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

V. Contribution of products of current photosynthesis after heading to the accumulation of organic compounds in the grain of barley

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The main aims of investigations on spring barley 'PZHR Browarny' var. presented here were analogous to those of experiments with spring wheat, reported previously (Part IV, 1964):

1) to determine the degree of accumulation in plants, at ripeness, of photosynthates formed at various stages after heading,

2) to evaluate the contribution of particular green parts to the total plant photosynthetic activity by application of shading and defoliation treatments for some hours only.

METHODS

Seeds were sown into a soil-sand mixture on April 19, 1962. Basal and top dressings were analogous as in the aforementioned investigations on wheat. Full sprouting was noted on April 23, shooting — on May 21. The plants were thinned gradually to 12 per pot. The beginning of ear emergence was observed on June 16. The first sampling was completed on June 18, i.e. 54 days after sprouting. At that time each plant had two ear-bearing shoots (the very few plants, which had a second small tiller, were removed). Only four upper leaf laminae on each shoot were fully green, the fifth — the lowest one was only partially (1/3) green. During the period from heading to full maturity six samplings * were completed at 7 — 10 day intervals.

In the middle ** of each period between samplings (the last one excepted) a group of plants was placed for three and a half hours (immediately after noon) in a plexiglass chamber (out-of-doors), into which ^{14}C-labelled CO_2 was introduced. The treatments applied before introducing the plants into the chamber as well as the procedures *** after

* Unfortunately the plants sampled for chlorophyll determination were lost by accident.

** The first experiment with $^{14}C—CO_2$ was carried out a little later.

*** Plants deprived of the flag-leaf lamina only were not investigated.

Table 1

Conditions under which plants* were kept in the plexiglass chamber

No.	Date of experiment	CO_2 content		mo	^{14}C-content in plants - % of the total radioactivity applied	Fluctuations of temperature °C	Weather conditions
		g	%v				
I	25.VI	1.45	0.11	1.5	65	26 - 30	sunny
II	2.VII**	1.96	0.14	2.3	25	20 - 23	clouded
III	9.VII	1.45	0.11	1.5	43	24 - 31	sunny
IV	16.VII**	1.40	0.10	1.5	4	17 - 28	varying cloudiness (rain)

*Expt I each shoot had three fully green leaf laminae (including the flag leaf); the fourth one - green only at its base; expt. II - two fully green leaves, the third leaf lamina half green; expt. III - only flag leaf fully green, the second one partially (1/3) green, the ear still fully green; expt. IV - all vegetative organs completely yellow; awns and glumes turning yellow.

**Together with lupine plants from another experiment.

their removal from it were analogous as in the aforementioned experiments with wheat, carried out in the same vegetation period.

The tiller was treated in the same way as the main shoot. In expts. II and III a group of additional plants was deprived of the tiller immediately before they were placed in the chamber.

In Table 1 the conditions, under which the plants were kept during exposure to ^{14}C-CO_2, are presented.

RESULTS

Immediately after ear emergence the weight of the main shoot was one and a half times that of the tiller (Table 2), owing mainly to differences in the weight of the stem including sheaths (Figs. 1 and 2). As in previous investigations (Part II, 1963) the highest total increment took

Table 2

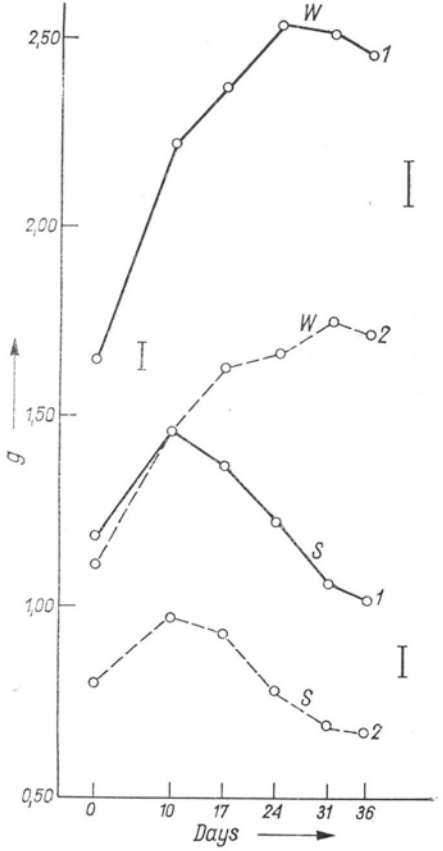
Weight of barley - g.d.m. per plant

Date of sampling	Main shoot			Tiller			Aerial part total	Root
	shoot	grain*	total	shoot	grain*	total		
18.VI	1.56	0.09	1.65	1.06	0.05	1.11	2.76	0.78
28.VI	1.84	0.38	2.22	1.23	0.24	1.47	3.69	0.81
5.VII	1.71	0.66	2.37	1.17	0.46	1.63	4.00	0.73
12.VII	1.55	0.98	2.53	1.00	0.67	1.67	4.20	0.70
19.VII	1.37	1.14	2.51	0.91	0.84	1.75	4.26	0.65
24.VII	1.34	1.11	2.45	0.91	0.81	1.72	4.17	0.62

*Mean number of kernels: main shoot - 26; tiller - 23.

place during the first 10 days, being greater in the main shoot than in the tiller. Over the subsequent 21—26 days *, the weight increase was smaller and the same for both shoots.

