Changes in the Carbohydrate Composition during Development and Maturation of the Wheat and Barley Kernel[1]

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ABSTRACT

Studies have been made on the change of the high-molecular carbohydrate composition (starch, pentosans, crude fiber) and the principal alcohol-soluble sugars in the developing wheat and barley kernel. Samples were collected from the fields at 9 to 49 days after flowering at intervals of 3 to 4 days, immediately immersed in liquid nitrogen, freeze-dried, and ground. Carbohydrate analyses were carried out with adequate methods which result in values of good precision and reproducibility. The results are expressed on a 1,000-kernel weight basis, which permits one to distinguish between the carbohydrates accumulating in the kernel (mainly starch, pentosans, and crude fiber) and those which arise by an intermediate pathway (mainly glucose and sucrose). The results are given as a function of a climatic factor, the cumulative daily mean temperature from the point of flowering. Thus it is possible to compare not only one cereal grown in different years and various regions but also all cereals among each other. Starch development was found to be essentially identical in the two cereals. Pentosans of wheat develop analogously to starch in the case of the Joss variety, while they follow the evolution of crude fiber in the case of the Cappelle variety. Barley, a covered cereal, shows a very rapid and parallel accumulation of pentosans and crude fiber. The alcohol-soluble sugars increase in the very early stage of development and then decrease to a more or less constant value. Some important phases in the formation of the carbohydrates become apparent and the relationship between the development of these components and the hydration of the kernel is discussed.

A considerable amount of information is available on the carbohydrate composition of mature wheat (1) and barley kernels (2–7), but relatively few studies have been published on the change of the total and the individual carbohydrates during the development of these cereal kernels. Early research was mostly concerned with starch development in wheat grain (8–13).

In 1950 the Laboratory for Biochemistry and Physico-Chemistry for Cereals of the French National Institute of Agronomic Research (14) reported the results of an investigation on the change of various biochemical constituents during different developmental stages of the wheat kernel. According to this work, the starch content, expressed on a dry matter basis, increased slowly and regularly but not in a linear way. The pentosans decreased in the beginning of maturation but they then increased, whereas the crude fiber content went up in two stages, declined quite sharply, and increased again. Sucrose showed a first maximum in the early stage of kernel development (22 days after flowering) and a second one a few days before maturity. Levosine (13), or nowdays called glucofructosans (6), followed the development of sucrose, and reducing sugars decreased progressively during whole kernel formation.

However, of particular interest is the fact that the results of these investigations

[1]Presented at the 56th Annual Meeting, Dallas, October 1971.

[2]This work constitutes parts of a University thesis for the degree of Doctor of Science.

have been also reported on a per kernel basis. Expressing the results in this manner enables one to obtain a better idea of kernel physiology. Presented in this way, dry matter, starch, and pentosans develop regularly, showing a typical S-shaped curve of growth. On the other hand, sucrose and glucofructosans pass through a maximum 22 days after flowering. In addition, sucrose showed another increase 13 days later and then decreased as did the glucofructosans. Belval (13) has already indicated the same findings in 1924.

Menger (15), studying the change of soluble sugars by paper chromatography, contributed to a more detailed knowledge of the development of these constituents during maturation of durum wheat (*Triticum durum*). She found that fructosyl-raffinose, maltose, glucose, fructose, and sucrose are present at the very early stage of the kernel development, and that only their concentrations change during maturation. Menger (15) also mentioned that the relatively high maltose values for immature wheat are probably explained by a partial degradation of starch that occurred during preparation of the sample.

Harris (3,16,17) recorded that the development of starch during ripening of barley followed a more or less logarithmic form when expressed on a per kernel basis. Sucrose and fructosans showed a maximum 4 weeks after ear formation, glucosans presented 2 maxima, the first one 5 weeks after ear formation, the second one 3 weeks later. Furthermore, Harris showed that fructose, sucrose, fructosans, and glucodifructose are present in the kernel at the beginning of maturation and that raffinose appears only at a later stage.

MacGregor et al. (18) indicate in a recent study that starch and crude fiber, expressed on a per kernel basis, reached their maximum values 32 to 36 days after ear emergence, but that sugars rose to a maximum 16 days after ear emergence and then declined.

In spite of this research, our knowledge of the development of carbohydrate composition of cereals during ripening remains fragmentary, and it seemed worthwhile to study some aspects more precisely.

