

Dynamics of phosphorus compounds in ripening and germinating cereal grains

Part I. Changes in phosphorus compounds content during ripening of wheat, barley and rye grains

J. TEUCZKIEWICZ AND W. BERENDT

Institute of Plant Biology, Agricultural-Technical Academy, Olsztyn

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Abstract

The dynamics of phosphorus compounds was followed in ripening wheat (Grana), barley (Kosmos) and rye (Pancerne) seeds. In the investigated ontogenesis period the content in the seeds of total and acid-soluble phosphorus doubled. The phosphorus of free phytin and phytin that bound with proteins increased to the end of maturation. In dormant seeds the contribution of phosphorus bound with phytin was 62-70 per cent of total P. As the seeds ripened, the content of inorganic and nucleotides-P decreased, while that of saccharides-P and their metabolites started to decrease from the moment of wax ripeness. Later RNA-P and DNA-P level decreased only slightly and that of lipids-P markedly. Phosphoproteid content diminished at the beginning of ripening and further remained at almost the same level. Wheat, barley and rye seed exhibited similar dynamics of metabolically active (nucleotides, saccharide-P esters and their metabolites), functional (nucleic acids) and structural (phospholipids) phosphorus compounds. Accumulation of storage forms (phytin) of phosphorus was higher in wheat and successively lower in rye and barley.

INTRODUCTION

Numerous authors (Asamov and Valizanov, 1971; Grze-siuk, 1967, 1971; Jennings and Morton, 1963; Kulka, 1966) report that phosphorus compounds start to accumulate rapidly in seeds at the initial stages of development.

As the seeds ripen, the total phosphorus content increases, it decreases, gradually, however, in relation to the seed weight and is lowest at full morphological maturity (Grzesiuk, 1967; Jennings and Morton 1963; Kulka, 1966; Kulka and Grzesiuk, 1965).

In forming seeds the inorganic-P content first increases and then decreases consistently. Towards the end of ontogenesis the inorganic phosphates level is usually low (Assamov and Valizanov, 1971; Bourdet and Feillet, 1967; Fink, 1963).

With the fall of the inorganic-P level, there occurs a rapid accumulation in the seeds of phytin phosphorus (Asanov and Valizanov, 1971; Grzesiuk, 1972; Prokofiev et al., 1967; Suvorov and Sobolev 1972). Phytin synthesis in seeds starts around the 15th day after pollination and lasts to the end of ripening (Grzesiuk, 1972; Prokofiev et al., 1967; Sobolev and Radionova, 1966; Williams, 1970).

Jennings and Morton (1963) noted a considerable decrease in acid-soluble P (nucleotides-P and saccharides-P), together with enhanced phytin deposition in the endosperm and seed integuments of ripening wheat grains. Precise analysis of the nucleotide dynamics in wheat grain revealed a 3-4-fold decrease in ATP, ADP, UDP and NAD contents from the 12th day to the end of maturation (Jenner, 1968).

Phospholipid content in whole ripening cereal seeds increases up to the middle of ontogenesis (Jennings and Morton, 1963; Kulka, 1966). In wheat endosperm the phospholipid level is slightly depressed from mid ripening (Jennings and Morton, 1963). In developing embryos the amount of phospholipids increases to the end of embryogenesis (Asanov and Valizanov, 1971; Kulka 1966).

The two types of nucleic acids — RNA and DNA were found to occur in large quantities in newly set seeds (Grzesiuk, 1971; Jennings and Morton, 1963; Kulka and Grzesiuk, 1965). The nucleic acids content in forming cereal seeds increases, reaching maximum at wax ripeness (Grzesiuk, 1967, 1971; Kulka, 1966). In wheat endosperm intensive DNA and RNA synthesis occurs beginning with the 14th day after pollination and continues to the stage of wax ripeness (Jennings and Morton, 1963). In older endosperm the nucleic acids level falls to values lower in this tissue than in the period of wax ripeness (Grzesiuk, 1967; Jennings and Morton, 1963; Kulka, 1966; Kulka and Grzesiuk, 1965).

