

Photosynthetic activity and productivity before and after ear emergence in spring barley

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In previous investigation on barley (published in 1964) the attempts to examine changes in the share of particular vegetative organs with ageing in the total plant photosynthetic activity were not very successful. On the other hand some data obtained allowed to suppose that carbon assimilated before ear emergence might contribute in some degree to the organic matter accumulated finally in the kernels.

In the reported two-year experiments the role of particular green parts was investigated by exposing intact plants grown on two nitrogen levels to ^{14}C -labelled CO_2 for a short time at various stages of development (before and after heading). Changes in the distribution of assimilates were followed during the whole time from their formation to ripeness. The same as previously spring barley variety — 'PZHR Browarny' — was used. The environment conditions of growth were the same as in experiments with spring wheat (Birecka, Dakic-Włodkowska 1966).

METHODS

Experiment 1963. Full sprouting of plants was observed on April 23, beginning of tillering and shooting was noted after 13 and 30 days, respectively. The plants were thinned gradually to 11 per pot (the total amount of nutrients added was: N 0.7, P_2O_5 0.6, K_2O 0.8 g). On the 35th day they were divided into two groups; the first was given 0.2, the second 0.7 g N per pot. Heading of the main shoot and tillers in both groups was observed after 46—47 and 49—51 days of growth, respectively. Full ripeness was noted on the 84th day after sprouting.

Experiment 1964. Sprouting was observed on April 22, tillering and shooting after 12 and 30 days, respectively. The plants were thinned to 8 per pot (the total amount of nutrients added was: N 0.8, P_2O_5 0.8, K_2O 1.2 g). On the 31th day of growth they were given 0.2 or 0.8 g N per pot. Heading of the main shoot was observed after 46—48, and ripeness after 83 days of growth, without significant differences in dependence on nitrogen supply.

In both experiments the plants were sampled for dry matter determination several times at various intervals. In the middle of each period between samplings

(the last one excepted) groups of plants representing two N levels were exposed* in a plexiglass box out-of-doors to ^{14}C -labelled CO_2 for 20–30 min. In table 1 the conditions, under which they were kept in the box are listed.

In 1963 the labelled plants were sampled successively six times: immediately after exposure, at 8 p.m. on the same day, on the next day at 8–9 a.m., on the days of the next two samplings for dry matter determination and at ripening. The 1st, 3rd and 6th samplings represented plants of two N levels, the remaining — only those grown on the low N dose. In 1964, plants representing always both N levels were sampled five times: immediately after exposure, on the days of the next three samplings for dry matter determination and at ripeness. On the day of each exposure chlorophyll content in the particular green parts as well as the lamina area (expt. I) were determined.

All technical procedures applied were the same as in the experiments with spring wheat. Similarly, the data concerning the radioactivity of plants exposed at various stages to $^{14}\text{CO}_2$ were referred to the specific activity of ^{14}C -labelled CO_2 applied at the first exposure in the 1963 as the 1964 experiments.

RESULTS

Although the total final weight and the grain yield of the main shoot in control plants were in both experiments similar (Table 2), some differences in the weight of leaves as well as in chlorophyll and nitrogen content could be observed. Thus in expt. I the weight of the laminae was lower and that of the sheaths higher than in expt. II (Figs. 1 and 2). Analogous differences — even more pronounced as regards the sheaths — were found in chlorophyll content at the early stage after heading (Tables 3 and 4). Although the total nitrogen amount in the main shoot was in 1964 higher (Table 5), the ageing process of its green parts was much more rapid than in 1963, owing probably to the higher temperature in June**. This is reflected also in changes of chlorophyll content in the ear***. The enhanced senescence in the second experiment is — as seems — mainly responsible for the fact that weight increments of the main shoot after heading were noted during a shorter period. However, even in the first experiment the greatest shoot weight was already reached 15 days before ripening.

The higher rate of productive tillering in 1964 — due mainly to the smaller number of plants per pot and to a better supply especially of N — was accompanied by a greater total weight of the shoots as well as of their kernels.

* In addition, at exposures II and III some plants with their uppermost internode and sheath shaded were introduced into the box. The covers were removed immediately after exposure.

** Mean temperature in June: 1963 — 17.1; 1964 — 20.2°C.

*** In spite of a similar dry weight the ear contained more chlorophyll in 1963 than in 1964, even in the first period after heading.

Table 1

Conditions, under which plants were kept in the plexiglass box

No.	Age of plants days	CO ₂ concentration vol %	¹⁴ CO ₂ assimilated — per cent of total activity applied	Fluctuations of temperature °C	Weather conditions
Experiment 1963 ¹ — I					
I	43	0.075	68	26—33	sunny
II	56	0.05	54	22—28	var. cloudiness
III	65 ²	0.048	50	27—34	sunny
IV	72	0.035	26	28—34	„
Experiment 1964 ¹ — II					
I	37	0.09	70	27—33	sunny
II	44	0.09	58	24—30	
III	53	0.09	76	30—35	
IV	60 ²	0.08	63	21—26	cloudy
V	67	0.035	17	17—21	„ (rain)

¹ Beginning of exposures to ¹⁴C-labelled CO₂: in 1963 — at 1¹⁵ p.m., in 1964 — at 10 a.m.² Milk stage of kernels.

Table 2

Weight of barley — g d.m. per plant

Age of plants days	Low nitrogen dose				High nitrogen dose			
	main shoot		tillers ¹		main shoot		tillers ¹	
	total	grain only ²	total	grain only	total	grain only	total	grain only
Experiment I								
41	1.26		1.01		1.23		1.08	
50	2.02	0.13	1.80	0.11	1.79	0.13	2.06	0.11
62	2.55	0.53	2.70	0.54	2.36	0.60	3.25	0.59
69	2.77	0.95	3.00	1.02	2.53	1.00	3.91	1.17
76	2.85	1.22	2.99	1.38	2.70	1.28	4.54	1.96
84	2.88	1.33	2.90	1.40	2.68	1.26	4.70	2.29
Experiment II								
33	0.64		0.84		0.61		0.85	
40	1.23		1.83		1.13		2.11	
47	1.68	0.08	2.91	0.10	1.64	0.07	3.37	0.07
56	2.27	0.35	3.95	0.54	2.35	0.30	5.38	0.57
63	2.80	0.82	5.11	1.52	2.86	0.82	7.35	1.96
71	2.87	1.16	5.50	2.37	3.03	1.23	8.21	3.41
83	2.79	1.19	5.38	2.41	2.82	1.25	8.32	3.95

¹ Mean number of fertile tillers in 1963, low N — 1.4, high N — 3.4; in 1964 — 2.6 and 4.0, respectively. The weight of sterile tillers varied on both N levels in 1963 between 0.32 and 0.13 g, in 1964 between 0.16 and 0.07 g.² Mean number of kernels in the main shoot — equal on both N levels — in 1963 — 27, in 1964 — 28; in tillers in 1963: low N — 32, high N dose — 67; in 1964 — 60 and 99, respectively.