It appears that one has not always paid sufficient attention to the preparation and stabilization of the immature material, which has led occasionally to high maltose values. The indication of the physiological kernel age has sometimes been given on the basis of quite subjective observations.

The basis chosen for expressing is also of great importance. Calculating the results of analysis on a dry basis cannot lead to conclusive information because the dry matter of the developing kernel changes continuously and some of the constituents show an apparent decrease simply because the accumulation of starch is so important and so fast. These concepts are often overlooked and account for some of the apparent discrepancies in the literature. One can only get a real idea about what takes place in the growing kernel when the analytical results are used to calculate actual quantities present in the kernel.

Another point which seems important is the way the results are presented. It is well known that climatic conditions which vary considerably from one country to the other affect the formation and the development of the plant. Therefore, it appeared preferable to present the results not as a function of time, as is commonly done, but as a function of a climatic factor (19), the cumulative daily mean temperature from the point of flowering. Thus, it is possible to compare not only one cereal grown in different years and various regions but also all the cereals among each other.

TABLE I. DATA FOR THE 1967 CROP OF CAPPELLE WHEAT
(SOWING NOVEMBER 15, 1966; FLOWERING JUNE 14, 1967)

Sample	Collecting Date	Days after Flowering	Σ dmt° C.
1	June 22	8	100
2	June 26	12	190
3	June 29	15	240
4	July 3	19	330
5	July 5	21	405
6	July 8	24	460
7	July 11	27	545
8	July 15	31	605
9	July 18	34	705
10	July 22	38	795
11	July 26	42	880

The purpose of our studies was to take all these aspects into consideration and to try to contribute to a better knowledge of the development of the carbohydrate composition during the ripening of wheat and barley kernels.

MATERIALS AND METHODS

Materials

Two wheat varieties and one barley variety were examined. Cappelle wheat and Iris barley were grown in 1967 in the center of France (Clermont-Ferrand); Joss wheat was grown in the Parisian area in 1968 (Tables I, II, and III). The samples, at the same stage of physiological development, were collected from the fields 4 to 49 days after flowering. A small portion of each sample was taken for moisture determination and another part was immediately immersed in liquid nitrogen. The kernels from the middle part of the ear, after being threshed, were freeze-dried and ground in the presence of carbon dioxide ice to a particle size of less than 0.5 mm.

Methods

Moisture. The moisture content of the fresh kernels and the freeze-dried material was determined by drying the sample to a constant weight at 102° to 105°C. in an oven (20) with conditioned air and by adding a constant correction factor, which is 0.3 for ground cereals.

TABLE II. DATA FOR THE 1968 CROP OF JOSS WHEAT
(SOWING NOVEMBER 9, 1967; FLOWERING JUNE 12, 1968)

Sample	Collecting Date	Days after Flowering	Σ dmt° C.
1	June 27	15	200
2	July 1	19	275
3	July 4	22	335
4	July 8	26	405
5	July 11	29	465
6	July 15	33	525
7	July 18	36	570
8	July 22	40	630
9	July 25	43	680
10	July 29	47	745

Kernel Weight. A sufficient amount of each sample was divided into ten equal batches. From each batch 100 to 200 kernels depending on their size were counted, weighed, and corrected for their moisture content.

Starch. Starch was determined by the enzymatic method (21) with glucoamylase after extraction of the ethanol-soluble sugars from the material. The Ewers method (22), which consists of the determination of starch by extraction and dispersion with hydrochloric acid, was also used.

Crude Fiber. This was estimated by the modified Weende method (23), which consists of weighing the residue remaining after an acid and alkaline treatment of the sample.

Pentosans. These were determined by aniline-acetate (24) after conversion into furfural during steam distillation (25).

Sugars. The total alcohol-soluble sugars after two extractions with hot 80% ethanol, two washings, and purification of the extract (24) were determined by the anthrone method (26). They were qualitatively estimated by paper chromatography (27,28,29). Fructose and fructosans were determined by the anthrone method at 50°C. (30). Glucose was determined by the action of glucose-oxidase (21,24). Finally sucrose was determined by the glucose-oxidase method after hydrolysis by invertase (24,30).