The increase in nucleic acids content in seeds at middle ripening occurs mainly in the embryo (Kulka and Grzesiuk, 1965). It was demonstrated that synthesis of nucleic acids in the embryo lasts to the end of grain ripening (Grzesiuk, 1967, 1971; Kulka, 1966). ^{32}P in-

corporation both into RNA and DNA in barley embryos was found to occur to the end of full ripeness (Chang Chong, 1963).

As reported by Jennings and Morton (1963) the content of phosphorus bound with proteins in ripening wheat grains increases to the end of ontogenesis.

In dormant barley seeds the inorganic phosphorus and phospholipids content slightly diminishes, whereas the amount of phosphorus of the acid-soluble fraction remains unchanged (Kulka and Sobieraj, 1969).

The aim of the present investigations was:

1. to record the quantitative changes in phosphorus compounds in ripening wheat, barley and rye grain.
2. to compare the dynamics of phosphorus compounds in the above mentioned three cereal species during ripening.

MATERIAL AND METHODS

1. Material

The object of investigations consisted of grain of the 3 cereal species: winter wheat (Grana), spring barley (Kosmos) and winter rye (Pancerne). The grain was collected from plants cultivated in 1974 on plots (150 m²) of the Institute of Plant Biology, Agricultural University, Olsztyn. Fertilization over the entire vegetation period amounted to 60—N, 100—P and 120—K kg/ha.

Seeds for analysis were taken at the following periods of ontogenesis determined on the basis of ripening criteria (Grzesiuk, 1967):

- a) milk ripeness: 19-20 days after pollination,
- b) wax ripeness: 30-32 days after pollination,
- c) full morphological ripeness: 43-48 days after pollination.

Laboratory analyses at these dates were performed on freshly collected grain removed free-hand from the ears. Grain was taken from the middle of the ear in order to obtain possibly equal material as regards ripeness. Further analyses were carried out in the period of post-harvest seed dormant that is 30-35 days after the harvest.

2. Methods

a) Acid-soluble fraction

The phosphorus compounds of this fraction were extracted according to Konariiev (1967). The samples (100 grains) were ground in a mortar and pestle with cold 7 per cent trichloroacetic acid (TCA):

Extraction with TCA was repeated and then the samples were washed with ice-cold water. Each time the homogenized tissue was centrifuged at $5000\times g$ in the cold (further centrifugations were done under identical conditions). The supernatants were combined and fractionated to acid-soluble compounds.

Inorganic phosphorus and phytin were separated from the acid-soluble components by means of a magnesium-ammonium mixture (Bourdet and Feillet, 1967). The precipitate of magnesium-ammonium salt of both phosphates was sedimented by centrifugation and dissolved in 0.5 N HCl. Phytine sedimented in the form of a hardly soluble calcium salt (Bourdet and Feillet, 1967).

Phytine bound with proteins was isolated from the TCA extract by means of a 4 per cent sodium molybdate solution (Prokofiev et al., 1967).

Nucleotides adsorption at $0-2^{\circ}\text{C}$ on active carbon was run directly from the TCA extract (Kochetavkin, 1965; Konariiev, 1967). They were desorbed from the carbon by 3-fold treatment with a 1 per cent ammonia solution in 50 per cent ethanol.

Phosphate esters and their metabolites were isolated together with the nucleotides from the TCA extract from which inorganic phosphorus and phytin had been previously removed. The latter compounds were precipitated in the form of insoluble barium salts at pH 8.5 (Kochetavkin, 1965, Sobolev, 1971).

b) Phospholipid fraction

Phospholipids were extracted by the method of Konariiev (1967). The samples were treated with a mixture of ethyl ether and ethanol (1:1). The phospholipids were dissolved at 55°C on a water bath within 30 min. Extraction was repeated with a mixture of chloroform and methanol (1:1). The extracts were then combined and evaporated to dryness.

c) Nucleoproteid fraction

Nucleic acids were isolated by the method of Ogura and Rosen in Holden's modification (1952). The samples were treated with 1 N HClO_4 and kept at 4°C for 16 h with stirring from time to time. After centrifugating off the dissolved RNA the sample was washed with 1 N HClO_4 and the solutions were combined.

DNA was isolated by 2-fold treatment with 0.5 N HClO_4 at 70°C for 30 min. Proteid phosphorus isolated together with DNA in mineral

form was precipitated with a magnesium mixture as was done in the case of inorganic phosphorus.

