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Chloroplast Lipoquinones in Ontogenesis of Winter Wheat

Lipochinony chloroplastowe w ontogenezie pszenicy ozimej

Пластидовые липохиноны в онтогенезе озимой пшеницы

INTRODUCTION

Chloroplast lipoquinones comprise three groups of compounds: plastoquinones (PQA and its homologues PQB, PQC and PQD), tocopherol-quinones (α -T and α -TQ) and naphtoquinone (vit. K₁).

The synthesis of these compounds takes place with the simultaneous formation of the interior structure of chloroplasts (28, 37, 42, 43, 48). From the studies carried out in recent years by Bishop (13), Krogmann and Oliviero (29), Trebst (47), Crane and Henninger (20) it is known that plastoquinones participate in photosynthetic electron transport. There is, however, no evidence to indicate if the accumulation of plastoquinones in leaves, occurring in much higher quantities than might appear from the role attributed to them so far, is connected with some other processes. This can be concluded from the data concerning the function of α -T in plant development (6, 7, 10, 15, 36, 39, 40, 41), the structure of which — particularly its oxidized form α -TQ — approximates the structure of plastoquinones. Therefore, a comparison of the distribution of plastoquinones in the ontogenesis of winter-wheat, subdued to the effect of low temperature and control growing under noninduced conditions, might render some initial information as to the role of plastoquinones in plant development. The role of plastoquinones in the developmental processes is not known at present. Fragmentary studies of Bucke and Hallaway (16), Tendille et al. (45), Barr and Crane (5), reported the appearance of the particular

homologues PQs in various stages of plant development, but they do not allow more general conclusions.

In this paper, then, it was decided:

- 1) to study the dynamics of lipoquinones in the ontogenesis of winter wheat;
- 2) to examine the distribution of the above compounds in single leaves in definite growth stages;
- 3) to determine the composition and amount of lipoquinones in the wheat seed during its maturing.

MATERIAL AND METHODS

The material used in the studies consisted of kernels of winter wheat of the Dańkowska white variety which came from the Plant Breeding Station in Dańków. Wheat seeds were vernalized according to Lewicki's technique (30) for 60 days. After this period, the kernels were sown in experimental plants. At the same time non-vernalized wheat was sown. The material for the analyses from the vernalized plants was taken in the particular phenological stages according to Rudenko (quot. 35). They involved leaves, stems, spikes and kernels. The above-ground portions of non-vernalized wheat were examined every 15 days from the beginning of tillering, because — except for the first phenological stages, i.e., shoots, the stage of the third leaf and tillering — no other stages could be distinguished in its growth. In both experimental series (vernalized and non-vernalized wheat) a medium sample of all leaves present on the stalk was taken for analyses. From the beginning of the shoot stage (stem-formation) (vernalized wheat) the individual leaves were also analyzed. Plastoquinones were analyzed according to Lichtenthaler's method (33). The content of plastoquinones was spectrophotometrically measured on the basis of difference in extinction between the oxidized and reduced form, with the use of KBH_4 . Extinction-measurements were carried out at a wavelength of 225 nm, $E_{1\text{ cm}}^{1\%} = 198$ for PQS (19), for α -TQ at a wavelength of 262 nm, $E_{1\text{ cm}}^{1\%} = 397$ (21). α -T and PQA H_2 were identified from the reaction of Emmerie and Engel (23). The content of PQA H_2 was calculated assuming $E_{1\text{ cm}}^{1\%} = 225$ whereas α -T was calculated according to the formula of Green (24), assuming $E_{1\text{ cm}}^{1\%} = 98$. Vit. K_1 was determined according to the method of Lichtenthaler and Tevini (31). Chlorophyll was determined by the Hager's and Bertenrath's method (27). The results obtained are presented in $\mu\text{g/g}$ of the dry matter or of the whole plant, or in $\mu\text{M/mg}$ of chlorophyll.

The studies were carried out in 1970 and 1971. In the 1970—1971 experiments a great coincidence was found in the course of dynamics of the compounds studied. The data presented in this paper concern 1971.