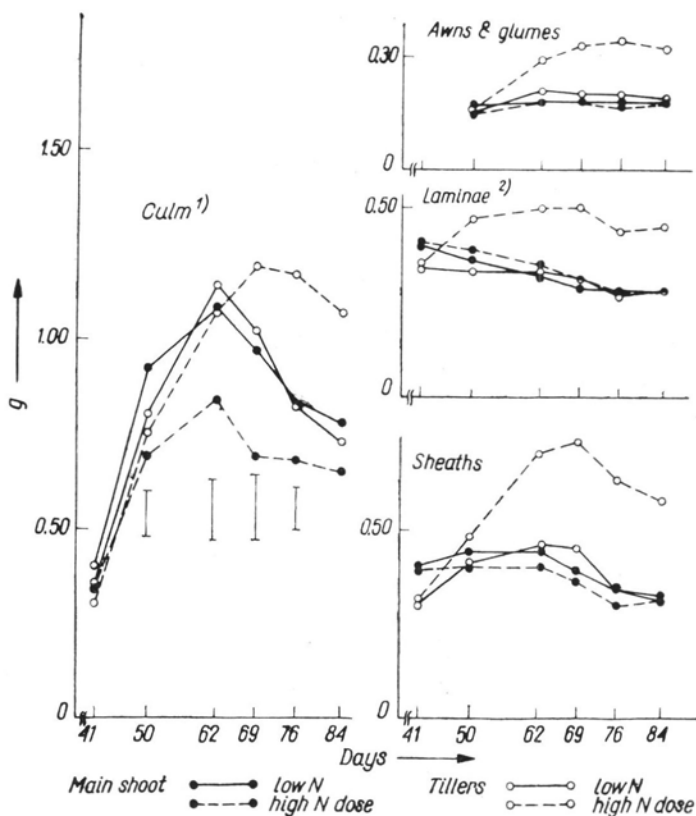


Fig. 1. Dry weight of particular plant parts. Experiment I.

1) Including rachis; length of the main shoot culm: low N- 97, high N dose- 94cm. Vertical lines represent L.S.D. values ($p = 0,05$) for the weights of the main shoot culm. 2) Seven leaves; changes in weight of the first and second (from the top) laminae—low N: 32–22 and 76–52, high N dose: 33–25 and 79–56 mg, respectively.

In the main shoot and tillers of control plants, while intensive grain filling still occurred without any significant total shoot increments, a marked decrease in the weight of the culm was observed. It is worth noting that in both years the grain: shoot ratio in the tillers was even slightly higher than that in the main shoot.

In expt. I the higher N dose applied at shooting had no influence on the total lamina area of the main shoot; the green lamina area was only a little higher than in corresponding leaves of control plants, even at later development stages (Table 6). Differences in the total weight of laminae depending on N supply were in most cases insignificant. Neither were differences in the weight of awns & glumes found. On the other hand the weight of sheaths and especially of the culm was markedly lower. So, in spite of the fact that the better N supply caused a significant increase of chlorophyll content in all green parts of the main shoot (in laminae per area unit mainly) at all stages under investigation, its total weight was always smaller than that of the controls. However, no significant differences in the grain yield were found.

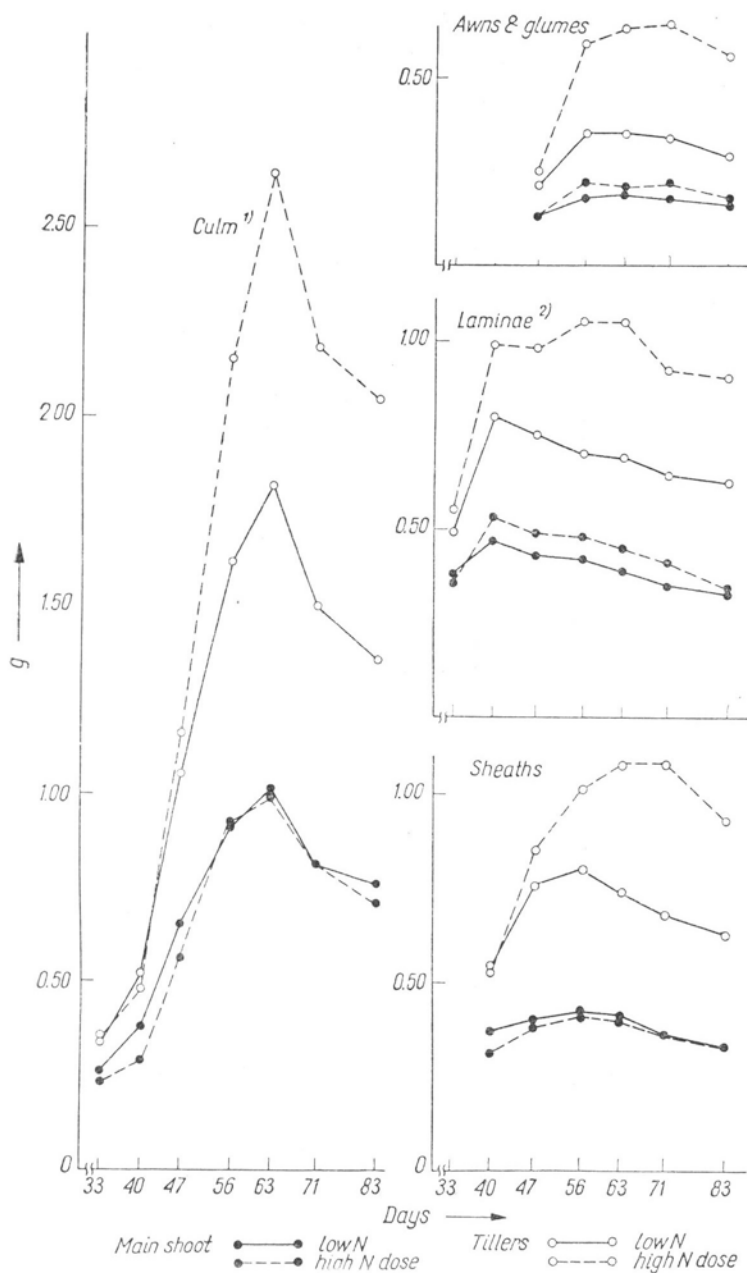


Fig. 2. Dry weight of particular plant parts. Experiment II.

1) Including rachis; length of the main shoot culm: low N-101, high N dose-99 cm. 2) Eight leaves (at first sampling-no flag leaf); the mean weight of the lowest lamina: 0.01-0.02 g.

Table 3
Chlorophyll content in the main shoot — mg per plant
Experiment I

Plant parts ¹	Low nitrogen dose				High nitrogen dose			
	age of plants — days							
	43	56	65	72	43	56	65	72
laminae								
1 st	0.30	0.36	0.25	} tra- ces	0.41	0.46	0.33	} 0.08
2 nd	0.82	0.75	0.49		1.02	1.14	0.79	
3 rd	1.06	0.67	0.18		1.26	1.05	0.38	
remaining	1.62	0.17	—		2.35	0.36	—	
total	3.80	1.95	0.92		5.04	3.01	1.50	0.08
sheaths								
1 st	0.40	0.56	0.46	0.07	0.47	0.79	0.66	0.20
2 nd	0.20	0.22	0.25	0.02	0.45	0.45	0.41	0.05
3 rd	0.15	0.15	0.09	—	0.24	0.18	0.10	—
remaining	0.20	0.14	0.03	—	0.30	0.15	0.04	—
total	0.95	1.07	0.83	0.09	1.46	1.57	1.21	0.25
internodes								
1 st		0.19	0.14	} 0.02		0.26	0.17	} 0.02
2 nd	0.21	0.14	0.09		0.34	0.17	0.13	
3 rd		0.04	0.02			0.05	0.02	
remaining		0.06	0.04			0.10	0.09	
total	0.21	0.43	0.29	0.02	0.34	0.58	0.41	0.02
ear	0.11	0.55	0.61	0.31	0.28	0.67	0.65	0.35
kernels		0.16	0.21	0.12		0.16	0.19	0.14
total	5.07	4.16	2.86	0.54	7.12	5.99	3.96	0.84

¹ 1st — uppermost.

In the second experiment, in contrast to the first one, better N supply caused a marked increase in the weight of laminae. Unfortunately their surface area was not measured, but the differences in weight, especially of the upper laminae indicate that their area on higher N level must have been greater. The weight of awns was also somewhat higher. No reaction to N after heading could be observed either in the culm or in the sheaths.

The higher N dose caused a significant increase in chlorophyll content in all green parts of the main shoot [changing somewhat the chlor.a/chlor.b ratio], however, it did not delay markedly the process of their dying. The highest shoot weight was reached at a similar time as in the control; the final total yield as well as grain yield were in both treatments analogous.