RESULTS AND DISCUSSION

Qualitative Aspect

The paper chromatograms show the ethanol-soluble sugars of Joss wheat (Figs. 1 and 2). Chromatograms for Cappelle wheat and Iris barley are not shown since the results obtained are virtually identical with those of Joss wheat (for the sample numbers see Table II). The spots on the chromatograms correspond to the same amount of total sugars for each sample. It has been operated in this way because the sugar content of the samples, collected at different stages of maturity, varied so greatly. In this manner the different sugars are distinguished and some are identified by authentic samples of known sugars as controls. Thus a proximate idea is obtained concerning the relative concentrations of the individual sugars in the alcohol-soluble fraction. Unfortunately the chromatograms are poorly reproduced; the very faint details of the color and small traces which appear immediately after the development are difficult to reproduce.

TABLE III. DATA FOR THE 1967 CROP OF IRIS BARLEY (SOWING FEBRUARY 24, 1967; FLOWERING MAY 29, 1967)

Sample	Collecting Date	Days after Flowering	Σ dmt°C.
1	June 6	8	140
2	June 10	12	195
3	June 13	15	235
4	June 16	18	280
5	June 19	21	315
6	June 22	24	360
7	June 26	28	455
8	June 30	32	525
9	July 6	38	670
10	July 12	44	760
11	July 17	49	870

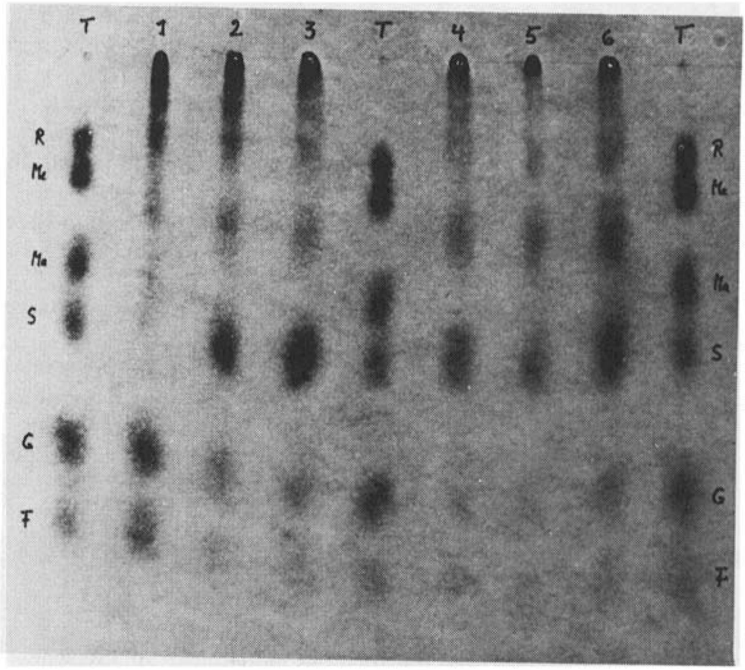


Fig. 1. Paper chromatograms of the 80% ethanol-soluble sugars sensitive to the diphenylamine-aniline reagent (28). The solvent mixture used was butanol:acetic acid:water (4:1:5). F - fructose, G - glucose, S - sucrose, Ma - maltose, Me - melibiose, R - raffinose, T - standard mixture. Wheat Joss sample 1-6.

Paper chromatography reveals in wheat as well as in barley the presence of glucose, fructose, sucrose, gluco-difructose, or possibly neokestose (31) located between melibiose and maltose and very small traces of maltose. At the end of maturation raffinose appears (samples 7–11). The spot overlapping raffinose and present from the beginning of kernel development is supposedly a fructosyl-raffinose (15), but it is certainly not raffinose. This can be affirmed by the color of the spot after development with aniline-diphenylamine. These observations are in agreement with those of Harris and MacWilliam (16) and Menger (15), who recorded the appearance of raffinose at the end of kernel development only. The same findings have been indicated by Cerning (24) in maturing corn kernels.

Furthermore one can observe near the starting line a carbohydrate fraction believed to be higher molecular weight glucofructans (6) inasmuch as they yield fructose and smaller amounts of glucose after acid hydrolysis. All sugars, except raffinose, are present in the grain from the earliest stage of development; only their concentrations change during maturation. It is important to underline that the carbohydrate composition of the mature kernels, as observed here, corresponds to that of grains harvested in optimal conditions. The occasionally high values for maltose as well as the presence of melibiose found by some workers (15) are believed to be partly due to the enzymatic breakdown of starch or raffinose, which may arise either from poor harvesting conditions and insufficient stabilization of the material or from alteration during storage.

