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

III. Spring wheat — photosynthesis and the daily accumulation of photosynthates in the grain

H. BIRECKA, L. DAKIĆ-WŁODKOWSKA

The experiments reported here constitute a continuation of investigations begun in 1960 (part I, 1963). Plants of three spring wheat varieties, i. e. an awned „Chłopicka" and two awnless ones — „Opolska" and „Fortunata" are the subject. The experiments (in pots) were carried out in 1961 in the greenhouse of the Central College of Agriculture in Warsaw.

METHODS

The soil-sand mixture and nutrients applied were analogous to those in the experiments with wheat carried out in the same year at Puławy (part I, 1963). Seeds were sown on April 27. Full sprouting was noted on May 2. The plants were thinned gradually to 12 per pot. Ear emergence in Chłopicka and Opolska var. was observed on June 17, in var. Fortunata on June 20 (the shoots of the first two varieties were much higher than those of the third one). Flowering was noted between June 20 and 23. At this time all varieties had 1—2 very small tillers per plant, which were removed; among six leaves (including the flag leaf) on the main shoot in Chłopicka and Opolska only three and in Fortunata — four upper ones were green. The average dry weight of the removed yellow leaf laminae together with the tillers amounted in Chłopicka to 0,43, in Opolska to 0,32, in Fortunata to 0,31 g per plant.

The plants were sampled seven times. The dates of sampling and the state of plants are presented in table 1. In the middle of each period between samplings (except for the last harvesting) some plants of each variety were placed (always early in the morning) in a plexiglass chamber, into which ^{14}C — labelled CO_2 was introduced. Following treatments were investigated: 1. controls, 2. plants with flag leaf only (2—3 lower leaf laminae removed), 3. flag leaf lamina removed, 4. ear removed, 5. ear shaded, 6. all vegetative parts shaded (ear only exposed to light). The appropriate technical procedures were analogous to those

Table 1

The state of wheat plants during the period from anthesis to full maturity

Date of sampling and observations	The state of plants
23.VI	Var. Chłopicka and Opolska — three, var. Fortunata — four green leaves, stems (with leaf sheaths) green
3.VII	Var. Chłopicka and Opolska — two leaves (including the flag leaf) fully green, the third one yellow, var Fortunata — three green leaves, the fourth one yellow
10.VII	Var. Chłopicka and Opolska — flag leaf fully green, the lower leaf only half green, var. Fortunata — two leaves (including the flag leaf) green, the lower ones yellow. Stems from the second internode green.
17.VII	All varieties — the flag leaf only half green, Chłopicka and Fortunata — stems green to $^2/_3$, Opolska to $^1/_2$ of their length
24.VII	All varieties — all leaves yellow, stems green only in their upper parts (peduncle), var. Chłopicka — awns still fully green
31.VII	Plants turned yellow (even the awns of the var. Chłopicka)
7.VIII	Plants at full maturity

in the experiment with barley (part II, 1963). In Table 2 the conditions under which the plants were kept in the plexiglass chamber, are reported. The plants were removed from the chamber after 24 hours, immediately killed at —60°C and analysed in the same way as in the experiment with barley.

RESULTS

At the stage immediately after anthesis the investigated three wheat varieties differed from each other as regards the total plant weight (Tab. 3) as well as the weight of particular organs (fig. 1 and 2). The plants var. Chłopicka showed the comparatively highest total dry weight, the highest weight of the stem (including sheaths) and the lowest weight of green leaf laminae. The lowest weight of the whole plant as well as of the stem *, and at the same time the highest weight of leaf laminae was shown by Opolska var.

During the first 10 days of investigations the weight of leaf laminae did not change significantly, on the other hand the weight of the stem and to a certain extent of glumes was increasing. The lowest stem increment was shown by var. Opolska, in which — also in contrast to other varieties — the weight of the flag leaf lamina even increased

* Strictly speaking stem with leaf sheaths; the word stem will be used subsequently with this meaning.

during this time. In the later period the weight of all leaf laminae was gradually decreasing, showing the lowest value already 24 days after anthesis, i. e. at the time they were almost completely dead. And in this respect var. Opolska differed from other varieties, i. e. the weight of its leaves was undergoing the smallest changes with ageing. The gradual decreasing of the stem weight began only about 17 days after anthesis. At full maturity the weight of this plant part in all varieties was similar to that at the starting point of investigations.

The process of grain filling proceeded at a different rate depending on the stage of development and the variety (fig. 3). During the first 10 days its rate was very low in Chłopicka and Fortunata var. and relatively higher in var. Opolska. In the following period it was high already in all varieties.

Table 2

Conditions under which plants were kept in the plexiglass chamber

No.	Date of experiment	CO_2 content*		Total radioactivity applied mc	^{14}C content in plants** per cent of the total activity applied	Fluctuations of temperature in the chamber in the daytime	Weather conditions
		g	%				
I	29-30.VI	5.1	0.35	1.5	73	23—30	sunny
II	6-7.VII	4.4	0.30	1.5	56	18 - 22	varying cloudiness
III	13-14.VII	3.9	0.27	1.5	62	19—30	mostly sunny
IV	20-21.VII	2.2	0.15	0.75	37	20—29	varying cloudiness
V	27-28.VII	1.45	0.10	1.12	1.7	25—35	sunny

* Including the normal CO_2 content in the air volume of the chamber.
** In their aerial parts (the varieties together).

