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

IV. Contribution of products of current photosynthesis after heading to the accumulation of organic compounds in the grain of spring wheat

H. BIRECKA, L. DAKIĆ-WŁODKOWSKA

In previous investigation on spring wheat (part III, 1963) we paid attention mainly to the daily accumulation, in the grain, of products of current photosynthesis at various stages after heading. In the experiments reported here the changes in the amount of these products till full maturity of the plants were followed. We tried also to find, whether the defoliation or shading technique applied for a shorter time than in previous experiments would enable to obtain more reliable data for estimation of the contribution of particular green organs to the total photosynthetic activity of the plants.

Two spring wheat varieties were investigated: the awned — "Chłopicka" var. and the awnless — "Fortunata".

METHODS

Seeds were sown into a soil-sand mixture similar to that used in previous experiments (part I, 1963). The plants received basal and top dressings — at the stage of tillering and shooting; the total amount of nutrients applied was: N — 850, P_2O_5 — 600, K_2O — 800 mg per pot. The soil humidity was maintained at 60% of its water capacity. Full sprouting was noted on May 2, 1962, shooting on June 6. The plants were thinned gradually to 12 per pot. In Chłopicka var. full ear emergence was observed on June 24*, i.e. 53 days after sprouting, flowering on June 29. In Fortunata var. the two processes were noted a day earlier than in Chłopicka var.

The first sampling of plants of the two investigated varieties was completed on June 28 after having removed 1—2 very small tillers per plant. At that time, in both varieties, only four upper leaf laminae on the main shoot were fully or partially green (the completely yellow leaves were also removed). During the period from flowering to full ripeness

* A very cool spring.

Table 1

Conditions under which plants were kept in the plexiglass chamber

No.	Date of experiment	CO ₂ content*		mc	¹⁴ C content in plants — % of the total radio-activity applied	Fluctuations of temperature C°	Weather conditions
		g	% vol.				
Chłopicka var.							
I	3.VII	2.05	0.15	1.5	57***	23—26	varying cloudiness
II	13.VII	1.03	0.07	0.75	68	14—28	varying cloud. (rain)
III	21.VII	1.03	0.07	0.75	62	29—36	sunny
IV	28.VII	0.62	0.045	1.5	38***	26—32	varying cloudiness
Fortunata var.							
I	3.VII	together with plants of var. Chłopicka				24—32	mostly sunny
II	12.VII	1.03	0.07	0.75	67		
III	20.VII**	1.12	0.08	0.90	38	29—35	sunny
IV	28.VII	together with plants of var. Chłopicka					

* Including the normal CO₂ content in the air volume in the chamber.

** Together with some lupin plants from another investigation.

*** Including plants of var. Fortunata.

six samplings were completed: 1) for dry matter determination (3×10 plants each time) and, simultaneously, 2) for chlorophyll content determination (3×2 plants per sampling).

In the middle of each period between samplings (except for the last harvest) some plants of each variety were placed in a plexiglass chamber (out-of-doors), into which ¹⁴C — labelled CO₂ was introduced. Plants subjected to following treatments were investigated: 1) controls (a greater number), 2) flag leaf lamina removed, 3) lower leaf laminae removed, 4) stem shaded, 5) ear shaded, 6) all vegetative parts shaded, i.e. only ear exposed to light (a greater number of plants). In some experiments plants deprived of awns (Chłopicka var.) or plants deprived of all leaf laminae (Fortunata var.) were also investigated. The appropriate technical procedures* were analogous to those in previous experiments. The plants were placed in the chamber immediately after noon. In Table 1 the conditions in the chamber are reported. After three and a half hrs all plants were removed, 6 plants (3×2) per each treatment were immediately killed at -60°C . The remaining controls and plants,

* Applied immediately before the plants were put into the chamber.

whose ears only were exposed to light*, were placed under conditions similar to those, under which plants were kept in the greenhouse. They were harvested gradually (6 per treatment each time): after 20 hrs (except for expt. I), 2. on the day of the following experiment with $^{14}\text{C} - \text{CO}_2$, 3. at full maturity.

Particular parts of plants sampled for analysis on chlorophyll were macerated and extracted with acetone. The content of chlorophyll ($a+b$) was determined in a Unicam SP. 700 spectrophotometer at $\lambda = 652 \text{ m}\mu$ (Arnold 1949, Bruinsma 1961). The radioactive plant material was homogenized, extracted with 80% ethanol. The total radioactivity and the activity in the soluble fraction was determined by means of a G.M. counter with counting efficiency at the geometry applied about 50%. The amount of plant material on the planchette did not exceed 0.5 mg/cm^2 .

RESULTS

At the stage of flowering the total plant weight in Chłopicka var. was greater than in Fortunata var. (Table 2). This was mainly due to differences in the dry weight of the stem (Figs 1 and 2). At the fourth

Table 2
Weight of wheat g d.m. per plant

No.	Date of sampling*	Chłopicka var.				Fortunata var.			
		aerial parts			roots	aerial parts			roots
		shoot	grain**	total		shoot	grain**	total	
1	28.VI.	2.58	0.01	2.59	1.51	2.21	0.01	2.22	1.34
2	8.VII.	3.27	0.08	3.35	1.44	2.64	0.22	2.86	1.36
3	16-17.VII.	3.50	0.54	4.04	1.51	2.41	0.72	3.13	1.25
4	24-25.VII.	3.52	1.16	4.68	1.28	2.14	1.40	3.54	1.00
5	1.VIII.	3.00	1.67	4.67	1.22	2.00	1.69	3.69	0.88
6	9-13.VIII.	2.74	1.84	4.58	0.97	1.97	1.70	3.67	0.77
	L.S.D. ($p = 0.05$)		0.10	0.25			0.11	0.30	

* Plants var. Fortunata at the third and fourth harvest were collected one day, at the last harvest (at full maturity) — four days earlier than the plants of var. Chłopicka.