Quantitative Results

As mentioned above the results are not given as a function of time, as is common, but as a function of a climatic factor, which is obtained by adding up the daily mean temperature from the time of flowering according to the formula:

$$\text{dmt}^\circ\text{C. } \Sigma = \frac{\text{maximum + minimum of daily temperature }^\circ\text{C.}}{2}$$

This factor is from now on referred to as Σ dmt°C.

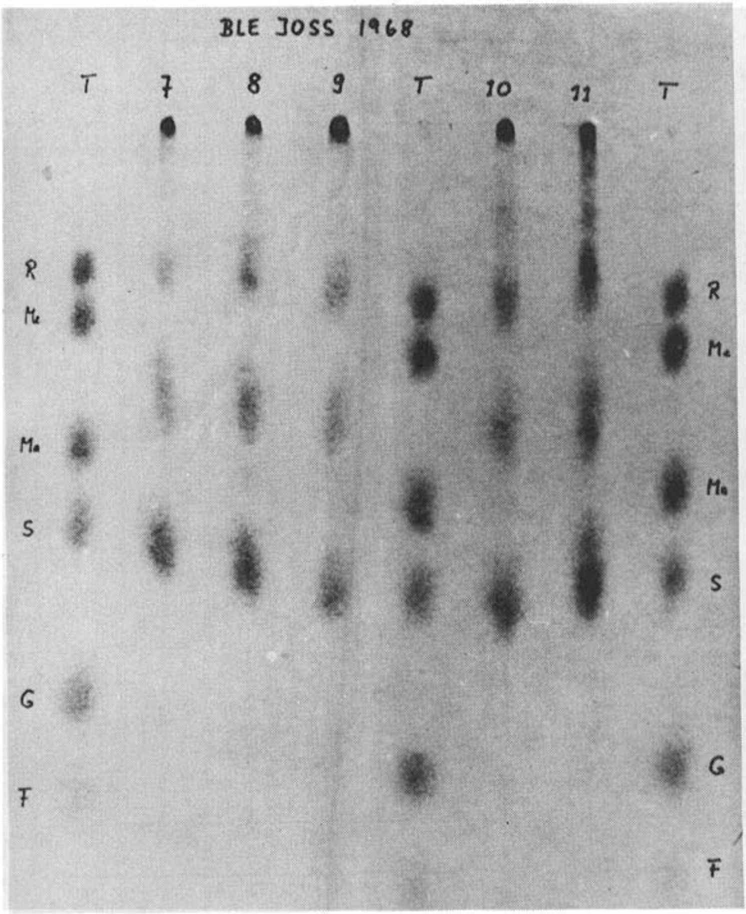


Fig. 2. Paper chromatograms of the 80% ethanol-soluble sugars sensitive to the diphenylamine-aniline reagent (28). The solvent mixture used was butanol:acetic acid:water (4:1:5). F - fructose, G - glucose, S - sucrose, Ma - maltose, Me - melibiose, R - raffinose, T - standard mixture. Wheat Joss sample 7-11.

1,000-Kernel Weight and Water

Figure 3 shows, as an example for wheat, the change of dry matter (curve 1) and of the water quantity contained in 1,000 kernels (curve 2) as a function of Σ dmt°C. The time elapsed after flowering is also indicated in all figures to facilitate comparison with the kernel age. The percentage of water from the kernels (curve 3) as harvested is also shown, since it is with these values and those of the 1,000-kernel weight that we have calculated the amount of water in the kernel (curve 2). The 1,000-kernel weight (curve 1) increases regularly showing a typical S-shaped curve of growth. The quantity of water in 1,000 kernels increases rapidly in a linear way between Σ dmt = 200° and 300°C., remains constant during 12 days, and desiccates rapidly following an almost linear rate.