In the awnless varieties the grain reached its greatest dry weight already two weeks before full maturity, in Chłopicka, however, a significant increment occurred still during the last but one week. At these stages also the particular varieties showed the highest total weight. The total plant increment during the whole period under investigation was the greatest in Chłopicka and the lowest in Opolska var. The rate of the weight increase in all varieties was the highest during the first 10 days. Its magnitude after this period was analogous to that found after the following three weeks. It is worth noting that within seven days, when the weight of the stems began decreasing and simultanously grain filling was already rather intense, the total weight

of the investigated plants was not changing markedly. This period coincided with the milk stage of the grain.

Taking into account the gradual diminishing of the assimilating plant area, smaller and smaller amounts of labelled CO_2 were applied in consecutive experiments with ^{14}C. The fluctuations of temperature

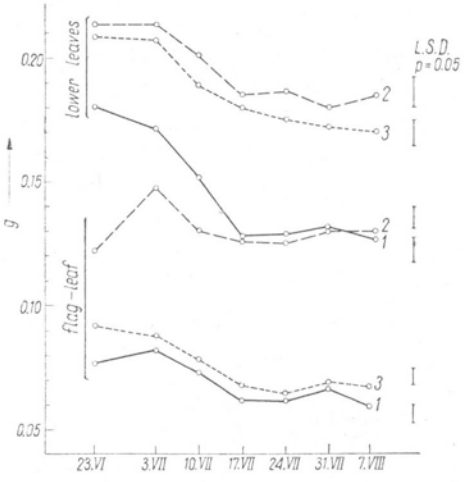

Fig. 1. The weight of leaf laminae * — g d. m. per plant
1 — var. Chłopicka; *2* — var. Opolska; *3* — var. Fortunata
* Var. Chłopicka and Opolska — two, var. Fortunata three lower leaves; the weight of the lowest leaf lamina in the latter var. was about 0.06—0.05 g.

in the chamber in daytime — except for exper. II — were similar (Tab. 2). The data obtained for the plant radioactivity in particular experiments were converted — as in investigations with barley —

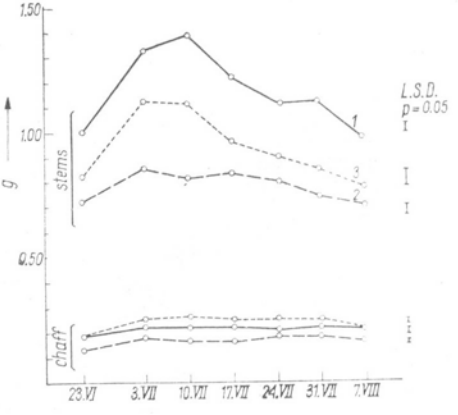

Fig. 2 The weight of stems* and chaff** g d. m. per plant
1 — var. Chłopicka; *2* — var. Opolska; *3* — var. Fortunata
* Including the sheaths and rachis; the weight of the rachis on June 23 was: in Chłopicka — 0.036, Opolska — 0.035, Fortunata — 0.051 g; in the later period — 0.043; 0.040 and 0.062 g respectively. ** In var. Chłopicka — glumes and awns

according to the specific activity of CO_2 applied in exper. II, i. e. $35{,}5 \times 10^3$ cpm per mg CO_2. Therefore the results of all experiments (Tab. 4, 5 and 6) are comparable. The roots of plants, from which soil was previously washed away and which were put into the chamber (exper. II) showed after 24 hours a radioactivity about $5{,}5 \times 10^3$ cpm

per plant — in Chłopicka and Opolska var., and $8{,}7 \times 10^3$ cpm — in var. Fortunata. These values constitute barely 0.5 — 0.6% of the activity found in the aerial parts of the investigated plants.

The plant radioactivity — as has already been discussed in detail in part II — characterises in particular experiments a value between the true and net assimilation, a value more approaching the first one.

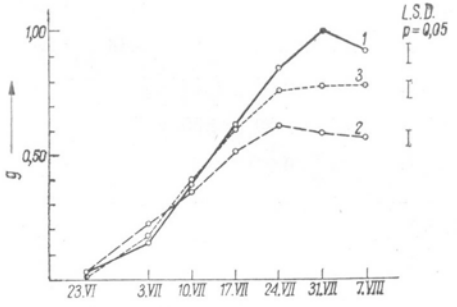

Fig. 3. The weight of the grain — g d. m. per plant
1 — var. Chłopicka; *2* — var. Opolska; *3* — var. Fortunata

The amount of ^{14}C — assimilates in controls found after 24 hours was the greatest in the first period of investigation. At that time the content of labelled carbon was the highest in var. Fortunata.

In the first experiment, with the highest dose of CO_2 applied, only obout 75% of its amount was found in the plants; in the subsequent experiments in spite of diminishing the doses the degree of CO_2 utilisation by all plants was still less*. Therefore it can be assumed that the differences in the CO_2 concentration in the chamber was not a factor significantly influencing the content of carbon assimilated by plants in daytime. If also one takes into account that the temperature was in particular experiments similar (a greater deflection in minus occurred only in exper. II), it can be assumed that the changes in the amounts of photosynthates found after 24 hours in controls at various stages of development were mainly due to changes in the physiological state of the investigated plants. As the obtained results show (additional calculations in tab. 7), these amounts were diminishing with ageing of the plants. However the greatest and relatively the most rapid decrease in CO_2 assimilation could be found in Opolska var. It is worth noting that within the period, when the weight increment of plants in the greenhouse was insignificant, their assimilating capacity was still relatively high.

* The CO_2 concentration at the moment of plant removing from the chamber in all experiments was higher than the concentration (about 0.01%), at which CO_2 is of little availability for assimilation.

