity, especially in the later period. It is worth noting, that in exper. I and II the amount of photosynthates translocated to the grain of the main shoot was higher than that translocated to the grain of the tiller, in the subsequent experiments it was the same * (Tab. 4 and 5). Analogous differences between the first 10 day period of investigation and the following 15 day period could be found, when the absolute increase in the dry weight of the grain of these shoots is considered.

New assimilates accumulating daily in the grain derived from various sources. One of them were the green parts ** of the ear itself. The average contribution of their photosynthates to the total amount of ^{14}C — assimilates accumulated in the grain accounted in experiments I—IV for about 50%. Between the 20th and 25th day after heading almost all these assimilates derived from the green parts of the ears. It should be added that in all experiments about 80% of photosynthates formed in these parts were translocated during 24 hours to the grain. The radioactivity of awns and glumes in treat. 1, 6 and 7 indicates that a certain amount of assimilates was translocated to them from vegetative organs. However this amount *** found after 24 hours (treat. 6) was very small.

The two remaining sources, i. e. leaf laminae and the stems supplied the grain with ^{14}C — assimilates daily to a different degree at particular stages of filling. The data presented in tab. 7 seem to indicate that in the first stage the photosynthates of leaf laminae played a greater role in this process. Within the period between the 10^{th} and 15^{th} day after heading a certain preponderance of assimilates formed in

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* In these experiments the relative accumulation of ^{14}C — assimilates in grain — calculated as percent of the total activity found in each shoot — is higher in the tiller than in the main shoot (in their stems a reversed relationship can be observed). This fact can be due to the supposed translocation of assimilates from the vegetative parts of the tiller to the main shoot.

** Not only awns, glumes and flowering glumes can be numbered among the assimilating parts of the ear, but also the seed coat, which remains green for a long time. In our considerations of assimilate accumulation the word grain is used as including both kernel and the flowering glume.

*** Though in most cases the sum of the radioactivity of awns and glumes of plants, whose ears were shaded, and of plants, whose ears only were exposed to light, corresponds to the radioactivity of these organs in the control, it can not be certain that the observed translocation of assimilates to the green parts of the shaded ear was not caused by the treatment of shading itself.

Table 7

Translocation of ^{14}C — labelled assimilates to the grain — per cent of the total activity of each shoot of control plants

Treatment	Plants parts	Experiment									
		I		II		III		IV		V	
		main shoot	tiller	main shoot	tiller	main shoot	tiller	main shoot	tiller	main shoot	tiller
Control	total	100	100	100	100	100	100	100	100	100	100
	in stem* only	50	48	31	33	31	21	34	26	7	5
	in grain only	36	38	50	49	58	70	57	66	85	84
Leaves removed	total	54	56			64	75	84	87		
	in stem* only	23	24			15	15	18	17		
	in grain only	26	26			44	54	59	64		
Only ears exposed to light	total	23	28	24	28	33	35	36	34		
	in grain only	19	22	20	21	27	29	29	29		
L.S.D.** (p=0,05)	Stems	2.7		7.9		3.4		4.5			
	Grain	3.4		5.4		3.9		5.0			

* The reported data comprise the carbon translocated to and assimilated by the stem (including the sheaths).

** The L.S.D. for stems and grain of plants deprived of leaves or with all vegetative parts shaded were calculated on the basis of differences between the activity of each replicate and the average activity in the control (the differences between replicates in the control plants were very small).

stems over those formed in the leaf laminae could be found in the grain; between the 15th and 20th day the leaf laminae did not supply with any marked amounts of photosynthates.

The observed tendency of changes in the role of leaf laminae and of stems in the daily accumulation of ^{14}C — assimilates in the grain corresponds to the tendency of changes in the contribution of these organs to the total CO_2 assimilation. However it should be borne in mind that the translocation of photosynthates from stems to the grain in plants deprived of leaf laminae — and it is mainly on their behaviour, that the conclusions about the contribution of ^{14}C — assimilates from vegetative parts were based — could have been more intense than in the controls because of the treatment applied. Thus the participation of photosynthates formed in stems in the total amount of daily translocated carbon from the vegetative parts to the grain

could have been in fact smaller, especially at the latest stages, than it would have seemed from the data obtained.