** Mean number of kernels per plant: var. Chłopicka — 46, var. Fortunata 54. At first sampling — only generative organs.

week after flowering the plants of both varieties reached their greatest weight, which did not change till full maturity, i.e. during the following 15-19 days. The total increase in Chłopicka var. was much higher than in Fortunata var.

* The paper covers were removed immediately after exposure to $^{14}\text{C} - \text{CO}_2$.

The two varieties investigated differed from each other in the behaviour of their stems and in grain filling. In Chłopicka var. the stem weight increased till the beginning of the milk stage of the grain (third sampling) and started dropping only at the beginning of the wax stage. At full maturity it remained higher than at flowering. In Fortunata var. an increase of the stem was to be observed only during the first period, afterwards its weight diminished; at full maturity it was smaller than at the stage of flowering.

Fig. 1. Weight of stems*, grain and of whole plants, g d. m. per plant.

G — grain, S — stem, T — total; O = 57 days after sprouting

* Including rachis (0.06–0.08 g) and sheaths; their weight in Chłopicka var. was about 0.45–0.51 g (due to the increase of the flag leaf sheath at the second sampling), in Chłopicka var. about 0.37 g.

During the first period after anthesis the grain filling in Chłopicka var. was slower than in Fortunata var. The difference in its weight increase subsisted till the end of the milk stage (fourth sampling). Within the following week the filling process in Fortunata var. slowed down markedly and at that time the grain weight reached its highest value, whereas in Chłopicka var. this process proceeded still intensively and lasted for a longer time. The final grain yield in the latter variety was higher than in Fortunata var.

As the data presented in Table 3 show, the two investigated varieties differed from each other as regards the total chlorophyll content, its distribution between particular plant parts and changes with ageing. At flowering the higher chlorophyll content in Fortunata than in Chłopicka var. was mainly due to differences between their leaf laminae. In the later period a reverse phenomenon could be observed. It resulted mainly from: 1) a relatively more rapid decomposition of chlorophyll in the leaf laminae in Fortunata *, 2) a marked increase of this pigment in the part of the uppermost internode, not covered by the sheath, in Chłopicka var., 3) the higher and longer lasting chlorophyll content in

Fig. 2. Weight of leaf laminae and chaff*.

C — glumes (Fortunata var.) and awns (Chłopicka var.); F.L. — flag leaf laminae; L.L. — lower leaf laminae. * The weight of awns was: sampling I — 0.08, II — 0.11, at the later ones 0.14—0.13 g.

the ear of the latter variety. The gradual decrease of the total chlorophyll content — more rapid in Fortunata than in Chłopicka var. — was accompanied during the 24 days after flowering by an increase of the share of the stem, including sheaths, and of the ear in its total amount.

* However its total amount remained higher than in laminae of Chłopicka var. The decrease of chlorophyll with ageing in the laminae of both varieties was revealed when calculated per unit of their total surface area as well as per unit of their green surface area.

Table 3

Chlorophyll content, mg per plant

Plant parts		Chlopicka var.					Fortunata var.				
		Date of sampling									
		I 28.VI	II 8.VII	III 17.VII	IV 25.VII	V 1.VIII	I 28.VI	II 8.VII	III 16.VII	IV 24.VII	V 1.VIII
Leaf laminae ¹	1 (flag) leaf	0.96	0.94	0.66	0.16	—	1.26	1.08	0.83	0.22	—
	2 leaf	0.93	0.70	0.55	0.06	—	1.12	0.80	0.57	0.02	—
	3 leaf	0.31	0.16	—	—	—	0.81	0.19	0.07	—	—
	4 leaf	0.04	—	—	—	—	0.12	—	—	—	—
Leaf sheaths	1 (flag) leaf	0.65	0.56	0.53	0.31	0.02	0.54	0.42	0.42	0.17	0.01
	2 leaf	0.27	0.22	0.20	0.03		0.20	0.13	0.12	0.06	
	3 leaf	0.10	0.08	0.09			0.06	0.04	0.04		
	4 leaf	0.02 ⁴					0.04				
Internodes ²	1a ³	0.11	0.65	0.71	0.51	traces	0.39	0.48	0.50	0.23	0.01
	1b ³	0.24	0.23	0.19	0.09		0.22	0.21	0.18	0.02	
	2	0.16	0.07	0.08	0.02		0.17	0.09	0.07	0.01	
	3	0.08	0.09				0.04	0.04	0.03		
	remaining	0.06		0.08							
Ear	rachis	0.03	0.04	0.04	0.04	0.02	0.09	0.07	0.06	0.04	0.01
	grain	—	0.02	0.15	0.14	0.04	—	0.04	0.16	0.11	—
	glumes	0.39	0.40	0.43	0.27	0.15	0.46	0.38	0.33	0.23	0.09
	awns	0.34	0.35	0.37	0.35	0.10	—	—	—	—	—
total		4.69	4.51	4.00	2.03	0.33	5.60	3.97	3.38	1.11	0.12

¹ Leaf lamina surface area in var. Chlopicka: first (flag) leaf — 27.8 second — 38.1; third — 34.7 and fourth 26.6 cm²; in var. Fortunata 30.0; 32.5; 31.1 and 31.0 cm², respectively.