Table 3

Weight of wheat — g d. m. per plant

Date of sampling	Var. Chłopicka				Var. Opolska				Var. Fortunata			
	aerial parts			roots	aerial parts			roots	aerial parts			roots
	shoot	grain*	total		shoot	grain*	total		shoot	grain*	total	
23.VI	1.45	0.02	1.47	0.63	1.20	0.02	1.22	0.38	1.32	0.01	1.33	0.65
3.VII	1.79	0.15	1.94	0.58	1.37	0.22	1.59	0.39	1.68	0 17	1.85	0.69
10.VII	1.82	0.39	2.21	0.57	1.29	0.36	1.65	0.30	1.63	0.40	2.03	0.63
17.VII	1.61	0.63	2.24	0.46	1.30	0.52	1.82	0.30	1.42	0.61	2.03	0.54
24.VII	1.52	0.85	2.37		1.30	0.61	1.91		1.39	0.76	2.15	
31.VII	1.55	1.00	2.55		1.24	0.59	1.83		1.32	0.77	2.09	
7.VIII	1.43	0.93	2.36	0.31	1.27	0.57	1.84	0.17	1.20	0.78	1.98	0.33
L.S.D. p=0,05	0.053	0.061	0.090		0.065	0.060	0.109		0.115	0.070	0.124	

* Mean number of kernels per plant: Chłopicka — 23, Opolska — 24, Fortunata — 26.

The attempts to determine the role of leaf laminae and of the ear in the total CO_2 assimilation yielded different results depending on the variety investigated. In Chłopicka var. the removal of the flag leaf lamina as well as of laminae of the lower leaves in the first period did not influence the plant activity significantly (Tab. 4). The activity of all leaf laminae in the control amounted after 24 hours to about 10 % of the total plant activity. Taking into account the translocation of photosynthates to other organs at that time, it can be supposed that the true contribution of leaf laminae to the total CO_2 assimilation was much higher. Thus the phenomenon of recompensation for the removed organs, and already during a dozen or so hours after the removal procedure, occurred in all probability in the discussed experiment. It is hard to judge, how reliable the results of the exper. II are; according to them the contribution of the flag leaf lamina at that time would have been equal to that of the lower leaf and together would have accounted for about 30 %. The same is true for the exper. III, in which the contribution of the flag leaf lamina would amount to 12 % ± 10 %. It can be assumed that the plant capacity for recompensation in later stages must decrease.

In Opolska var. in exper. I the removal of the two lower leaf laminae did not have an influence on the total amount of assimilated carbon either (Tab. 5). On the other hand the removal of the flag leaf lamina caused a decrease in the photosynthate content of about 50 %. In the later period the contribution of this lamina to the total

Table 4

Radioaktivity of wheat plants var. Chłopicka after 24 hrs. exposure to $^{14}CO_2$ — 10^3 cpm per plant

Date of experiment	Plant parts*	Control	Flag leaf laminae remov.	Lower leaves laminae remov.	Ear remov.	Ear shaded	Only ear exposed to light***	L. S. D. ($p = 0.05$) for all treat.	L. S. D. ($p = 0.05$) for treat No. 6
		1	2	3	4	5	6		
I June 29 — 30	fl. leaf	33	—	46	123	92	0	31	
	l. leaves	136	95	—	59	90		32	
	stem	983	1098	1010	1077	1115		Te < Tt	
	rachis	70	42	49	—	36	28		
	glumes**	260	248	234	—	133	175	51	
	grain	198	245	182	—	226	231	42	15
	Total	1680	1728	1521	1259	1692	434	161	8
II July 6 — 7	fl. leaf	73	—	74	133	84	0	22	
	l. leaves	70	57	—	62	69		Te < Tt	
	stem	596	349	375	616	286		43	
	rachis	30	26	27	—	16	9		
	glumes	133	146	121	—	42	97	17	
	grain	432	541	545	—	466	315	65	31
	Total	1334	1119	1142	811	963	421	74	29
III July 13 — 14	fl. leaf	46	—	39	48	48	0	Te < Tt	
	l. leaves	14	8	—	17	18		Te < Tt	
	stem	413	340	386	501	286		52	
	rachis	26	30	31	—	13	10		
	glumes	134	153	124	—	44	89	24	
	grain	761	683	732	—	620	392	99	18
	Total	1394	1214	1312	566	1029	491	141	25
IV July 20 — 21	fl. leaf	33			27	15	0	6	
	stem	257			349	145		43	
	rachis	32			—	3	12		
	glumes	156			—	22	127	14	
	grain	473			—	252	249	63	31
	Total	951			376	437	388	134	36
V July 27 — 28	stem	1			4				
	rachis	1			—				
	glumes	17			—				
	grain	62			—				
	Total	81			4			6	

* fl. — flag, l. — lower leaf laminae. Exp. I — three green leaf laminae (including the flag leaf), the lowest one begins turning yellow, exp. II — two green leaves, exp. III — flag leaf green, the lower leaf green at its base only, exp. IV — flag leaf green only at its base, exp. V — no green leaf laminae. The rachis of three replicates were analysed together.