All the separated organic phosphorus compounds were mineralized by digestion in a mixture of concentrated H_2SO_4 and 30 per cent HClO_4 (1:1) (Prokofiev et al., 1967). The inorganic phosphorus separated after hydrolysis was determined by the Fiske-Subbarov method (1925).

RESULTS

The phosphorus content increases consistently in the grain of 3 cereal species (Fig. 1). Total phosphorus increased most rapidly between milk and wax ripeness of the grain. In the period between milk and full ripeness the amount of total-P in the grains doubled.

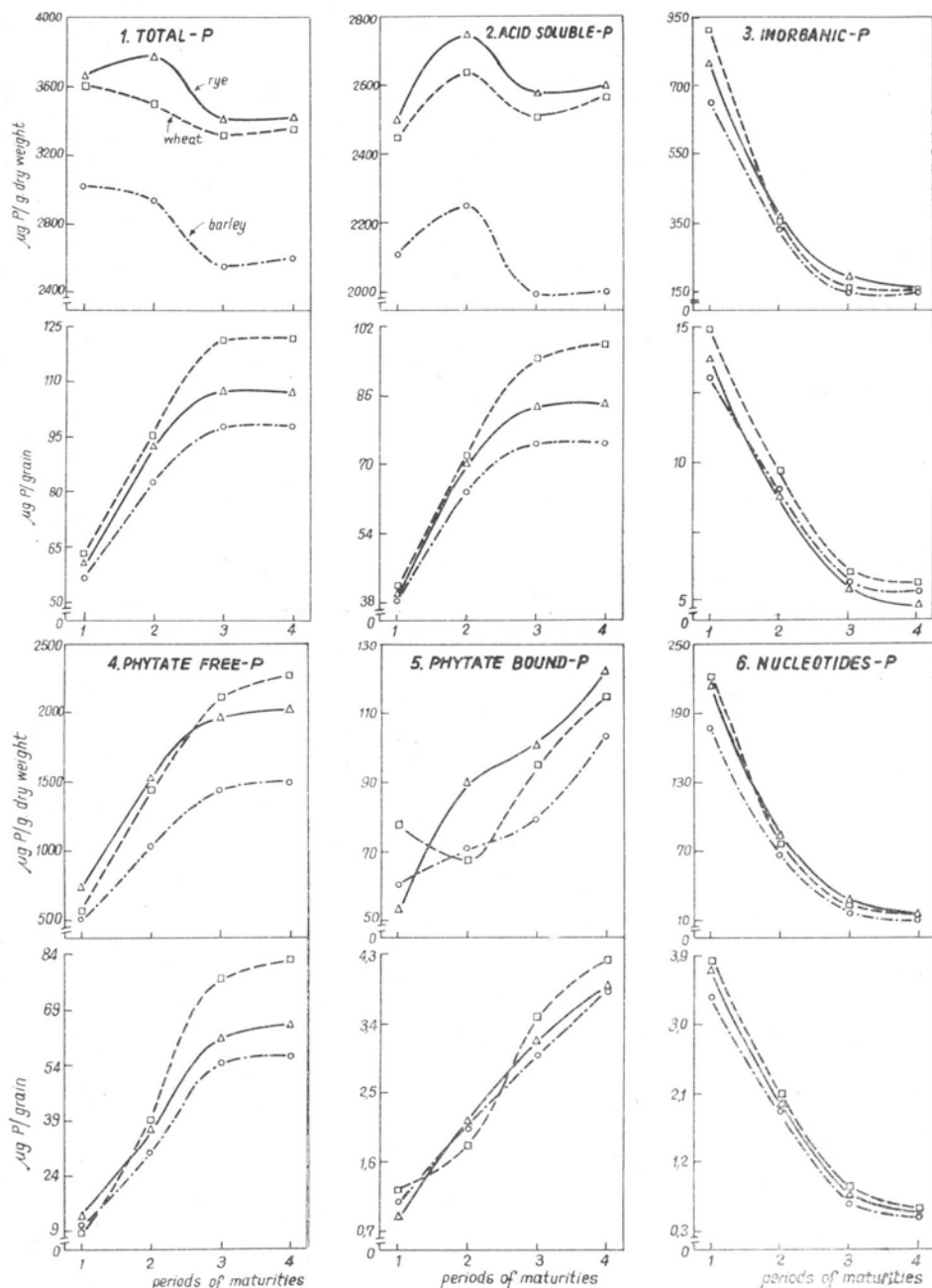
The dynamics of total-P in 1 g of dry weight of ripening grain showed a different course (Fig. 1). The relative content of phosphorus substances in the seeds remained at first at the same level and then decreased. Wheat grain showed the highest phosphorus content at ripening, it was lower in rye and lowest in barley.