² In var. Chlopicka the total length of the stem at the 1-st sampling was 96.6 cm, at the 2-nd — 121.6 cm (this increase was due to the elongation of the uppermost internode from 37 to 63 cm). In var. Fortunata the stem length was 65 and 71 cm, respectively. No significant increase in either varieties was observed in the later period.

³ 1a — uncovered, 1b — covered by the flag leaf sheath. In var. Chlopicka at the 1st sampling 1a—9, 1b—28 cm, at the 2nd 31 and 33 cm, respectively. In var. Fortunata at the 1st sampling 1a — 10, 1b — 18 cm; at the 2nd — 15 and 19 cm.

⁴ Including the sheaths of the lower completely yellow leaves.

Taking into account the differences in the specific activity of ¹⁴C—CO₂ applied (Table 1), the data obtained for the plant radio-activity in particular experiments* were converted — as in previous investigations — according to the specific activity of CO₂ in expt. I. Therefore the results of all experiments (Tables 4, 5) are comparable.

* In expt. I both investigated varieties had four leaves (including the flag leaf lamina), the lowest green only at its base; expt. II — only two upper leaves fully green, the third partially green; expt. III — the flag leaf only fully green, the second in Chlopicka var. green at its base only, in Fortunata-half green; expt. IV — only the flag leaf partially green.

Table 4

Total radioactivity of wheat Chłopicka var. immediately after exposure to $^{14}\text{C} - \text{CO}_2$
 10^3 cpm per plant

Treatment	Plant parts *						Contribution of invest. part per-cent
	fl.l.	low.l.	stem	glumes, awns	grain	total	
Experiment I — July 3							
Control	114	354	1234	269	25	1996	100
Fl.l. removed	—	353	945	248	18	1564	22
Low.l. removed	121	—	1046	270	19	1456	27
Stem shaded	151	297	464	278	17	1207	39
Ear shaded	130	462	1293	61	19	1965	
Veg. parts shaded	traces		44**	246	16	306	15
L.S.D. (p = 0.05)	17	35	88	26	6	138	
Experiment II — July 13							
Control	98	197	546	358	123	1322	100
Fl.l. removed	—	173	445	302	101	1021	23
Low.l. removed	105	—	428	320	104	957	27
Stem shaded	120	129	193	336	88	866	34
Awns removed	95	192	581	202	94	1164	
Ear shaded	107	283	541	80	65	1076	
Veg. parts shaded	traces		17	234	58	309	23
L.S.D. (p = 0.05)	17	26	43	19	17	93	
Experiment III — July 21							
Control	110	33	419	60	282	904	100
Fl.l. removed	—	22	274	56	208	560	38
Low.l. removed	111	—	432	60	285	888	
Stem shaded	92	47	144	51	215	549	39
Awns removed	93	41	378	33	191	736	
Ear shaded	130	27	449	4	105	715	
Veg. parts shaded	0	0	20	55	185	260	29
L.S.D. (p = 0.05)	17		40	9	26	70	
Experiment IV — July 28							
Control	11	—	153	150	107	421	
Fl.l. removed	—	—	148	144	77	369	12
Stem shaded	8	—	13	145	57	223	47
Awns removed	12	—	151	66	61	290	
Ear shaded	9	—	117	5	37	168	
Veg. parts shaded	0	—	7	145	49	201	48
L.S.D. (p = 0.05)			22	21	15	41	

* Fl.l. — flag, Low.l. — lower leaves; stem including the rachis and leaf sheaths; activity of rachis in expts I, II, III and IV: control — 63, 54, 43 and 21, in the treatment with ear shaded — 52, 34, 29 and $5 \cdot 10^3$ cpm, respectively.

** Only the rachis was radioactive — in all experiments.

Table 5

Total radioactivity of wheat Fortunata var. immediately after exposure to $^{14}\text{C} - \text{CO}_2$
 10^3 cpm per plant

Treatment	Plant parts								Contribution of invest. part-per cent
	laminae		sheaths		stem*	glumes	grain	total	
	fl. l.	low. l.	fl. l.	low. l.					
Experiment I — July 3									
Control	174	440	42	40	396	236	36	1364	100
Fl.l. removed	—	293	48	58	313	122	23	857	37
Low.l. removed	163	—	65	48	268	197	35	776	43
Stem shaded	98	282	59	55	314	138	26	972	29
Ear shaded	158	407	71	77	444	133	42	1332	
Veg. parts shaded	0	0	0	0	12	122	4	138	10
L.S.D. (p = 0.05)	18	51	14	15	29	21	10	85	
Experiment II — July 12									
Control	201	250	87	75	356	129	336	1434	100
Fl.l. removed	—	190	69	51	266	128	208	912	37
Low.l. removed	165	—	105	41	286	121	262	980	32
All l. removed	—	—	75	41	190	101	158	565	61
Stem shaded	189	218	31	17	182	118	210	965	33
Ear shaded	224	280	110	71	368	50	277	1380	
Veg. parts shaded	0	0	0	0	10	93	48	151	11
L.S.D. (p = 0.05)	21	29	11	10	41	16	25	108	
Experiment III — July 20									
Control	108	78	—	—	247	117	287	837	100
Fl.l. removed	—	60	—	—	172	87	185	504	40
Low.l. removed	95	—	—	—	167	87	206	555	33
All l. removed	—	—	—	—	133	78	168	379	55
Stem shaded	86	62	—	—	88	94	162	492	41
Ear shaded	85	73	—	—	203	37	267	665	
Veg. parts shaded	0	0	—	—	9	80	41	130	15
L.S.D. (p = 0.05)	16	11			27	14	40	95	
Experiment IV — July 28									
Control	24	—	—	—	57	44	46	171	100
Fl.l. removed	—	—	—	—	46	43	38	127	26
Stem shaded	25	—	—	—	14	50	28	117	32
Ear shaded	13	—	—	—	72	2	25	112	
Veg. parts shaded	0	—	—	—	5	43	17	65	38
L.S.D. (p = 0.05)					6	4	7	16	