** Together with awns — in all experiments.

*** The direct counting of samples of the vegetative plant parts gave the back ground value.

Table 5

Radioactivity of wheat plants var. Opolska after 24 hr. exposure to $^{14}CO_2$ — 10^3 cpm per plant

Date of experiment*	Plant parts**	Control	Flag leaf laminae remov.	Lower leaf laminae remov.	Ear remov.	Ear shaded	Only ear exposed to light	L.S.D. (p=0.05) for all treat.	L.S.D. (p=0.05) for treat. no. 6
		1	2	3	4	5	6		
I June 29 — 30	fl. leaf	190	—	198	202	219	0	26	
	l. leaves	65	28	—	39	62		17	
	stem	697	301	811	1113	673		117	
	rachis	33	23	32	—	27	8		
	glumes	172	116	200	—	70	74	26	
	grain	547	397	586	—	520	152	92	12
	Total	1704	865	1827	1354	1576	234	151	20
II July 6 — 7	fl. leaf	141	—	117	131	96	0	30	
	l. leaves	23	35	—	19	41		18	
	stem	295	225	292	535	269		47	
	rachis	28	20	25	—	14	5		
	glumes	111	77	115	—	27	53	24	
	grain	472	319	300	—	315	97	106	5
	Total	1070	676	849	685	762	160	143	6
III July 13 — 14	fl. leaf	86	—	96	56	68	0	30	
	l. leaves	23	26	—	17	20		12	
	stem	248	205	207	503	196		53	
	rachis	26	20	25	—	9	9		
	glumes	73	67	76	—	14	61	11	
	grain	604	493	579	—	455	106	95	19
	Total	1060	811	983	576	762	176	130	22
IV July 20 — 21	fl. leaf	43			42	43	0	10	
	stem	82			107	94		12	
	rachis	15			—	9	6		
	glumes	100			—	8	88	31	
	grain	239			—	187	46	27	11
	Total	479			149	341	140	67	9

* In the experiment carried out on July 27—28 only traces of radioactivity were found in the investigated plants.

** Exp. I — three green leaf laminae (including the flag leaf), the lowest one only half green, exp. II — two green leaves, the lower one getting yellow, exp. III — the flag leaf green, the lower one green only at its base, exp. IV — the flag leaf green only at its base. exp. V — no green leaf laminae.

CO_2 assimilation would amount to about 36% and of the lower one — partially yellow — to 20%. The contribution of the flag leaf lamina in exper. III would account for about 24%.

The greatest influence of the removal of the leaf laminae is to be found in var. Fortunata (Tab. 6). So in exper. I and II the

Table 6

Radioactivity of wheat plants var. Chłopicka after 24 hr. exposure to $^{14}CO_2$ — 10^3 cpm per plant

Date of experiment	Plant parts*	Control	Flag leaf laminae removed	Lower leaf laminae removed	Ear removed	Ear shaded	Only ear exposed to light	L.S.D. (p=0.05) for all treat.	L.S.D. (p=0.05) for treat no 6
		1	2	3	4	5	6		
I June 29 — 30	fl. leaf	52	—	60	59	54			
	l. leaves	123	61	—	102	107	0	28	
	stem	1243	390	732	1172	1057		132	
	rachis	40	36	49	—	34	14		
	glumes	205	175	232	—	109	116	49	
	grain	310	205	268	—	195	116	56	5
	Total	1973	867	1341	1333	1556	246	243	21
II July 6 — 7	fl. leaf	73	—	84	101	80		19	
	l. leaves	77	53	—	123	88	0	30	
	stem	657	205	332	855	391		128	
	rachis	24	18	28	—	14	6		
	glumes	84	79	107	—	27	55	24	
	grain	503	341	353	—	540	188	85	27
	Total	1418	696	904	1079	1140	249	219	31
III July 13 — 14	fl. leaf	62	—	29	71	76		30	
	l. leaves	23	25	—	9	63	0	12	
	stem	262	202	246	475	274		61	
	rachis	31	17	23	—	18	7		
	glumes	108	96	105	—	33	55	22	
	grain	672	598	710	—	569	141	101	26
	Total	1158	938	1113	555	1033	203	208	29
IV July 20 — 21	stem	103			312	84	0	72	
	rachis	12			—	5	4		
	glumes	42			—	6	27	10	
	grain	552			—	386	143	71	21
	Total	714			312	481	174	120	26
V July 27 — 28	stem	traces			traces				
	rachis	3			—				
	glumes	9			—				
	grain	55			—				
	Total	67			traces			5	

* Exp. I three leaf laminae (including flag leaf) fully green, the fourth one turning yellow, exp. II — two leaves green, the third one getting yellow the lowest one completely yellow, exp. III — only the flag leaf fully green, the second one green only at its base, exp. IV — no green leaf laminae.

decrease — as compared to the control — in the radioactivity of plants deprived of the flag leaf lamina accounted for 50%, and of the plants deprived of 3—2 lower leaf laminae for about 30%. The contribution of the flag leaf lamina to the total CO_2 assimilation in exper. III would amount to about 20%. In exper. IV the role of this leaf lamina was not investigated, for in var. Fortunata it was completely yellow and in the other varieties it was green only at its base. Its activity in this experiment accounted in Chłopicka for 3 and in Opolska var. for 9% of the total plant activity. However the true contribution of the flag leaf lamina at that time was in all probability higher than these values seem to indicate.

The contribution of the ear to the total carbon assimilated by the investigated plants could be estimated from results of three treatments (4, 5 and 6). In all varieties and in all experiments the sum of the activity of plants, whose ears were shaded and of plants, whose all vegetative parts were shaded, was similar to the total activity of the controls (within the limits of the standard error). The only exception in this respect was Chłopicka var. in exper. I, in which the activity of plants with ears shaded was equal to that of the controls. The activity of plants deprived of the ear was in all cases less than that of plants with ear shaded. It does not seem that this is due to a possible increase — because of the treatment applied — in the translocation of assimilates to the roots. For the observed differences occurred and even to a greater extent also at the late stages of grain filling, i. e. in the period, when the roots were partially decomposing. It would be more likely that ear removal had a negative influence on the rate of photosynthesis in the vegetative organs of the plants. Therefore the results from these plants can not serve as basis for the estimation of the role of the ear.