RESULTS

1. THE DYNAMICS OF LIPOQUINONES IN THE ONTOGENESIS OF VERNALIZED AND NON-VERNALIZED WHEAT

The content of benzoquinones (PQA, α -TQ and their reduced forms PQA H_2 , α -T) and naphthoquinone vit. K_1 — in terms of the chlorophyll

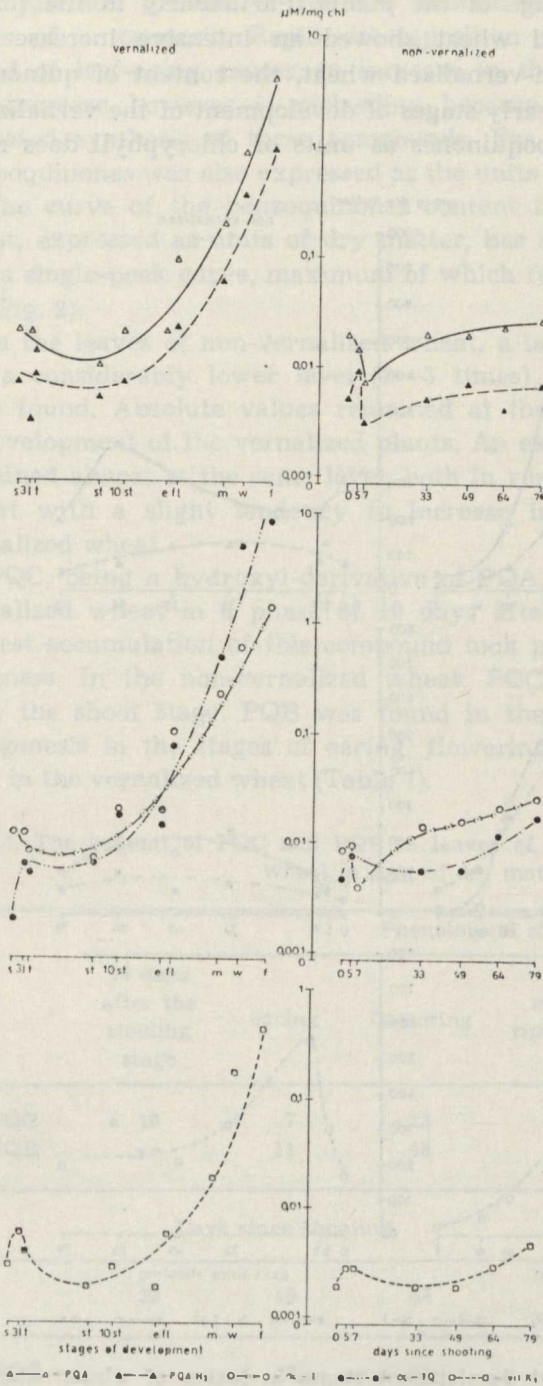


Fig. 1. Plastiquinones in different development stages in leaves of winter wheat in $\mu\text{M}/\text{mg}$ chlorophyll: s — shooting, 3l. — third leaf stage, t — tillering, st — stooling stage, 10st — 10 days after the stooling stage, e — earing, fl — flowering, m — milk ripeness, w — wax ripeness, f — full ripeness

unit — increased with the age of the plants. Particularly in the final stages of growth, vernalized wheat showed an intensive increase in quinones (Fig. 1). In the non-vernalized wheat, the content of quinones remained at the level of the early stages of development of the vernalized wheat. The expression of lipoquinones as units of chloryphyll does not