In both experiments, especially in the first one, under the influence of N the number of fertile tillers was much higher. This fact is reflected in the weight of all parts of these shoots. It is worth noting that 1) a significant weight increase of the tillers occurred also in the period, when in control plants no more increment was obser-

Table 4

Chlorophyll content — mg per plant

Experiment II

Plant parts	Low nitrogen dose				High nitrogen dose			
	age of plants — days							
	53 ¹		67 ²		53 ¹		67 ²	
	M	T	M	T	M	T	M	T
laminae								
1 st	0.41(3.0)	0.76	0.04	0.17	0.60(2.9)	1.17	0.10	0.70
2 nd	0.82(2.9)	1.85	—	0.21	1.42(2.7)	2.96	0.04	0.81
3 rd	0.75(2.7)	1.59	—	—	1.01(2.4)	2.07	—	—
remaining	0.31(2.4)	0.76	—	—	0.57(2.2)	1.13	—	—
total	2.29	4.96	0.04	0.38	3.60	7.33	0.14	1.51
sheaths								
1 st	0.38(2.9)	0.74	0.11	0.43	0.52(2.7)	1.50	0.24	1.04
2 nd	0.17(2.7)	0.33	—	0.03	0.28(2.5)	0.80	traces	
3 rd	0.10(2.1)	0.21	—	—	0.23(2.3)	0.84	—	—
remaining	0.07	0.11	—	—	0.12(2.0)	0.29	—	—
total	0.72	1.39	0.11	0.46	1.15	3.43	0.24	1.04
culm	0.44(2.0)	0.76			0.56(2.0)	1.10		
rachis	traces	0.02	traces		traces	0.03	tr.	0.02
glumes & awns	0.40(2.4)	0.80	0.25	0.70	0.52(2.2)	1.17	0.31	0.92
kernels	0.10(2.0)	0.18	0.08	0.16	0.11(1.9)	0.20	0.09	0.20
total	3.95	8.11	0.48	1.70	5.94	13.26	0.78	3.69

¹ M — main shoot, T — fertile tillers. Number of remaining laminae: at low N — 1, at high N-2. In parantheses — chlor.a: chlor.b ratio.

² The first sheath was analysed together with the uppermost internode.

Table 5

Total nitrogen content — mg per plant

Age of plants days	Low nitrogen dose				High nitrogen dose			
	main shoot		tillers		main shoot		tillers	
	total	grain only	total	grain only	total	grain only	total	grain only
Experiment I								
41	21		23		24		30	
84	25	19	26	20	31	24	58	45
Experiment II								
33	23		34		26		43	
83	30	20	51	36	35	25	93	73

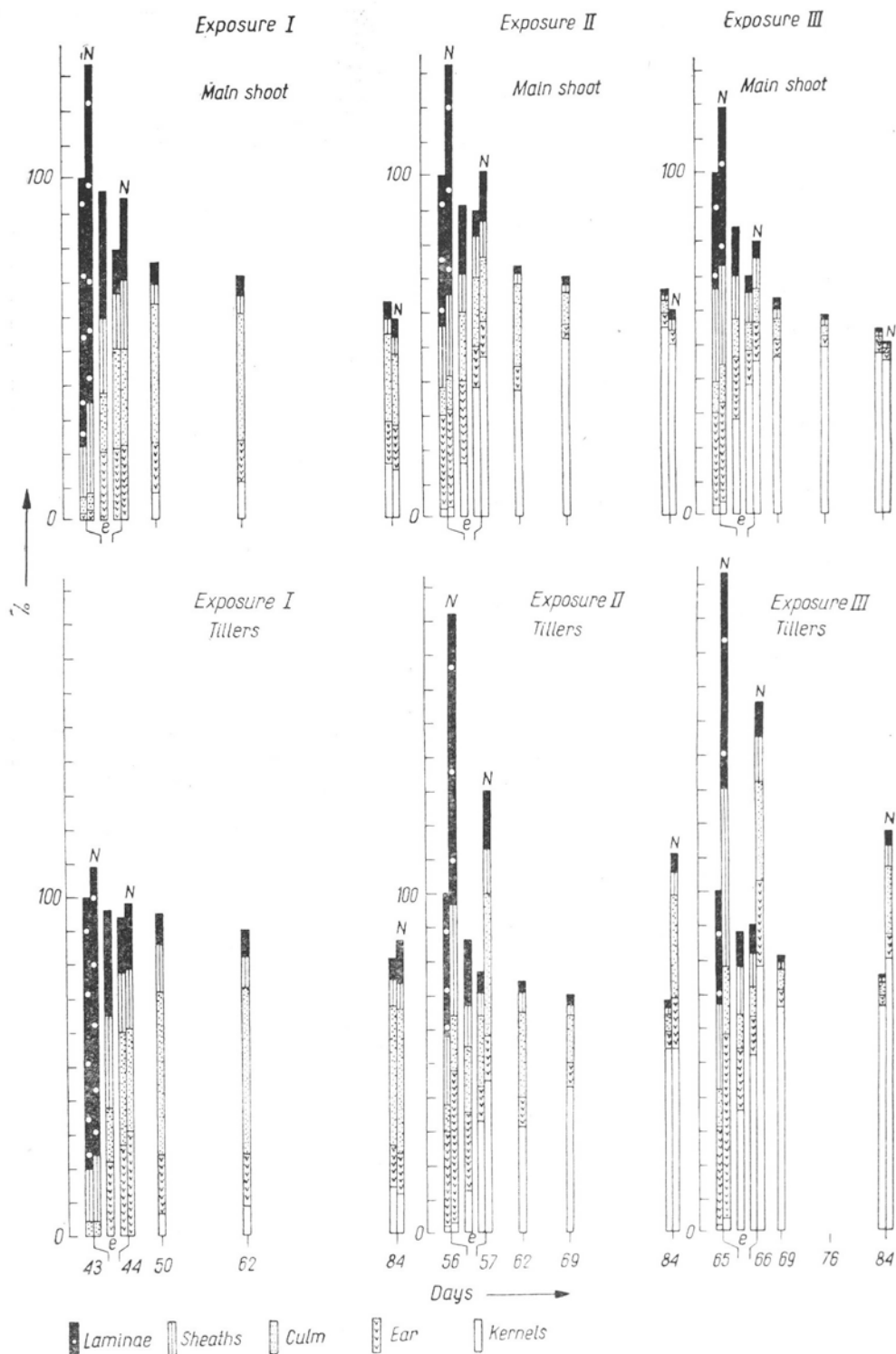


Fig. 3. Changes in radioactivity of shoots after exposure to $^{14}\text{CO}_2$ (activity immediately after exposure — 100%). Experiment I.*

* In this experiment as well as in expt. II bars denoted N represent plants on high N level. Radioactivity of successive laminae immediately after exposure is indicated by distances between white points; e — plants sampled in the evening on the day of exposure.

Table 6
Green lamina area of the main shoot (cm²)
Experiment I

Laminae ¹	Low nitrogen dose				High nitrogen dose			
	age of plants — days							
	43	56	65	72	43	56	65	72
1 st	9.2	8.0	7.1	2.8	9.7	8.8	7.6	3.7
2 nd	22.5	19.4	18.9	1.1	23.6	21.9	18.9	2.5
3 rd	28.0	26.1	13.4		30.1	28.4	17.5	
4 th	34.1	15.7			33.5	18.1		
5 th	25.8				27.9			
6 th	9.7				19.7			
total	129.3	69.2	39.4	3.9	144.5	77.2	44.0	6.2

¹ first lamina = flag leaf lamina.

ved, 2) the decrease in culm weight at later stages, especially in expt. I was relatively smaller than in the control and 3) the grain yield was much higher than that observed in tillers on low N level.