The rate of dry matter accumulation in the grain during the period under investigations was (except for the last interval) almost constant,



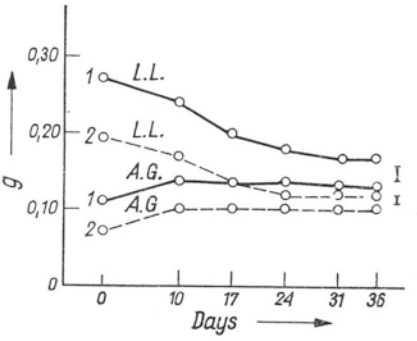


Fig. 2. Weight of leaf laminae * and awns & glumes — g d.m. per plant
L.L. — leaf laminae; *A.G.* — awns & glumes. *1* — main shoot; *2* — tiller.

* Four leaves including the flag leaf, which weighed 0.033—0.021 g (M.S.) and 0.025—0.018 g (T.); the lowest one (the fifth L.L.) weighed at the first sampling 0.07 (M.S.) and 0.05 g (T.).

Fig. 1. Total dry weight and stem * weight — g d.m. per plant
W — total; *S* — stem; 0 = 54th day after sprouting; vertical lines represent least significant differences (p = 0.05) in figs 1, 2 and 3. 0—54 days after sprouting.
1 — main shoot; *2* — tiller.

* Including leaf sheats and rachis, its weight: 0,03 (M.S.) and about 0.02 g (T.); increase of the stem length between the first and second harvest: from 86 to 99 cm (M.S.) and from 73 to 85 cm (T.).

but higher in the main shoot than in the tiller (Fig. 3). It is worth noting that the transient increment of the stem in the former was also higher. At ripeness its weight in both shoots was significantly lower than immediately after heading. The grain yield ** at that time was higher than the total weight increase of the plant.

The data obtained in the particular experiments for the plant radioactivity were referred to the specific activity of CO_2 in expt. I. There-

* Within the period between the 8th and 18th day after the first sampling the mean day temperature was very low, varying from 12 to 15°C.

** The difference between its weight at ripeness and immediately after heading.

fore the results of all four experiments are comparable (Tabs. 3 and 4). However, taking into account the differences in CO_2 concentration and temperature between the first three experiments * (Table 1) only expts. I and III can give more reliable information about changes in photosynthesis with ageing. During the two-week period between these experiments the total photosynthetic activity of the investigated plants

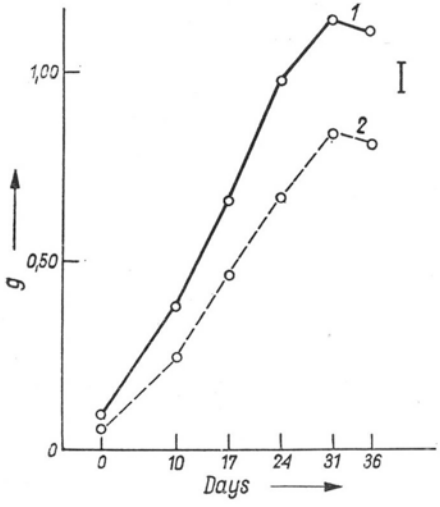


Fig. 3. Weight of grain — g d.m. per plant. *1* — main shoot; *2* — tiller.

diminished by about 50%, without significant changes in ear photosynthesis when treat. 5 is taken into consideration. The very low activity of the plants investigated on the 28th day after heading, constituting only about 4—6% of the activity found in the plants three weeks earlier, resulted mainly from their physiological state.

The radioactivity of the main shoot of plants deprived of the tiller — in expts. II and III — did not differ significantly from that found in the control (data not presented in Table 4).

In all experiments — except the last one — the photosynthetic activity of the main shoot (controls) was higher than that of the tiller, but the differences with ageing diminished from about 34 to 19% (Fig. 4).

The attempts to determine the contribution of particular green parts to the total photosynthetic activity of the plant were not very successfull, especially when the leaf laminae and the stem (including sheaths) are taken into consideration. The data of expts. I and II indicate that removal of leaf laminae, respectively stem shading may have had influence not only on ^{14}C-assimilate translocation, but also on the photosynthetic activity of organs exposed to light. An indirect indication supporting

* The results obtained in expt. II may perhaps be due also to the presence of lupin plants in the chamber.

Table 3

Radioactivity of barley immediately after exposure to $^{14}C-CO_2$ - 10^3 cpm per plant

Experiment I - June 25

No.	Treatment	Shoot[1]	Plant parts								Contribution of investig. part per cent
			laminae		sheats		stem[3]	awns and glumes[4]	grain	total	
			fl.l.	low.l.	fl.l.	low.l.					
1	control	M.S.	81	387	157	192	601	325	335	2078	100
		T.	62	261	101	136	338	217	254	1369	100
2	l.lam. removed	M.S.	-	-	115	103	276	223	258	975	53
		T.	-	-	92	86	215	168	203	764	44
3	stem shaded	M.S.	51	360	30	45	258	234	226	1204	42
		T.	61	222	30	35	167	151	131	797	42
4	ear shaded	M.S.	60	534	156	194	593	46	228	1811	13
		T.	51	330	114	123	452	31	182	1283	6
5	veg.parts shaded[2]	M.S.	traces				10	285	178	473	23
		T.					9	207	140	356	26
L.S.D. all treats			16	44	23	21	34	29	30	137[5]	
L.S.D. treat.5.								14	34	41	

[1] In all experiments: M.S.-main shoot; T.-tiller; fl.l.-flag leaf; low.l.-lower leaves.