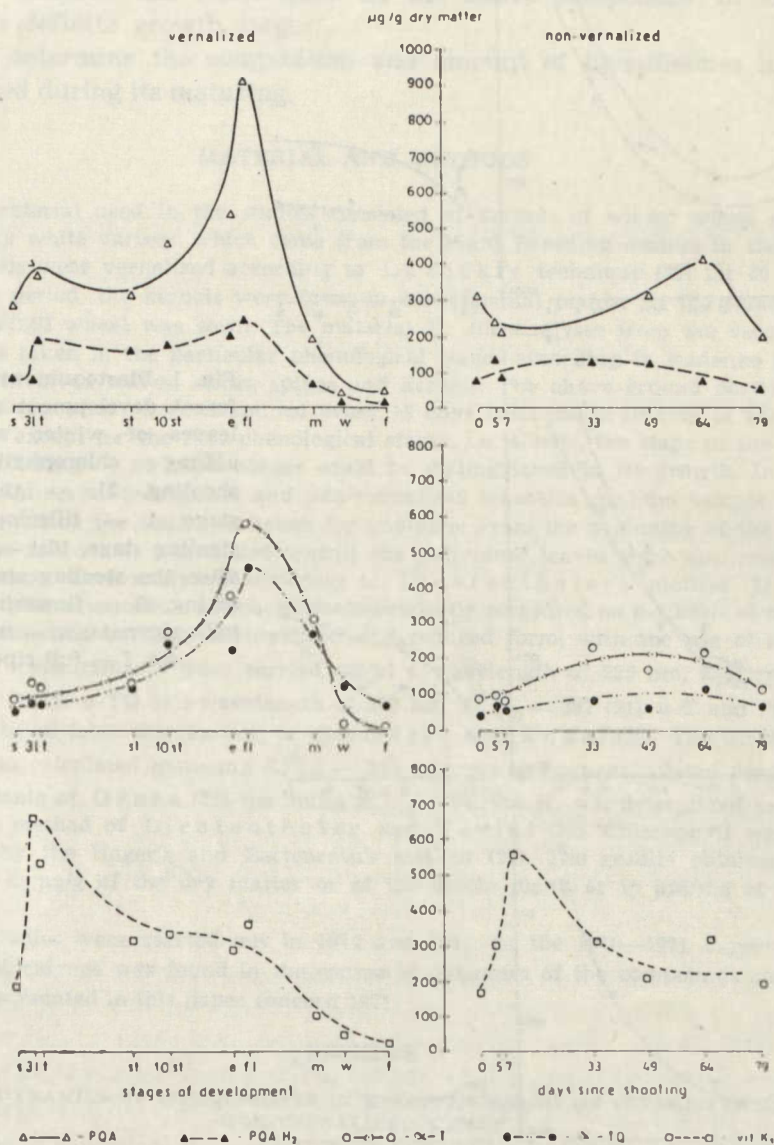


Fig. 2. Plastoquinones in different development stages in leaves of winter wheat in $\mu\text{g/g}$ dry matter; explanations as in Fig. 1

seem justified because of the low content of chlorophyll in the final stages of ontogenesis. Rapid decomposition of chlorophyll during the period of leaf-aging causes an increase in the content of lipoquinones. This increase, however, is misleading, because it does not result from an increased synthesis of these compounds. For this reason, the dynamics of lipoquinones was also expressed as the units of dry matter.

The curve of the benzoquinones content in the leaves of vernalized wheat, expressed as units of dry matter, has a quite different character. It is a single-peak curve, maximum of which fell on the period of flowering (Fig. 2).

In the leaves of non-vernalized wheat, a lack of a distinct maximum, and a considerably lower level (2—3 times) of the compounds studied were found. Absolute values remained at the level of the early stages of development of the vernalized plants. An exception was PQAH₂, which remained almost at the same level, both in vernalized and non-vernalized wheat with a slight tendency to increase in the flowering period of vernalized wheat.

PQC, being a hydroxyl-derivative of PQA, appeared in the leaves of vernalized wheat in a phase of 10 days after stem formation, and the highest accumulation of this compound took place in the period of milk-ripeness. In the non-vernalized wheat, PQC appeared within 49 days after the shoot stage. PQB was found in the leaves by the end of the ontogenesis in the stages of earing, flowering and milk ripeness — but only in the vernalized wheat (Table 1).

Tab. 1. The content of PQC and PQB in leaves of vernalized, and non-vernalized wheat in $\mu\text{g/g}$ of dry matter

	Phenological stages					
	10 days after the stooling stage	earing	flowering	milk ripeness	wax ripeness	full ripeness
PQC	19	7	13	28	8	4
PQB	—	11	48	13	—	—
	Days since shooting					
	33	49	64	79		
PQC	—	22	31	18		

The amount of naphthoquinone vit. K₁ was found to decrease steadily up to the end of the studies, after a rapid increase in the first stages of development (falling in leaves of vernalized plants in the stage of the third leaf, and in non-vernalized — in the stage of tillering). No distinct accumulation was observed in the period of plant flowering. The content of vit. K₁ in both experimental combinations was similar, and about 10 times lower, than that of benzoquinones (Fig. 2). In order to determine whether the synthesis of lipoquinones took place during the entire ontogenesis, the general condition of these compounds in the whole plant is presented, taking not only the leaves into consideration, but the stem, ears and seeds as well (Fig. 3).