A number of results of exper. III and IV indicate that the treatments applied could have caused an increased translocation of assimilates from the stem to the grain, i. e. the treatments of awn removal or of ear shading. However the kernels exercising as acceptors of organic compounds a marked influence on the translocation of photosynthates from the stem did not effect their translocation from the leaf laminae at all. The evidence for this is the great accumulation of labelled carbon in the stems of plants deprived of ears; at the same time the leaf laminae of these plants do not differ significantly from those of the controls as regards their radioactivity.

The above reported experiments permitted an approximate estimation of only the daily translocation of products of current photosynthesis in green parts of barley to its grain. The fact, that relatively great amounts of them remain after 24 hours in the vegetative parts does not allow any conclusion to be drawn about the true role of particular investigated organs in the accumulation of assimilates in the grain. In 1960 in the investigations with barley carried out in the greenhouse (see part I, 1963) several days after ear emergence, i. e. on June 23 some plants deprived previously of tillers were placed in the plexiglass chamber, into which ^{14}C — labelled CO_2 was introduced. Control plants, plants with ear shaded and plants with all vegetative parts shaded vere investigated *. They were sampled after one and two weeks exposure to $^{14}CO_2$ (each treatment in 3 replicates, 2 plants each). The labelled carbon in equal amounts and of equal specific activity was introduced at 2—3 day intervals in the first week — three times, in the second one-twice. It should be remembered that — as it was discussed in detail in the quoted publication — in the period under investigation in the greenhouse: 1) the control plants showed the highest weight increase, 2) shading of vegetative organs for 15 days caused a more intense growth of awns, 3) ear shading at that time brought about an increase in the weight of the flag leaf lamina and in the translocation of organic compounds from the green plant parts to the grain.

As the results of the experiment 1960 with labelled carbon show (Tab. 8), the total weight increment of controls after two weeks was not lower than that of analogous plants under greenhouse conditions. However the weight of their leaf laminae was lower. The observations of vegetative organs indicated that the ageing of plants in the plexiglass chamber was quicker than in the greenhouse.

* The shading treatments were applied immediately before the plants were placed in the chamber.

Table 8

Dry weight * and radioactivity of barley plants after one and two week exposure to $^{14}CO_2$ (per plant)
Experiment 23.VI—7.VII.1960.

Plant parts	After one week				After two weeks			
	I	II	III		I	II	III	
	control	only ear shaded	only ear exposed to light	L.S.D. p=0.05	control	only ear shaded	only ear exposed to light	L.S.D. p=0.05
			dry weight g d.m.					
Leaf laminae	0.19	0.20	0.16		0.19	0.16	0.17	
Stem**	1.06	1.04	1.01		1.04	1.04	0.93	
Glumes and awns	0.18	0.16	0.16		0.18	0.15	0.15	
Grain	0.59	0.54	0.47		0.92	0.79	0.65	
Total	2.02	1.94	1.80		2 33	2.14	1.90	
			radioactivity 10^3 cpm					
Leaf laminae	28	31			60	49		
Stem**	146	77	7***		182	156	6***	
Glumes and awns	37	15	27		62	17	33	
Grain	699	603	208	39	1623	1050	543	37
Total	910	726	242	32	1927	1272	582	53

* The total dry weight of the control on June 20 was 1.67 g (leaf laminae 0,35 stem 1.02, chaff 0.15 grain 0.14 per plant); on July 6 the total weight of the control in the greenhouse was 2.29 g (leaf laminae -0.25, stem 1.04, chaff -0.16, grain 0.84). The final dry weight of the grain was 1.45 g.

