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Some conclusions concerning a series of investigations on the dynamics of growth and development in cereals

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INTRODUCTION

The early literature on growth in cereals is concerned with the studies on the uptake of mineral nutrients (N. Ardent 1859; G. Liebscher 1887, and successors). It has already been reviewed (P. Strebeyko 1961). The first analysis of cereal crop from the morphological point of view was carried out by F. L. Egledow and S. N. Wadham, 1923. The pertinent literature was reviewed by D. J. Watson (1952). The present experiments dealt with growth and development in wheat, barley, rye, and oats. The relevant literature has been cited in previous publications. (Strebeyko & Góra 1964; Strebeyko & Madej 1963; Strebeyko & Rosiek 1964; Strebeyko, Wisłocka & Krzywacka 1963).

METHODS

Nine pot experiments were carried out in 1960 and 1961. Plants were grown in sand to facilitate removal of roots. Moisture was kept at 60 per cent of the capillary water-holding capacity of the sand. Each pot contained 8 kg sand and fertilizers added in the following quantities: 0.5 g N, 0.5 g K_2O and 0.25 g P_2O_5. Small amounts of microelements were supplied in Hoagland's A—Z nutrient solution. Plants were harvested at intervals of 4—5 days. At each harvest, determinations of leaf, stem, and root dry weight were carried out and at later developmental stages seed weight was also recorded. The change in the plant assimilatory surface area with the lapse of time was established. Photographic records of the growing point and ear development were kept. Duration of the successive phases of the vegetative period was noted and expressed as the number of days reckoned from seedlings emergence. Increases in dry mass and in assimilatory surface area are given in per-cent of the final value taken as 100. The leaf assimilatory surface areas were found by weighing the silhouettes cut out of light sensitive paper, the weight of 1 sq. dm. of this paper being established beforehand. Leaf area was calculated only on the side usually directed towards the light. Stem assimilatory surface was calculated as circumference times length of the individual internodes. Ear assimilatory surface was not measured because of technical difficulties. Ear tissue in cereals nevertheless gains importance as an active assimilatory surface when the growth of leaves and stems is nearing completion. The method of measuring ear and panicle area was developed later (Strebeyko, Bacławska, & Skośkiewicz 1964).

RESULTS

Length of the vegetation period and final dry mass yields

In 1961, sowing took place sooner than in 1960. Wheat and rye were sown 17 days earlier and barley was sown 25 days earlier. Table 1 shows the final dry mass yields obtained in the two years. In the case of earlier sowing the vegetation period was longer. There were noticeable differences in the final yields. For wheat, the total dry mass yield was higher by 10 per cent in 1961 and for barley it was higher by 7 percent. The difference between the two years in the length of the vegetation period was smaller for barley, too. For rye, the final yield tended to be smaller in 1961, the final seed yields being nearly one-half as large. Lower temperatures and shorter days prevailing at the beginning of vegetation in 1961 may well have been the factors responsible for the differences mentioned. The day was shorter by one hour at the time of emergence in 1961. The average temperatures within the period from emergence to ear formation in wheat were over 16°C in 1960 and only 13°C in 1961.

Table 1

Length of the vegetation period and dry mass yields

Cereal	Sowing date	Length of vegetation period, days	Dry mass yield, g			
			grain	straw	roots	total
Wheat	1960/22/IV	96	13	30	6	49
	1961/5/IV	107	14	33	7	54
Barley	1960/22/IV	87	15	24	5	44
	1961/28/III	91	14	28	5	47
Rye	1960/23/IV	93	11	25	3	39
	1961/6/IV	105	6.5	26	3.5	36
Oats	1961/27/III	101	18	31	7	56

Leaf growth

Maximum green leaf area was attained before leaf development was complete. Afterwards the green leaf area decreased quickly (Fig. 1). The lower leaves began yellowing and drying before the development of the upper leaves was complete. Yellowing began 1—3 weeks before the increase in leaf mass ceased.

1. For barley and rye, the leaf growth period was 5—6 weeks, whereas for wheat and oats it was 6—7 weeks.

2. Leaf growth was fast in each cereal studied, lasting 5—7 weeks, which is approximately 40 percent of the vegetation period.