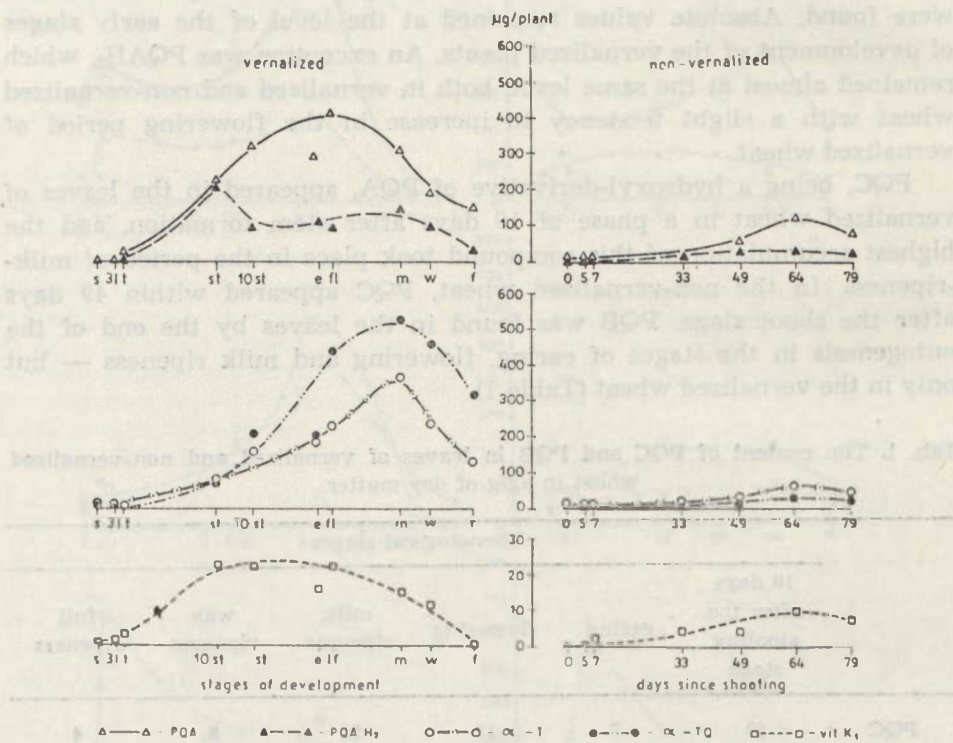


Fig. 3. Plastoquinones in different development stages of winter wheat in μg per plant; explanations as in Fig. 1

The curves for vernalized wheat are similar to those concerning the dynamics of the compounds studied in the unit of dry matter. The level of lipoquinones was not observed to increase by the end of vegetation. Only the maximum of α -T and α -TQ was shifted to the stage of milk ripeness. It can thus be assumed that the synthesis of lipoquinones does

not take place by the end of plant vegetation. In non-vernalized plants, the level of the compounds studied was exceptionally low, due to the development having been inhibited in the initial phase of ontogenesis.

Variations in the content of plastoquinones in relation to the age of the leaf can be most easily observed in the individual leaves. Upon development, the lower leaves die off and those located higher and higher reach their maximum growth. The curves illustrating the content of the plastoquinones studied for one unit of chlorophyll in the third and fifth leaves are substantially similar to those concerning plastoquinones analogically expressed (per chlorophyll unit) of all quantities taken as whole (Figs. 4, 5, cf. Fig. 1).

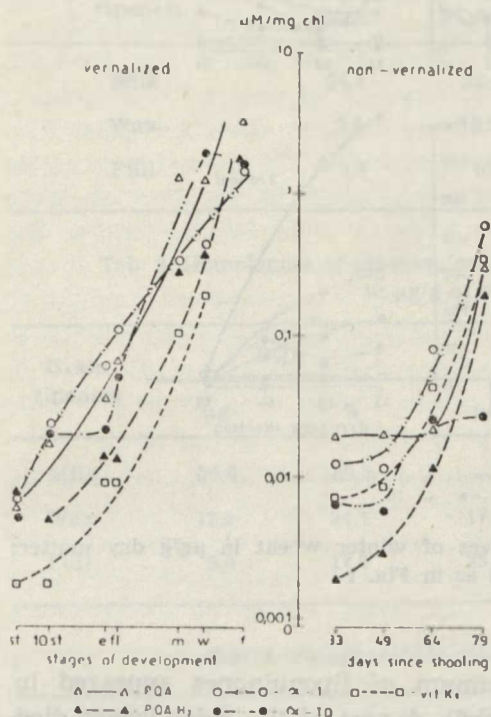


Fig. 4. Lipoquinones in 3rd leaf of winter wheat in $\mu\text{M}/\text{mg}$ chlorophyll; explanations as in Fig. 1