** Including the rachis.

*** These data represent mainly the activity of the rachis.

The average amount of carbon assimilated by the controls during the first an the second week was similar. After the first seven days about 77 % of this amount was translocated to the grain. In the vegetative organs 19 % could be found (in leaf laminae barely 3 %). After the subsequent week the content of photosynthates in the grain increased more than twice constituting just about 84 % of their total amount in plants at that time. As average for the two week period the contribution of vegetative organs to the total CO_2 assimilation accounted — according to the results of treat. II (ear shaded) — for 66 %, the contribution of the ear — according to treat. III (ear only exposed to light) — for 30 %. Thus the contribution of the vegetative parts would oscillate between 66—70 % and of awns and glumes between 30—34 %

(the standard error is less than 3 %). However during the first week only — according to analogous calculations — the contribution of vegetative parts would amount to 74—80 % and that of the ear to 20—26 %. These results — similar to the results of exper. 1961 — clearly indicate that with ageing of the leaves the relative role of green parts of the ear increases.

The contribution of vegetative organs to the accumulation of products of current photosynthesis in the grain for the whole period under investigation would account for 65—70 %. The remaining amount would be due to assimilates formed in the ear itself. It should be stressed that the results of the first week are from this point of view rather divergent. So the contribution of the ear to the accumulation of ^{14}C — assimilates in the grain at that time according to treat. III would amount to 30 %, but according to treat. II barely to 14 % of their total content. However the radioactivity of the stem in the latter treatment indicates that the translocation of photosynthates from this part was markedly greater than in the control. Taken this into account the magnitude of the ear contribution would be about 23 % instead of 14 %.

In the reported experiment — in contrast to the experiment in the greenhouse (in 1960) — it was hard to find a clear reaction of plants to the shading treatment (which lasted for a long time!), a reaction, which would have been revealed in an increased rate of photosynthesis in organs exposed to light. It is possible that the lack of this reaction was due to the accelerated ageing of barley under the conditions of the chamber.

DISCUSSION

The above reported results of the experiment 1961 under greenhouse conditions are very similar to those obtained in the experiment with the same variety of barley carried out at Puławy. The similarity is revealed partly by the weight increment of the plants, which during the first approximately 10 days after heading (when at least 2—3 leaves on each shoot were still green) was higher than during the subsequent 15—25 days. The standard error is rather high in comparison to the magnitude of the weight increment within particular five day periods, so it is difficult to determine to what degree these increments were diminishing with ageing of the plants. Thorne (1960, 1961) investigating barley under constant conditions found that the rate of net assimilation (per unit of green leaf area) with ageing of the plants was diminishing weekly by about 15 %. Under uncontroled conditions the magnitude of the weight increment is obviously a resultant of the influence of the physiological state of the plant as well as of the influence of external factors. The latter can act in plus or in minus. Therefore also the experiments with ^{14}C carried out at five day intervals did not give the possibility of determining the changes in the

rate of photosynthesis with ageing of the investigated barley variety. It seems, however, that the assimilating capacity of plants at the milk stage of their grain (exper. III) was greater than would have resulted from the weight increase at that time (between June 22 and 27). For in this period — in contrast to the following one — the total increment was minimal, statistically even insignificant. This can be due to the relatively great losses of organic compounds at the milk stage, losses due to respiration mainly of the developing kernels (Grzesiuk 1961 a, b).

The behaviour of plants deprived of the tiller, which indicate the possibility of translocation of photosynthates in the control from this shoot to the main one in the later period of grain filling, is worth noticing. Thorne (1962) points to the possible occurrence of this phenomenon in barley. But her remarks concern tillers, which did not bear ears and which died early after the ears of other shoots had emerged. In our experiments this was not the case. The problem of translocation of assimilates from one shoot to another demands more detailed investigations, the more so because Terentiew and Cariewa (1959) observed in barley a reverse direction of movement, i. e. from the main shoot to the tillers.

