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# The dynamics of acid-soluble phosphorus compounds in the course of winter and spring wheat germination under various thermic conditions

## Part I. Fractionation of wheat germs extracts

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Abstract

Results of investigations are reported on the role of acid-soluble phosphorus compounds in the process of winter wheat vernalization. Fractionation of germ extracts by the precipitation method revealed the dynamics of phosphorylated glycolysis metabolites during germination. The variability curves for spring wheat germinated at 1.5° and 22° and for winter wheat at 1.5° had a similar course, only that for winter wheat germinated at 22° showed differences. It is concluded that glycolysis is essential in the process of vernalization.

## INTRODUCTION

Acid-soluble tissue extracts contain free nucleotides and physphorylated compounds of initial carbohydrate metabolism as well as phytin and inorganic phosphorus. In view of the key role played by free nucleotides ATP and ADP, in the coupling of enzymatic reactions in the organism and NAD and NADP in oxidation reactions, and by carbohydrates as essential substrates of synthesis and breakdown, acid-soluble phosphorus compounds are of high importance in the general cell metabolism.

Investigation of the dynamics of the biochemical changes occurring in the earliest phase of plant life is particularly interesting in connection with the bioinduction observed in nature (P a c z o s k i 1947) when the effect becomes manifest at a later phase of development.

Flowering of winter plants depending on thermoinduction was investigated in this Laboratory. The studies concerned mostly the differences in metabolism between the winter and spring wheat forms during germination at low vernalizing temperatures and higher ones excluding vernalization (Markowski, Madej 1962 a, 1962 b; Markowski, Myczkowski, Łebek, 1962; Markowski, Piskornik 1964; Markowski, Madej 1968; Markowski, Filek, Madej 1968; Myczkowski 1967; Wojtaszek 1964 a, 1964 b). In a series of such investigations Markowski *et al.* (Markowski, Madej 1962 a, 1962 b; Markowski, Madej 1968; Markowski, Filek, Madej 1968), analysed the most important groups of phosphorus compounds, without tackling the separation of acid-soluble fraction. The latter problem was undertaken in the present study. It was the more timely, since studies on acid-soluble phosphorus compounds in the process of vernalization published in the available literature deal only with the whole acid-soluble extract, and mostly do not confront the metabolism of these compounds with the process in the spring form. Finch and Carr (1956) in the search for a relationship between the nucleic acid content and vernalization and devernalization of the winter rye Petkus, determined additionally acid-soluble phosphorus; they did not, however, observe any influence of vernalization in the course of germination at low temperature. It results from the investigations of Stoletov et al. (1965) that the spring forms of wheat examined by them had a lower acid-soluble phosphorus content than the winter varieties. Proskuryakov and Strazhevskaya (1948) observed a temperature-dependent decrease in acid-soluble phosphorus content in winter wheat germs during vernalization at 0° and 2°C with a simultaneous increase of the inorganic phosphorus content at the lower vernalization temperature. Markowski and Madej (1962) demonstrated a greater dependence of the acid-soluble phosphorus content on germination temperature than on the variety used. Ponomareva (1957), investigating the dynamics of phosphorus compounds in early ontogenesis of spring wheat, observed a high content of labile compounds in the whole acid-soluble extract, she did not succeed, however, in detecting noticeable quantities in the fraction precipitated by mercury salts.

Therefore, the aim of the present study was to investigate the changes in the fractions of acid-soluble extracts, during germination of winter and spring wheat at low and higher temperatures. It was believed that the finding of eventual differences in metabolism might contribute to the detection of the unknown mechanism of flowering initiation.

## MATERIAL AND METHODS

Material. Winter and spring wheat varieties, differing widely in their thermic requirements as regards transition to the generative phase, were used in the experiments. The winter variety of awned wheat 'Ostka Złotokłosa' requires about 60 days of vernalization for coming into ear, when low temperatures during vegetation are excluded. The spring awned wheat 'Ostka Chłopicka', on the contrary, sown under these conditions passes to the generative phase without previous thermic induction. The seeds of both wheat forms were germinated in dark vernalization chambers at 1.5° for periods of 0, 14, 35, 49, 63, and 70 days, and parallelly, in thermostats at 22° for 20, 60, 72, 84, 96, and 103 h. The germination period at 22° was adjusted so that the germs would reach the same physiological age — determined in terms of dry weight produced (Markowski, Madej 1962) — as the plants in the above mentioned germination periods at low temperature. Before vernalization the seeds were soaked and pregerminated for 72 h at 10°, and before germination at higher temperature — for 20 h at 22°.

Extraction. One-gram germ samples were subjected to fourfold extraction with trichloroacetic acid (TCA), in the first, 10 per cent, and in the following ones, 5 per cent TCA being used. During extraction and in the course of fractionation, temperature was maintained at 0°. The material was found to contain 5 - 15 mg of phosphorus in 50 ml of the basic extract.