[2] I.e.only ears exposed to light; covers were removed immediately after exposure to $^{14}C-CO_2$ (in all experiments).

[3] Including rachis; its radioactivity: control-20 (M.S.) and 17 (T.), treats. 2,3, and 4-about 12 and 11 x 10^3cpm respectively; in treat. 5 only rachis was radioactive; in the shaded stem as well as in the leaves only traces of activity were found.

[4] Radioactivity of glumes: control-43 (M.S.) and 35 (T.), treat.4 - 14 and 9, treat.5 - 29 and 23 x 10^3 cpm, respectively.

[5] L.S.D. for the tiller only: 107 x 10^3 cpm.

($p = 0.05$).

this supposition is the low activity of awns & glumes in the treatments discussed, even significantly lower * than that found in the same parts of plants with all vegetative organs shaded. It is worth noting that such differences were not observed in expt. III, when ^{14}C-assimilate translocation to the developing kernels was very intensive, much more

* The differences are greater when the possible afflux of a certain amount of ^{14}C-assimilates from vegetative organs to these parts of the ear are also taken into account; this possibility — if it is not an artefact — is shown by plants, whose ears were shaded.

Table 4

Radioactivity of barley immediately after exposure to $^{14}C\text{-}CO_2$ - 10^3 cpm per plant

Experiment II - IV

No.	Treatment		Plant parts: shoot	laminae: fl.l.	laminae: low.l.	stem[1]	awns and glumes[2]	grain	total	Contribution of investig. part per cent
						Experiment II - July 2				
1	control	M.S.	46	195		306	157	378	1082	100
		T.	51	111		232	140	282	816	100
2	l.lam. removed	M.S.	-	-		157	80	226	463	57
		T.	-	-		111	78	194	383	53
3	stem shaded	M.S.	45	110		100	107	263	625	42
		T.	43	60		57	79	201	440	46
4	ear shaded	M.S.	37	136		211	13	223	620	42
		T.	36	62		127	9	179	413	49
5	veg.parts shaded	M.S.	0	0		4	129	185	318	29
		T.	0	0		5	99	158	262	32
L.S.D. all treats.			16	42		36	21	33	114[3]	
L.S.D. treat. 5							18	30	41	
						Experiment III - July 9				
1	control	M.S.	14	15		194	259	437	919	100
		T.	13	14		159	207	356	749	100
2	l.lam. removed	M.S.	-	-		202	288	272	762	17
		T.	-	-		149	244	249	642	14
3	stem shaded	M.S.	23	5		63	287	219	597	35
		T.	24	5		47	192	182	450	40
4	ear shaded	M.S.	41	33		224	22	124	444	52
		T.	50	24		187	17	170	448	41
5	veg.parts shaded	M.S.	0	0		11	258	177	446	48
		T.	0	0		7	189	174	370	49
6	awns removed	M.S.	17	7		113	41	208	386	58
		T.	19	6		91	39	194	349	53
L.S.D. all treats						30	30	38	75[3]	
L.S.D. treat. 5							35	37	41	
						Experiment IV - July 16				
1	control	M.S.				3	28	48	79	
		T.				4	23	53	80	

[1] Including leaf sheats (which were not analysed separately) and rachis; its radioactivity was: expt II, control - 13 (M.S.) and 12 (T.), treats. 2,3,4 - about 8 and 6 x 10^3 cpm; expt II: control - 21 and 20, treats. 2,3 - 16 and 15; treat. 4,6 - about 8 x 10^3 cpm. In expts II, III, IV, treat. 5 - rachis only radioactive.

[2] Radioactivity of glumes: expt II - control - 24 and 22, treat. 5 - 19 and 16 x 10^3 cpm; expt III - control - 38 and 26, treat. 5 - 31 and 23 x 10^3 cpm.

[3] L.S.D. for the tiller only: expt II - 83, expt III - 58 x 10^3 cpm. ($p = 0.05$).