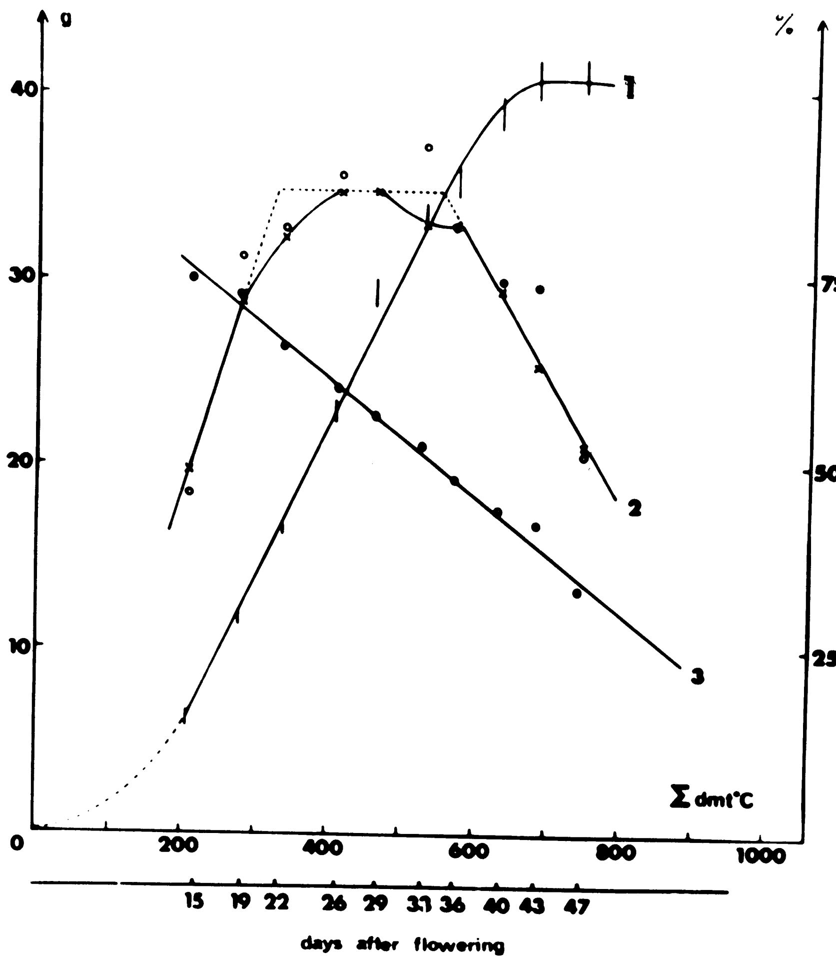


Fig. 3. Change of the dry matter (curve 1) and water (curve 2) expressed on a 1,000-kernel weight basis and of the water percentage (curve 3) of the kernel at sampling time as a function of Σ dmt°C. for Joss wheat. Left ordinate: g./1,000 kernel; right ordinate: % water.

It seems relevant to discuss briefly a peculiar aspect of curve 2 which is traced at the constant water level as a dashed line and as a continuous line. The solid line is drawn from the experimental values, and the dashed line represents the theoretical constant water level which is obtained by extrapolation of the initial and final linear parts of this curve and by locating their intersection with the experimental constant water level. This curve corresponds to the findings of Geslin and Jonard (19), provided climatic conditions are relatively uniform. The experimental disparities are due to the particular high temperature of dry air which occurred at that stage. Thus the first point of divergence between the theoretical and the experimental curve corresponds to the absolute temperature maximum registered in 1968 at Σ dmt = 325°C. (33,1°C.), the second one (Σ dmt = 550°C.) to another important raise of temperature.

High- and Low-Molecular-Weight Carbohydrates

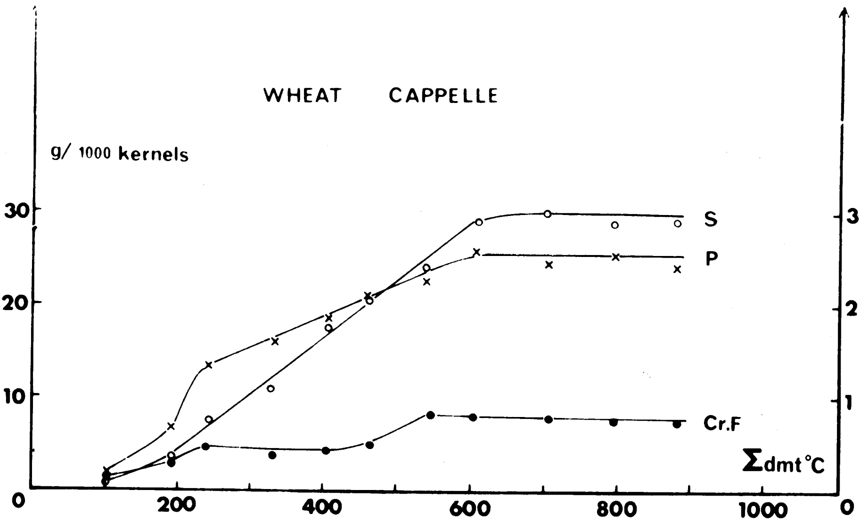
Cappelle Wheat. Figure 4 demonstrates the change of high- and low-molecular carbohydrates in Cappelle wheat during maturation. Starch increases regularly between Σ dmt = 200° and 600°C., reaching a constant value at Σ dmt = 625°C. Pentosans and crude fiber are synthesized first rapidly between Σ dmt = 100° and 225°C. The pentosans then accumulate steadily reaching their maximum value at Σ dmt = 600°C.; the crude fiber quantity remains practically unchanged up to Σ dmt = 475°C., and then increases to a maximum value at Σ dmt = 550°C.