3. The maximum green leaf area attained per plant was 1.5 sq. dm for wheat and rye and 2 sq. dm for barley and oats.

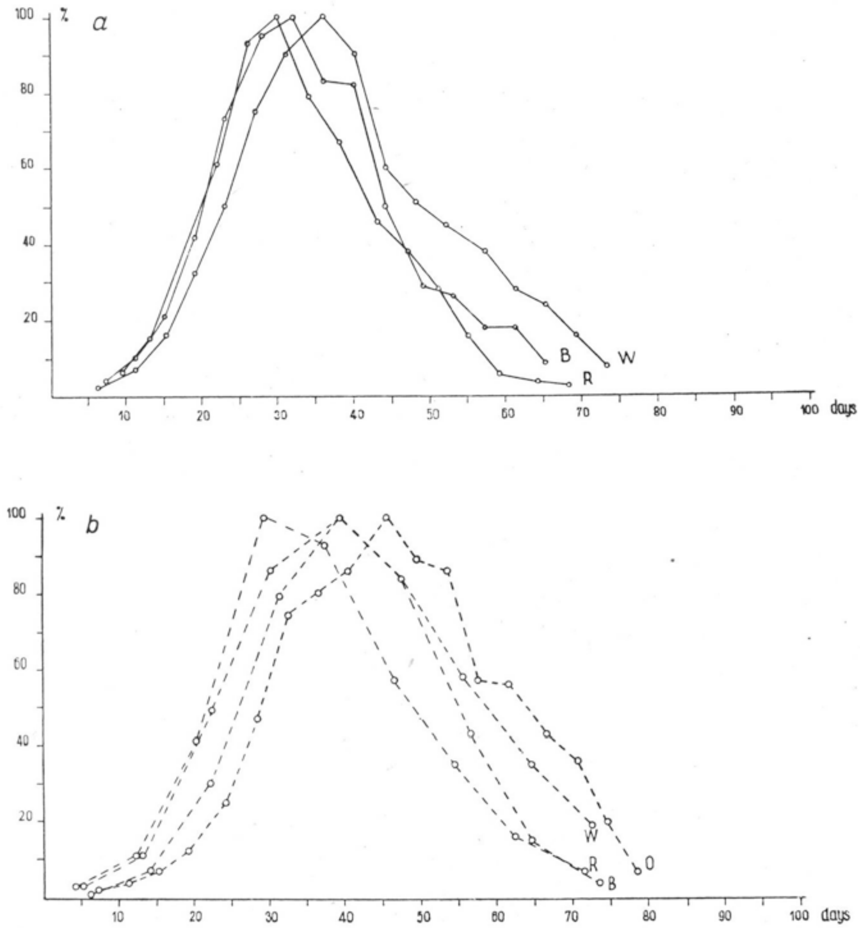

Fig. 1. Increase in leaf assimilatory area in cereals:

a — in 1960, *b* — in 1961. Days reckoned from emergence. Surface area expressed in percents of the maximum attained (taken as 100%). *W* — wheat; *B* — barley; *R* — rye.

It is a characteristic of cereals that the assimilatory surface of leaves develops quickly. Almost as soon as the maximum surface area is attained it begins to decrease owing to the yellowing and drying of the lowest leaves and simultaneously the period of rapid growth of the stem's assimilatory surface begins. The lowest leaves begin to yellow before the last of the young leaves have finished unfolding.

Stem growth

It would be unjustified, particularly in the case of cereals, to measure leaves alone and to disregard stems in calculating the photosynthetically active surface. Stem growth enters a rapid phase at the time when leaf growth stops (Figs. 2 and 3). When leaves ceased growing, stems assumed the photosynthetic function of the

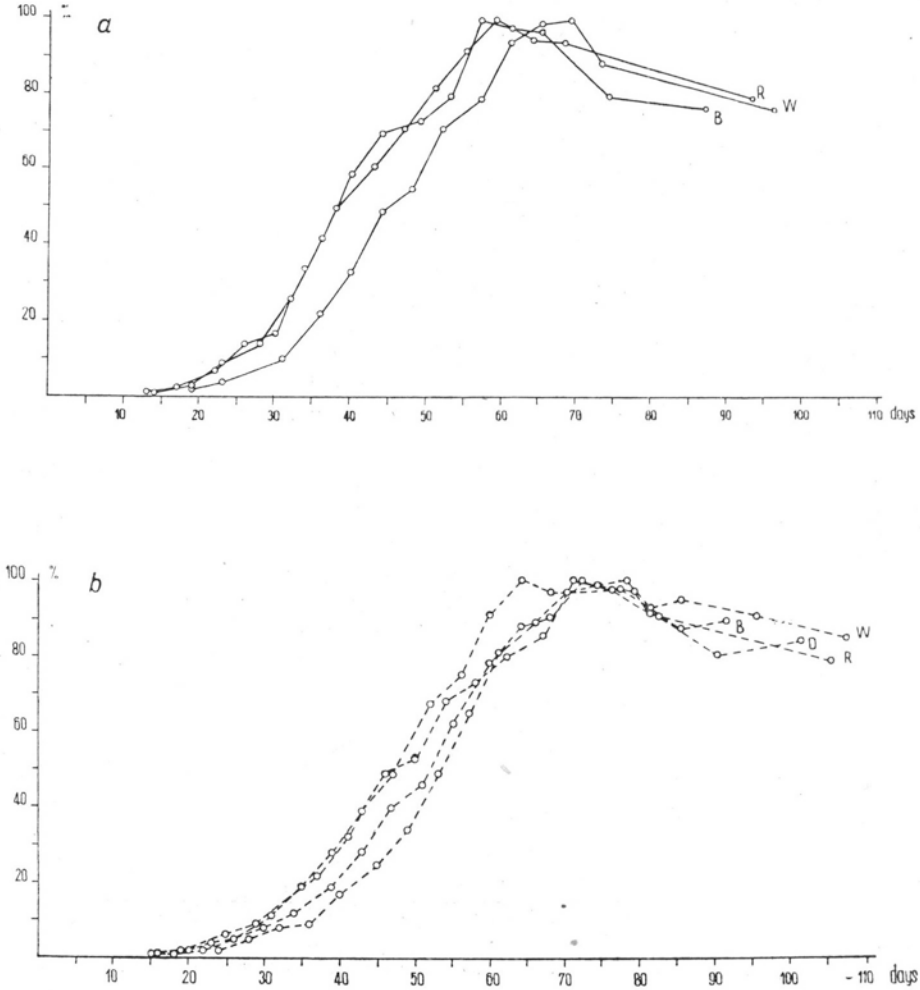

Fig. 2. Increase in stem dry mass expressed in percents of the final dry mass (taken as 100%): *a* — in 1960, *b* — in 1961. Days reckoned from emergence. *W* — wheat; *B* — barley; *R* — rye.