Among the first two treatments the data obtained from plants, whose ears only were exposed to light, are burdened — similarly as in the investigations on barley — with the relatively smallest error, for: 1° in this case the error due to differences between replicates in the rate of photosynthesis in vegetative organs is eliminated, 2° the possible increase — because of shading the vegetative parts — in the rate of this process in the ear itself would bring about an increment of assimilated carbon, which would constitute a small value as compared to the total amount of carbon assimilated by the whole plant, especially in the first two weeks of investigations. Therefore the results from treat. 6 were taken as a basis for the estimation of the ear contribution to the total CO_2 assimilation. This contribution was the highest in var. Chłopicka and with ageing of the vegetative organs it was increasing from about 25 to 40% (Tab. 8). In var. Fortunata and Opolska it was significantly less, increasing during the investigation period from

12—14% to 24—29%. In the last experiment, i. e. 10 days before full maturity the green parts of the ear only in fact were capable of photosynthesizing (except for Opolska var.).

It is worth noting that the absolute amounts of carbon assimilated by the ear in particular experiments carried out during the month after anthesis did not undergo great changes (the visual estimation of the ear greeness would be an indirect confirmation of this).

Table 7

The radioactivity of plants in particular periods after anthesis — per cent of the total plant activity found in the first period

Variety	Experiment									L.S.D. p = 0.05
	I		II		III		IV		V	
	total	due to photosynt. in the ear	total	due to photosynt. in the ear	total	due to photosynt. in the ear	total	due to photosynt. in the ear	total	total
Chłopicka	100	26	79	25	83	29	57	23	5	4.3
Opolska	100	14	63	9	62	10	23	8	traces	4.6
Fortunata	100	12	72	13	59	10	36	9	3	11.5

As the data in Table 7 show, one of the main causes of the relatively small decrease with ageing in the CO_2 assimilation in plants var. Chłopicka was a greater assimilating capacity of their ear as compared to other varieties.

Table 8

The contribution of photosynthesis in the ear to the total CO_2 assimilation — per cent of the total activity of controls in particular experiments

Experiment	Variety		
	Chłopicka	Opolska	Fortunata
I	26	14	12
II	31	15	17
III	35	17	18
IV	41	29	24
V	95	—	100

The estimation of the role of leaf laminae, especially from the results of the first two experiments being uncertain, it is hard to determine the role of the stem at that time. According to the following

two experiments, in which the observed „artefacts" were perhaps of a lesser importance, the contribution of this plant part to the total CO_2 assimilation would amount in the period under investigation in Chłopicka var. to about 50%, in other varieties to about 60% (in Fortunata in exper. IV, when all leaf laminae had turned yellow, to about 75%).

Table 9

The distribution of assimilates between particular plant parts — per cent of the total activity of the controls

Treatment	Plant parts	Experiment					L.S.D. (p=00.5)
		I	II	III	IV	V	
Control	total	100	100	100	100	100	
		var. Chłopicka					
Control	Leaf laminae	10**	11	5	3	—	1.5
	Stem *	63	47	31	30	2	3.1
	Glumes, awns	15	10	10	17	20	2.0
	Grain	12	32	54	50	73	4.4
Only ear exposed to light	Glumes, awns	10	7	6	13		
	Grain	14	24	28	26		
		var. Opolska					
Control	Leaf laminae	15***	15	10	9		1.6
	Stem *	43	31	26	20		2.8
	Glumes	10	10	7	21	traces	1.2
	Grain	32	44	57	50		4.0
Only ear exposed to light	Glumes	4	5	6	18		
	Grain	9	9	10	10		
		var. Fortunata					
Control	Leaf laminae	9**	11	7	0	—	1.0
	Stem *	65	48	26	17	5	3.8
	Glumes	10	6	9	6	13	1.1
	Grain	16	35	58	77	82	4.5
Only ear exposed to light	Glumes	6	4	5	4		
	Grain	6	13	12	20		

* Including the rachis.
** Mainly lower leaf laminae.
*** Mainly the flag leaf.

The distribution of assimilates between particular parts of the control plants after 24 hours (Tab. 9) varied depending of the development stage and variety. In the first two experiments, which can characterise the period of about 18 days immediately after anthesis, Chłopicka and Fortunata var. showed great similarities. The daily accumulation of photosynthates in the grain during the first period after anthesis was relatively small, constituting about 12—16% of their total amount found in the plant. A week later it increased markedly to

about 32—35%. At that time the greatest amount of photosynthates was accumulating in stems. In both experiments only 10% of the total carbon assimilated could be found in the leaf laminae of these varieties. On the other hand plants var. Opolska already in the first period were accumulating daily in the grain about one third of photosynthates and in the following week even more. At the same time this variety showed a relatively much smaller accumulation of assimilates in the stem retaining a greater amount of them in leaf laminae, especially in the flag leaf (an analogous phenomenon in the leaf laminae of Opolska var. occurred also at later stages). These differences between the investigated varieties are reflected also in the data concerning the dry weight of plants.

During the following two weeks the daily translocation of photosynthates to the grain in all varieties increased markedly, exceeding 50% of their total amount. At the same time the relative content of labelled carbon in the stem was significantly lower, however its value was the highest in Chłopicka var., which in this period showed the greatest assimilating capacity in comparison with other varieties.