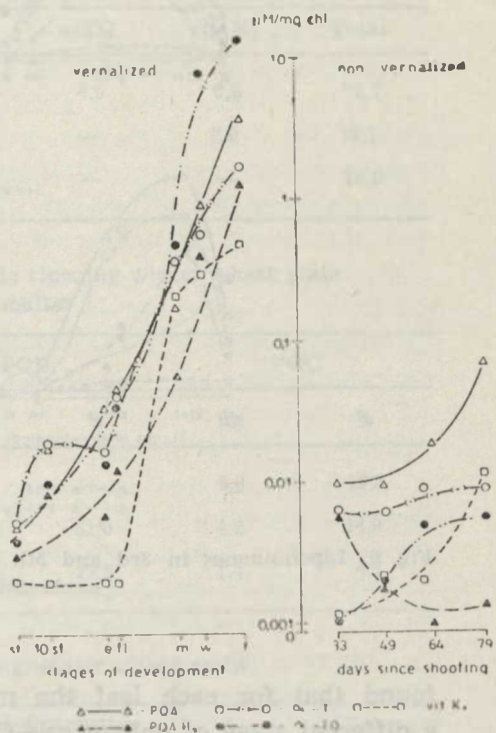


Fig. 5. Lipoquinones in 5th leaf of winter wheat in $\mu\text{M}/\text{mg}$ chlorophyll; explanations as in Fig. 1

It was found that with the age of the leaf the level of all plastoquinones studied increased per chlorophyll unit. It should be stressed that the content of the compounds studied was higher in all leaves of vernalized wheat. Expressing the data in terms of dry-matter units, it was

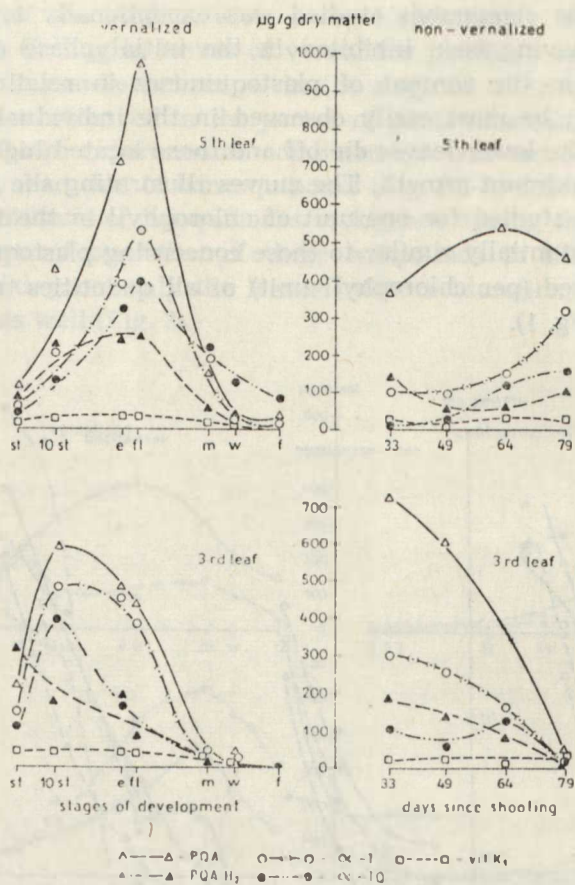


Fig. 6. Lipoquinones in 3rd and 5th leaves of winter wheat in $\mu\text{g/g}$ dry matter; explanations as in Fig. 1

found that for each leaf the maximum of lipoquinones appeared in a different stage of ontogenesis (Fig. 6). A part of the older leaves died off before the plant reached full development. For example, the second leaf reached the highest level of PQA in the stoling stage, the 4th, 5th and 6th leaves — in the flowering period, and the values were 780, 974 and 666 $\mu\text{g/g}$ of dry matter, respectively. Older leaves reached the maximum of PQA in the early stages of plant development, younger ones did so later. These variations were similar for the benzoquinones left. It should be noticed that in the leaves of non-vernalized wheat, no distinct uniform maximum of the content of plastoquinones was observed.