leaves. For the sake of accuracy, it should be added that leaf vaginae were also included into stem area. The total assimilatory area of the stem is lower than the leaf assimilatory area and amounts to 1 sq. dm for each cereal, except rye, for which it reaches 1.5 sq. dm. per plant, very nearly equal to the maximum value for the assimilatory surface of leaves.

Seed growth

Seed development lasts from just after flowering until the doughty stage (Fig. 4). This is a period of 4—5 weeks. The growth of seed mass is the fastest in barley and the slowest in rye.

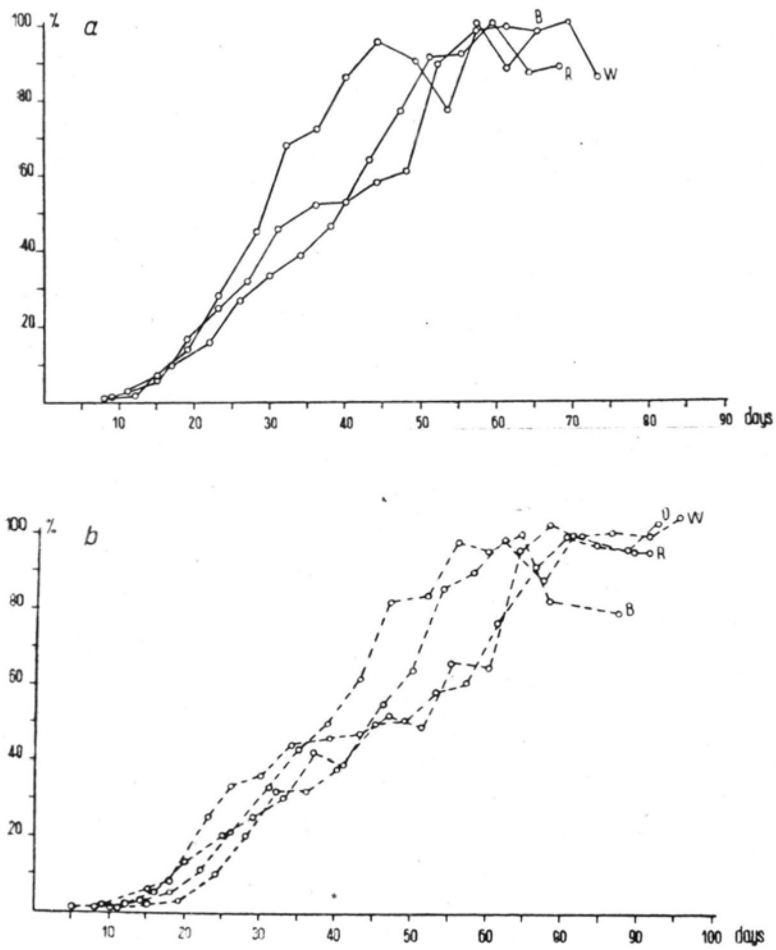

Fig. 3. Increase im stem assimilatory area:

a — in 1960, *b* — in 1961. Days reckoned from emergence. Surface area expressed in percents of the maximum attained (taken as 100%). *W* — wheat; *B* — barley; *R* — rye

Root growth

Root growth generally lasts 6—7 weeks. Root growth ceases gradually, coming to an end soon after the leaves stop growing (Fig. 5). This is the time of transformation into the ear.

Growth of the whole plant

The vegetation period lasted 12.5—15 weeks, reckoned from emergence. When considered in terms of increases in the masses of various plant components the growth period may be looked upon as consisting of the following phases: leaf growth 5—7 weeks, root growth 6—7 weeks, and stem growth 9—12 weeks. At