* Including the rachis, in expts III and IV — also the leaf sheaths: the activity of the rachis in experiments I, II, III and IV: control 44, 46, 25 and 9, in treatment with ear shaded — 50, 51, 17 and 5×10^3 cpm respectively.

The plant radioactivity immediately after exposure to $^{14}\text{C} - \text{CO}_2$ may be considered as an index closely approaching true assimilation. Taking into account the degree of $^{14}\text{C} - \text{CO}_2$ utilization by all plants placed in the chamber, its concentration does not seem to have been a factor limiting the photosynthesis rate.

The total activity of control plants of Chłopicka var. (Table 4) gradually diminished in consecutive experiments. However, partly, the rather marked differences in temperature between particular experiments do not allow to consider the data obtained as values determining the exact degree of the decrease of photosynthetic capacity with ageing. Nevertheless, it is worth noting that, at the stage when the plants showed no more dry weight increase, their radioactivity accounted for about 20% of that in the first period.

When the role of particular green parts in the total plant photosynthetic activity is to be estimated on the basis of the data obtained, one must take account of the possible artefacts, which could have occurred after the appropriate treatments were applied. Actually, they are manifest first of all in plants with ear shaded, particularly in expt. I. The total radioactivity in this treatment is similar to that in the control, whereas the activity of plants with all vegetative parts shaded indicates a contribution of the ear accounting for about 15%. It must be stressed that — as in previous investigations — in all experiments with Chłopicka as well as Fortunata var. the deviation from the mean values of the radioactivity found in this treatment did not exceed 5%. As discussed in detail previously (part III, 1963), exactly this treatment can yield more reliable informations about the contribution of the ear to the total plant photosynthetic activity. The higher — as compared to the control — radioactivity in lower leaf laminae (without any marked differences in the stems) in plants with ear shaded indicates that a compensation for the shaded organ took place. A similar phenomenon is to be observed in expt. II. Some artefacts — if not in the photosynthesis rate, then in the translocation (leaf laminae) — can be found also in plants, whose stems were shaded (in both experiments). The plants deprived of leaf laminae do not supply any indications in this respect.

Thus, according to the data obtained, the contribution of leaf laminae to the total photosynthetic activity diminishing with ageing would change from about 50% during the first 18 days to about 40% (mainly the flag leaf) at the milk stage of grain. The contribution of the stem (including sheaths) within this period would vary between 34 and 39%, that of the ear would increase from 15 to 29%. At the wax stage its contribution would be similar to that of the stem amounting to about 47% of the rather low photosynthetic activity of the investigated plants. The participation of awns in ear photosynthesis was important and increased with ageing.

Plants of *Fortunata* var. in expts I and IV (Table 5) — when placed in the chamber together with *Chłopicka* var. — show a lower total radioactivity than the latter. In expt. IV the activity accounted only for about 12% of that in expt. I. Within the period under investigation the contribution of the ear to the total photosynthetic activity was much lower and that of the leaf laminae higher than in *Chłopicka* var. Two facts are worth noting: 1) the reaction of plants to ear shading was similar to that in *Chłopicka* var., 2) the contribution of leaf laminae calculated on the basis of the radioactivity of plants deprived of all leaves is significantly lower than that based on the activity of plants without the flag leaf and plants deprived of lower leaf laminae. Thus, it may be supposed that the data obtained from the latter two treatments overestimate the contribution of the leaf laminae and that at any rate a partial defoliation could have a negative influence on the assimilation rate in other green parts. The lower radioactivity in the lower leaf laminae after removing the flag leaf, especially in expt. I when grain filling was relatively slow, may, partly, serve as evidence for this supposition. Such a phenomenon was not observed in *Chłopicka* var.

The radioactivity of leaf sheaths — as compared to other green parts — was rather low. It is, however, difficult to estimate their contribution to photosynthesis because of the translocation process, which took place during the plant exposure to $^{14}\text{C} - \text{CO}_2$. Actually, if the data characterizing the contribution of the leaf laminae in *Chłopicka* var. are assumed as reliable, then, during this time (expts I and II) about 50% of the total amount of assimilated carbon flowed out of them. The translocation rate from the flag leaf lamina seems to be greater than that from the lower laminae. The amount of labelled assimilates found in the laminae after 20 hrs (Table 6) accounted for about 10%, and at full maturity — only for 2—3% of their initial total. In *Fortunata* var. a similar behaviour of the leaf laminae assimilates* could be observed (Table 7).

In all experiments** — except for the first — the differences in the total plant radioactivity at various times after exposure indicate that the relatively greatest losses of ^{14}C — photosynthates occurred during the first 20 hrs. In spite of the lack of direct evidence it can be assumed

* In all experiments (with both varieties) after exposure to $^{14}\text{C} - \text{CO}_2$ about 80% of the total laminae radioactivity was found in the ethanol soluble fraction; with time the activity of this fraction diminished to about 20—35% depending on the development stage, at which labelled carbon was applied.