When the role of investigated plant parts in the total CO_2 assimilation is estimated on the basis of the results obtained one has to take account of some additional errors, which could have been caused by the treatments applied. The first one is the possible increased rate of photosynthesis in organs exposed to light during a dozen or so hours immediately after shading or removal of appropriate plant parts. It seems, however, that these recompensation processes could have played a certain role during the first 10 days of investigations. In the later period, when the leaf laminae and sheaths were gradually turning yellow, they were in all probability of litle significance. Therefore in the first period, the period of the greatest dry matter increase, the role of the leaf laminae in the total CO_2 assimilation could have been higher (and the role of ears perhaps slightly lower) than the data obtained seemed to indicate.

There is, however, another source of errors, which could have influenced the results, i. e. differences between particular investigated treatments in the degree of participation of ^{14}C — assimilates in respiration. E. g. the degree of utilisation of ^{14}C — assimilates in respiration in stems and ears of plants deprived of leaf laminae —

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* Even if assumed that the increased — as compared with the normal — CO_2 concentration in the chamber did not influence the photosynthesis rate in particular organs to a different degree; it has to be verified.

** The influence of carboxylation processes, which might have occurred in the shaded organs — as the results show — was insignificant.

if the rate of this process was not lowered — could have been relatively higher than in analogous organs of the controls. The same stricture concerns the ears of plants whose all vegetative parts were shaded. The resulting error, however, does not seem to be great, if one takes into account that a barley ear (including the grain), i. e. the plant part, which respires perhaps most intensely, produced at night within the period from its emergence to full maturity — according to Porter and others (1950) — a total amount of CO_2, which constituted only 10% of the amount of CO_2 assimilated (true photosynthesis) by awns and glumes in the daytime during that period.

As it was mentioned above the CO_2 assimilation calculated from the plant radioactivity in exper. 1961 was nearer the value of the true than the net assimilation. On the other hand the data obtained from exper. 1960 — taking into account the much longer exposure to labelled carbon — are nearer the value of the net assimilation. The physiological state of plants investigated in 1960 was similar to the state of plants investigated in 1961 within the period between the 5th and 20th day after full ear emergence.

The contribution of all vegetative parts of these plants to the total content of ^{14}C — assimilates accounted for 66—70% and the contribution of the ear for 30—34%. These values are very similar to those obtained in exper. 1961. The results from the experiments with ^{14}C in both years clearly indicate a significantly greater role of the vegetative parts of barley within the investigated period of its development than it would seem from the data obtained in the experiment without application of labelled carbon (part I).

However it should be borne in mind that the estimations of the role of particular organs in CO_2 assimilation within the period from ear emergence to full maturity of barley plants are approximate. For they may undergo some changes especially under field conditions depending partly on the rate of ageing of the leaves and also on the intensity of the light, to which particular organs are exposed. It is worth stressing in this connection that: 1) the number of completely green leaves on each shoot of barley, sampled in the field in 1962 (part I) immediately after heading, and the rate, at which they were yellowing, did not differ significantly from that observed in pot cultures; 2) under field conditions the most privileged plant part with respect to the illumination is the ear, and the lower parts may often be exposed to light intensities below the point of saturation (Stalfelt 1960). On the other hand in our experiments the light intensities, to

* It should be added, that in fact the dry weight (and green area) of vegetative parts of the main shoot in 1960 was higher than that in 1961, but the ageing process proceeded quicker.

which particular plant organs were exposed, were rather similar. However, there is no doubt that the character of the changes in the role of particular green organs in the CO_2 assimilation, observed after heading in barley plants grown in pots will be similar also under field conditions. For the differences between various green parts in the rate of ageing are in both cases similar (leaf laminae ⟩ sheaths and stem ⟩ ear).

The data from exper. 1961 concerning the translocation of assimilates — as was mentioned above — gave only limited informations about the contribution of particular plant parts to the accumulation of photosynthates in the grain. For it can be assumed that at least a proportion of ^{14}C — assimilates remaining after 24 hours in green organs, especially in the stems * can be translocated afterwards to the grain. On the other hand the possibility of utilisation of a certain amount of assimilates, just accumulated in the kernels, in respiration in the later period is also to be taken into account.