Fractionation. Acid-soluble phosphorus compounds were separated by the method of LePage-Umbreit (1948) based on the different solubility of barium salts of phosphorus compounds, and applied in the modification adapted to material containing starch. The extract was separated into three fractions: 1) barium-insoluble salts, 2) barium--soluble alcohol-insoluble salts, and 3) barium-soluble alcohol-soluble salts. This procedure allows to include into fraction I, adenosinedi- and -triphosphates, hexosediphosphate, phosphoglyceric acid, phytin and inorganic phosphorus, and in fraction II, hexose-6-phosphates, glucose-1-phosphate, phosphotrioses, phosphopyruvic acid, pentose phosphate, adenosinemonophosphate and finally to include in fraction III unidentified phosphorus compounds (Benson 1955; Samotus 1963).

In each experimental combination several or some dozen replications were performed in dependence on the kind of determination and repeatability of the results obtained. Phosphorus determination was carried out by the Fiske-Subbarov method in Müller's modification 1935: inorganic P was determined immediately after obtention of the fraction, total P after acid digestion, organic P was indirectly determined as the difference between total and inorganic P.

For determination of phytin P, 300-mg samples were separately extracted, and the content was determined after McCance-Widdowson (1968).

## RESULTS

The results of phosphorus determination in the germs of both varieties and at both germination temperatures are plotted in diagrams (Figs. 1 - 5).

The dynamics of acid-soluble phosphorus compounds was followed in the whole germ extract in the course of 0 to 63 days of seed germination at 1.5° and between the 20 and 96th hour of germination at 22°, and the following observations were made.

In both varieties and at both temperatures the amount of total and organic phosphorus calculated in terms of dry germ weight (Fig. 1, left side) decreased drastically with the progress of germination, while inorganic phosphorus showed only a slight increasing tendency. The trend of changes was different when observed in a single germ (Fig. 1, right side). The amount of total and inorganic P increased, whereas organic P showed a tendency to decrease. In this case the curve reached a maximum after 14 days or, respectively, 60 h of germination at higher temperature. Within this time the initial values usually were doubled; after reaching its peak, the phosphorus content gradually decreased so that towards the end of the experiment organic P content was as a rule lower than at the beginning of germination.

In the whole extract of acid-soluble phosphorus compounds the influence of the germination temperature was more pronounced than that of the variety; the curves of the winter and spring variety ran closer to each other than those for the two varieties at both experimental temperatures.

Phosphorus content in fraction I had a similar course as in the whole extract (Fig. 2), the dependence of P content on germination temperature being more pronounced than the influence of the variety.

Phytin phosphorus. During germination of both varieties at both temperatures a drastic and continuous decrease in the content of inositophosphoric acid salts was noted (Fig. 3). This change is in agreement with the commonly noted breakdown of this storage form of phosphorus during seed germination. In view, however, of the exaggerated results of analyses, the changes in phytin P are not recalculated to 1 germ. This is due to the unsatisfactory method of phytin P determination (Fink 1963).

The metabolism of the organic phosphorus compounds, in fraction II (Fig. 4) was similar in the case of spring wheat germinated at both the