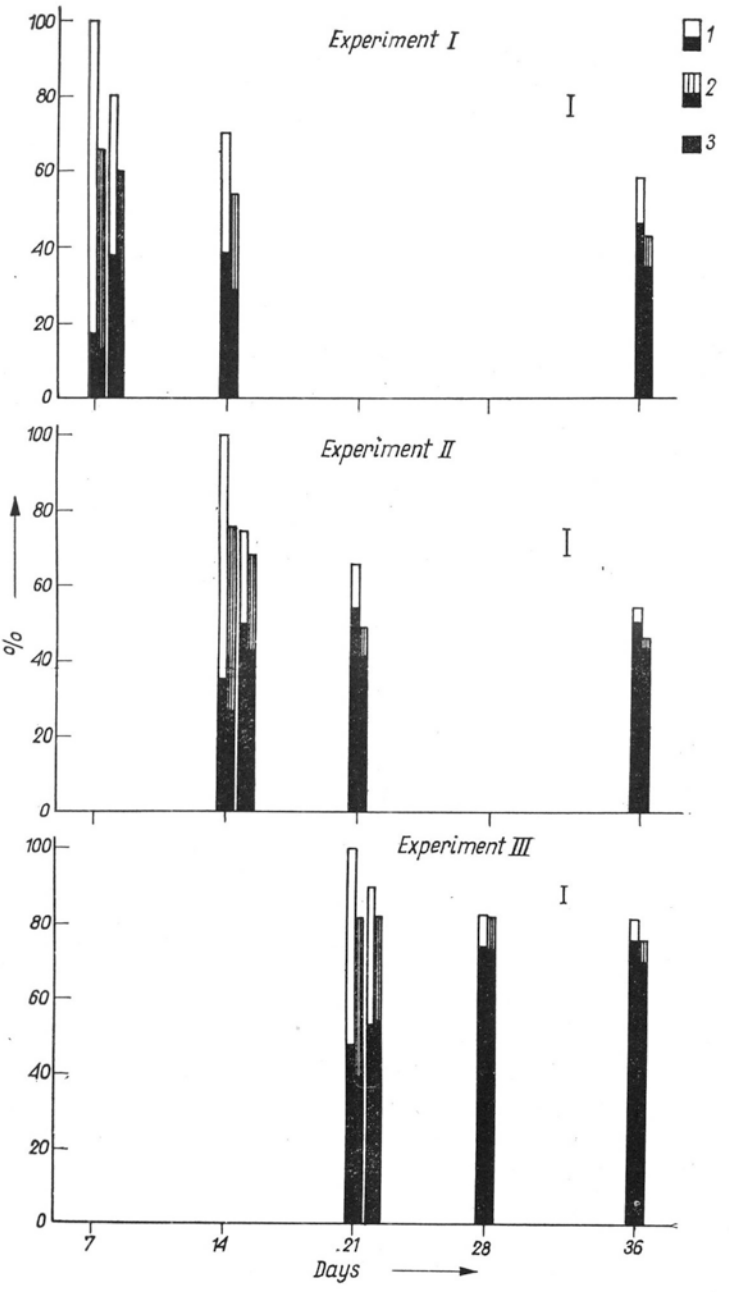


Fig. 4. Changes in radioactivity of control plants — per cent of the total activity found in the main shoot immediately after exposure to $^{14}C—CO_2$.

Vertical lines represent L.S.D. ($p = 0.05$) for the differences between the main shoot and the tiller.

1 — total, main shoot; *2* — total, tiller; *3* — grain.

so than in expt. I. Hence, the data obtained in the first two experiments seem to exceed the true contribution of leaf laminae and/or of the stem to the photosynthetic activity of the investigated plants.

The contribution of the ear can be evaluated from the results of treats 4 and 5. However, the data obtained from plants with ears shaded (treat. 4) are very divergent. The much higher radioactivity — than in the control — in lower leaf laminae (M. S.) as well as in the stem (T.) in expt. I allows to suppose that, at the investigated development stage, a compensation for the shaded ear in photosynthesis could have taken place (the radioactivity found in grain — when compared with the control and treat. 5 — does not indicate any marked disturbance in ^{14}C-assimilate translocation to the ear). A reverse phenomenon seems to have occurred a week later, in expt. II.

The data obtained from plants, whose ears only were exposed to $^{14}C—CO_2$ (treat. 5) may be considered as much more reliable, for 1) similarly as in previous investigations, the L.S.D. values is in this treatment relatively small, 2) the possible compensation in photosynthesis for shaded vegetative organs — even high as compared to the true assimilation rate in the ear — would be relatively low in comparison with the total photosynthetic activity of the plant, especially in the first two experiments (the radioactivity of awns & glumes as well as of the grain — as compared to the control — does not indicate any high degree of compensation). It should be added that in expt. III * the results of treat. 5 are similar — within the limit of the error — to that of treat. 4. Thus the contribution of the ear — close in both shoots — to the total photosynthetic activity of the plant would have changed from about 24% — a week after heading to about 48% — two weeks later.

The distribution of photosynthates, immediately after plant removal from the chamber (Tables 5 and 6) **, shows that their translocation from leaf laminae and green parts of the ear during the three and a half hours of exposure to $^{14}C—CO_2$ was intensive. After 20 hrs (overnight) these organs contained only about one third of the amount found immediately after exposure, and 10% or even less of the amount in the whole plant determined simultaneously (expts. I and II).

The amounts found in leaf laminae as well as in the green parts of the ears after the next six days were already very small and did not

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* The radioactivity found in plants deprived of awns in this expt. indicates some artefacts at least in ^{14}C-assimilate translocation.

** There were no significant differences — either in the total or in the grain yield — between plants exposed to labelled CO_2 and those kept during the whole vegetation period in the greenhouse. The L.S.D. ($p = 0.05$) expressed as percentage of the total activity of each shoot at time 0 were calculated from the absolute values of plant radioactivity (including the controls at time 0).

Table 5

Changes in radioactivity of barley from after exposure to $^{14}C\text{-}CO_2$ to full maturity per cent of the total activity in control plants