** The L.S.D. ($p = 0.05$) values, presented in tables 6 and 7 as percentage of the activity in controls at time 0, were calculated from the absolute values of the plant radioactivity (including the controls).

Table 6

Changes in radioactivity of wheat *Chlopicka* var. from after exposure to ^{14}C — CO_2 to full maturity-per cent of the total activity in control plants (at time 0)

Time after exposure	Control plants						Plants with veg. parts shaded				
	leaf laminae	stem		rachis awns glumes	grain		whole plant	rachis awns glumes	grain		total
		total	soluble only		total	soluble only			total	soluble only	
Experiment I — July 3											
0	23.4	58.7	51.1	16.7	1.2	0.8	100.0	84.4	14.5	0.8	15.3
10 days	1.7	54.6	26.2	7.8	8.5	3.0	72.0	33.5	7.6	5.7	13.3
at full maturity	0.9	28.1	2.6	6.2**	21.8	3.1	57.0	6.8	2.9	7.7	10.6
Experiment II — July 13***											
0	22.3	37.2	35.8	31.2	9.3	8.2	100.0	85.5	19.0	4.4	23.4
20 hrs	4.5*	27.9	25.0	16.7	22.2	13.5	71.3	54.3	—	—	—
8 days	1.5	22.3	17.8	6.9	34.8	6.5	65.5	27.9	2.7	7.9	10.6
at full maturity	1.0	4.3	1.4	5.0**	39.0	3.7	49.3	7.1	1.8	8.2	10.0
Experiment III — July 21***											
0	15.8	41.6	35.3	11.4	31.2	17.9	100.0	74.6	8.4	20.4	28.8
20 hrs	5.2*	18.5	15.9	4.5	64.1	14.5	92.3	36.6	—	—	—
7 days	2.6	15.9	11.6	2.0	67.7	9.1	88.2	22.6	—	—	—
at full maturity	2.0	4.9	2.0	1.3	78.8	6.9	87.0	10.7	0.9	24.6	25.5
Experiment IV — July 28***											
0	2.5	31.5	30.4	39.5	25.5	20.0	100.0	84.4	36.1	11.6	47.7
20 hrs	0.8	10.2	7.9	16.8	58.2	25.4	86.0	67.2	—	—	—
at full maturity	0.3	traces	traces	9.6**	65.5	3.7	75.4	5.4	3.6	27.0	30.6

L.S.D. in experiments I, II, III, IV for the controls: grain — 3.2; 2.5; 6.0; 7.1; whole plants — 5.1; 5.2; 6.7; 6.6, respectively.

L.S.D. in experiments I, II, III, IV for the plants with veget. parts shaded: grain — 0.5; 0.8; 3.0; 4.5; total 2.5; 2.3; 4.0; 5.6, respectively.

* In lower leaves — 3.0 (expt. II) and 3.5% (expt. III).

** Mainly in glumes and awns.

*** Mean night temperature — July 14: 13°; July 22 and 29: 15° C.

Table 7

Changes in radioactivity of wheat *Fortunata* var. from after exposure to $^{14}\text{C} - \text{CO}_2$ to full maturity-per cent of the total activity in control plants (at time 0).

Time after exposure	Control plants							Veget. parts shaded			
	leaf laminae	leaf sheaths	stem		rachis & glumes	grain		whole plant	rachis & glumes	grain	total
			total	soluble only		total	soluble only				
Experiment I — July 3											
0	45.0	6.0	25.8	21.0	20.5	2.7	2.5	100.0	82.6	9.8	10.1
9 days	2.1	3.2	34.0	29.8	11.0	18.1	7.3	68.4	45.2	3.0	6.3
at full maturity	1.7	0.9	7.7	2.3	8.3**	44.3	3.7	62.9	8.6	1.5	4.5
Experiment II — July 12***											
0	31.4	11.3	21.6	20.0	12.2	23.5	14.9	100.0	80.0	7.2	10.5
20 hrs	6.8*	5.6	14.6	14.0	10.7	45.5	15.1	83.2	49.3	—	—
8 days	2.9	2.0	11.3	7.2	4.0	61.0	10.8	81.2	25.5	1.1	8.4
at full maturity	1.4	0.7	2.3	0.9	2.6	66.0	4.0	73.0	6.0	0.8	7.1
Experiment III — July 20***											
0	22.2	26.5	17.5	17.0	17.0	34.3	15.4	100.0	60.4	10.6	15.5
20 hrs	8.3*	8.5	7.2	11.7	11.7	62.8	15.7	91.3	37.3	—	—
8 days	2.8	2.5	1.5	3.0	3.0	65.7	5.9	74.0	8.1	2.0	10.4
at full maturity	2.7	1.7	1.0	2.6	2.6	58.8	3.5	65.8	7.0	1.0	9.0
Experiment IV — July 28											
0	14.0	27.8	26.3	31.2	31.2	27.0	15.9	100.0	83.2	28.0	38.0
20 hrs	4.8	11.1	12.2	10.1	10.1	64.1	24.5	90.1	48.0	—	—
at full maturity	1.6	3.4	6.0	6.0**	6.0**	66.7	8.6	77.7	13.7	5.5	25.9

L.S.D. in experiments I, II, III, for the controls: grain — 3.1; 5.0; 7.3 whole plants — 5.0; 5.3; 4.0, respectively.