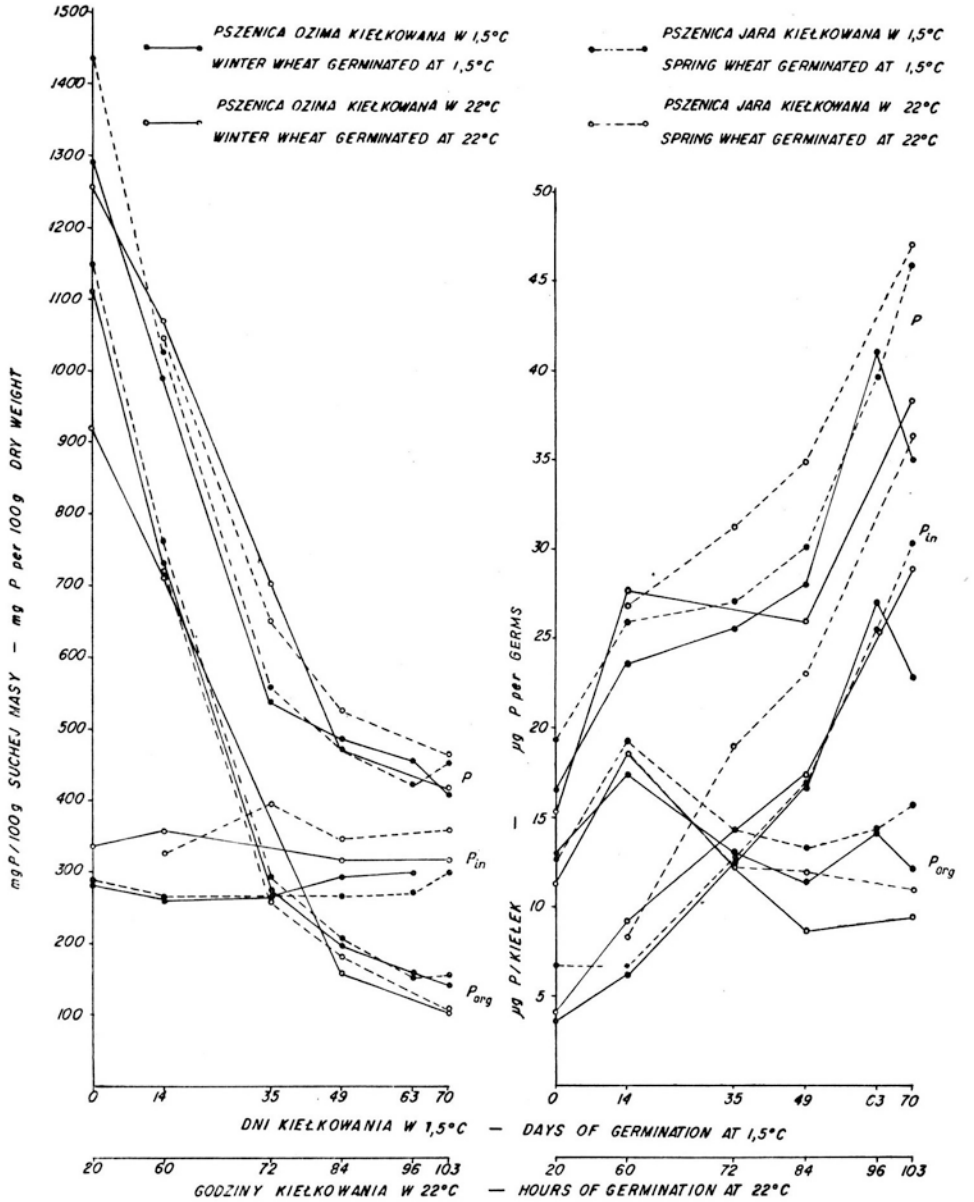


Fig. 1. Changes in total (P), organic ($P_{org}$) and inorganic ($P_{in}$) phosphorus content in whole extracts of winter, and spring wheat in the course of germination at 1.5° and 22°. Left side : P expressed as percentage of dry weight of germs; right side : P per 1 germ