The total alcohol-soluble sugars (Fig. 5) increase in the early stage of kernel development and show a pronounced maximum at about Σ dmt = 200°C.; afterwards a progressive decrease is observed. Sucrose, fructose, and fructosans exhibit a similar trend in that an alternating increase and decrease of these sugars is observed. Very little glucose is found in the immature kernel and it becomes negligibly small on maturation.

Joss Wheat. Starch development in Joss wheat resembles that of Cappelle (Fig. 6); however, the synthesis slows down slightly between Σ dmt = 475° and 620°C. This observation may be explained by the fact that this wheat has come under the influence of particularly high temperature at this stage. Starch synthesis is completed when the water starts to decrease in the kernel. Pentosans are accumulated regularly following the same pattern as starch, while crude fiber synthesis increases progressively up to Σ dmt = 415°C. and then tapers off to a fairly constant level.

As we have already observed for Cappelle wheat, the total alcohol-soluble sugars (Fig. 7) show a maximum in the beginning of kernel formation at Σ dmt = 200° to 300°C. and then decrease more or less progressively. Sucrose, fructose, and fructosans seem to develop in a comparable way with, however, a slight displacement of their minima and maxima. Here again, the glucose concentration remains low, but it is to be noted that the little maximum at about Σ dmt = 450°C. corresponds to the time when starch accumulation slowed down.

Iris Barley. Barley shows a much more distinct difference between the synthesis of starch (Fig. 8) on the one hand and that of pentosans and crude fiber on the other. As is seen, starch development during ripening follows again a more or less logarithmic form, while pentosans and crude fiber show a very rapid and parallel accumulation which occurs in two stages. Both carbohydrate constituents reach their maximum accumulation very early, pentosans at about Σ dmt = 350°C. and crude fiber at Σ dmt = 450°C.



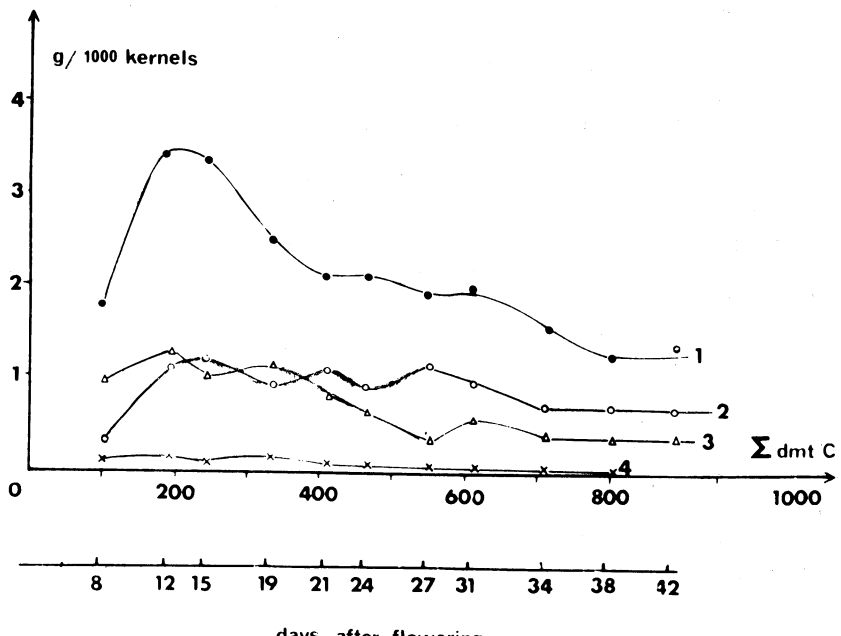
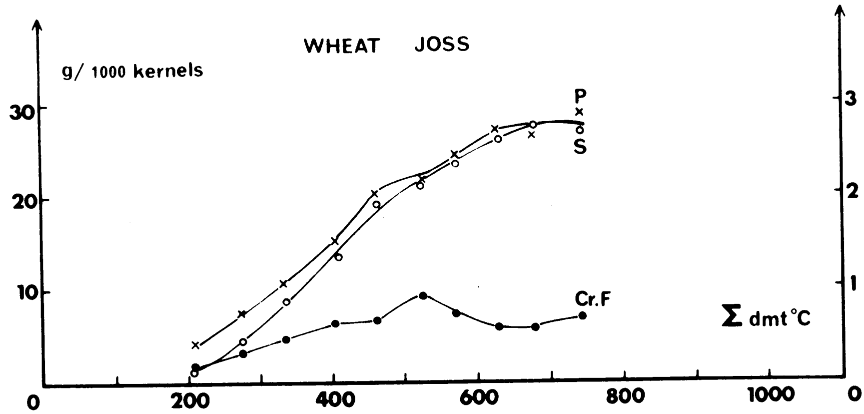