L.S.D. in experiments I, II, III, for plants with veget. parts shaded: total — 1.6; 1.7; 1.6, respectively.

*In lower leaf laminae 4%.

** Mainly in glumes.

*** Mean night temperature — July 13: 13°; July 21: 14° C.

that this was also the case in the first period after flowering. However in most experiments the losses of carbon a week and more after its assimilation were also considerable. Thus, the mature plants of *Chlopicka* var. contained only about 50% of carbon assimilated on the fifth and fifteenth day after flowering, i.e. within the period of a relatively low translocation rate of photosynthates to the grain. In this period, particularly at its beginning an intensive elongation of the uppermost

Fig. 3. ^{14}C -assimilates accumulated in the grain — per cent of the total radioactivity found in mature control plants.

A — control plants; B — plants, whose ears only were exposed to light (dashes—grain)
I, II, III, IV — period of exposure to ^{14}C .

internode and a weight increase of glumes was observed. These two facts caused that only about 40% of carbon assimilated in the first period and found in the plant at the end of its vegetation* was accu-

* In all experiments there were no differences — either in the total or in the grain yield — between plants exposed to labelled carbon and those kept during the whole vegetation period in the greenhouse.

culated in the mature grain (Fig. 3). It is worth noting that a marked proportion of assimilates found in the stem 10 days after exposure must have been translocated to the grain in the later period (on the tenth day the most part of the previously formed assimilates detected in the grain came from the ear itself).

The accumulation of carbon assimilated on the fifteenth day in the mature grain amounted to as much as 80% of the total found at the end of vegetation. The relative accumulation of photosynthates formed in the later period is still greater. Within this period: 1) the rate of translocation of assimilates to the grain as well as the rate of their transformation there into ethanol-insoluble compounds was much more rapid, 2) the relative losses of photosynthates after exposure — in the later period — were much smaller than in the earlier two experiments and 3) a significant translocation of labelled carbon from the stem to the grain in the late stage of its development can be assumed (expt. III).

It is worth stressing that during plant exposure to $^{14}\text{C} - \text{CO}_2$ the translocation of ear assimilates to the grain — as compared to that from the vegetative parts — was relatively more intensive. In plants with ears only exposed to light the radioactivity found in the grain 8—10 days after exposure did not differ markedly from that at the end of their vegetation. The contribution of the ear to photosynthates accumulated in the grain at full maturity depended on its participation in the assimilatory activity of the whole plant, on the degree of incorporation of assimilates into still growing parts of the mother-plant and on the losses of photosynthates, in particular in the ear itself. It varied from 20 to 40%. It may be mentioned that the greatest losses of ear assimilates took place at the stage when the losses of the total plant assimilates were relatively the greatest, i.e. at the milk stage of grain.

The differences in the behaviour of plants of *Fortunata* var. — as compared to those of *Chłopicka* var. — consisted in: 1) relatively smaller losses of assimilates formed on the fifteenth day after flowering; a reverse phenomenon was observed with the carbon assimilated at the milk stage, 2) relatively smaller retention and incorporation in the stem of photosynthates, especially those formed in the first period after anthesis, 3) more rapid translocation of assimilates to the grain within the first 2—3 weeks (a higher rate of their transformation into insoluble compounds in expt. II is worth stressing), 4) relatively greater degree of accumulation in the mature grain of assimilates formed within the first two weeks after anthesis and found at the end of vegetation, 5) much smaller contribution of the ear to the photosynthates accumulated in the grain, especially to those formed in the first period. As in plants of *Chłopicka* var. a large proportion of assimilates, formed on the fifth day after anthesis and stored in the stem during the following

9 days, was later translocated to the grain. The degree of radioactivity losses in plants with ears only exposed to light was correlated with that in the controls.

DISCUSSION

The main differences in the character of growth and development between the two investigated varieties in the present experiments are similar to those in previous investigations (part I and III, 1963). However, in both varieties the total plant weight at flowering as well as the total increment in the later period and the grain yield were much higher. These facts — it seems — are partly connected with the slower senescence of the vegetative organs after heading. The distribution of chlorophyll clearly showed that in this period the two uppermost leaves with the corresponding internodes as well as the green parts of the ear were mainly responsible for the plant's photosynthetic activity. It is precisely to these plant parts, especially to the flag leaf that the main attention of various authors has recently been drawn (Anisimow 1961, Grodzinski 1959, Stoy 1963).

The results reported above indicate that the marked differences in the magnitude of the total weight increments after anthesis between varieties were due to differences in the photosynthetic capacity of the upper internodes (including sheaths) and of the ear*. For, the ageing process — within the period under investigation — precisely of these plant parts is slower than that of the leaf laminae. The higher (and longer-lasting) chlorophyll content in the leaf laminae** in *Fortunata* than in *Chłopicka* var. could not compensate the differences between the other green parts.

It must be stressed, however, that the values of weight increments at particular stages after flowering as well as of the total plant increase do not indicate the exact amount of organic compounds due to current photosynthesis. For, according to the data obtained considerable losses of carbon occurred over a long time after it has been assimilated. It is also probable that a certain part of photosynthates accumulated in the plant before flowering was also lost in the later development stages. The true losses of photosynthates — in particular within the first 24hrs and at the early stages of grain filling — must have been greater than

* This was reflected in differences between varieties in absolute values of the radioactivity due to photosynthesis in the stem and ear (especially in expts I and IV when the two varieties were placed together in the chamber) and in the chlorophyll content in these plant parts.