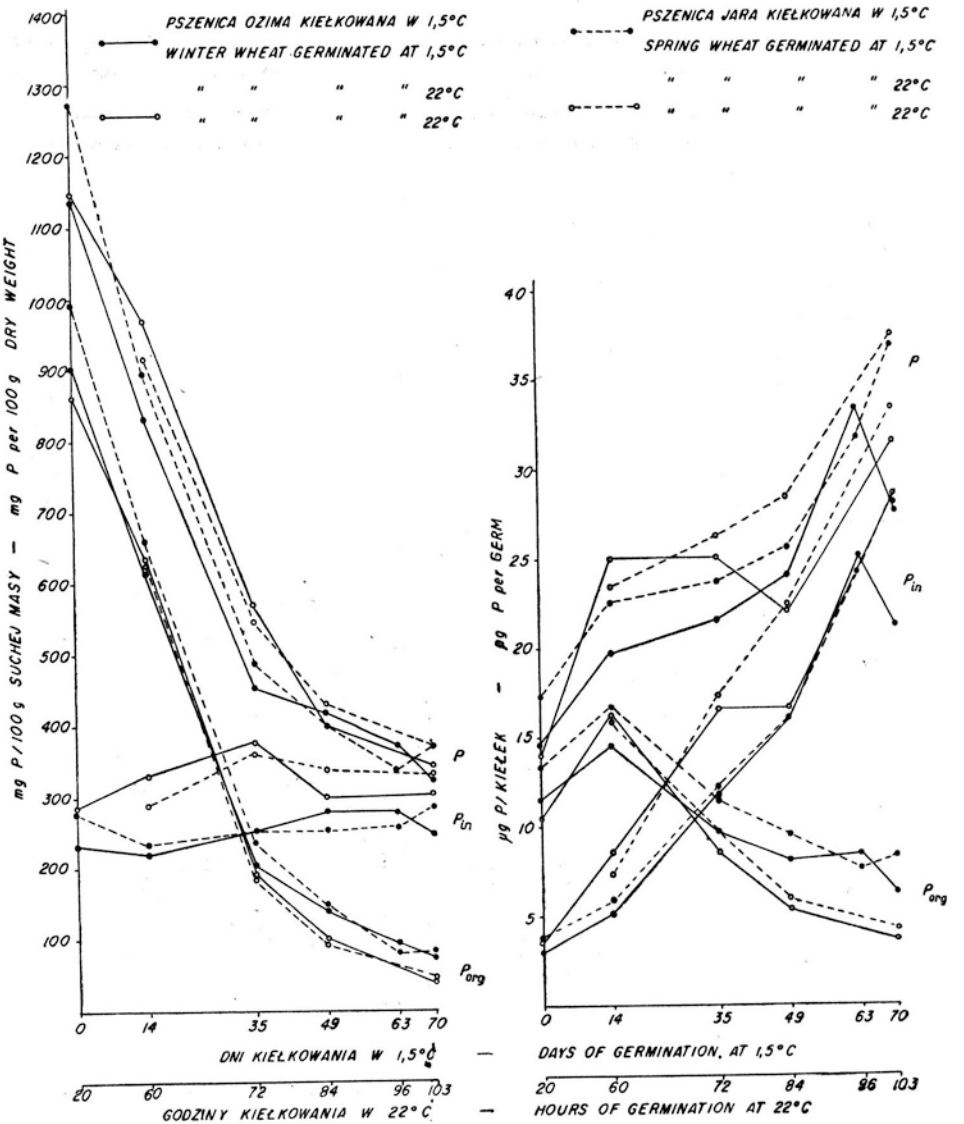


Fig. 2. Changes of phosphorus content in the barium-insoluble fraction of extracts from winter and spring wheat germs in the course of germination at 1.5° and 22°. For each experimental combination total (P), organic ($P_{org}$) and inorganic ($P_{in}$) phosphorus is given in dry weight of germs (left side) and per 1 germ (right side)

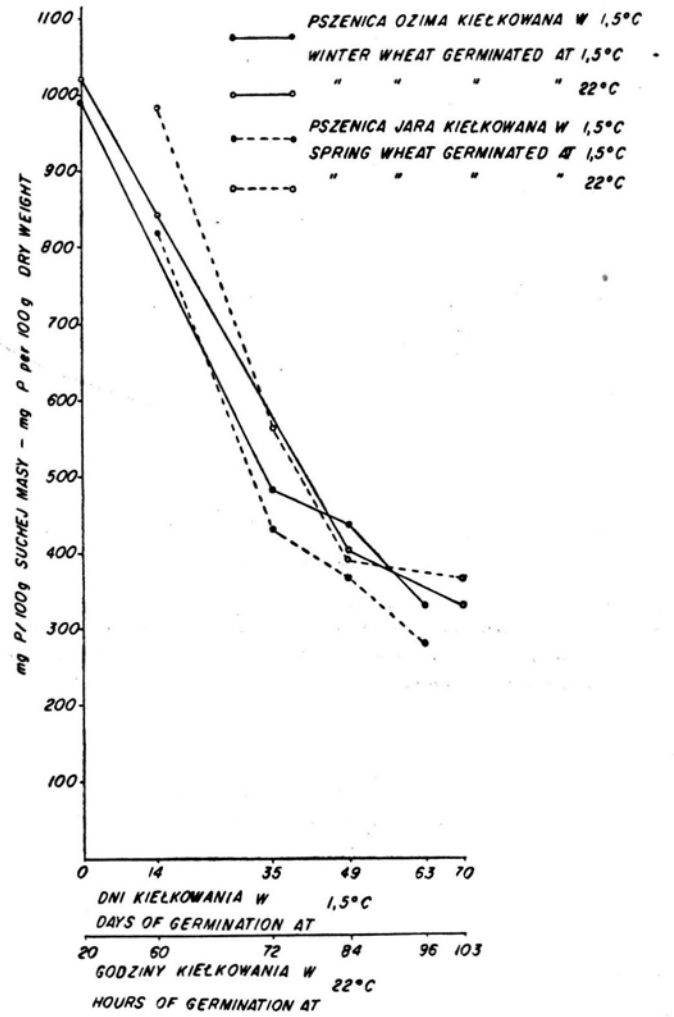


Fig. 3. Changes in content of phosphorus of phytic acid compounds in the course of germination of winter and spring wheat at 1.5° and 22°.

experimental temperatures and of winter wheat at 1.5°, it was only different for winter wheat at 22°. In the three above named combinations, marked changes were observed in the phosphorus content during germination. The maximum percentual P content in dry weight fell to the 60th hour of germination at 22° and the 14th day at 1.5°, thereafter a distinct fall occurred. Consequently, the content of phosphorus was only two times higher towards the end than at the beginning of germination. On the other hand, in the course of germination of the winter variety at 22°, the amount of phosphorus in relation to the dry weight