Experiment I - June 25

Time after exposure[1]	Shoot	Control									Vegetative parts shaded[5]			
		leaf lam.[2]	leaf sheaths	stem		rachis awns glumes	grain		whole plant		rachis awns glumes	grain		total
				total	ethan. sol.		total	ethan. sol.	total	ethan. sol.		total	ethan. sol.	
0	M.S.	22.5	16.8	28.0	27.5	16.6	16.1	13.5	100.0	80.6	14.2	8.5	6.8	22.7
	T.	23.6	27.3	23.4	22.4	17.1	18.6	13.6	100.0	73.7	15.8	10.2	8.4	26.0
	total	22.9	17.0	26.2		16.8	17.1		100.0		14.8	9.2		24.0
20 Hrs	M.S.	8.9[3]	8.1	20.4	17.5	5.1[4]	37.5	12.5	80.0	44.9	-	-	-	-
	T.	8.1	8.4	22.7	15.9	5.3	45.5	14.0	90.0	45.5	-	-	-	-
	total	8.6	8.2	21.3	-	5.2	40.7		84.0					
7 Days	M.S.	2.5	4.3	22.5	14.6	2.5	38.1	5.2	69.9	24.8	1.8	16.7	2.4	18.5
	T.	2.4	5.7	28.0	18.2	3.1	42.3	9.2	81.5	34.1	2.3	18.4	4.4	20.7
	total	2.4	4.9	24.7		2.8	39.8		74.6		2.0	17.4		19.4
Full maturity	M.S.	1.2		8.3	2.4	1.7	45.9	3.7	58.1	7.2	0.8	15.9	1.4	16.7
	T.	1.7		9.6	4.5	1.2	52.2	4.0	64.7	9.2	0.8	18.4	1.8	19.2
	total	2.0		8.8		1.5	48.4		60.7		0.8	16.8		17.6
L.S.D.	M.S.						5.1		8.5			2.6		3.2
	T.						5.4		9.1			3.1		3.9

[1] Mean night temperature between the first and second samplings: 16° C.

[2] Ethanol-soluble fraction in all leaf laminae of both shoots at samplings: I - about 70, II - 65, III - 45 and IV - 30% of the total radioactivity found at corresponding times in these organs; this fraction in leaf sheaths constituted about 70% at each sampling.

[3] In lower leaf laminae 8,1% (M.S.) and 7,2% (T.).

[4] Rachis radioactivity: about 0,6% in both shoots.

[5] Only during exposure to $^{14}C\text{-}CO_2$.

Table 6

Changes in radioactivity of barley from after exposure to $^{14}C\text{-}CO_2$ to full maturity - per cent of the total activity in control plants

Experiment II - IV

Time after exposure[1]		Control									Vegetative parts shaded[4]			
		shoot	leaf lem.	stem		rachis awns glumes	grain		whole plant		rachis awns glumes	grain		total
				total	ethan. sol.		total	ethan. sol.	total	ethan. sol.		total	ethan. sol.	
1		2	3	4	5	6	7	8	9	10	11	12	13	14
Experiment II - July 2														
0	M.S.	22.2	27.1	21.9	15.7	35.0	22.8	100.0	71.8	12.2	17.2	12.1	29.4	
	T.	19.8	27.0	19.6	18.6	34.6	23.7	100.0	69.3	12.8	19.3	13.4	32.1	
	total	21.1	27.1		17.0	34.8		100.0		12.4	18.2		30.6	
20 Hrs	M.S.	5.6[2]	13.9	9.1	5.3	49.7	15.9	74.5	31.8	-	-	-	-	
	T.	7.6	19.6	13.4	7.2	55.7	19.1	90.1	44.1	-	-	-	-	
	total	6.5	16.3		6.2	52.3		81.3						
7 Days	M.S.	1.7	8.3	5.0	1.9	53.7	6.7	65.6	13.1	1.0	20.2	2.3	21.2	
	T.	1.1	6.8	5.1	1.7	54.6	5.8	64.2	12.2	1.0	20.7		21.7	
	total	1.4	7.7		1.8	54.1		65.0		1.0	20.4		21.4	
Full maturity	M.S.	1.0	1.7	1.0	0.9	50.3	3.8	53.9	5.1	0.4	17.9	1.4	18.3	
	T.	1.0	1.7	0.9	1.0	57.1	4.5	60.8	5.6	0.6	17.3	1.6	17.9	
	total	1.0	1.7		0.9	53.2		56.8		0.5	17.6		18.1	
L.S.D.	M.S.					6.2		7.4			4.1		5.1	
	T.					6.4		8.7			4.2		5.5	
Experiment III - July 9														
	M.S.	3.2	18.9	14.8	30.4	47.5	35.6	100.0	72.0	29.2	19.3	15.4	48.5	
	T.	3.6	18.5	13.7	30.5	47.4	34.6	100.0	72.3	26.2	23.2	18.0	49.4	
	total	3.4	18.7		30.4	47.5		100.0		27.9	21.0		48.9	

1	2	3	4	5	6	7	8	9	10	11	12	13	14
20 Hrs	M.S.	2.3	19.9	14.9	14.7[3]	53.1	23.9	90.0	50.2	12.8	29.8	13.4	42.6
	T.	1.6	16.4	11.0	16.8	67.0	28.5	101.8	53.4	13.9	32.5	16.2	46.4
	total	2.0	17.9		15.6	59.5		95.0		13.3	31.0		44.3
7 Days	M.S.	0.8	4.0	2.1	4.0	73.9	10.4	82.7	13.6	-	-	-	-
	T.	1.0	4.5	2.2	5.3	91.0	12.1	101.8	16.5	-	-	-	-
	total	0.9	4.2		4.6	82.0		91.7					
	M.S.	0.8	1.8	0.2	3.5[3]	75.3	5.3	81.4	6.4	3.8	37.3	3.3	41.1
	T.	0.8	2.0	tr.	4.0	86.6	6.8	93.4	7.9	2.4	45.6	4.4	48.0
	total	0.8	1.9		3.8	80.6		87.1		3.2	41.1		44.3
L.S.D.	M.S.					9.0		8.3			6.1		6.6
	T.					8.9		8.6			6.0		7.2
Experiment IV - July 16													
0	M.S.	0	tr.		39.2	60.8	38.0	100.0	66.0				
	T.	0	tr.		33.7	66.3	51.8	100.0	75.1				
Full maturity	M.S.	0	tr.		4.0	84.9	15.2	88.9	16.5				
	T.	0	tr.		2.8	101.2	10.2	104.0	11.1				

[1] Mean night temperature between the first and second samplings: expt II - 10° C; expt III - 9° C.