The daily translocation to the grain of photosynthates derived from the green parts of the ear varied. So in Chłopicka and Fortunata var. in the first period, when the rate of grain filling was wery low and the glumes (and awns in Chłopicka var.) were increasing in weight, only about half of these assimilates were translocated to the grain. In the following stages the mean magnitude of the daily translocation amounted to about 75% of ear assimilates. In Opolska var. on the other hand already in the first period it accounted for 60% and did not undergo significant changes in the two subsequent experiments. In the later period it diminished to about 35%. Thus the contribution of photosynthesis in the ear to the total amount of ^{14}C — assimilates accumulated daily in the grain varied depending on the investigated variety and the development stage. In var. Chłopicka it was as follows: in exper. I — 100, in exper. II — 75, in two subsequent ones — about 50%; in var. Fortunata in the first two experiments about 40, in the following ones 20—25%. In both varieties at the latest stage of grain filling almost the whole amount of photosynthates — in fact very small — was due already to the assimilating activity of the ear only. In var. Opolska the contribution of photosynthesis in the ear to the daily accumulation of assimilates in the grain was varying from 30 (in exper. I) to about 20% in the later period.

It should be noticed that the removal of leaf laminae or ear shading either had no influence at all (at the first stages) or effected only to a very small degree the amount of photosynthates accumulated in the grain. Thus the reaction of plants to these treatments was

revealed not only in changes in the rate of photosynthesis but also in the translocation of assimilates to the ear. This reaction was to be seen most clearly in var. Chłopicka.

DISCUSSION

The character of growth of the three investigated wheat varieties after heading and the differences between them, found in the experiments reported above, do not seem incidental. Investigations carried out for several years by G e j (1962) in our laboratory showed that the total yield and the yield of the grain of plants var. Chłopicka were usually greater than that of plants var. Opolska (even under optimal water supply), and the differences in the weight increment occurred mainly in the later period of development i. e. after ear emergence. An analogous phenomenon was revealed in experiments carried out at Puławy as well as in the reported ones. The yield of plants of both varieties in investigations at Puławy was significantly higher. It should be added that the results obtained with var. Fortunata in these investigations were also similar to those in the reported experiments.

In investigations carried out in Warsaw and at Puławy analogous differences between varieties in the size of green leaves and stems too, as well as in the changes of their weight during the last month of growth were found. The plants Opolska var. were to be distinguished by the greatest area and weight of the leaf laminae, and the plants var. Chłopicka by the smallest. As concerns the weight of stems the relationship was reversed.

The experiments with ^{14}C showed, that in the first period after heading (i. e. about 7—8 days after anthesis) the amount of carbon assimilated by the vegetative organs of plants var. Opolska as well as Fortunata was greater than that in the var. Chłopicka. A week later the assimilating capacity * of these organs was higher only in var. Fortunata (a greater number of green leaves!). In the third week the differences between the varieties were already nil in this respect and in the fourth week the vegetative organs in var. Opolska markedly conceded to those in other varieties. These facts clearly indicate that the ageing process in vegetative organs of Opolska var. was the quickest. It is possible that this phenomenon was caused by a more rapid decomposition of the roots, which moreover were relatively small. The accelerated maturation of Opolska plants was revealed also in the relatively low degree of translocation of assimilates from glumes to the grain in the last period of filling. This variety differed from other ones also in the first period after anthesis — as was discussed

* Assuming that the influence of CO_2 concentration applied on the rate cf photosynthesis was analogous in all investigated varieties.

above in detail. It seems, however, that an additional important cause of the relatively low yield of Opolska plants is the small assimilating capacity of the ear itself. On the other hand one of the main causes of the high yield of the whole plants as well as of the grain in var. Chłopicka is probably the relatively high assimilating capacity of the ear.

The still marked weight increment observed in this variety during the fifth week after anthesis resulted in all probability also from a longer maintainance — as compared to the vegetative organs — of this capacity. In the experiment with ^{14}C carried out at that time plants Chłopicka var. showed in fact only 5% of the activity found in the first week after anthesis, but at the investigated stage a difference of 3—4 days between the experiment and the preceding sampling could have been of significant importance.

The great influence of the photosynthetic capacity of ears on the grain yield in wheat has been stressed by Asana and others (1958 a, b). It is possible that the presence of awns in var. Chłopicka was the main cause of the relatively high assimilating capacity of the ear as compared to awnless varieties. It is worth noting that the contribution of the ear in this variety to the total CO_2 assimilation was analogous to that of an awned barley variety Browarny PZHR grown under similar conditions (part II, 1963). It is obvious that the characteristics of the role of the ear, found in the reported experiments, may undergo some changes deepnding on the physiological state of the vegetative organs of plants.

It is difficult to determine from the results obtained, what was the true contribution of photosynthesis in the ear to the yield of the grain in the investigated varieties. For one must take into account that assimilates remaining after 24 hours in the green organs may still in the later period be translocated at least partially to the grain. On the other hand a proportion of them can be utilised in respiration. This latter remark is perhaps of little significance when the advanced stages of grain filling are considered because of the relatively high rate of starch synthesis in the grain and of the diminished rate of respiration (Rejowski 1962 a, b, Szczukina 1929, Wood 1960). However in the earlier period, especially at the milk stage the losses brought about by respiration can be great. It seems that this is the main cause of the differences between the rate of photosynthesis and the dry weight increase of plants at that time. It is also possible that at this stage not only products of current photosynthesis served as respiration substrate, but also to some extent organic compounds accumulated in the stem during the earlier period. The role of these compounds in grain filling at later stages needs — as in the case of barley — more detailed investigations.