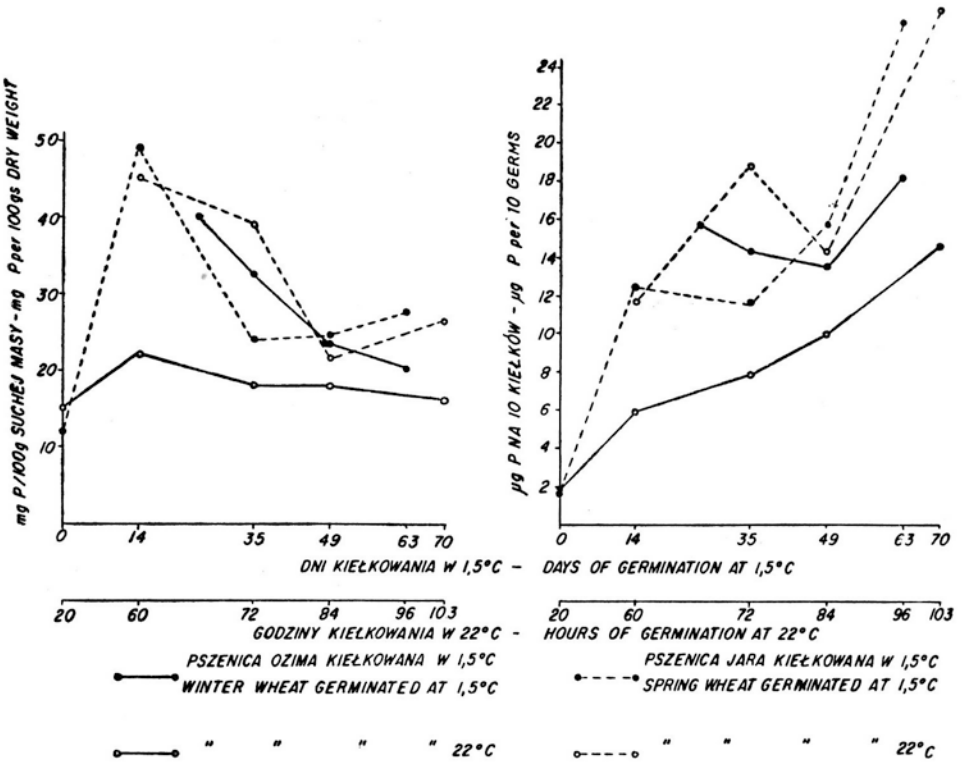


Fig. 4. Changes in phosphorus content of the barium-soluble, alcohol-insoluble fraction of extracts from winter and spring wheat germs in the course of germination at 1.5° and 22°.

of the germs remained unchanged — with the exception of a temporary slight increase after 60 h. When calculated to one germ, the phosphorus content increased in both the groups discussed, but in the above named three combinations it was almost twice higher towards the end of the period investigated than in the winter variety germinated at 22°.

Phosphorus of fraction III is shown in fig. 5. For a short period, during germination up to 14 days at 1.5° and up to 20 h at 22°, the proportion of phosphorus in the dry weight of the germs increased, and then it gradually fell. However, over the entire period investigated the phosphorus amount in this fraction increased. In relation to the constant number of germs, the amount of phosphorus increased drastically in the course of the entire period of germination. The course of phosphorus content in the form of barium-soluble alcohol-soluble salts is, therefore, similar to the phosphorus level variation in fraction II, but the differences between the results in the three combinations and those for winter wheat examined at higher temperature were less pronounced.