In expt. I plants with their uppermost internode shaded did not show immediately after exposure (II and III) any significant differences — as compared to the unshaded ones — in the radioactivity of the ear and only traces of ¹⁴C in the covered part of their culm were found. Thus, the very small activity immediately after exposure in the kernels (Fig. 3) could result mainly from photosynthesis in situ or in the awns. At exposure I (before heading) a very small proportion of ¹⁴C was found in the ear; this could be due only to ¹⁴C-assimilate translocation.

In control plants the total photosynthetic activity of the main shoot was somewhat higher than that of the tillers, with exception of the last period, when the contribution of vegetative organs was already very small (Table 7). However, the relative losses of carbon in tillers during the period from its assimilation to ripening were lower* (the same was observed in previous investigations).

Changes with ageing in the contribution of particular green parts to the total photosynthetic activity were similar in both shoots. Some days before heading the contribution of laminae amounted to about 80% or even somewhat more (if ¹⁴C translocation is taken into account). It diminished rather rapidly afterwards and 13 and 22 days later dropped to about 42–45 and 33%, respectively. The much larger contribution of the two lower leaf laminae as compared to that of the uppermost one not only before but also after heading is worth noting (Table 8). On the other hand the contribution of the flag leaf sheath was significantly higher than that of the remaining ones and also markedly exceeded that of its own lamina. Nevertheless the data clearly show that the lower leaves together with the corresponding internodes are of great importance for shoot photosynthesis not only before but also after ear emergence. Even on the 65th day of growth the activity of the second leaf

* Assimilate translocation from the main shoot to tillers in the period under investigation can be considered as negligible (unpublished date).

Table 7

Plant radioactivity immediately after exposure to $^{14}\text{CO}_2$ and at ripeness (10^3 cpm per plant)

N dose		¹⁴ CO ₂ assimilated on the ²⁾														
		(37 th day)			43 rd (44) day			56 th (53) day			65 th (60) day			72 nd (67) day		
		immedi- ately	at ripeness		immedi- ately	at ripeness		immedi- ately	at ripeness		immedi- ately	at ripeness		immedi- ately	at ripeness	
total	in grain % total		total	in grain % total		total	in grain % total		total	in grain % total		total	in grain % total		total	in grain % total
Experiment I																
low	M			569	355	25.6	340	224	82.6	350	187	88.8	77	41	83.1	
	T			410	332	17.8	318	210	80.0	297	223	87.9	98	76	83.4	
high	M			758	334	24.8	449	200	84.7	416	171	90.0	113	66	83.2	
	T			446	353	14.1	580	348	50.9	574	350	68.0	529	303	88.0	
Experiment II																
low	M	509	314	9.8	305	206	21.6	361	228	66.2	322	180	89.4	30	27	93.3
	T	673	452	8.9	512	420	21.0	641	448	60.2	555	358	82.4	94	81	92.6
high	M	495	295	10.0	436	230	16.3	489	232	60.0	378	202	87.6	63	38	92.1
	T	785	560	6.9	820	666	12.3	1,220	798	48.1	1,005	665	87.0	214	156	93.0

¹ M — main shoot, T — fertile tillers. Radioactivity of sterile tillers in 1963 at exposure I — on both N levels — was about 140×10^3 cpm (at ripeness — about 40 % of the initial), at exposures II and III on high N level — 71 and 50×10^3 cpm. respectively. In 1964 it varied between 120 (exp. I) and 40 (exp. III, high N level).

² In parentheses — age of plants in experiment II.

Table 8

Contribution of particular green parts to the total photosynthetic activity of shoots (%)

Plant parts ¹	Experiment I								Experiment II					
	age of plants — days													
	43		56		65		72		53		60		67	
	nitrogen dose													
	low	high	low	high	low	high	low	high	low	high	low	high	low	high
main shoot														
total	100	100	100	100	100	100	100	100	100	100	100	100	100	100
ear			30	24	30	26	90	84	25	20	23	22	77	57
1 st leaf														
lamina	8	9	9	9	10	13	tr.	2	10	11	14	16	7	17
sheath	6	8	11	11	17	14	6	7	9	7	7	8	16	11
1 st intrn.			5	4	6	6	4	3	5	5	5	5		7
total	14	17	25	24	33	33	10	12	24	23	26	29	23	35
2 nd leaf														
lamina	19	18	16	19	20	21	tr.		18	17	21	21		6
sheath	4	5	4	4	7	6		4	3	2	3	3		1
2 nd intrn.	1	1	2	3	2	2			3	3	3	3		1
total	24	24	22	26	29	29		4	24	22	27	27	—	8
3 rd leaf														
lamina	22	20	15	17	3	4			15	15	13	12		
sheath	3	2	2	2	2	3			1	1	3	2		
3 rd intrn.	2	2	1	tr.	1	1			1	1	3	3		
total	27	24	18	19	6	8	—	—	17	17	19	17	—	—
tillers														
total	100	100	100	100	100	100	100	100	100	100	100	100	100	100
ear			30	26	31	30	80	48	25	20	24	23	63	52
1 st leaf														
lamina	10	10	11	9	13	10	1	8	11	13	14	16	10	14
sheath	5	8	15	13	17	17	12	16	8	7	7	7	8	7
1 st intrn.			5	4	8	5	2	4	6	3	4	5	6	6
total	15	18	31	26	38	32	15	28	25	23	25	28	24	27
2 nd leaf														
lamina	19	18	17	16	17	18		9	15	17	23	23	10	20
sheath	5	5	3	3	6	6	3		3	2	4	3		
2 nd intrn.	1	1	2	3	2	2		12	2	2	3	3	3	1
total	25	24	22	22	25	26	3	21	20	21	30	29	13	21
3 rd leaf														
lamina	20	17	12	14	3	5			14	14	12	12		
sheath	2	2	1	2	2	3	2	3	2	2	4	2		
3 rd intrn.	2	2	1	2	tr.	2			1	1	3	2		
total	24	21	14	18	5	10	2	3	17	17	19	16	—	—

¹ 1st — the uppermost; intrn. — internode; ear — including kernels. Radioactivity of the 1st internode is due mainly to its part non covered by the sheath.

Table 9

Chlorophyll content (mg) and ^{14}C assimilated (10^3 cpm) per dm^2 of green lamina (main shoot)
Experiment I

La- minae	Age of plants — days											
	43 ¹				56				65			
	nitrogen dose											
	low		high		low		high		low		high	
	chlor	¹⁴ C	chlor	¹⁴ C	chlor	¹⁴ C	chlor	¹⁴ C	chlor	¹⁴ C	chlor	¹⁴ C
1 st	3.2	480	4.2	691	4.7	341	5.2	449	3.5	506	4.4	702
2 nd	3.6	483	4.3	590	3.9	277	5.2	401	2.6	362	4.2	448
3 rd	3.7	434	4.2	503	2.6	175	3.6	263	1.3	74	2.2	80
4 th	2.5	287	3.5	283	1.2	64	2.0	82				
5 th	2.0	201	2.8	221								
6 th	1.4	152	2.1	160								

¹ $480 \cdot 10^3$ cpm corresponds to about $12 \text{ mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$.

was not much lower than that of the uppermost one including the internode and amounted in the main shoot to 29 and in the tillers to 25%. The contribution of the ear accounted in both shoots for about 30% and only at late stages of growth increased rapidly to 90 (main shoot) and 80% (tiller) of the total photosynthetic activity.

The better N supply caused an increase in photosynthesis already 8 days after its application (at exposure I); at that time its influence on the main shoot was much higher than on the tillers. However, 13 days later, when the increase in photosynthesis in the main shoot accounted also for about 30%, in the tillers it reached more than 80% and at the last period it was five times higher than in the tillers of the control.