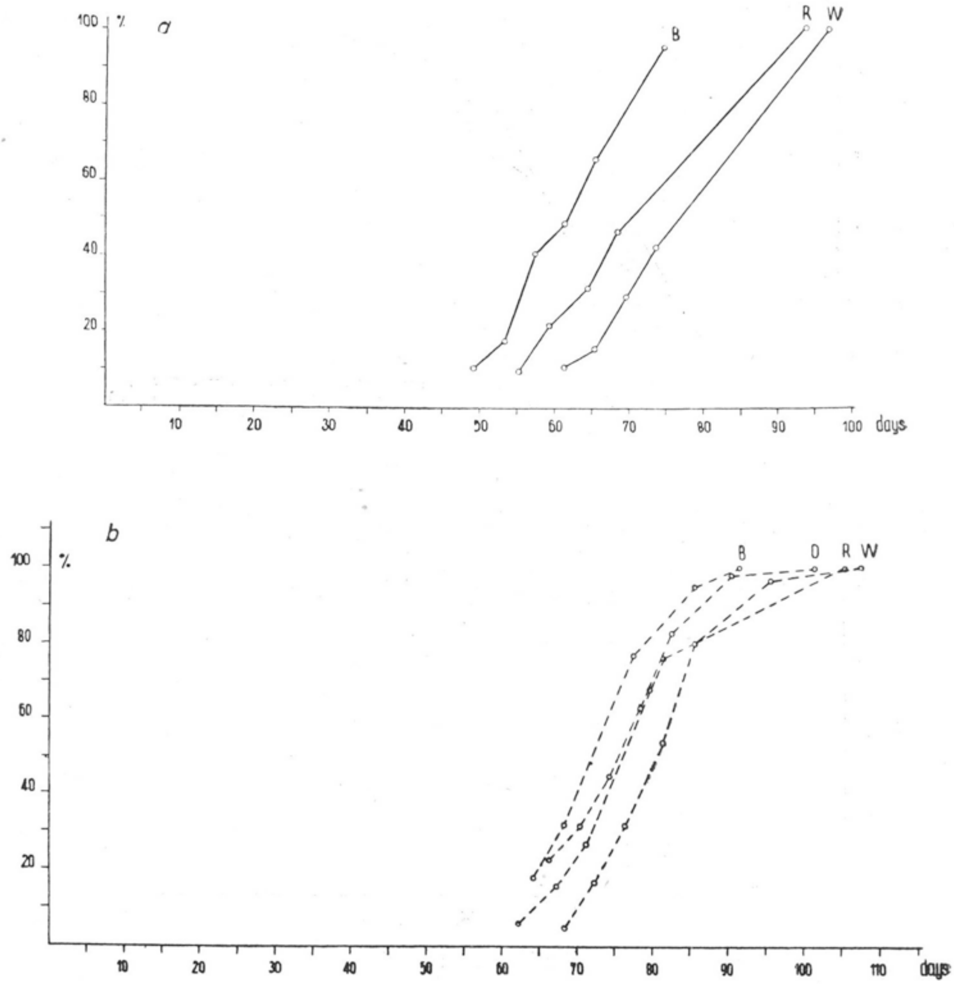

Fig. 4. Increase in seed dry mass.

a — in 1960, *b* — in 1961. Legend as above.

the milky stage of the grain the growth usually ceased to continue, except in barley, where it lasted until the doughy stage of the grain. Figure 6 shows that the plots representing the percentual increases in the dry mass of the plant during the two experimental years are very similar. When presented as a single plot (Fig. 7), these results, which refer to all the cereal species tested, give a very regular straight line.

The growth of a cereal plant fits the growth formula of T. B. Robertson (1907) fairly well

$$\log \frac{x}{A - x} = k\,(t - t_{1/2})$$

where x is the dry mass after t days of vegetation, A is the final maximum dry mass,