During ontogenesis the acid-soluble-P level rose rapidly in the grain up to ripeness (Fig. 2). In the dormant period the content of this phosphorus in rye and barley grains remained unchanged. In wheat a further slight increase in the amount of this fraction was observed. The largest quantities of acid-soluble-P accumulated during ripening in wheat, less so in rye and markedly less in barley. The ratio of acid-soluble-P to dry weight of the grain increased in wheat, while it diminished in barley and rye.

The initial high inorganic P level decreased as the grain ripened (Fig. 3). Mineral-P content decreased on the average 3 times in the period from milk maturity to post-harvest rest. The inorganic P level also fell in relation to dry weight of the developing seeds (Fig. 3). The ripening cereal grains did not differ from one another in inorganic P content.

In ripening seeds a considerable increase of the amount of phytin-P was observed (Fig. 4). This phosphorus was rapidly stored up to full ripeness, and its amount still continued to increase slightly during the period of post-harvest dormant. The rise in phytin-P level during ontogenesis was noted even in relation to the increase in dry weight of the grain (Fig. 4). From among the seeds investigated, wheat exhibited the highest phytin-P values, next came rye and barley showed the lowest.

Paralelly with the increase in free phytin content in the grain, the level of phytin bound with proteins also rose (Fig. 5). The phosphorus content in protein-phytin complexes increased less when calculated to



Figs 1-6 Changes in total, acid-soluble, inorganic and phytin phosphorus (free and bound with protein) and nucleotide phosphorus in ripening wheat, barley and rye seeds:

1 — milk ripeness, 2 — wax ripeness, 3 — full ripeness, 4 — post-harvest dormant, data from 2-3 experiments

Triangles — rye; squares — wheat; circles — barley

Upper curves: P content per dry weight; lower curves: P content per grain

the dry weight of the seeds. During the entire period of ripening the barley and rye grain showed similar contents of phytin-protein complexes. More bound phytin was formed towards the end of ripening in wheat grain.