In the main shoot, the higher N dose — the last period excepted — had a relatively small influence on photosynthesis in the ear as well as in the culm; the contribution of the former to the total photosynthetic activity even diminished as compared to that in the control. A much stronger reaction to N was shown by the sheaths, and especially by the leaf laminae. As the data presented in tables 6 and 9 indicate, the higher photosynthetic activity of the latter was mainly due to the higher rate of carbon assimilation per area unit. It is worth noting that at low N level the greatest photosynthesis rate (very close to true photosynthesis) in the youngest leaf laminae, with chlorophyll content $3.2\text{--}3.6 \text{ mg} \cdot \text{cm}^{-2}$, accounted for about $12 \text{ mg CO}_2 \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$; its markedly smaller values in the lower leaves (4th–6th, exposure I) could be due not only to their advanced senescence, but also to the lower light intensity. This as a limiting factor may have been also partly responsible for the fact that the better N supply did not bring about any increase in the rate of photosynthesis in these leaves. The same applies to the lowest, 4th leaf at exposure II. However, it should be added that the second (from the top) leaf lamina, to which shading effect can not be applied, showed — as compared to the flag leaf — a lower rate of photosynthesis after heading not only on low but also on high N level, in

spite of the fact that in the latter case the chlorophyll content per area unit was similar in both of them.

The much higher photosynthetic activity of tillers under N influence, especially at later stages, was obviously due to their greater number and — calculated per shoot — it was even lower than in the control, the last period excepted. However, the differences between the investigated tillers in the activity of the particular green parts were greater than the differences in their weight; thus the higher photosynthetic activity at larger N dose was partly due also to a higher rate of photosynthesis in these organs. It is worth stressing that in the last period (exposure IV) the contribution of the first as well as the second leaf was much greater and that of the ear much smaller than on low N level.

In experiment 1964 the photosynthetic activity of fertile tillers, whose number in the control exceeded that in 1963, at all investigated stages was higher than that of the main shoot. Similarly as in the first experiment, the total losses of assimilated carbon in the tillers were relatively smaller (Fig. 4); its amounts found at ripeness were higher than those in the main shoot. Changes with ageing in the contribution of particular green parts to the total photosynthetic activity were similar in the tillers and main shoot. In comparison with the first experiment, the contribution of the ear and sheaths was somewhat lower and that of the laminae somewhat higher. The differences between the experiments in lamina and sheath contribution find support in differences in their weight and also chlorophyll content.

Already on the 6th day after application of the higher N dose an increase in the photosynthetic activity of the tillers could be observed. In the later period it became manifest in the main shoot and markedly augmented in the tillers. The extent, to which the activity of both shoots increased, was similar to that in the first experiment. The reaction of particular green parts to the higher N dose was also similar, with exception of the fact that the increase of the activity of the laminae was greater and that of the sheaths smaller than in 1963. However, in relative values—when compared to the control — in most cases it was analogous especially as regards the laminae. The greater in the second experiment differences between treatments in the weight of the main shoot laminae indicate that their higher photosynthetic activity could have resulted to a significant extent also from a larger green area.

At all investigated stages assimilate translocation from leaf laminae was rapid. According to the data obtained in the experiment I, six hours after exposure, in control plants before heading only less than 50 and at later stages about 30% of the initial amounts could be found in these organs, without significant differences between the main shoot and tillers. Overnight the ¹⁴C-assimilate content in the laminae dropped to about 20–15% and further diminished in the later period.

The main acceptors of assimilates formed before heading were the culm, especially in tillers, and the ear. Photosynthates formed after heading translocated in relatively great proportions during the first 20 hours to the kernels and partially accumulated in the culm. Similarly as in previous experiments with barley, this organ played the role of a temporary store for assimilates, which afterwards moved to the ear. The marked decrease in their content in the culm occurred at the milk

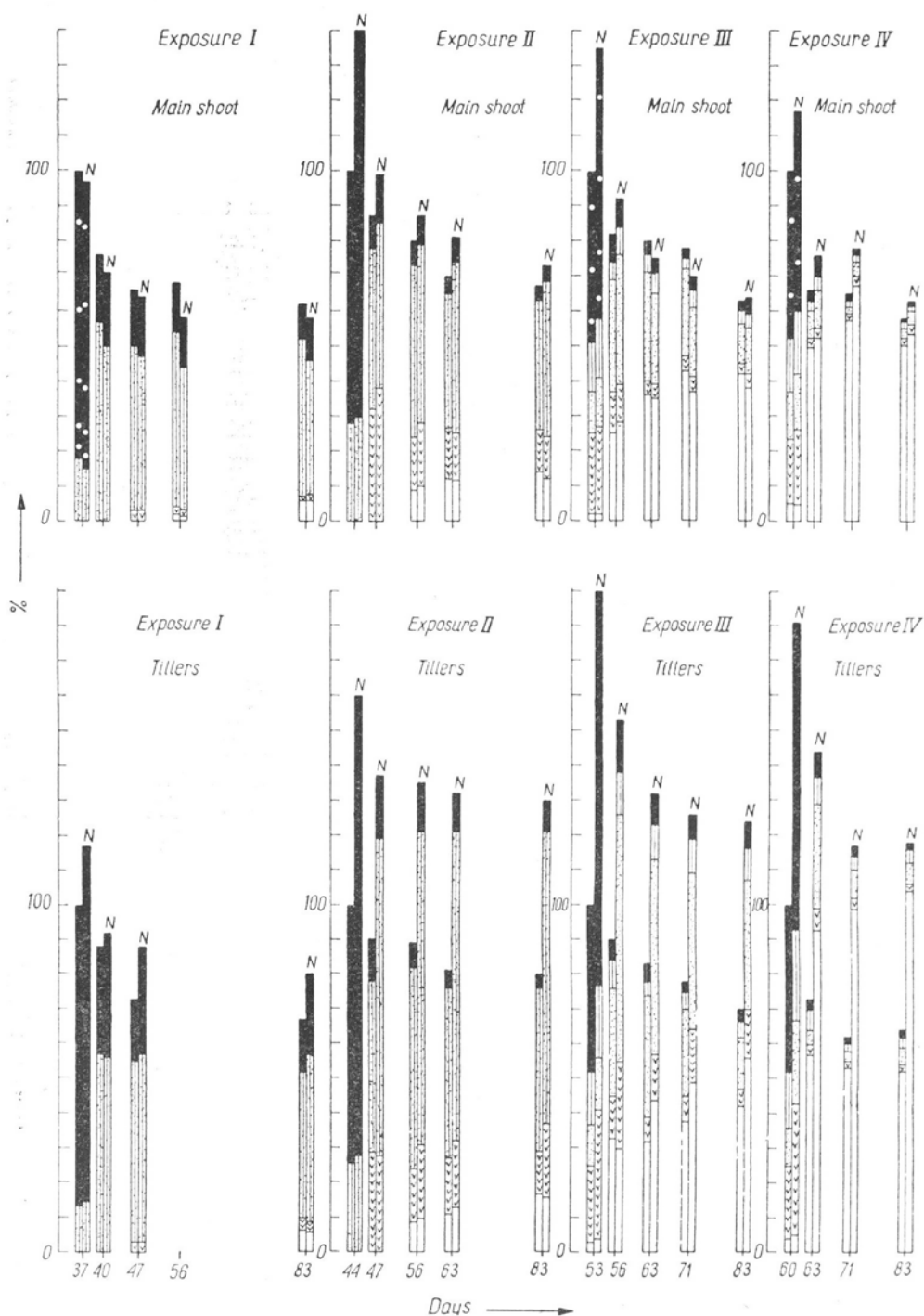


Fig. 4. Changes in radioactivity of shoots after exposure to $^{14}\text{CO}_2$ (activity immediately after exposure — 100%). Experiment II.