There is no doubt that the stem in wheat as well as in barley is capable of a transient accumulation of assimilates and that:

1. The translocation to it of photosynthates from leaf laminae depends little on the ear and on the physiological stage of the developing kernels. For in all varieties the amount of photosynthates found after 24 hours in the laminae was relatively small even within the period, when the rate of grain filling was wery low. The rapid translocation of photosynthates from leaf laminae in wheat has already been stated by a number of workers (Pietinow 1962, Shen and others 1959, Żółkiewicz and others 1958). Some differences between varieties in this respect can in fact occur but they do not change the main features of the phenomenon observed.

2. On the other hand the period, during which photosynthates are retained in the stem, seems to be dependent on the rate of accumulation of organic compounds in the grain, on the total photosynthetic capacity of the plants and also on the photosynthetic capacity of the ear itself. The small increment of the stem in Opolska var. — as compared to others — in the first period after anthesis (this was confirmed in experiments with ^{14}C) can be explained mainly by a more intense translocation of photosynthates to the grain and by the relatively low contribution of the green parts of the ear to this process. On the other hand in Chłopicka var. the great increment of the stem at that time was favored by the small grain increase and the simultanous high photosynthetic activity of the ear; in Fortunata var. apart from the similar behaviour of the grain the main factor was the high — higher than in other varieties — assimilating capacity of the vegetative organs. The dependence of the translocation of photosynthates on the above mentioned factors could be found also at the later stages of grain filling.

One of the aims of the experiments was to estimate the contribution of not only the ear but also of particular vegetative parts to the total CO_2 assimilation. It seemed that removing the flag leaf or lower leaf laminae for a relatively short time, for a dozen or so hours, it would be possible to avoid — in contrast to previous experiments — the reaction of organs exposed to light to the treatment applied. As it came out, even within such a short period this reaction could not be avoided. It must be stressed that each investigated variety reacted similarly as in the experiments mentioned above. First of all the great capacity of plants var. Chłopicka to recompensate in photosynthesis the removed leaf laminae is worth noting. Similarly their vegetative organs reacted in the case of ear shading in the first period of investigation (not to mention the changes in the translocation of photosynthates). Taking into account the short

period of the influence of the treatments applied, it can be assumed that the increased amount of carbon assimilated by these organs resulted from an increase in the rate of photosynthesis only, and not also from the increased growth rate; this latter phenomenon was to be observed in the previous investigations. It is difficult to judge from the experiments, what part of the plant reacted most strongly in the case of lamina removal or ear shading. This problem seems to be worth further investigations.

The plants var. Fortunata — in contrast to the Chłopicka ones — showed after the removal of flag leaf or lower leaf laminae a significantly smaller amount of assimilated carbon. The behaviour of plants var. Opolska was intermediary in this respect. It is possible that in both these varieties the contribution of leaf laminae to the total CO_2 assimilation was in fact as high as the obtained data seem to indicate (thus the role of the stem with sheaths would have been wery small in the first two weeks after anthesis). However it is uncertain, whether in this case a negative reaction to the treatments applied might not have occurred, perhaps a phenomenon known in literature as „traumatogenic reaction". In connection with this the fact of the negative influence of ear removal on the photosynthesis rate in all wheat varieties is worth stressing. This phenomenon was not observed in barley *.

The degree of the recompensation capacity of the plant or its negative reaction — independently of the theoretically physiological aspect — may be of great importance in agricultural practice. For under normal field conditions injuries or dying of a part of vegetative organs can and often does occur as a result of diseases, insects, mechanical factors, drought etc. The greater the recompensation capacity of the plant with regard to photosynthesis, the lesser the negative effects of these factors, which could be expected. It is probable that one of the main causes of the yield stability of the var. Chłopicka under field conditions is just its great recompensation capacity. It seems that a better understanding of this capacity in various plant populations may be of great importance especially for breeding.

Unfortunately taking into account the immediate aim of our investigations this phenomenon caused great difficulties.

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* The experiments with barley var. Browarny PZHR showed that the shading or removal of appropriate organs bring about mainly a reaction of recompensation (but a much weaker one than in wheat var. Chłopicka). This was one of the main reasons., why the role a particular leaf laminae of barley especially of the flag leaf, which is wery small, was not investigated.

CONCLUSIONS

Among the results obtained from the reported, preliminary experiment the following are worth noting;

1. Three investigated (in pots) varieties of spring wheat, an awned — Chłopicka and two awnless Opolska and Fortunata showed significant differences in growth and translocation of photosynthates within the period from anthesis to maturity. The total weight increment and the grain yield were the highest in var. Chłopicka and the lowest in var. Opolska. This was due mainly to differences between these varieties in the rate of ageing of vegetative organs and in the photosynthetic capacity of the ear.

2. The greatest weight increase in all varieties occurred during the first 10—18 days after anthesis, when the plant had 3—2 green leaves. At the milk stage, when the total increment was minimal, the assimilating capacity of the plants was still relatively high.

3. In the first period after anthesis the contribution of photosynthesis in the ear to the total amount of carbon daily assimilated by the plants amounted in var. Chłopicka to about 25%, in the awnless varieties to about 12—14%. Its contribution with ageing of vegetative parts was increasing and in the fourth week after anthesis accounted respectively for about 40% and 24—29%.

4. The daily translocation of photosynthates from the leaf laminae was intense at all stages of grain filling. The degree of accumulation of photosynthates in the stem (including sheaths) depended in the investigated varieties on the rate of grain filling, on the total assimilating capacity of the plant as well as on the assimilating capacity of the ear itself.