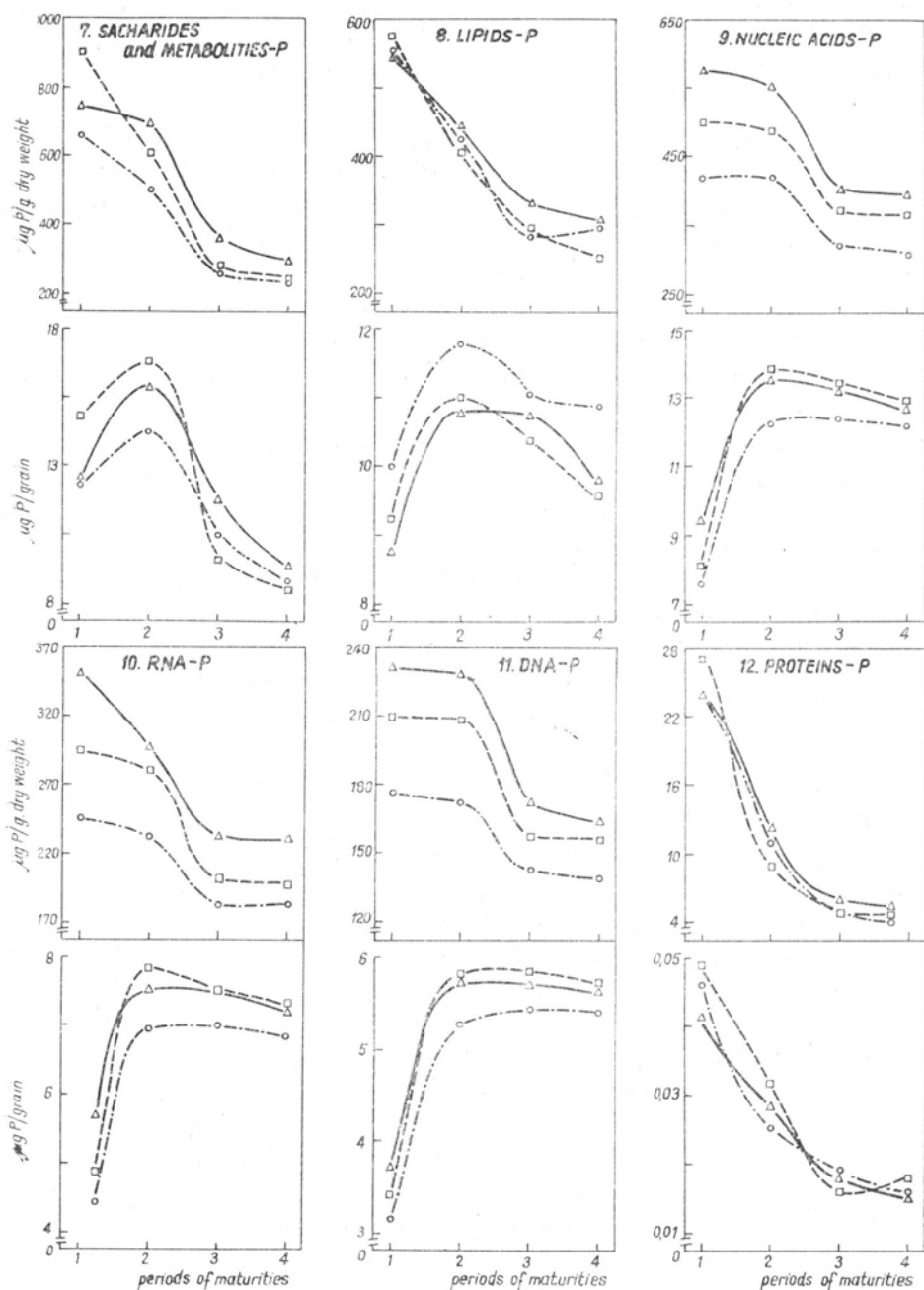
In maturing cereal seed nucleotides-P content fell rapidly (Fig. 6). The quickest fall of this P level occurred between milk and wax ripeness. In the period from milk ripeness to post-harvest dormant the nucleotides content decreased 7-8 times. A still more rapid fall of the nucleotides level was observed in reference to the dry weight content of the grains (Fig. 6). At the beginning of ripening the investigated cereal grains did not differ in nucleotides-P content. Towards the end of maturation barley seed contained somewhat less nucleotides than the remaining cereal species.

The ripening grain up to the stage of wax ripeness was characterized by a high saccharide phosphate esters and their metabolites content (Fig. 7). To the period of post-harvest dormant the content of phosphorus of these compounds diminished two times. Over the entire period of ontogenesis the content of phosphorylated saccharides decreased in relation to the dry weight of the seeds (Fig. 7). The studied cereal species differed only slightly in the saccharides-P and their derivatives level.

The amount of lipid phosphorus in ripening grain increased up to wax ripeness (Fig. 8). In further stages of ontogenesis the phospholipids content diminished. During post-harvest dormant they returned to the level of the milk ripeness stage. Phospholipids content in relation to dry mass of the ripening grain decreased (Fig. 8). The lipids-P level was higher in barley seeds than in wheat and rye.

In ripening seeds the content of nucleic acids-P rapidly increased to the stage of wax ripeness and then slightly diminished (Fig. 9). The dynamics of changes in RNA (Fig. 10) and DNA (Fig. 11) phosphorus ran a similar course in developing seeds. Over the entire period of ontogenesis the RNA content was higher than that of DNA but the ratio of RNA-P to DNA-P decreased on the average from 1.6 to 1.2. Calculated in reference to dry weight of the grain, the content of nucleic acids diminished consistently, but differently in the case of RNA and DNA (Figs 9, 10 and 11). From among the grains analysed, ripening wheat showed the highest nucleic acids content and barley the lowest.

During ripening the amount of phosphoproteids drastically decreased to the stage of wax ripeness and then remained at a constant level (Fig. 12). Over the entire period of ontogenesis the phosphoproteids content diminished on the average 4-5 times. Similar quantitative changes in protein-bound P occurred in relation to dry weight (Fig. 12). The studied cereal species showed no major differences in phosphorylated proteins content.