The relative magnitude of the daily accumulation of photosynthates in the grain — expressed as percentage of their total content in the control plants — was increasing significantly in the course of the investigations. This, it seems, resulted mainly from the changes in the physiological state of the mother-plant and of the kernels. It is hard to assume that the differences in temperature in the plexiglass chamber between particular experiments could have played an important role in this phenomenon. For a number of facts indicate that there was no clear relationship between the translocation of photosynthates to the grain — found after 24 hours — and the temperature (an analogous relative rate of translocation from green parts of the ears in all experiments, a similar relative accumulation of photosynthates in the grain in exper. III and IV in spite of differences in temperature etc.). The comparatively small degree of translocation of ^{14}C — assimilates to the grain at the first stage of filling (exper. I 1961) is also confirmed by the relatively small weight increase of the grain of plants under greenhouse conditions at that time.

The mean contribution of photosynthates from the green parts of the ear accounted about 50% of the total amount daily accumulating in the grain. According to the results of exper. 1960 the contribution of the ear itself to the accumulation of products of current photosynthesis within a two week period would account for 33—35%, the remaining proportion would be due to the assimilating activity of the vegetative organs. This value is very similar to the value given by Porter and

* The transient accumulation of assimilates in these plant parts, revealed by their weight increase in the first period after heading, was confirmed also by the results of exper. I with ^{14}C.

others (1950) for the contribution of the green parts of the ear of a two rowed barley variety to the total amount of organic compounds accumulated in the grain at full maturity. It should be remember, however, that in exper. 1960 the ageing process of the vegetative organs proceeded quicker than under normal conditions. This could have influenced the obtained results.

It is worth noticing that even in a period of intense accumulation of organic matter in the grain above 15% of the total content of assimilates, found in the plants after two weeks exposure to ^{14}C — CO_2, remained in their green parts, mainly in stems. This indicate that it would be purposeful to examine — under conditions more approaching the normal ones — what proportions of assimilates formed at various stages after heading are in fact translocated to the grain and remain in it till full maturity.

CONCLUSIONS

Among the results obtained from the reported, preliminary experiments the following are worth noting:

1. The dry weight increase of spring barley plants var. „Browarny PZHR" (grown in pots) within the period from ear emergence to maturity amounted to about 40% of their final weight; the increment during the first 10 days after heading was even higher than that after the following 15—25 days. At the milk stage of the grain, when the total weight increase was minimal, the photosynthetic capacity of the plants was still relatively high. The grain yield at full maturity corresponded to the size of the total plant increment.

2. Within the first 10 days after heading the main shoot of plants deprived of the tiller — after 24 hours exposure to ^{14}C — labelled CO_2 in a plexiglass chamber — did not differ as regards its radioactivity from the control one. Within the later period its radioactivity was less as compared to the control. This latter fact indicates a possible translocation of assimilates from the tiller to the main shoot.

3. The contribution of particular green parts to the total amount of carbon assimilated by the plant within the period under investigation was changing markedly; at the first period after heading the contribution of leaf laminae was the greatest amounting to 45%, in the later period it was gradually diminishing, accounting between the 15th and 20th day after heading for only 15%. The contribution of the stems (including sheaths) was changing within this period from 30 to about 50%; the contribution of the ear from 25 to about 35%. At the end of growth, when the assimilating capacity of the plants was wery small, almost all the assimilated carbon was due to ear activity only.

4. At all investigated stages the translocation of photosynthates from leaf laminae and from green parts of the ears was relatively

rapid. During 24 hours about 80% of carbon assimilated by these parts in daytime was translocated, the assimilates from leaf laminae to the stem and grain, from awns and glumes to the grain only.

5. The daily accumulation of photosynthates in the grain was different at particular stages of its development. In the first week after heading it accounted for about 37%, in the later stages for 50 to 63% of the total amount of carbon daily assimilated by the plant. An average of about half of the amount accumulating in the grain derived from the green parts of the ear.