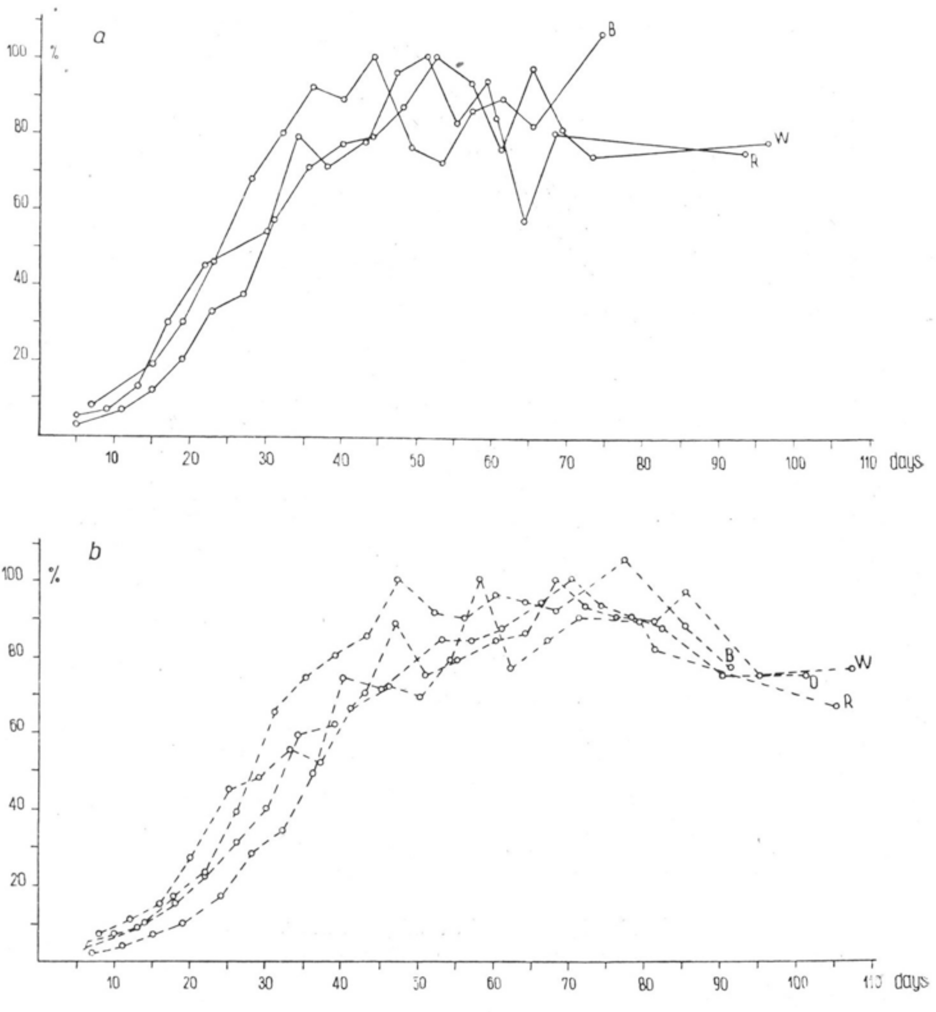

Fig. 5. Increase in root dry mass.

a – in 1960, *b* – in 1961. Legend as above.

$t_{1/2}$ is the time necessary to obtain the half of the maximum dry weight, and k is a constant.

In our experiments, A was 100 percent and $t_{1/2}$ was 43 days, reckoned from emergence. The k value varied from 0.5 at the beginning of vegetation to 0.03 in the middle of the growth period and to 0.05 towards its end. With 0.04 taken as the mean k value, the growth equation becomes:

$$\log \frac{x}{100 - x} = 0.04\,(t - 43)$$

where x is the plant dry weight expressed in per cents of the maximum dry weight within t days after emergence.

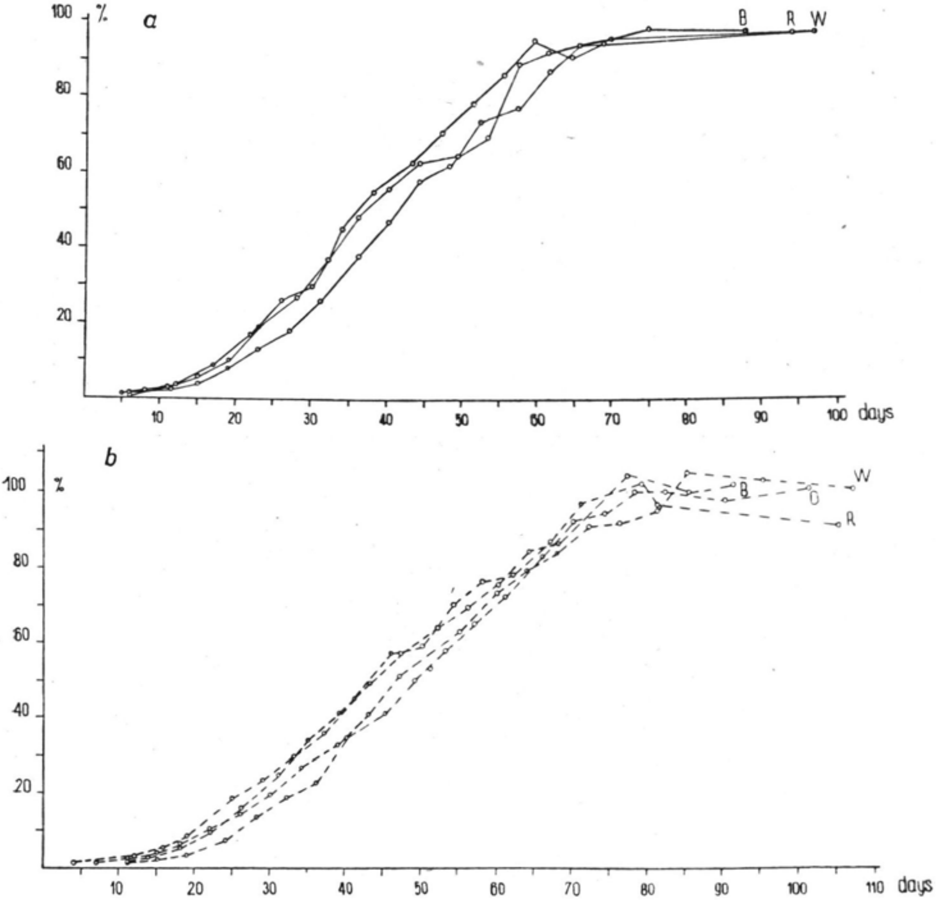

Fig. 6. Increase in total plant mass.

a — in 1960, *b* — in 1961. Legend as above.