Figs 7-12 Changes in phosphorus of saccharides and their metabolites, lipids, nucleic acids, RNA, DNA and protein phosphorus in ripening wheat, barley and rye seeds (explanations as for Fig. 1-6), data from 2-3 experiments

DISCUSSION

The process of wheat, barley and rye grain ontogenesis is characterized by a definite orientation of the phosphorus transformations. As the seed ripens the total-P content consistently increases in the grain and its concentration in relation to the dry weight of the grain decreases. Phosphorus accumulation in the grain was more rapid in the early stage of ripening than in the end period. Similar relations in the phosphorus dynamics have been observed in ripening cotton seeds (Assamov and Valizanov, 1971), wheat (Jennings and Morton, 1963) and rye (Kulka 1966).

The quantitatively largest groups of phosphorus compounds in developing cereal grains consisted of the acid-soluble fraction. Its level amounted to 68-71 per cent of total-P at milk ripeness and 77-82 per cent at post-harvest dormant. The increase in acid-soluble-P content in the period of ontogenesis was reported in cotton seed by Asamov and Valizanov (1971) and in wheat grain by Jennings and Morton (1963).

At milk ripeness phytin-P was already present in large amounts (21-23% of total P). The observations of some authors (Jennings and Morton, 1963; Prokofiev et al., 1967, Sobolev and Radionova, 1966, Suvorov and Sobolev, 1972) demonstrated that synthesis of free and protein-bound phytin starts simultaneously on the 16-20th day after pollination and lasts to the end of maturation. A slight rise of the phytin-P level was noted in the present study even during post-harvest dormant. Phytin accumulated the major part of phosphorus in ripe grain: 62-67 per cent of total-P and 80-86 per cent of acid-soluble-P. The data concerning phytin content in ripe grain agree with those of other authors (Bourdet and Feillet, 1967; Fink 1963; Suvorov and Sobolev, 1972; Williams, 1970).

In the early period of grain formation inorganic-P was the basic component of the acid-soluble fraction (24-26% of total P). Towards the end of ripening the level of inorganic P was depressed in various seeds (Grzesiuk, 1967; Jennings and Morton, 1963; Kulka 1966).

The decrease in the nucleotides content in ripening grain observed in the present study was also reported by other investigators (Jenner, 1968; Prokofiev et al., 1967, Williams, 1970). A close connection between changes in nucleotides content and phytins synthesis was detected by Jennings and Morton (1963) and Williams (1970). The decrease in nucleotide content is also related with the synthesis of nucleic acids (Kulka and Grzesiuk, 1965) phospholipids (Grzesiuk, 1971) and starch (Jenner, 1968). The main cause of decrease in nucleotides concentration during ontogenesis would seem to be, however, inhibition of the respiration and oxidative phosphoryla-

tion processes — the main processes producing these substances in seeds (Tluczkiwicz, 1974).

The seeds at the stage of wax ripeness were characterized by a high level of saccharide phosphorus and its metabolites. The rise in the level of these compounds is due to the translocation of phosphosaccharides to the seeds from photosynthesizing tissues (Grzesiuk, 1972) and to the increased number of plastids functioning in the grain cells in the first half of the period of ripening (Grzesiuk et al., 1970). At this stage of development there also occur intensive respiratory processes in the grain (Grzesiuk, 1971; Tluczkiwicz, 1974) which supply phosphorylated metabolites. Depression of the phosphosaccharides content in cotton seeds after the first half of the period ripening has also been observed by Asamov and Valizanov (1971).

In the dynamics of lipids-P characteristic was its increase up to the stage of wax ripeness. Grzesiuk et al. (1970) demonstrated that, up to this development stage, the number of plastids and mitochondria increases in the grain and so does the phospholipids content in these organelles. The fall of the phospholipid level in the end stage of ontogenesis of rye grains was also observed by Kulka (1966) and Kulka and Rejowski (1970). Other investigations (Asamov and Valizanov, 1971; Jennings and Morton, 1963) report that the lipids-P level slightly increased to the end of seed ripening.