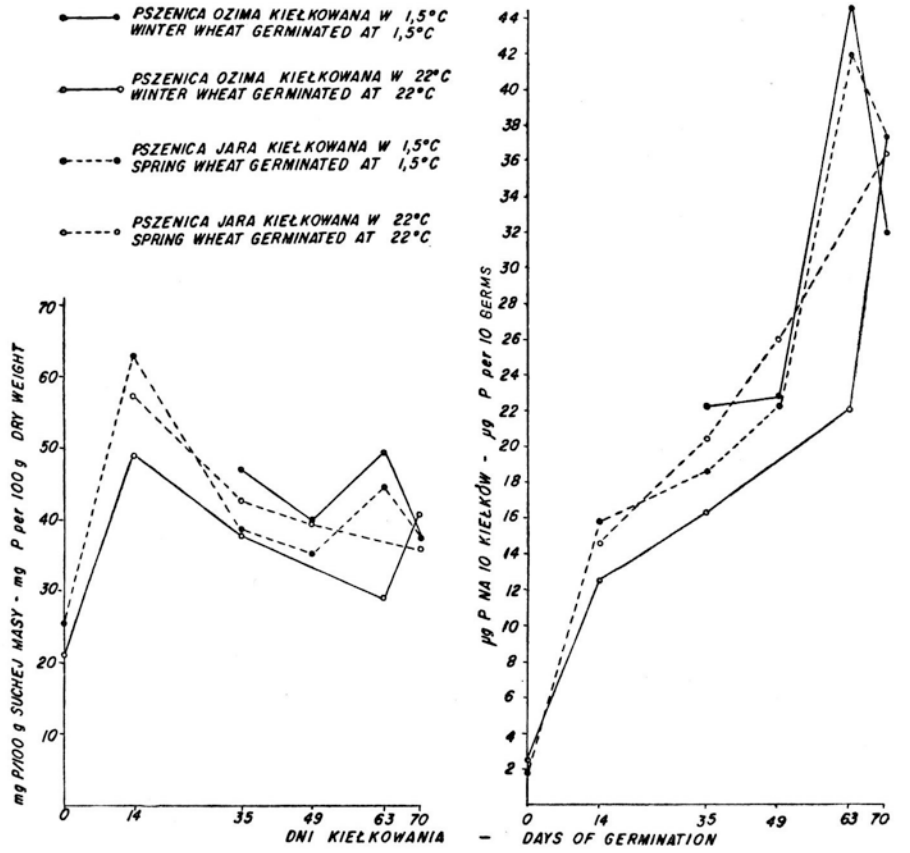


Fig. 5. Changes in phosphorus content of the barium-soluble, alcohol-soluble fraction of extracts from winter and spring wheat germs in the course of germination at 1.5° and 22°.

## DISCUSSION

The changes in phosphorus content in the whole acid-soluble extract and in its organic and inorganic compounds show a higher dependence on the germination temperature than on the variety. Similar results have been obtained by Markowski and Madej (1962 a, 1962 b).

In the course of wheat germination, both in the winter and in the spring forms, a drastic decrease of the organic acid-soluble phosphorus compounds content was observed in the germ extract at both temperatures tested (Fig. 1). The acid-soluble extract contains all the essential storage phosphorus in phytin as well as all the organic phosphorus of the tissues. It was, therefore, to be expected that the phytin breakdown observed (Fig. 3), responsible for the drastic fall

of the organic phosphorus level in the extract, would be associated with a corresponding rise of inorganic phosphorus content. However, since no such rise was noted, it is supposed that, in the process of wheat germination, inorganic phosphorus is not accumulated, but phosphorylation of organic compounds occurs simultaneously with abstraction of the phosphorus rests from inositol. The compounds thus formed seem, however, to be insoluble in acids. Similar relations were observed by Mihailovic (1965) in wheat and maize. On the other hand, Hall and Hodges (1966) found that in oats, the total phytin phosphorus appeared in the germs as inorganic phosphorus towards the end of germination. The investigations of Hiller (1967) confirm the different course of phytin breakdown in oats than in wheat and rye.

In fraction I precipitated by barium, similar variations in total and organic phosphorus were observed as in the whole extract. This results from the simple fact that phytin compounds and total inorganic phosphorus pass from the extract to this fraction. Since inositol salts constituted the major part of the organic compounds, and inorganic phosphorus occupied quite an important place, it is understandable that variations in the content of other organic phosphorus compounds present in this fraction in much smaller amounts did not find a reflection in the total and organic phosphorus content of this fraction.

The phosphorus in fraction II is contained in: glucose-6- and fructose-6-phosphate, trioses, phosphopyruvic acid, adenilic acid, pentose phosphate, NAD and NADP. Since inorganic and phytin phosphorus, constituting as already mentioned the main bulk of phosphorus compounds in the acid-soluble extract pass to fraction I, it was possible to follow the changes in other organic phosphorus compounds occurring in relatively small amounts and present in fraction II. This fraction included mainly phosphorylated metabolites of glycolysis and adenilic acid (LePage, Umbreit 1948). The similarity of the curves of phosphorus content in this fraction for the winter wheat variety at low temperature and the spring variety at both temperatures seems to indicate that in the winter variety glycolysis occurs under the influence of low temperature with an intensity similar to that found in the spring variety. On the other hand, the low phosphorus content in this fraction during germination of the winter variety at 22° seems to be evidence of a low degree of glycosis. These results lead to the conclusion that glycolysis must be an essential step in the process of vernalization of winter wheat seeds, which makes possible the further course of metabolism controlled by thermic induction. In the light of the well known increased respiration intensity under the influence of higher temperature, and on the basis of the investigations of Wojtaszek (1964) on oxygen uptake during germination of the wheat varieties 'Ostka

Złotokłosa' and 'Ostka Chłopicka', the above described results may be interpreted as follows. 1. The similar intensity of glycolysis in both varieties at low temperature and in spring wheat at higher temperature — in spite of the differences in oxygen uptake under the influence of temperature — seems to suggest that at low temperature, glycolysis metabolites are utilised more readily for other conversions than in the tricarboxylic acids cycle, and this would restrict the step of oxygen respiration. 2. The lower content of glucose metabolites in the winter variety during germination at higher, nonvernalizing temperature seems to indicate that the step of glycolysis is here substituted by oxidation on a different pathway than that of Embden Parnass. Direct determinations of glycolysis intensity confirm the conclusion of Wojtaszek, after investigation of the influence of respiratory inhibitors on the generative development of spring wheats, in which he stresses the role of glycolysis in the chemism of vernalization.