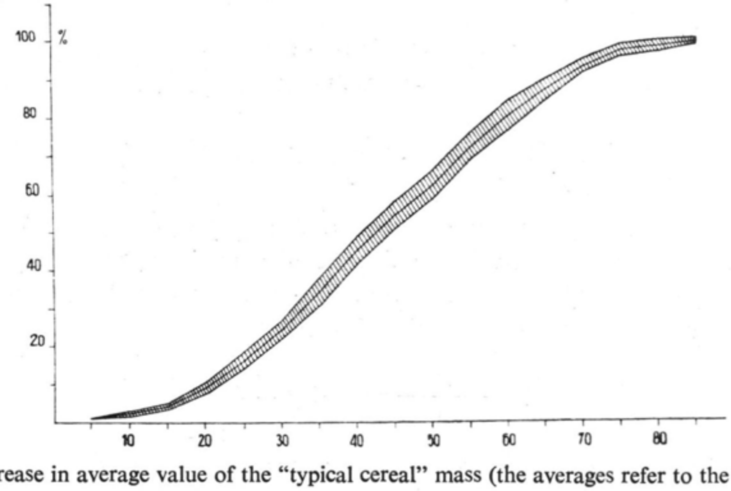

Fig. 7. Increase in average value of the "typical cereal" mass (the averages refer to the four species studied and to the experiments from both years).

Further calculations carried out by Z. Sęp, M. Sc., enabled the cereal growth to be expressed by the following equation:

$$M = \frac{100}{10^{\sinh(-0.038t+1.6968)} + 1}$$

Generative development

The time required to attain a given stage of the generative development, expressed in days reckoned from emergence, was compared in the cereal species studied. Results are presented in Table 2 and the number of leaves at each stage as well as the final dry weight (the 1961 data) are given. All the four cereal species yielded very similar results. Rye was an exception, because the growing point and flower differentiation occured earlier than with the other cereals. By the time pollen maturity was reached this difference disappeared and in subsequent development stages rye did not differ from the other three species.The growing point began to differentiate within 2—3 weeks after emergence, when 3—4 leaves were present and the dry mass was 3—6 per cent of the final value. Two weeks later flowers started to develop.

Table 2
Cereal growth and development

		Wheat	Barley	Oats	Rye	All together
Beginning of growing-point differentiation	Days from emergence	18	18	19	12	
	Number of leaves	4	4	4	3	
	Dry mass, %	6	5	3.5	3	4
Beginning of flower differentiation	Days from emergence	30	31	36	20	
	Number of leaves	6	6	6	5	
	Dry mass, %	19	24	22	10	22 without rye
Formation of pollen mother cells	Days from emergence	51	43	49	37	
	Number of leaves	8	8	8	8	
	Dry mass, %	52	48	40	38	40-50
Flowering	Days from emergence	64	60	61	58	
	Number of leaves	8	9	9	9	
	Dry mass, %	78	79	71	83	max 70-80
Beginning of seed formation	Days from emergence	68	64	66	62	
	Number of leaves					
	Dry mass, %	83	83	83	84	83
Beginning of the milky stage in mature seeds	Days from emergence	72	68	70	67	
	Number of leaves					
	Dry mass, %	90	85	91	94	90

There were 5—6 leaves present and the dry weight was 22 percent of the final value. The pollen grain mother cells appeared in another 2—3 weeks and flowering took place 2 weeks later after all the leaves had developed and the total dry weight attained 70—80 percent of the final value. Seeds appeared 4—5 days after flowering and reached the milky stage in another 4—5 days. When seeds began appearing the dry mass was 83 percent of the final value. It is in this period that the ear gains importance as a photosynthetic organ, because at that time it constitutes the youngest plant tissue. At the milky stage of the seed the plants attained 90 percent of the final dry weight.

Photosynthesis rate

In one series of experiments the dry weight increase rate during the time from ear formation till the end of growth was compared in defoliated and in normal plants. It was found that in rye and in wheat the stem assimilation rate was 60 and 70 percent respectively of the leaf assimilation rate. Therefore, in calculating the total assimilatory surface and the net assimilatory rate it was assumed that 1 sq. dm. area of the stem assimilatory surface (including ears) is equivalent to 2/3ds sq. dm. of the leaf assimilatory surface. There was an error in the stem assimilatory area owing to the fact that the area of the ear was not measured.

The average assimilatory surface area was calculated as the leaf surface area plus 2/3ds of the stem surface area. The sum of all assimilatory surface areas for each developmental phase multiplied by the length of that phase in days gives the photosynthetic index (Σ (sq.dm $\times$ days)). This index gives some information on the plant's photosynthetic potential but not on the rate or intensity of photosynthesis. The rate of photosynthesis is obtained by dividing the dry mass increment by the photosynthetic index. In our experiments, the apparent photosynthesis rate — decreased by respiration — or the net assimilation rate (Table 3) averaged e.g. 40 mg (sq.dm) day.

Table 3

Net assimilation rate, mg/sq.dm/day

Species	Year: 1960	1961
Wheat	43	46
Barley	34	28
Rye	37	36
Oats		41

In four years' experiments with barley F. G. Gregory (1926) found the net assimilation rate to be 546 mg per week or 80 mg per day. In his experiments only leaves were considered to assimilate. The present results are considered to be virtually the same because at the time of ear formation the leaf and stem areas are equal. In wheat, a 1-sq.dm leaf surface produced 50 mg dry mass per day and a 1-sq.dm stem surface gave 35 mg per day, the total dry mass increase baing 85 mg per day.