[2] In lower leaf laminae - 4,5% (M.S.) and 5% (T.); ethanol-soluble fraction about 60% of the total.

[3] Rachis radioactivity: sampling II - about 1,5%; IV - 0,3% - in both shoots.

[4] Only during exposure to ^{14}C-CO_2.

differ much from those at full maturity (in all expts.). It is very probable that the decrease of the ^{14}C-assimilate content observed in these organs at that time occurred mainly during the second and third day after exposure.

The changes in radioactivity of the leaf sheaths in expt. I indicate that these are able to retain a certain proportion of the photosynthates (mostly in ethanol-soluble form) for a longer time than the leaf laminae — at the early stage of grain filling, when photosynthates are transiently accumulated in the stem.

The relatively greatest loss of assimilated carbon occurred during the first 20 hrs after exposure (especially in the main shoot). However the losses after a week and more were also considerable (in the expt. IV the differences are not statistically significant). Almost in all cases the ^{14}C-photosynthate content in the tiller (Fig. 4) was lower than in the main shoot, but the differences between them diminished with time and at full maturity they were rather small (except for the first expt.). This fact is due not only to the decrease of differences in their photosynthetic activity with ageing, but also to the greater losses in the main shoot as compared to the tiller during the period between exposure and ripeness.

The relative and absolute losses of carbon assimilated on the 7th and 14th day after ear emergence were much higher than those of carbon assimilated in the later period. Thus the plants at ripeness contained only about 60% of assimilates formed within the first two weeks after heading, whereas the relative amount of carbon assimilated later was much higher — about 87% (expt. III).

The radioactivity of the grain immediately after exposure $^{14}C—CO_2$ shows that the relative extent of photosynthate translocation to it in both shoots increased in the period under investigation. This phenomenon is also reflected in the proportions of assimilates found in the stem and in their changes during the first week after exposure in the particular experiments. The data obtained clearly show that a proportion of the assimilates retained for a period of time in the stem was afterwards translocated to the grain. As supporting evidence may serve the changes in the radioactivity of grain, awns & glumes and of the stem between the 7th day after exposure and ripeness in expt. I, and within the second and seventh day after exposure in expt. III.

It is worth noting that in the period, when no increment of labelled carbon could be detected in the grain, the loss of assimilates in the ear itself — as indicated by plants, whose ears only were exposed to $^{14}C—CO_2$ — was high, especially at the milk stage (expt. II). The losses established in these plants can be considered as underestimating the true utilization of previously assimilated carbon in ear respiration, in parti-

cular in the developing kernels. As indicated by the radioactivity of awns & glumes, for instance 20 hrs after exposure, the translocation of ear photosynthates to the grain was relatively more rapid * than from the vegetative organs. They could have been transformed quickly into insoluble compounds and the ^{14}C-assimilates supplied afterwards to the grain from the vegetative organs could have served to a relatively higher extent as respiration substrate. This possibility is confirmed by the relatively significant proportion of labelled carbon present in the grain for a long time in ethanol-soluble form. All this may have been one of the causes of the unchangeable amounts in the grain of previously assimilated carbon — notwithstanding its afflux from vegetative organs — within the period of high respiration rate in developing kernels.

It is worth stressing that the degree of ^{14}C-assimilate accumulation in grain at particular times after exposure — although higher in the tiller than in the main shoot when expressed as percentage of their photosynthetic activity — was in both shoots analogous when compared

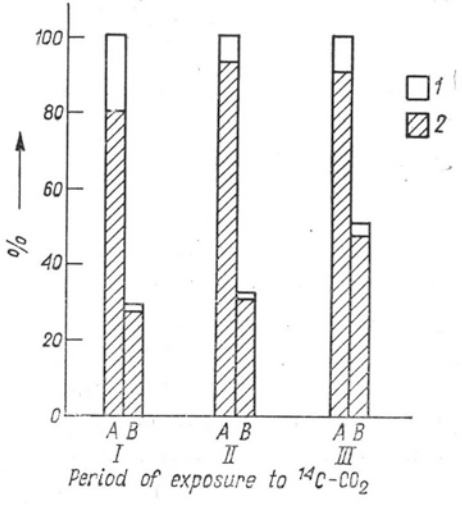

Fig. 5. ^{14}C-assimilates accumulated in grain — per cent of the total radioactivity found in control plants at ripeness

A — controls; *B* — plants with ears only exposed to ^{14}C—CO_2.
1 — mother plant; *2* — grain.

to the amounts of labelled carbon found in them at each time of examination. The absolute amounts of photosynthates in the grain of the tiller in most cases were lower than in that of the main shoot.

The accumulation in grain at ripeness of carbon assimilated in the first period after heading accounted for about 80% of its total amount found at full maturity (Fig. 5); about 14% was retained by the stem.