Glycolysis reduction may be the cause of the higher asparagine concentration found by Myczkowski (1967) in the course of winter wheat germination at higher temperature as compared with that in vernalized plants, and noted by Grzesiuk and Kulka (1963) under the same conditions in rye. It is, namely, to be expected as the consequence of decreased glycolysis that the amount of alphaketoacids necessary for amino acid synthesis will also decrease, this leading to an accumulation of amides. The different effect of temperature on the course of glycolysis in the two wheat varieties seems to support the conclusions of Myczkowski as to the higher enzymatic sensitivity of winter wheat to this factor.

It is to be expected that the difference in the course of the first phase of glucose oxidation in the winter variety germinated at low and higher temperatures will become manifest in the over-all carbohydrate metabolism in the vernalization process. The role of saccharides in the ontogenetic development of plants has been the subject of extensive investigations (Duperon 1956, Trione 1966). Their results cannot be directly compared with those here presented, but there is an essential agreement as regards the changes in saccharide content in dependence on the germination temperature, particularly towards the end of this process. It is probable that these difference occur owing to a different saccharide metabolism at the two temperatures applied, the dependence of glycolysis on germination temperature being a manifestation of this.

In fraction III containing unidentified phosphorus compounds, a decreasing tendency of the phosphorus values was noticed in the winter wheat variety germinated at 22° as compared with the three other combinations. This might indicate that the so far unidentified phosphorus

compounds present in this fraction have some influence on the induction of flowering in the winter forms of the plants. It is possible that their synthesis depends on the level of glycolysis metabolites and the content of ATP-type nucleotides (Barbaro, 1971).

The organic phosphorus content in the whole extract, in fractions I, II, and III shows interesting dynamics in the course of seed germination. For a short time after the beginning of germination an increase of phosphorus content in the germ is noticeable, then its maximum is reached and a gradual decrease occurs. A similar intensification of the enzymatic processes in the first few days of germination and their later decline are reported by authors investigating the metabolism of germination (Blaim 1965, Cherry 1963, Hanson 1960). Cherry (1963) on the basis of electron microscope microphotographs explains the observed peak of enzymatic activity by a progress in the organisation and structure of the endosperm mitochondria and their subsequent disappearance.

## SUMMARY AND CONCLUSIONS

The results of investigations on the dynamics of the acid-soluble compounds in the course of winter and spring wheat germination revealed the following relationships:

1. In the whole extract of acid-soluble phosphorus compounds, with progressing germination at the temperatures of 1,5° and 22°, both in winter and spring wheat, there occurs a drastic diminution of the total and organic phosphorus content as per cent of the germ dry weight. This results from the breakdown of phytin which was very intensive during germination. This decrease was not associated with a corresponding increase in inorganic phosphorus content.

2. The amount of phosphorus in the whole acid-soluble extract, both in the form of organic and inorganic compounds varied in the course of germination more under the influence of temperature than in dependence on the wheat variety.

3. In the fraction precipitated by barium salts (fraction I), the dynamics of the phosphorus compounds content was similar as in the whole acid-soluble extract. Parallelly performed phytin analysis seems to indicate that this was due to a high content of inositol salts in both the fractions, which masked the variation in other organic phosphorus compounds.

4. In the fraction of phosphorus compounds forming soluble barium salts precipitable with alcohol (fraction II) an interaction was revealed between germination temperature and variety. The curves of phosphorus content had a similar course for the spring variety at both temperatures

and for the winter variety at temperture of vernalization. Differences were, however, noted in the case of the winter variety germinated at 22°. In the latter case, contrary to the three other ones, the phosphorus content calculated to the germ dry weight did not increase in the course of germination.

5. On the assumption resulting from the analytical procedure that the main bulk of fraction II consists of phosphorylated glycolysis metabolites, it may be considered that in the winter variety the metabolism of carbohydrate oxidation becomes similar under the effect of low temperature to the type characteristic for the spring variety. It has been attempted to explain these relations against the widely known enhancement of respiration intensity under the influence of higher temperature.

The results here obtained give support to the opinion that glycolysis is an essential step in the process of vernalization of the winter wheat variety 'Ostka Złotokłosa', making possible a further course of metabolism associated with thermic inductions.

6. The interaction between temperature and variety, similar as in fraction II, but somewhat less pronounced was observed in fraction III containing unidentified phosphorus compounds. The author cannot exclude the possibility that these unidentified compounds may play some role in the induction of flowering of the winter and spring wheat varieties. It is possible that their synthesis may depend on the course of glycolysis and on the ADP and ATP nucleotides level. Investigations on the variability of labile phosphorus compounds will be reported in part II of the present paper (Barbaro, 1971).