6. After a two-week exposure to ^{14}C-labelled CO_2 85% of assimilates accumulated in the plant could be found in the grain; about one third of this amount derived from the ear itself.

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STRESZCZENIE

W roku 1961 przeprowadzono doświadczenia wazonowe z jęczmieniem jarym odm. PZHR Browarny. Badano przyrost suchej masy w okresie od wykłoszenia do dojrzałości. Sprzętu dokonywano siedmiokrotnie przeważnie w odstępach pięciodniowych. W połowie każdego okresu część roślin umieszczano na dobę w kamerze z pleksiglasu, do której wprowadzono znakowany ^{14}C dwutlenek węgla. Uwzględniono następujące kombinacje: 1. rośliny kontrolne, 2. pozbawione pędu bocznego, 3. pozbawione blaszek liściowych, 4. pozbawione ości, 5. pozbawione kłosów, 6. rośliny z kłosami zaciemnionymi, 7. rośliny z wszystkimi organami wegetatywnymi zaciemnionymi. W omówieniu badań uwzględniono wyniki doświadczenia przeprowadzonego w 1960 r., w którym umieszczano rośliny w atmosferze zawierającej znakowany CO_2 na okres dwóch tygodni.

Uzyskane wyniki pozwalają stwierdzić, że:

1. Przyrost suchej masy roślin w okresie od wykłoszenia do dojrzałości wynosił około 40% ich końcowego plonu; przyrost w ciągu pierwszych 10 dni po wykłoszeniu był nawet większy niż w ciągu następnych 15—25 dni. W fazie mlecznej dojrzałości, kiedy przyrost ogólny był minimalny, zdolność fotosyntetyczna roślin była jeszcze stosunkowo duża. Wysokość plonu ziarna odpowiadała wielkości ogólnego przyrostu masy roślin.

2. W okresie pierwszych 10 dni po wykłoszeniu radioaktywność pędu głównego roślin pozbawionych pędu bocznego — po 24 godzinach ekspozycji na znakowany CO_2 — nie różniła się od aktywności stwierdzonej w kontroli. W późniejszym okresie aktywność pędu głównego analogicznych roślin była niższa w porównaniu z kontrolą. Ten fakt wskazuje na ewentualne przemieszczanie się asymilatów z pędu bocznego do głównego w okresie intensywnego wypełniania się ziarna.

3. Udział poszczególnych organów roślin w ogólnej asymilacji CO_2 ulegał zmianom w badanych fazach: w pierwszym okresie po wykłoszeniu udział blaszek

liściowych był największy, wynosząc około 45%, w okresie późniejszym ulegał stopniowemu zmniejszeniu i między 15 a 20 dniem po wykłoszeniu wynosił tylko około 15%. Udział źdźbła wraz z pochwami wzrastał od około 30 do 50%; udział zaś kłosa od 25 do 35%. Pod koniec wegetacji, kiedy aktywność fotosyntetyczna rośliny była bardzo mała, prawie cała ilość zasymilowanego CO_2 przypadała już tylko na kłos.

4. We wszystkich badanych fazach przemieszczanie asymilatów z blaszek liściowych i zielonych części kłosa było stosunkowo bardzo intensywne. W ciągu 24 godzin około 80% zasymilowanego przez te organy węgla uległo przemieszczeniu, z blaszek liściowych do źdźbła i ziarna, z ości i plew tylko do ziarna.

5. Względna akumulacja asymilatów w ciągu doby w ziarnie była różna w poszczególnych fazach jego wypełniania. W pierwszym tygodniu po wykłoszeniu wynosiła około 37%, w późniejszych fazach 50 do 63% ogólnej ilości produktów fotosyntezy stwierdzonej w roślinach po upływie doby. Przeciętnie około połowa ilości tych związków pochodziła z zielonych części kłosa.

6. Po upływie dwóch tygodni ekspozycji na znakowany CO_2 w ziarnie stwierdzono około 84% nagromadzonych w roślinie asymilatów, z tej ilości około jedna trzecia pochodziła z zielonych części kłosa.

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