In rye, the yield from 1-sq.dm leaf surface was 50 mg per day and from 1-sq. dm stem surface 30 mg per day, i.e. a total of 80 mg per day.

The photosynthesis rate (F) for a given part of the developmental cycle is given by

$$F = \frac{M_2 - M_1}{S \cdot t}$$

where $M_2 - M_1$ is the dry weight increase during time t and S is the average assimilatory area.

Since the increase both in the assimilatory surface area and in dry mass is continuous, the principles of calculus apply and the equation of Briggs, Kidd, West (1920) and Gregory (1926) is more suitable.

$$R = \frac{M_2 - M_1}{t} \cdot \frac{\log_e S_2 - \log_e S_1}{S_2 - S_1}$$

where R is the apparent photosynthesis rate, M_1 and M_2 — original and final dry masses, S_1 and S_2 — original and final assimilatory surface areas, and t — time.

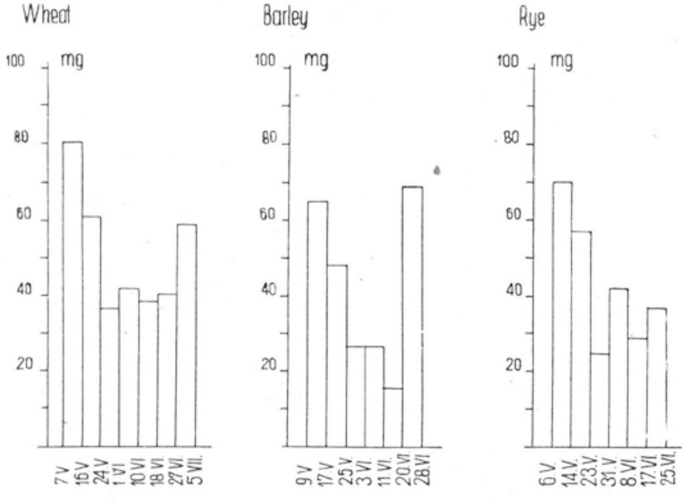

Fig. 8. Net assimilation rate per 1 sq.dm. assimilatory surface area per day in 1960. The total assimilatory area was obtained by adding the green leaf area to 2/3 ds of the green stem area.

In wheat, rye and barley, the rate of photosynthesis is seen to fluctuate considerably (Fig. 8). At first it decreased and at the time of ear formation it rose rapidly. The importance of the ear area at certain developmental phases should not be overlooked. The reason for photosynthetic fluctuations in earlier phases is unknown.

According to F. G. Gregory (1926) and O. V. S. Heath and F. G. Gregory (1938), the photosynthesis rate per 1 sq.dm leaf surface is the same in a large number of different species, but this depends on environmental factors. Light is of primary importance. Grass yields are almost proportional to the amount of energy available per unit soil area during the vegetation period if water is not limited (H. L. Penman 1956).

The data on the illumination intensity conditions near Warsaw were obtained from the Electrotechnical Institute at Międzylesie. This research centre was 40 km away from the site of our experiments. Nevertheless, the results are more uniform when expressed per 10 000 luxes per 1 sq.dm per day (Fig. 9*a* 1960 experiments). This correction does not affect the fall in the photosynthesis rate which occurs with age and is least-marked in wheat and most-marked in barley. The rapid increase

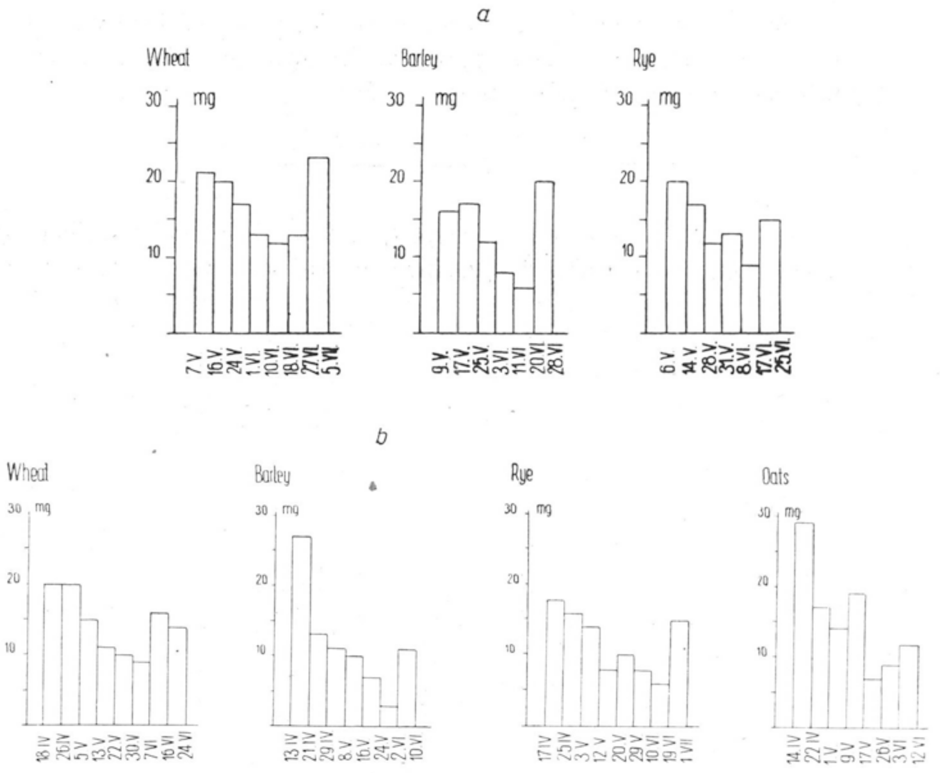

Fig. 9. Net assimilation rate per 10 000 luxes.
a — in 1960, *b* — in 1961.