5. The daily accumulation of photosynthates in the grain was different at particular stages of its development. In Chłopicka and Fortunata var. it accounted in the first period for about 12—16% only, increasing afterwards to more than half of their total amount found in the plants. In Opolska var. the relative accumulation of assimilates in the grain at the first stage was much higher.

6. The contribution of photosynthesis in the ear to the total amount of assimilates daily accumulated in the grain at all stages of filling was the greatest in var. Chłopicka. In the first period the ear only supplied the grain with photosynthates; when the filling process was increasing, the contribution of ear photosynthates was gradually diminishing to about 50%. In the awnless varieties the amounts of assimilates from the ear accounted in the first period for 30—40%, at the later stages for about 20—25% of the total amount daily accumulated in the grain.

7. The removal of particular leaf laminae or ear shading in var. Chłopicka caused during the following hours a marked reaction of the plants, which was revealed in an increased rate of photosynthesis in organs exposed to light. This recompensation capacity was manifested especially strongly in the first period after anthesis. The investigated varieties showed great differences in their reaction to these treatments.

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

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STRESZCZENIE

W roku 1961 przeprowadzono doświadczenie wazonowe z trzema odmianami pszenicy jarej, a mianowicie Ostką Chłopicką, Opolską i Fortunatą. Badano przyrost suchej masy roślin w okresie od zapłodnienia do pełnej dojrzałości. Sprzętu dokonywano w tym czasie siedmiokrotnie w odstępach najczęściej tygodniowych. W połowie każdego okresu część roślin umieszczano na dobę w kamerze z pleksiglasu, do której wprowadzano znakowany ^{14}C dwutlenek węgla. Uwzględniono następujące kombinacje: 1) kontrola, 2) rośliny pozbawione 2—3 liści dolnych, (oprócz flagowego), 3) pozbawione tylko liścia flagowego, 4) pozbawione kłosa, 5) rośliny z kłosem zaciemnionym, 6) z wszystkimi organami wegetatywnymi zaciemnionymi.

Uzyskane wyniki pozwalają stwierdzić, iż:

1. Trzy badane odmiany pszenicy jarej wykazały istotne różnice we wzroście i przemieszczaniu związków organicznych w okresie od zapłodnienia do dojrzenia. Wielkość przyrostu suchej masy oraz wielkość plonu ziarna była największa u Chłopickiej, najmniejsza zaś u Opolskiej. Fakt ten był głównie spowodowany różnicami w szybkości obumierania organów wegetatywnych i zdolności fotosyntetycznej kłosa.

2. Największy przyrost suchej masy u wszystkich odmian wystąpił w ciągu pierwszych 10—18 dni po zapłodnieniu, kiedy rośliny miały po 3—2 zielone liście. W fazie mlecznej dojrzałości ziarna, kiedy przyrost był minimalny, intensywność fotosyntezy była jeszcze stosunkowo duża.

3. Udział kłosa w ogólnej asymilacji CO_2 przez rośliny w pierwszym okresie po zapłodnieniu wynosił u Chłopickiej około 25% u odmian bezostnych był o połowę mniejszy. W miarę żółknięcia organów wegetatywnych udział jego zwiększał się i w czwartym tygodniu po zapłodnieniu u Chłopickiej wynosił około 40%, u Opolskiej i Fortunaty 24—29%.

4. Odpływ asymilatów z blaszek liściowych w ciągu doby we wszystkich fazach wypełniania ziarna był intensywny.

Stopień gromadzenia się asymilatów w źdźble (wraz z pochwami liściowymi) zależał u badanych odmian od intensywności akumulacji związków organicznych w ziarnie, a także od zdolności asymilacyjnej samego kłosa.

5. Akumulacja produktów fotosyntezy w ziarnie w ciągu doby była różna w poszczególnych fazach jego wypełniania. U Chłopickiej i Fortunaty w pierwszym okresie wynosiła zaledwie około 12—16%, a w późniejszych fazach wzrosła do ponad połowy ogólnej ich ilości stwierdzonej w roślinach. U Opolskiej względna akumulacja asymilatów w ziarnie w pierwszym okresie była znacznie większa.

6. Udział produktów fotosyntezy przebiegającej w kłosie w ogólnej ich ilości gromadzącej się w ziarnie w ciągu doby we wszystkich fazach jego wypełniania był największy w roślinach odm. Chłopickiej. W pierwszym okresie asymilaty przemieszczone do ziarna pochodziły wyłącznie z kłosa; w miarę zwiększania się intensywności akumulacji udział kłosa zmniejszał się stopniowo do 50%. U odmian bezostnych ilość asymilatów pochodzących z zielonych części kłosa wynosiła początkowo 30 (Opolska) — 40% (Fortunata), w późniejszych zaś fazach 20—25% ogólnej ilości gromadzących się w ziarnie w ciągu doby produktów fotosyntezy.

7. Usunięcie poszczególnych liści bądź też zasłonięcie kłosa u roślin odm. Chłopickiej wywołało w ciągu następnych kilkunastu godzin wyraźną ich reakcję, przejawiającą się we wzmożeniu fotosyntezy w organach eksponowanych na światło. Ta zdolność do rekompensacji przejawiła się szczególnie silnie w pierwszym okresie po zapłodnieniu. Badane odmiany wykazują duże różnice w swej reakcji na powyższe zabiegi.

Katedra Fizjologii Roślin SGGW
Zakład Fizjologii Roślin PAN

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