* In previous experiments (Part II) the radioactivity in the grain of plants, whose ears were exposed to labelled CO_2 for a day, accounted for about 80% of the total ear radioactivity.

The accumulation of assimilates formed in the later period accounted for more than 90%. The contribution of ear photosynthesis (calculated from the radioactivity found in plants, whose ears only were exposed to $^{14}C—CO_2$) varied from about 33% — when photosynthates formed within the first two weeks after heading are taken into consideration — to about 50% of those formed at the end of the third week. The very small amount of carbon assimilated in the latest period and found in the grain originated solely from ear photosynthesis.

DISCUSSION

The plants in the experiments reported above — in comparison with those investigated previously (Part I and II) — showed at ear emergence a total dry weight higher by about 30% *. Considerable differences in the weight of green leaves were also noted. However, the total weight increment during the following stages till ripeness was anologous — in spite of the fact that leaf ageing was slower in the reported experiments; perhaps this was due partly to the unusually cool 10-day spell (within this period) and in consequence to a lower photosynthetic activity of the investigated plants.

As mentioned previously the differences between shoots in their weight increase were observed only in the first stage after heading. Several causes may have brought about in the following period a similarity of both shoots in this respect (similarity observed also in the aforementioned experiments). One of them may be the decreasing differences between the main shoot and the tiller in their photosynthetic activity within this period; the second may consist in the higher — in absolute and relative values — losses of photosynthesis products in the main shoot, especially during the first day overnight.

According to previous investigations (Part II) the relative amount of ^{14}C-assimilates translocated daily to roots in the period under investigation was very small and could not have had a significant influence on the magnitude of the losses observed. Therefore it is respiration in the aerial plant parts, which was mainly involved. Hence, the greater loss of assimilates in the main shoot as compared to the tiller could have resulted from their greater utilization in respiration. There is another possibility, which is to be taken into account, i.e. translocation of a proportion of assimilates from the main shoot to the tiller, especially during a dozen hours or so after their formation. On investigation the main shoot of plants deprived of their tiller did not show any significant

* In the experiments reported here ear emergence was observed on the 54th day after sprouting, whereas in the previous ones 5—6 days earlier. The length of the period from heading to ripeness was similar.

differences in its radioactivity — as compared to the control — immediately after exposure to $^{14}C—CO_2$. In previous investigations, when such a treatment was applied at a similar development stage but with plants kept in the chamber for 24 hrs, the shoot was less radioactive than that of the control. Thus it was supposed that the direction of assimilate translocation might have been reverse to that expected in the experiments here reported. Further investigations are required for elucidating the discussed phenomenon.

It must be stressed that — as in similar investigations on wheat (Part IV) — the true losses of photosynthates must have been greater than shown by the data obtained, especially within the first 24 hrs and in the first stages of grain filling. According to Müller (1951, 1960) barley plants utilize in respiration an average of about 30—40% of their photosynthates. Obviously, the magnitude of assimilate loss within a particular stage of development depends on the environmental conditions controlling the rate of photosynthesis and respiration, and may change to some extent from year to year.

Considering that, within the period under investigation, the rate of respiration in the vegetative organs was relatively low, the main losses of assimilates seem to have occurred in the ear. This supposition is confirmed also by other investigations on barley (Thorne, 1963a), in which the flag leaf (the most intensively respiring leaf) with the corresponding uppermost internode utilized in respiration between heading and ripeness less than one fourth of the amount lost in respiration by the ear. Hence, the decrease in the amount of assimilates, accumulated in the stem during the first period after (and perhaps before) ear emergence, cannot be attributed mainly to respiration losses in situ (Archbold et al. 1944). As mentioned above, a marked proportion of these assimilates must have been transported to the grain.

In both shoots at ripeness the stem — although retaining certain amounts of carbon assimilated after heading * — showed a significantly lower weight than at ear emergence. This difference may be also partially due to organic compound translocation to the ear.

Although the grain yield was higher than the total plant increment within the whole period investigated, the exact contribution of products of photosynthesis before and after heading cannot be determined on the basis of the data obtained. The losses of carbon being considerable over a long period after its assimilation (similarly as in wheat), the values of weight increments at particular stages do not indicate the exact amount of organic compounds due to current photosynthesis. The carbon

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* The first expt. was carried out almost at the end of stem elongation. Therefore the amounts of photosynthates incorporated into this organ could have been greater than shown by the data observed.

assimilated before ear emergence should be labelled. Nevertheless the great importance of photosynthesis after heading cannot be denied, in particular ear photosynthesis whose rate is believed to influence even varietal differences in grain yield of barley (T h o r n e, 1963b). Indeed, the contribution of the ear to the total plant photosynthetic activity was relatively high and similar to that observed in previous investigations *, although the experimental procedures were somewhat different (Part II).

The ear contribution to the accumulation in grain at ripeness of assimilates formed in the first stage after heading was even greater than its contribution to the total plant photosynthetic activity at that period.

The values obtained in the experiments reported are similar to the estimations given by P o r t e r *et al.* (1950) for ear contribution to the grain yield of two-rowed barley. However, it must be borne in mind that, if the grain yield were due partially to organic compounds accumulated before ear emergence, the role of ear photosynthesis would be less.

It seems possible to evaluate the contribution of the barley ear to assimilate accumulation in the grain on the basis of its relative photosynthetic activity taking simultaneously into account that the data, particularly those concerning the first period after heading may be lower than the true values. However, the possible artefacts caused by the shading technique would be then completely eliminated.