Fig. 4. (top) Development of polysaccharides expressed on a 1,000-kernel weight basis as a function of Σ dmt°C. for Cappelle wheat. Left ordinate: S - starch; right ordinate: P - pentosans, Cr.F. - crude fiber.

Fig. 5. (bottom) Change of sugars expressed on a 1,000-kernel weight basis as a function of Σ dmt°C. for Cappelle wheat. 1) Total alcohol-soluble sugars, 2) sucrose, 3) fructose/fructosans, 4) glucose.

There is a maximum of alcohol-soluble sugars (Fig. 9) between Σ dmt = 150° and 200°C., then a decrease to a more or less constant value. Fructose and fructosans remain fairly constant up to Σ dmt = 525°C., whereas sucrose shows a minimum at Σ dmt = 450°C. The glucose content is so negligibly small in barley that the values could not be traced on the figure.



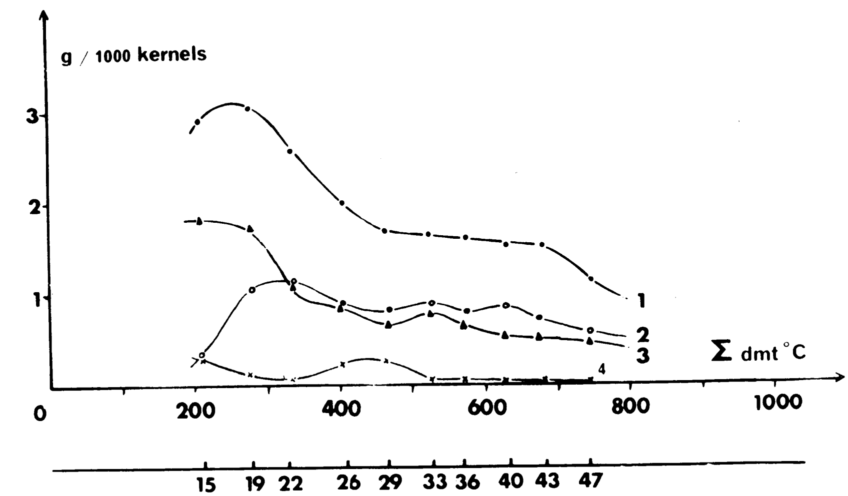
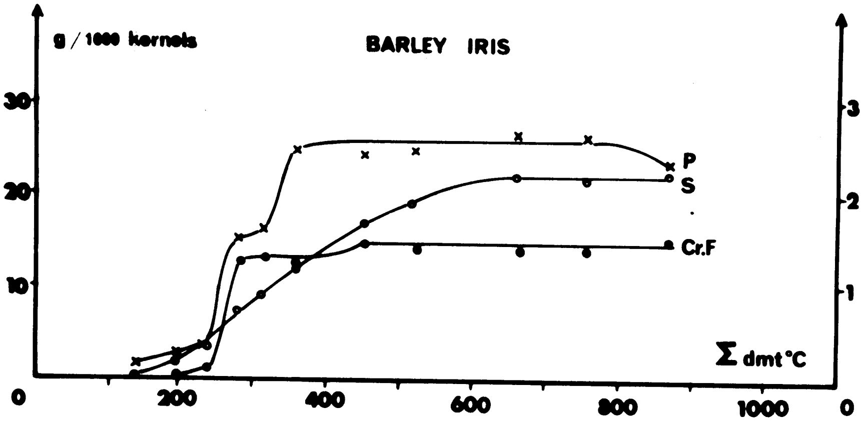


Fig. 6. (top) Development of polysaccharides expressed on a 1,000-kernel weight basis as a function of Σ dmt°C. for Joss wheat. Left ordinate: S - starch; right ordinate: P - pentosans, Cr.F. - crude fiber.