in the rate of photosynthesis visible at the end of the diagram (Fig. 9*a*) is connected with appearance of ears. The results of the 1961 experiments were essentially the same, the drop in photosynthesis rate with age being most-marked in rye and barley and least-marked in wheat (Fig. 9*b*).

The final yields depend directly upon the assimilatory surface area attained and upon the rate of photosynthesis.

The highest plant mass yields were obtained with wheat and oats and the lowest with rye (Table 1).

Certain small differences in the rate of photosynthesis were noticed. At the beginning of the vegetative period, the rate of photosynthesis in oats was greater than

25 mg. dry mass per 1 sq.dm per day per 10 000 luxes. With wheat and rye, the highest value obtained was 20 mg. and it decreased with age. Such differences may be compensated, if the assimilatory surface areas are taken into account; e.g. in barely, the leaf photosynthetic surface area attains 2 sq.dm per plant, which is 25 percent more than in wheat and rye.

It is possible therefore to simplify the investigations on the dynamics of growth of cereals by reducing the number of harvests. Table 2 shows that by 2 weeks, reckoned from the date of emergence, the plant had as few as 3 leaves and its weight attained as little as 3 percent of the final weight. The investigations may be started just within this period of time. Four weeks after emergence, the plant had 5 leaves and its weight was 15—20 percent of the final weight. In 8 weeks, the plant weight rose to 60—70 percent of the final weight and earing commenced. The last harvest would take place after completion of the vegetation, i.e. in the period of full maturity. It appears that the four harvesting dates comprise the most important stages of growth and will be sufficient for the purposes of characterization and comparison of the growth dynamics in various cereals. Such investigations can be carried out directly in the field by the author's method (1961), which involves harvesting of 100-plant samples.

SUMMARY

Nine pot experiments with wheat, barley, rye, and oats showed that these cereals exhibit a similar dynamics of growth.

1. An essential feature of the growth dynamics is the short period of leaf activity. Older leaves start yellowing and becoming dry before the youngest leaves are developed. The leaf growth period covers as little as 40 percent of the vegetation period. In later stages the function of leaves is taken over by the stem and ears which act as the photosynthetic assimilatory organs.

2. The assimilatory leaf area and the stem area were 1.5—2 and 1—1.5 sq. dm. per plant, respectively.

3. The average rate of photosynthesis was 40 mg. of dry mass increment per 1 sq.dm. per day or, when recalculated to an illumination intensity of 10 000 luxes, 20—25 mg. dry mass increment per 1 sq.dm. per day.

4. It appears that for agricultural purposes the number of harvests may be limited to four, viz., to those carried out after 2, 4 and 8 weeks, reckoned from the date of emergence, and one during the maturity period. Such investigations may be carried out in the field with 100-plant samples withdrawn in triplicate or quadruplicate according to method described by Strebeyko, Domańska and Nelken (1961).

5. Investigations on the growth dynamics could be useful for estimating the value of new plant varieties.

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Dynamika wzrostu i rozwoju zbóż jarych

Streszczenie

Na podstawie 9 doświadczeń wazonowych z pszenicą, jęczmieniem, żytem i owsem stwierdzono duże podobieństwa w dynamice wzrostu u badanych zbóż jarych.

1. Cechą charakterystyczną dynamiki ich wzrostu jest krótki okres aktywności liści. Dolne liście zaczynają żółknąć i usychać zanim się rozwiną najmłodsze. Wzrost liści wypełnia zaledwie 40% okresu wegetacyjnego. Później funkcje liści przejmują łodygi i kłosy — jako organa asymilacyjne.

2. Powierzchnia asymilacyjna liści sięgała 1,5—2 dcm^2, a powierzchnia łodyg 1—1,5 dcm^2 na roślinę.

3. Szybkość fotosyntezy odpowiadała przeciętnie ca 40 mg przyrostu suchej masy na dcm^2 i dzień, a w przeliczeniu na 10 000 luksów natężenia światła sięgała ona 20—25 mg suchej masy na dcm^2 i dzień.

4. Wydaje się, że dla celów rolniczych można ograniczyć liczbę terminów sprzętu roślin do czterech, mianowicie: po upływie 2, 4, i 8 tygodni od wschodów oraz w okresie dojrzałości nasion. Badania takie można prowadzić nawet w polu, sprzątając w 3—4 powtórzeniach po 100 roślin wg poprzednio stosowanej przez nas metody (1961).

5. Wydaje się, że badania dynamiki wzrostu mogą znaleźć szerokie zastosowanie przy ocenie wartości nowych odmian w hodowli roślin.