In the forming grains the content of nucleic acids-P and separately of RNA-P and DNA-P reached maximum at wax ripeness and then slightly decreased. Similar changes in nucleic acids dynamics in ripening seeds were noted by other authors (Asamov and Valizanov, 1971; Jennings and Morton, 1963; Kulka, 1966; Kulka and Grzesiuk, 1965). Over the entire ontogenesis period the contribution of nucleic acids-P to the total-P pool changed for RNA-P from 8-9 to 6-7 per cent and for DNA-P from 5-6 to 4-5 per cent. These data point to a relatively constant nucleic acids content in ripening grain cells. As shown by investigations on parts of forming caryopses, RNA and DNA synthesis occurs up to wax ripeness (Jennings and Morton, 1963; Kulka and Grzesiuk, 1965; Kulka 1966). On the other hand, in embryos RNA and DNA low-intensity production lasts to the end of maturation (Chang Chong, 1963; Kulka and Rejowski, 1970). The decrease in nucleic acids level towards the end of ripening may have been connected with their partial break-down in the endosperm by nucleases (Kulka, 1966).

As the grain ripens, the protein phosphorus level rapidly falls in them. In the studies of Jenninge and Morton (1963) the amount of phosphorus of these compounds in wheat grain increased during ripening. The difference in these results is probably due to the isola-

tion of phosphoproteids with different solvents. The sodium hydroxide solution used by the above named authors could additionally release phosphorus ester-bound with starch (Fink, 1963).

In view of the diverse metabolic functions of phosphorus compounds in seeds, further investigations in detail of their content during ripening will be useful for a better knowledge of the process of ontogenesis of seeds.

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Author's address:

*J. Tłuczkiwicz and W. Berendt
Institute of Plant Biology
Agricultural-Technical Academy
10-957 Olsztyn-Kortowo, Poland*

Dynamika związków fosforowych w dojrzewających i kielkujących ziarnach zbóż

Cz. I. Zmiany zawartości związków fosforowych podczas dojrzewania ziarna pszenicy, jęczmienia i żyta

Streszczenie

Analizowano dynamikę zmian związków fosforowych w ziarnach pszenicy (Grana), jęczmienia (Kosmos) i żyta (Pancerne) w etapach dojrzałości młeczej, woskowej, pełnej i spoczynku późniejszego. W dojrzewających ziarnach zbóż zwiększa się zawartość fosforu ogólnego i osiąga maksimum w dojrzałości pełnej. Najwyższe stężenie fosforu ogólnego mają ziarniaki pszenicy (Grana), nieco niższe żyta (Pancerne) i wyraźnie niższe jęczmienia (Kosmos). Zbliżoną do P-ogólnego dynamikę zmian wykazuje fosfor kwasorozpuszczalny. Do końca dojrzewania intensywnie odkładany jest fosfor fitynowy. Fosfor fityny stanowił 62-70% P-ogólnego i 80-86% P-kwasorozpuszczalnego. Do okresu spoczynku zwiększa się także w ziarnach ilość fityny związanej z białkami. Ze wzrostem wolnej i związanej fityny obniża się w dojrzewających ziarnach poziom fosforu nieorganicznego, nukleotydowego oraz estrów cukrowców i ich metabolitów od dojrzałości woskowej. Fosfor lipidów, RNA i DNA wzrasta w ziarnach do dojrzałości woskowej. Następnie poziom fosforu lipidów wyraźnie obniża się i nieco zmniejsza się ilość P-RNA i P-DNA. Ilość fosfoproteidów szybko spada na początku dojrzewania a dalej pozostaje na stałym poziomie. W miarę dojrzewania zawartość fosforu w przeliczeniu na suchą masę ziaren wzrasta u fityny wolnej i związanej z białkami, maleje natomiast u pozostałych związków. Dojrzewające ziarna pszenicy, jęczmienia i żyta mają zbliżoną dynamikę aktywnych metabolicznie (nukleotydów, estrów cukrowców i ich metabolitów), funkcjonalnych (RNA, DNA, fosfoproteidów) oraz strukturalnych (fosfolipidów) związków fosforowych. Zdolność odkładania zapasowych (fityna) form fosforu w procesie ontogenezy ma wyższą ziarno pszenicy, a odpowiednio niższą ziarno żyta i jęczmienia.