** The total surface area of the two upper leaf laminae was in *Chłopicka* var. 66, in *Fortunata* — 63 cm².

demonstrated in the reported experiments, because of the eventual utilization of new assimilates in respiration* during $^{14}\text{C} - \text{CO}_2$ photosynthesis and of the reassimilation of $^{14}\text{C} - \text{CO}_2$ lost in respiration in the green parts later, in daytime.

The degree of translocation of photosynthates to roots being relatively small within the period under investigation (part III, 1963), it may be assumed that the respiration process was mainly responsible for the losses observed during the later periods after exposure to $^{14}\text{C} - \text{CO}_2$. Taking into account the decrease in the respiration rate in leaf laminae with ageing (Strebeýko and others, 1963) the stem, showing a transient accumulation of assimilates, and the grain should be discussed in the first place. The ethanol-soluble compounds of assimilated carbon constituted the greatest proportion of its total amount present in the stem during several days after exposure. This fraction included only low molecular weight carbohydrates (mainly sucrose), but not high molecular weight fructosanes, present in relatively large quantities in the stem (Paech, Tracey 1955; Wanner 1958, Wood 1960). However, this fraction is the most interesting from the point of view of respiration substrates as well as of the form of transport of organic compounds. There is no doubt — according to the results obtained — that a great proportion of assimilates retained for a certain period in the stem (unless they were incorporated into the growing parts of the stem) is afterwards translocated and accumulated in the grain. Moreover, it seems that the main losses of photosynthates took place in the grain and not in the stem itself and that the degree of their translocation to the ear was greater than shown by the degree of accumulation in the grain. The changes in the radioactivity of the ear of plants, whose all vegetative parts were shaded, are an indirect evidence for such a supposition.

The extent of losses, in the grain, of current photosynthesis products within a particular stage would depend on their relative amounts translocated to it, on the rate of their transformation into insoluble compounds and on the afflux of organic compounds previously assimilated and retained in the stem. The much greater relative losses of assimilates formed at the end of the milk stage in *Fortunata* var. than in *Chłopicka* (expt. III) could be explained partly by the differences in the supply to the grain of assimilates previously accumulated in the stem (changes in its weight are proof for this supposition) and also by differences in the photosynthetic activity at that time. On the other hand, the differences between the two varieties in expt. II can be explained partly by differences in the rate of transformation into insoluble compounds.

* According to Weigl and others (1951) the utilization of current photosynthesis products in respiration under illumination is not supposed to be significant.

The results obtained show clearly that a greater or lesser proportion of assimilates from every stages after flowering can be found in the mother-plant at the end of its vegetation. This is particularly important when photosynthates formed at the first stage are taken into consideration. For, in this period — as compared to the later ones — the assimilatory capacity of the plant is the greatest and thus it can significantly influence the grain yield. The differences between varieties in this respect depended mainly on differences in stem elongation after flowering. Such differences are of genetic character (but — within a variety — they can be influenced to some extent by environmental conditions). At the same time it must be borne in mind that the uppermost elongating internode is photosynthetically active. The question to what extent this internode is self-sufficient in its growth process is worth examining.

The problem of the contribution of products of photosynthesis after flowering to the grain yield can not be fully elucidated by the results of the reported experiments. The fate of carbon assimilated in earlier stages (losses, direction of translocation and accumulation after anthesis) should be investigated. There is, however, no doubt that the photosynthetic capacity of the plant after heading is of great importance for the grain yield and that the ear itself can play a significant role in this respect. Great differences between the awned Chłopicka and the awnless Fortunata var. in the ear contribution to the plant photosynthetic activity and the daily accumulation of assimilates in the grain were found in previous investigations (Part III, 1963). The experiments reported confirm these results and, in addition, show that differences between these two varieties are even greater when the contribution of their ears* to photosynthates accumulated in mature grain is taken into consideration.

The smaller — as seems — role of the ear in photosynthesis of the plant, particularly in Chłopicka var. is, in all probability, due to the better — as compared to previous investigations — growth of vegetative organs. Nevertheless its contribution to photosynthate accumulation in the grain was considerable, amounting to 30—35%, whereas in Fortunata var. it accounted for 7—14%. Watson and others (1963) suggest that an increase in ear net photosynthesis could be one of the most important causes of the greater yields of some new varieties of winter and spring wheat. However, even when assumed that the grain yield is entirely due to assimilation after heading, the data presented by Buttrose (1962) seem to overestimate the ear contribution in wheat. Perhaps the results presented by Lupton (1961) are nearer the true situation.

* Including perhaps to some extent the green kernels themselves.

The estimation of the ear contribution in the experiments reported was based on the behaviour of plants with all vegetative parts shaded for a short time. The possible artefacts — as previously discussed — do not seem to be very significant. However, it is worth stressing that ear shading, defoliation or stem shading even for about three hrs can cause serious changes in the photosynthetic activity of other parts* or in translocation. In previous experiments it was impossible to determine the role of leaf laminae in Chłopicka var. because of an almost full compensation — for a dozen or so hours — in photosynthesis for the removed organs. The data obtained in the present experiments seem to be more reliable. The reaction of Fortunata var. did not differ from that in previous investigations.