1) For notations see Fig. 3; the culms of plants exposed to $^{14}\text{CO}_2$ before heading were analysed together with sheaths.

and wax stages of kernels, after the 62nd day of growth, i.e. in the period, when a significant decrease in its weight was also observed. At ripeness the amount of assimilates formed after heading constituted in the grain about 82–90% of its total found in the investigated shoots. Differences in their accumulation in kernels

Table 10

Radioactivity of ethanol-soluble fractions in the main shoot on low nitrogen level
(per cent of total shoot activity immediately after exposure)

Experiment I

Plant parts	Plant age on the day of exposure — days											
	I — 43				II — 56				III — 65			
	days after exposure											
	1	7	19	42	1	6	13	29	1	4	11	20
laminae	8	2	2	1	6	1	1	} tr.	2	1	tr.	} tr.
sheaths	11	1	1	} 3	8	2	1		6	2	1	
culm	15	10	9		16	22	6		1	7	2	
ear	} 6	2	1	tr.	8	2	1	1	4	2	1	1
kernels		1	tr.	tr.	14	8	6	3	13	6	5	2
kernels total ¹		8	11	16	38	37	51	55	38	46	49	47

¹ data reported represent total radioactivity of kernels.

between the 69th and 84rd day, especially in the main shoot, were not significant. It should be added that a marked proportion of carbon assimilated 3–4 days before heading was also gradually translocated to the kernels. At ripeness it amounted in the main shoot to about 25 and in the tillers to 18% of its total at that time. Changes with time in the ethanol-soluble fraction in particular plant parts, as when compared to changes in ¹⁴C accumulation in the kernels (Table 10), clearly show that the latter could not have resulted to a significant extent from reassimilation processes.

Translocation and redistribution of ¹⁴C-assimilates in the second experiment were similar as in the first one*. Two facts are worth noting: 1) a significant decrease in the amount of photosynthates accumulated in the kernels of the main shoot between the 71st and 83rd day (exposure IV), i.e. within the period, when only traces of available ¹⁴C were found in the culm. This decrease could be only due to loss in respiration. The high content of the ethanol-soluble fraction in kernels at that time (Table 11) supports such an assumption; 2) assimilates formed not only 3–4 but also about 8–9 days prior to ear emergence contributed to some extent to the accumulation of carbon in the grain. Their amount in kernels constituted about 9–10% of the total found in shoots at ripeness.

* Some differences in the degree of carbon accumulation in the kernels, especially of hat assimilated at exposure III were — as seems — due to differences in the stage of their development.

The efflux of ^{14}C -assimilates from leaves as well as the ear of the main shoot on high N level was in both experiments similar to that in the control. Their amounts found in kernels 20 hours (expt. I) or three days (expt. II) after exposure were higher than those on low N level (the share of the ethanol-soluble fractions was also a little greater). However, at ripeness in most cases (assimilates formed in the last period of growth excepted) the grain contained even somewhat less labelled carbon than it did in the control plants. Its total amount found in the shoot at ripeness was in the first experiment also somewhat lower except for the last stage, when the photosynthetic activity of the main shoot was very low. In the second experiment the differences in this respect (in plus as well as in minus) were insignificant, with exception of those for assimilates formed on the 44th day; in this case a greater than in the control amount of carbon was used for culm growth.

Table 11

Radioactivity of ethanol-soluble fractions in the main shoot on low nitrogen level
(per cent of total shoot activity immediately after exposure)

Experiment II

Plant parts	Plant age on the day of exposure — days																	
	I — 37					II — 44				III — 53				IV — 60				
	days after exposure																	
	3	10	19	46	3	8	19	39	3	10	18	30	3	11	23			
laminae	7	4	4	3	4	2	2	1	4	1	traces		1	1	} tr.			
sheaths	} 12	8	9	4	12	9	4	2	2	2	1	1	2	1				
culm		} tr.	1	1	tr.	} 5	1	1	1	5	tr.	traces		1		1		
ear			tr.	1	2		2	1	7	7	5	4	8	14				
kernels																		
kernels total																		
			2	6		9	12	14	25	36	43	42	50	57	50			

In both experiments the tillers on high N level incorporated much more photosynthates into their green parts, especially into their culms. The amounts of carbon assimilated before heading and finally found in the grain did not differ from those at low N dose. Neither did in experiment I the content of photosynthates formed soon after heading and found in kernels at ripeness exceed that in the control, in spite of the fact that 20 hours after exposure it was much higher. The larger amount of assimilates found finally in the grain of tillers was due only to carbon assimilated in the later period, when the photosynthetic activity under N influence was still relatively high. In 1964, when the higher N dose was applied some days earlier, a greater — as compared to the control — amount of carbon already assimilated on the 53rd day could be found in kernels not only soon after exposure but also at ripeness.

It should be noted that the losses of assimilates from tillers on high N level — although in relative values lower than those from aerial parts of the main shoot — in absolute amounts were in both experiments also considerable, especially after heading (Fig. 5). On both N levels the relatively greatest losses of photosynthates occurred during the first day (expt. I) or the first three days (expt. II) after their formation. However, in most cases they were also significant in the later period. The large differences in carbon loss caused by different N supply were manifest already during the first period.

It is worth noting that informations supplied by ^{14}C -labelled plants as regards assimilate redistribution with time, final accumulation in various parts of shoots as well as the influence of N on the productivity of photosynthesis find confirmation in changes in their dry weight, in final total yields of shoots as well as of their kernels. It is obvious that — carbon loss occurring for a long time after its assimilation — a dry weight increase at various intervals cannot be a satisfactory criterion of the efficiency of photosynthesis in a given period.

DISCUSSION

The photosynthetic activity of the investigated plants — represened by their radioactivity — being measured at different development stages at various CO_2 concentrations initially even twice or three times higher than under normal conditions, and at various temperature, cannot give reliable informations on the changes in total CO_2 assimilation with ageing. However, it may be assumed that the data obtained at earlier stages after heading represent a higher photosynthetic activity of particular shoots than those obtained in the later period. On the other hand, in contrast to our previous investigation on barley, the errors due to ^{14}C translocation being small and no artifacts occurring — the reported experiments supply satisfactory information as to the role of particular green parts in shoot photosynthesis*. In accordance with the results obtained previously the ear contribution to shoot photosynthesis does not change for a relatively long time after heading and only at the late stages of growth increases rapidly. It ranged — similarly as in aforementioned investigation — between 25 and 30% (the last period excepted) in both shoots, but was lowered by better N supply. The much weaker reaction to N of the ear as compared to that of the leaves was also observed in awned spring wheat varieties, in which the contribution of this organ was less than that in barley. However, it is hard to tell whether the observed difference is due to differences in the photosynthetic capacity of the barley and wheat ears (Thorne 1965a). It is true that in shoot photosynthesis the role of the flag leaf including the uppermost internode, to which great attention is paid (Watson et al. 1958; Thorne 1963, 1965 b), is very important and at high N dose even exceeds that of the ear; however, it seems that the role

* The contribution of particular parts to the total shoot photosynthetic activity did not alter markedly when changes in the rate of ^{14}C -labelled CO_2 fixation were induced by changing light intensity or CO_2 concentration (unpublished data).