As has been shown, defoliation or shading of stem or ear even for three and a half hours may cause changes in the photosynthetic activity of the other green parts, their character and magnitude being dependent on the development stage of the plant. It is worth noting that the reaction of barley to ear shading in the first period after heading was exactly the same as in wheat at an analogous development stage, especially in the awned 'Chłopicka' var. (Part IV). Special, more detailed investigations are required for better understanding of the artefacts observed.

In the reported experiments with barley as well as in those with wheat, it was assumed that the ^{14}C-photosynthates formed in the early afternoon represent the total carbon assimilated in daytime and in the particular period investigated. It should be noted that the relative accumulation of labelled carbon in the grain of barley 20 hrs after exposure — at various stages — was similar to that found in the experiments, in which plants were allowed to photosynthesize $^{14}C—CO_2$ over the whole daytime period. Nevertheless the errors resulting from such an assumption should be examined.

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* Some differences observed in this respect are due to differences in the age of the plants, at which the experiments were carried out.

Among the facts noted in the period from ear emergence to ripeness of the investigated plants the following are worth emphasizing:

1. The total dry weight increase of the plants amounted to about 35% of their final weight. The increment of the main shoot in the first stage after heading was higher than that of the tiller; in the subsequent period there was no difference between them in this respect. The grain yield was higher than the total plant increment.

2. The photosynthetic activity of the main shoot was higher than that of the tiller, but the differences diminished with ageing. The absolute and relative losses of current photosynthesis products in the main shoot were higher than in the tiller,

3. Considerable losses of carbon assimilated in various stages after heading occurred not only on the first day (overnight) following photosynthesis but also in the subsequent periods. Presumably they took place mainly in developing kernels.

4. A significant proportion of assimilates, accumulated transiently in the stem, was afterwards translocated to the grain.

5. The ear contribution to the total photosynthetic activity of the plant increased with ageing from about 24 to 48% at the end of the third week after heading.

6. The final accumulation in grain of assimilates formed in the first period after heading accounted for about 80% of their total amount found in plants at ripeness. The accumulation of assimilates formed in the later period exceeded 90%.

The contribution of ear photosynthesis to the amount of assimilates accumulated in grain varied from 33 to 50%, being similar in both shoots.

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Fotosynteza, przemieszczanie i akumulacja asymilatów w roślinach zbożowych w okresie kształtowania się ziarna

V. Udział produktów fotosyntezy wytworzonych po wykłoszeniu w akumulacji związków organicznych w ziarnie jęczmienia

Streszczenie

W 1962 r. przeprowadzono doświadczenie z jęczmieniem jarym odm. 'PZHR Browarny'. Badano przyrost suchej masy w okresie od wykłoszenia do pełnej dojrzałości, dokonując sprzętu roślin w odstępach 7—10-dniowych. Podobnie jak w poprzednich doświadczeniach z pszenicą jarą, w połowie każdego okresu między sprzętami część roślin umieszczano bezpośrednio po południu na trzy i pół godz. w kamerze z pleksiglasu, do której wprowadzano znakowany ^{14}C dwutlenek węgla. Niektóre z nich zbierano natychmiast po wyjęciu z kamery, pozostałe umieszczano w warunkach analogicznych do tych, w jakich znajdował się jęczmień w hali wegetacyjnej. Zbierano je: 1) po dobie; 2) w dniu następnego doświadczenia z $^{14}C—CO_2$; 3) w fazie pełnej dojrzałości.

Uzyskane wyniki pozwalają stwierdzić, że w okresie od wykłoszenia do pełnej dojrzałości:

1. Ogólny przyrost suchej masy roślin wynosił około 35% ich ciężaru końcowego. Przyrost masy pędu głównego w pierwszej fazie po wykłoszeniu był większy niż pędu bocznego. W okresie późniejszym nie było między nimi różnic pod tym względem. Ciężar ziarna był większy niż ogólny przyrost masy roślin.

2. Aktywność fotosyntetyczna pędu głównego była większa niż pędu bocznego, ale różnice między nimi ulegały zmniejszeniu w miarę starzenia. Bezwzględne i względne straty produktów fotosyntezy w pędzie głównym były większe niż w pędzie bocznym.

3. Znaczne straty węgla asymilowanego w różnych fazach po wykłoszeniu występowały nie tylko w ciągu pierwszej doby, ale również w okresie późniejszym. Straty te zachodziły najprawdopodobniej głównie w kształtujących się ziarniakach w procesie oddychania.

4. Znaczna część asymilatów gromadząca się przejściowo w źdźble ulegała następnie przemieszczeniu do ziarna.

5. Udział kłosów w ogólnej aktywności fotosyntetycznej roślin wzrastał od 24% w końcu pierwszego tygodnia do 48% — w końcu trzeciego tygodnia po wykłoszeniu.

6. Ilość asymilatów, wytworzonych w pierwszej fazie po wykłoszeniu, zakumulowana w dojrzałym ziarnie stanowiła około 80% ich ogólnej ilości stwierdzonej w roślinach w końcu wegetacji. Ilość zaś asymilatów wytworzonych w późniejszym okresie wynosiła odpowiednio ponad 90%.

Udział produktów fotosyntezy przebiegającej w kłosie w ilości asymilatów nagromadzonych w ziarnie wynosił 33—50%, będąc jednakowy w obu pędach badanych roślin.