Among the facts noted in the period from flowering to full maturity of the investigated plants the following are worth emphasizing:

1) the greater weight increase in the awned Chłopicka var. as compared to an awnless Fortunata var. was due mainly to a higher photosynthetic activity of the upper internodes (including sheaths) and the ear;

2) considerable losses of carbon assimilated at various stages after flowering took place not only on the first day following photosynthesis but also in the subsequent periods; it is supposed that they occur mainly in the developing kernels, in respiration;

3) a great proportion of assimilates, accumulated in the first stages in the stem, was translocated to the grain in the later period;

4) at the end of vegetation certain amounts of assimilates from every stage were found in the mother-plants, the share of photosynthates formed in the first period after flowering was the greatest; its magnitude depended mainly on differences in the degree of stem elongation between the investigated varieties;

5) the final accumulation in grain of assimilates formed in the first period after flowering accounted in Chłopicka var. for about 40%, and in Fortunata var. for 70% of their total amount found in plants at ripeness. The accumulation in grain of assimilates formed in the later period varied — in both varieties — from about 80 to 90% of their final amounts.

6) the contribution of ear photosynthesis to assimilates accumulated in the mature grain amounted in Chłopicka var. to about 30—35%, in Fortunata var. 7—14%, whereas its contribution to the total plant pho-

* In further (unpublished) experiments with intact plants, in which much shorter exposures to labelled carbon — in the morning, at noon and in the afternoon — were applied, the relative contribution of particular green parts did not differ significantly in dependance on the time of the day.

tosynthetic activity varied with ageing from 15 to 29%, and from 10 to 15%, respectively. At the very late period of vegetation it was higher;

7) ear shading, a partial defoliation or stem shading — even for about three hours—caused significant changes in the photosynthetic activity of organs exposed to light or in assimilate translocation. Differences in the reaction between the investigated varieties were manifested.

Dept. of Plant Physiology,
Central College of Agriculture, Warsaw
Plant Physiology Laboratory
of the Polish Acad. of Sciences

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

IV. Udział produktów fotosyntezy wytworzonych po wykłoszeniu w akumulacji związków organicznych w ziarnie pszenicy jarej

Streszczenie

W roku 1962 przeprowadzono doświadczenia z dwiema odmianami pszenicy jarej, a mianowicie z ościstą „Chłopicką” i bezostną „Fortunatą”. Badano przyrost suchej masy i zmiany w zawartości chlorofilu w okresie od zapłodnienia do pełnej dojrzałości, dokonując sprzętu roślin w odstępach najczęściej tygodniowych. W połowie poszczególnego okresu między sprzętami część roślin umieszczano bezpośrednio po południu na trzy i pół godziny w kamery z pleksiglasu, do której

wprowadzano znakowany ^{14}C dwutlenek węgla. Niektóre z nich zbierano natychmiast po wyjęciu z kamery, pozostałe natomiast umieszczano w warunkach analogicznych do tych, w jakich pszenica znajdowała się w hali wegetacyjnej. Zbierano je: 1) po dobie, 2) w dniu następnego doświadczenia z $^{14}\text{C} - \text{CO}_2$, 3) w fazie pełnej dojrzałości.

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

1) większy przyrost masy roślin odm. „Chłopickiej“ w porównaniu z odmianą „Fortunatą“ był wynikiem większej aktywności fotosyntetycznej dwóch górnych międzywęzli źdźbła (włączając pochwy liściowe) oraz kłosa;

2) istotne straty węgla asymilowanego w różnych fazach po kwitnieniu zachodziły nie tylko w ciągu pierwszej doby, ale również w okresie późniejszym. Straty te najprawdopodobniej miały miejsce głównie w kształtujących się ziarniakach w procesie oddychania;

3) stosunkowo duża część asymilatów, gromadząca się w źdźble w pierwszej fazie po kwitnieniu, ulegała w okresie późniejszym przemieszczeniu do ziarna;

4) pod koniec wegetacji w roślinach macierzystych znajdowano pewne ilości węgla zasymilowanego w poszczególnych badanych fazach rozwoju; udział produktów fotosyntezy przebiegającej w pierwszym okresie po kwitnieniu był stosunkowo największy. Jego wielkość zależała również od różnic między odmianami w stopniu wydłużania się górnego międzywęzła w tym czasie;

5) ilość asymilatów, wytworzonych w pierwszej fazie po kwitnieniu, zakumulowana w dojrzałym ziarnie, stanowiła u „Chłopickiej“ około 40%, a u „Fortunaty“ 70% ich ogólnej ilości, stwierdzonej w roślinach w końcu wegetacji; akumulacja zaś asymilatów, wytworzonych w późniejszym okresie wynosiła w obu odmianach 80—90% ich końcowej zawartości.

6) udział produktów fotosyntezy przebiegającej w kłosie w ilości asymilatów nagromadzonych w dojrzałym ziarnie wynosił u odmiany „Chłopickiej“ około 30—35%, u „Fortunaty“ 7—14%; udział kłosa w ogólnej aktywności fotosyntetycznej rośliny zmieniał się w miarę jej starzenia się; u „Chłopickiej“ od 15 do 29%, u „Fortunaty“ od 10 do 15%. W końcowej fazie wegetacji był większy;

7) zaciemnianie kłosa, częściowa defoliacja lub też zaciemnianie źdźbła — nawet na okres około trzech godzin — powodowało znaczne zmiany w intensywności fotosyntezy w organach eksponowanych na światło oraz w przemieszczeniu asymilatów. Badane odmiany ponownie wykazały istotne różnice w swej reakcji na powyższe zabiegi.

Katedra Fizjologii Roślin SGGW, Warszawa

Zakład Fizjologii Roślin PAN