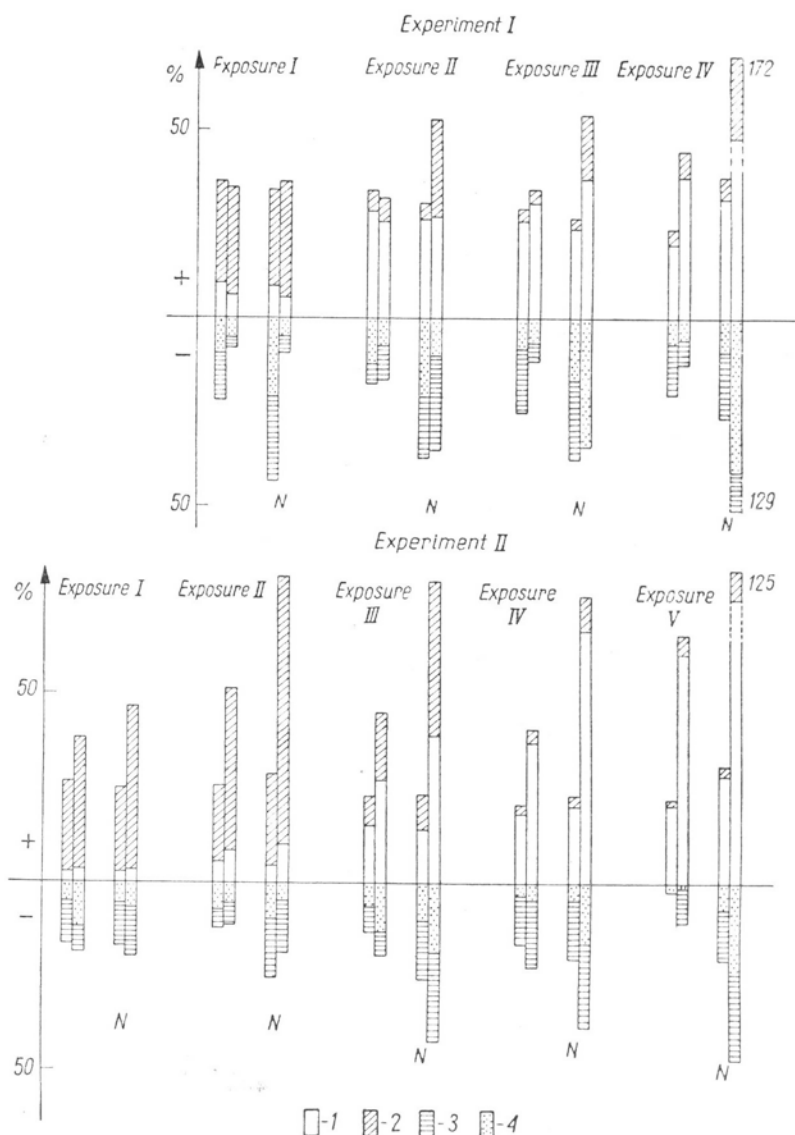


Fig. 5. Influence of nitrogen on photosynthetic activity of the main shoot and tillers and on assimilate loss (total plant radioactivity immediately after exposure on low N level — 100%).

At each exposure first two bars (left-main shoot, right-tillers) represent plants on low N, the second ones those on high N level. 1 — carbon found at ripeness in grain; 2 — carbon found at ripeness in remaining shoot parts; 3 — carbon lost during one (expt. I) or three (expt. II) days after exposure; 4 — carbon lost during the following period till ripeness.

of lower leaves, particularly of the second one is underestimated because: 1) its surface area in barley is larger than that of the uppermost one, 2) it maintains photosynthetic activity for a relatively long time after heading, 3) the shading effect exerted on it even under field conditions cannot be very great and 4) its photosyn-

thates (as well as those of the lower leaves) formed prior to heading may contribute to the organic matter accumulated in grain.

It is worth stressing that—similarly as in spring wheat—in later development stages differences in the rate of photosynthesis in laminae depending on their age (insertion order) were highly significant even when no differences in chlorophyll (relatively high) content occurred. These leaves exhibit—similarly as those of other species (Gej 1966)—some differences in the chlor.a: chlor.b ratio. However, these differences do not seem to be mainly responsible for the phenomenon observed. Other processes mentioned previously (Birecka, Dakic-Włodkowska 1966) must be the dominant determinants of the decrease in photosynthetic capability of leaves with ageing.

The mean rate of photosynthesis in the youngest leaves on low N level was about $12 \text{ mg} \cdot \text{dm}^{-2} \cdot \text{h}^{-1}$; it did not differ significantly from that observed by other authors in experiments with barley or other species under normal CO_2 concentration and high light intensity (Thorne 1959, 1963; Watson et al. 1965; Monteith 1962; Slavik 1963) as well as from the rate found in our investigation on wheat grown under the same conditions. However, in contrast to wheat, better N supply at shooting caused in barley a marked increase in the photosynthesis rate also in the youngest leaves of relatively young plants. The causes of such a difference in the reaction of these laminae to N are not clear; perhaps they were due only to some external factors. More detailed experiments are required for their elucidation. As it was mentioned above, the lack of reaction to N of older leaves in young plants could be partly due to the shading effect; however, differences in the reaction capability of leaves depending on their age should be also taken into account (Bourdu et al. 1965).

The results obtained clearly show that an increased photosynthetic activity of the main shoot does not necessarily lead to a higher productivity of photosynthesis. The uneffectiveness in this shoot of N applied at shooting, reflected in its total as well as grain yield and confirmed by the amounts of ^{14}C -assimilates found at ripeness, is not casual. It occurred in barley var. 'Skrzeszowicki' (Jackowska, personal communication). The small influence or none of a better N supply at shooting on other spring barley varieties was observed also under field conditions (Bezdek et al. 1964). On the other hand, our investigation on spring wheat showed that an increased by N (applied also at shooting) photosynthetic activity after anthesis resulted in its greater productivity reflected in assimilate accumulation not only in the tillers but also in the main shoot. The question can be put as follows: why is the reaction of the main shoot of barley to a higher N dose different from that in wheat, whereas the tillers respond in a similar way, what plant parts are mainly responsible for such a great assimilate loss in barley under better N conditions?

The main cause of the differences observed between the two species is—as seems—the fact that in barley the period from N application to heading of the main shoot (11 days—expt. I and 15 days—expt. II), and especially to anthesis (occurring 3–4 days before heading) was much shorter than in wheat (19 and 24

days, respectively). If in addition the relatively rapid cell division in the endosperm and embryo is taken into account (Wardlaw 1955; Grzesiuk 1961), it can be assumed that in the former N came into action to late to be capable of influencing the growth and differentiation of generative organs as well as of the developing young kernels*. Thus, if these processes determine the capacity of kernels to accumulate organic substances, the barley shoot under N influence was in a state of a "surplus" of photosynthates.

The amounts of assimilates that moved soon after their formation to the ear and especially kernels were higher than in the control (even higher than revealed by the data obtained). The lack of differences in the later period clearly indicate that they must have been lost there in respiration. The very high rate of this process in generative organs and seeds is a well known phenomenon (Sójka 1961; Grzesiuk 1961; Thorne 1963; Gaastra 1963); it can, as the data obtained seem to indicate, be even significantly increased owing to the increase in substrate concentration or to the preceding indirect N action. It is obvious, that a proportion of the high assimilate loss could be due to an increase in respiration of vegetative organs, especially of leaves, although its rate in these parts is relatively low (Thorne 1959, 1963); more assimilates, in particular those formed before heading, could have been translocated to the root. It seems, however, that the ear with its kernels is mainly responsible for the low productivity of photosynthesis in the main shoot on high N level. The fertile tillers, whose number under N influence was greater and the heading of which occurred later than in the main shoot, supplied for assimilates formed before and soon after heading two intensively growing acceptors: the culm and the ear with kernels. The relatively very high — due to N — photosynthetic activity of tillers at the late stage of development, especially in expt. I** clearly show that — in contrast to the main shoot — their senescence could be significantly delayed, similarly as it was delayed by N, applied at shooting of the main shoot, in all shoots in spring wheat. It should be remembered that, especially in tillers, the late development stages are of great importance for assimilate accumulation in grain.

Two problems are worth considering. The first one concerns the notion of advanced age as a factor limiting the influence of an environmental agent on various physiological processes, notion, which seems to be very relative. It was shown that N applied at shooting can influence greatly the rate of photosynthesis of already fully expanded and relatively old (but not very old) leaves for a long time; the rate of respiration in kernels could be increased either by substrate concentration or perhaps by other factors connected with N influence. However, such a process like grain filling which occurs in the later developmental stages is determined very early and at shooting the main shoot was already "too old" to be capable of reacting to nitrogen as regards the capacity of its intact undamaged ear, including kernels for incorporation of organic substances. Physiologically controlling "me-

* Neither were differences in their member depending on N supply found.