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## Dynamika kwasorozpuszczalnych związków fosforowych w czasie kiełkowania pszenicy ozimej i jarej w różnych warunkach termicznych Cz. I. Frakcjonowanie ekstraktów kiełków

Streszczenie

Autor przedstawił badania nad udziałem kwasorozpuszczalnych połączeń fosforowych w procesie jaryzacji pszenicy ozimej. Rozfrakcjonowanie ekstraktów metodą precypitacji soli barowych wg LePage-Umbreita (1948) pozwoliło na prześledzenie dynamiki ufosforylowanych metabolitów glikolizy w czasie kiełkowania pszenic. Analizy prowadzono w ekstraktach kiełków pszenicy ozimej i jarej kiełkowanych w ciemności przez okres 0, 14, 35, 49, 63 i 70 dni w temperaturze 1,5°C oraz równolegle przez 20, 60, 72, 84, 96 i 103 godziny w temperaturze 22°C. Ekstrakty rozdzielano na trzy frakcje a to: pierwszą zawierającą nierozpuszczalne sole barowe (frakcja I), drugą zawierającą sole barowe strącalne alkoholem (frakcja II) oraz trzecią — rozpuszczalnych soli barowych niestrącalnych alkoholem etylowym. We frakcjach oznaczano fosfor nieorganiczny i całkowity metodą Fiske-Subarowa wg modyfikacji Müllera; fosfor organiczny określano pośrednio jako różnicę całkowitego i nieorganicznego.

Uzyskane wyniki badań pozwalają wyłonić następujące zależności:

1. W pełnym ekstrakcie kwasorozpuszczalnym obserwowano w miarę postępu kiełkowania w obu temperaturach, 1,5 i 22°C, tak u pszenicy ozimej jak i jarej, gwałtowne zmniejszanie się procentowej zawartości fosforu całkowitego i organicznego w suchej masie kiełków. Wynikało ono z rozpadu fityny silnie przebiegającego w czasie kiełkowania. Obniżeniu temu nie towarzyszył odpowiedni wzrost fosforu nieorganicznego.

2. Ilość fosforu pełnego ekstraktu kwasorozpuszczalnego, tak jego połączeń organicznych jak i nieorganicznych, zmieniała się w czasie kiełkowania pszenicy w większej zależności od temperatury kiełkowania niż od badanych form pszenicy.

3. We frakcji strącalnej solami baru (frakcja I) dynamika zmian ilości związków fosforowych była podobna jak w pełnym ekstrakcie kwasorozpuszczalnym. Na podstawie wykonanych równolegle analiz fityny można sądzić, że przyczyną

tego była duża zawartość soli inozytolu w obu frakcjach, przykrywająca zmienność innych połączeń organicznych fosforu.

4. We frakcji połączeń fosforu tworzących rozpuszczalne sole baru strącalne alkoholem (frakcja II) stwierdzono współdziałanie między temperaturą a odmianą. Krzywe zmienności zawartości fosforu tej frakcji miały przebieg podobny u odmiany jarej w obu temperaturach i ozimej w temperaturze jaryzującej; natomiast odmienny u odmiany ozimej w temperaturze 22°C. U tej ostatniej, odwrotnie niż u trzech pozostałych obiektów nie obserwowano w czasie kiełkowania zwiększania się zawartości fosforu w przeliczeniu na suchą masę kiełków.

5. W oparciu o założenie — zgodnie z postępowaniem analitycznym — że główną masę frakcji II stanowią ufosforylowane metabolity glikolizy, można uważać, że u odmiany ozimej pod działaniem niskich temperatur metabolizm utleniania cukrów zbliżył się na etapie glikolizy do typu charakteryzującego odmianę jarą. Natomiast wyższa temperatura kiełkowania nie sprzyjała glikolizie u odmiany ozimej. W pracy przedstawiono próbę wyjaśnienia tych zależności na tle ogólnie znanego zwiększania intensywności oddychania pod wpływem podwyższonej temperatury.

Wyniki pozwalają sądzić, że glikoliza jest bardzo istotnym etapem w procesie jaryzacji pszenicy ozimej odmiany 'Ostka Złotokłosa', umożliwiającym dalszy bieg metabolizmu związanego z indukcją termiczną.

6. Podobne jak we frakcji II, jednak nieco mniej wyraźne współdziałanie między temperaturą i odmianą obserwowano również we frakcji III zawierającej nie oznaczone dotąd związki fosforowe. Autorka nie wyklucza możliwości, że te nie zidentyfikowane połączenia fosforu mogą mieć znaczenie w indukcji kwitnienia form ozimych i jarych pszenicy. Przypuszcza się, że ich synteza zależy, być może, od przebiegu glikolizy i osiągniętego poziomu zawartości nukleotydów ADP, ATP. Badania nad zmiennością labilnych połączeń fosforowych zostaną omówione w II części pracy nad dynamiką kwasorozpuszczalnych związków (Barbaro 1971).