Fig. 7. (bottom) Change of sugars expressed on a 1,000-kernel weight basis as a function of Σ dmt°C. for Joss wheat. 1) Total alcohol-soluble sugars, 2) sucrose, 3) fructose/fructosans, 4) glucose.



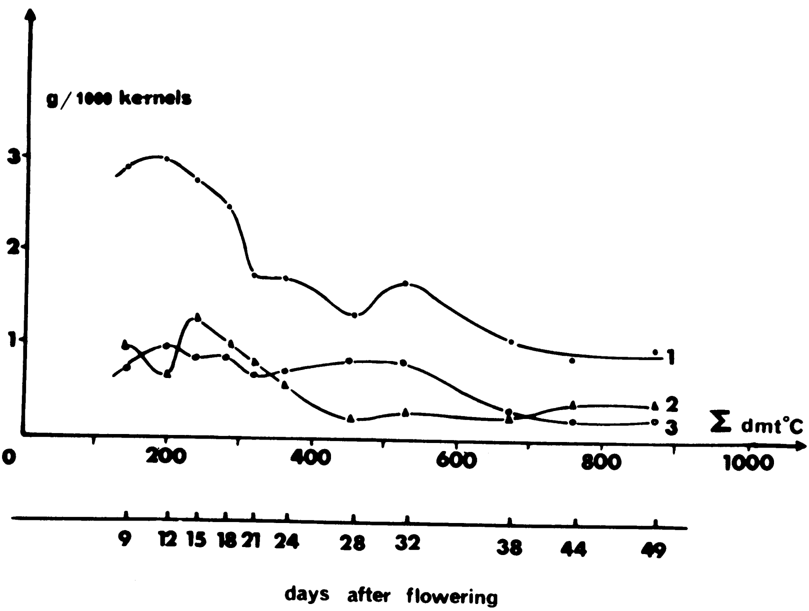


Fig. 8. (top) Development of polysaccharides expressed on a 1,000-kernel weight basis as a function of Σ dmt°C. for Iris barley. Left ordinate: S - starch; right ordinate: P - pentosans, Cr.F. - crude fiber.

Fig. 9. (bottom) Change of sugars expressed on a 1,000-kernel weight basis as a function of Σ dmt°C. for Iris barley. 1) Total alcohol-soluble sugars, 2) sucrose, 3) fructose/fructosans.

CONCLUSIONS

In general it may be concluded that the patterns of carbohydrate development in wheat and barley are about the same. However, two differences are to be noticed: crude fiber development differs from one wheat variety to another and barley, a covered cereal, shows a very rapid accumulation of pentosans and crude fiber.

Expressing the analytical results on a 1,000-kernel weight basis permits one to distinguish between the carbohydrates accumulating progressively in the kernel, mainly starch, pentosans and crude fiber, and those that show a trend to decrease in concentration before reaching a constant level. In general the mono-, di-, and oligosaccharides decrease during maturation. It seems as if they are degraded by an enzyme system to be used in polysaccharide synthesis or other metabolic processes. To consider glucose and sucrose as intermediate products is in agreement with the hypothesis of several authors (3), who found that starch is synthesized at the expense of reducing and nonreducing sugars. However, it is noteworthy to underline that such conclusions cannot be made on the basis of results which are reported as a percentage of the dry matter, since the latter changes continuously. This has been emphasized in the recent study by MacGregor et al. (18), whose results on starch and sugar development during growth of the barley kernel confirm our own findings.

The choice of a climatic factor as a function for presentation facilitates easier comparison of the results. Of particular interest is the fact that the end of starch accumulation is observed in all cases between Σ dmt = 600° and 625°C., while the difference between the days after flowering varied from 31 to 42 days.

If this way of expressing the results would be generally adopted, it would most certainly facilitate the comparison of results obtained in various countries with largely differing climatic conditions.

The present work was concerned only with the carbohydrate development in the kernel itself. A complete elucidation of what occurs during the ripening process can only be obtained when not only the kernel but all the other parts of the plant are included in the studies

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[Received June 20, 1972. Accepted October 30, 1972]