** In expt. II the photosynthetic capacity of tillers on high N level was not perhaps fully manifested because of the low light intensity and relatively low temperature (rain).

chanisms" (e.g. photosynthesis-respiration) may be —as seems—like the genetically determined features of particular organs (Börger et al. 1956) great influence on plant productivity.

The second problem concerns the relationship between donors and acceptors in assimilate translocation. It was demonstrated that in the main shoot in spite of the unchanged by N growth of kernels the amounts of assimilates that moved to them from the leaves, strictly speaking from the culm, were significantly higher. Thus not only the efflux per se but the rate of translocation was not — at least entirely — determined by the "sink power" depending on growth. It seems rather to be dependent on the culm capacity to retain assimilates and perhaps on their concentration in the conducting tissues. However, other possibilities should not be completely eliminated, e.g. that the increased (but not by substrate concentration) respiration rate or perhaps an increased hormone production in the kernels might have brought about a greater afflux of assimilates.

The fact that the culm not only in wheat but also in barley functions as a temporary store for photosynthates was in the reported experiment once more demonstrated. After all this organ in cereals has already for a long time been considered as a supplier for the ear of various organic compounds, even previously incorporated into it (Palejew 1940; Czebanowa et al., 1951; Terentiew et al. 1960).

The data obtained showed that carbon assimilated even about a week before heading contributes to some extent to the grain yield. Its relative amount found at ripeness in kernels was higher than in wheat. This results, at all probability, not only from the fact that anthesis in barley occurs much earlier, but also from the lemmas adhering to the kernels.

SUMMARY

The contribution of particular green parts to the total photosynthetic activity of the main shoot as well as tillers of spring barley plants changes significantly with ageing. The contribution of leaf laminae, accounting 9—4 days before heading for 85—75%, soon after ear emergence dropped rapidly to about 45% and further gradually decreased. The photosynthetic activity of the second (from the top) leaf including its sheath was before heading higher and after heading for a long time similar to that of the uppermost one. The contribution of the ear to the shoot photosynthetic activity accounted for about 25—30% and only at late development stages increased to 80—90%.

The higher nitrogen dose applied at shooting significantly increased the rate of productive tillering, chlorophyll content in green parts and the rate of photosynthesis per area unit of laminae, even of the youngest ones. The photosynthetic activity of the ear as well as of the culm in the main shoot increased very slightly. The influence of N on ageing of this shoot was very small.

Translocation of ^{14}C -labelled assimilates from leaves was rapid not only after but also before heading. They moved to the ear and also partially accumulated in the culm; a significant proportion of assimilates, especially of those formed after heading, was translocated afterwards from this organ to the kernels. On high N level greater amounts of photosynthates reached the kernels in the main shoot as well as the tillers. However, in spite of a much higher photosynthetic activity

of the main shoot as compared to that on low N level neither its grain nor its culm contained at ripeness more assimilates, independently of the development stage, at which they were formed. The much greater loss of assimilates on high N level were at all probability due to a large extent to the higher rate of respiration in the kernels.

The relative loss of photosynthates in tillers on high as well as on low N level was less than in the main shoot. Due to better N supply they contained at ripeness more assimilates formed before, but especially after heading.

The amount of carbon assimilated 9—4 days before heading and finally found in grain accounted in the main shoot for about 10—25%, respectively, of its total at ripeness. In the tillers it ranged between 8 and 20%. The higher N supply at shooting had no positive effect in this respect even in tillers. The contribution of assimilates formed after heading increased rapidly to 60—80% and later to about 90% of their corresponding total amounts found at ripeness in the investigated shoots. The greater amount of carbon found in grain of tillers on high N level was due mainly to their much higher—as compared to the control—photosynthetic activity at later stages, when the culm growth was already insignificant.

The causes of differences between the main shoot and tillers in their reaction to N applied at shooting as well as the relationship between the donor and acceptor of assimilates in connection with their translocation rate are discussed.

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*Aktywność i produktywność fotosyntezy w roślinach jęczmienia jarego
przed i po wykłoszeniu*

STRESZCZENIE

Udział poszczególnych organów w ogólnej aktywności fotosyntetycznej pędu głównego, jak i pędów bocznych jęczmienia, ulega istotnym zmianom w miarę starzenia się rośliny. I tak, udział blaszek liściowych, wynoszący 9—4 dni przed wykłoszeniem 85—75%, spadł wkrótce po wykłoszeniu do 45%, po czym nadal zmniejszał się stopniowo. Ogólna aktywność fotosyntetyczna liścia drugiego od wierzchołka (łącznie z pochwą) była przed wykłoszeniem większa, a w okresie późniejszym przez dłuższy czas analogiczna do aktywności liścia pierwszego (flagowego). Udział kłosa, w ogólnej aktywności fotosyntetycznej pędu, wynosił około 25—30% i tylko w późnych fazach rozwoju wzrastał do 80—90%.

Wyższa dawka azotu zastosowana w okresie strzelania w źdźbło spowodowała istotne zwiększenie stopnia produktywnego krzewienia, zawartości chlorofilu w poszczególnych organach wszystkich pędów oraz ich aktywności fotosyntetycznej. W pędzie głównym wystąpił znaczny wzrost intensywności asymilacji CO₂ w blaszkach liściowych (w przeliczeniu na jednostkę powierzchni); aktywność fotosyntetyczna kłosa i źdźbła zwiększyła się tylko w stopniu niewielkim. Wpływ azotu na szybkość starzenia się pędu głównego był bardzo słaby.

Odpływ asymilatów (znakowanych ¹⁴C) z liści był szybki, nie tylko po, ale również i przed kłoszeniem. Stosunkowo duże ich ilości przemieszczały się do kłosa, a także gromadziły się w źdźble, skąd w późniejszym okresie częściowo przemieszczały się również do ziarniaków.

W warunkach lepszego zaopatrzenia w azot (od strzelania w źdźbło) większe ilości asymilatów docierały do ziarniaków zarówno pędu głównego, jak i pędów bocznych. Jednakże w pędzie głównym — mimo jego znacznie większej pod wpływem tego składnika aktywności fotosyntetycznej — ani ziarno, ani też źdźbło nie zawierały w pełnej dojrzałości więcej asymilatów.

Znacznie większe straty węgla na wyższym poziomie azotowym były najprawdopodobniej wynikiem zwiększonej intensywności oddychania przede wszystkim w kłosie łącznie z ziarniakami.

Względne straty asymilatów w pędach bocznych zarówno na wyższej, jak i niższej dawce azotu były mniejsze niż w pędzie głównym. W warunkach lepszego zaopatrzenia w azot pędy te również pod koniec wegetacji zawierały więcej węgla, w szczególności zasymilowanego po wykłoszeniu.

W fazie pełnej dojrzałości w ziarniakach pędu głównego stwierdzono 10—25% pozostałej w nim ilości węgla zasymilowanego 9—4 dni przed wykłoszeniem; w ziarniakach pędów bocznych ilości te wynosiły odpowiednio 8—20%. Wyższa dawka azotu nie wywarła pod tym względem żadnego dodatniego wpływu nawet w pędach bocznych.

Względna akumulacja w ziarniakach asymilatów utworzonych wkrótce po wykłoszeniu wzrastała do 60—80%, a w przypadku asymilatów powstałych w fazach późniejszych dochodziła do około 90%. Większe ilości węgla w ziarnie pędów bocznych na wyższym poziomie azotowym były głównie wynikiem ich znacznie większej aktywności fotosyntetycznej w późniejszych fazach, kiedy wzrost źdźbeł był już nieistotny.

Przedyskutowano przyczyny różnic między pędem głównym a pędami bocznymi w ich reakcji na azot zastosowany w fazie strzelania w źdźbło, jak i zagadnienie zależności między donorem i akceptorem asymilatów w związku z intensywnością ich przemieszczania.