2. LIPOQUINONES IN THE PROCESS OF SEED-RIPENING

In the ripening seed, all quinones which appeared in leaves, were represented. Their amount rapidly decreased with ripening. α -TQ already disappeared in the stage of wax-ripeness of the seed, and vit. K₁ did so in full ripeness (Table 2). Detailed studies of the homologues of plastoquinones in the ripening seed made it possible to observe a decrease not only in the content of PQA, but of PQC as well, the amount of which was about 3—4 times smaller than that of PQA. In the stage of wax-

Tab. 2. Lipoquinones in ripening grain of winter wheat

Grain ripeness	$\mu\text{g/g}$ dry matter				
	PQA	PQAH ₂	α -TQ	vit. K ₁	Total
Milk	24,3	38,4	4,0	6,0	72,7
Wax	5,6	10,5	—	2,0	18,1
Full	3,2	6,8	—	—	10,0

Tab. 3. Homologues of plastoquinones in ripening winter wheat grain in $\mu\text{g/g}$ of dry matter

Grain ripeness	PQA		PQB		PQC	
	μg	%	μg	%	μg	%
Milk	24,0	80,5	—	—	5,8	19,5
Wax	12,9	34,1	17,8	51,0	4,2	14,9
Full	5,0	17,8	23,2	77,5	1,4	4,7

Tab. 4. Tocopherols in ripening winter wheat grain

Grain ripeness	$\mu\text{g/g}$ of dry matter									
	α -T		β -T		α_3 -T		β_3 -T		Total	
	μg	%	μg	%	μg	%	μg	%		
Milk	15,8	29,0	12,9	23,7	7,6	14,0	18,1	33,0	54,4	
Wax	17,4	30,1	10,8	18,7	4,4	7,6	25,2	43,6	57,8	
Full	16,4	22,0	16,1	21,6	7,3	9,8	34,6	46,4	74,4	

-ripening PQB appeared the amount of which was still higher in full ripeness (Table 3).

The dynamics of tocopherols in the ripening wheat seed were similar to that found in other cereal crops (Table 4). The total increase in the total of tocopherols during seed-ripening was accompanied by a decrease in the participation of trimethyl-derivatives and by increase of dimethyl-derivatives. This image corresponds to the previous belief that the demethylation of α -T appears with seed-ripening.

DISCUSSION

This paper deals with the fate of lipoquinones in ontogenesis of winter wheat. It is known from the papers of Lichtenthaler (34) and Rojek (38) that, parallel to the development of thylakoids and the synthesis of chlorophyll in chloroplast appear lipoquinones, reaching a high level only after several hours of the illumination of the etiolated leaves. Further synthesis of these compounds has not been closely studied. The influence of the age and development of plants on the level of isoprenolic phytoquinones and chromanols was studied by several investigators, however, the results of these studies are difficult to be interpreted for the following reasons:

- 1) the results of the studies are expressed in incomparable units;
- 2) the conditions of the development and growth of the plants studied are not specified. In some studies, e.g., seasonal variations in the content of lipoquinones in relation to the season of the year were observed, without taking into consideration the developmental stages (3, 44).

In this paper the dynamics of plastoquinones in wheat leaves was studied with regard to the content of chlorophyll and dry matter; at the same time these compounds were balanced in the whole plant. In the study of the dynamics of lipoquinones, attention was concentrated on plastoquinones, α -T and α -TQ and vit. K₁.

The qualitative content of plastoquinones in the above-ground parts of wheat agreed with the data of other investigators. It is known from the studies of Egger (22), Barr and Crane (3), Threlfall and Griffiths (46) that the basic plastoquinones of green tissues are: PQA, PQB and PQC. In this paper it was shown that PQA is the dominating quinone in wheat leaves. Moreover, it was found that PQB did not occur in the leaves of non-vernalized wheat; it appeared in the later stages of ontogenesis.

A number of authors (2, 3, 18, 44, 49) observed a distinct increase in the content of plastoquinones per chlorophyll unit in older leaves, in comparison with younger ones. The increasing accumulation of plasto-

quinones in relation to chlorophyll with the development of plants, particularly by the end of ontogenesis (also shown in this paper), does not find any reasonable explanation. Chlorophyll can be the proper fiducial point of lipoquinones only over the period of full photosynthetic efficiency of the leaf, because in this time, as it is known, plastoquinones are concentrated in about 95% in thylakoids. With the aging of plants the level of chlorophyll decreases and plastoquinones are accumulated in plastoglobules (1, 3, 22, 25). So far, the concentration of plastoquinones in the globules has not been explained. With the ageing of plants the lamellar system undergoes decomposition; chloroplasts become photosynthetically less active. Lichtenhaler (32) showed that with the ageing of chloroplasts the number and size of globules increased. In such a situation, the reason of the apparent increase in lipoquinones in the stage of plant ageing is the dramatical decrease in the accumulation of chlorophyll after the following period.

The accumulation of lipoquinones calculated in relation to dry matter of the material studied showed distinct differences in the level of lipoquinones in vernalized and non-vernalized wheat. The highest accumulation of lipoquinones in the leaves of vernalized wheat fell on the flowering period. In non-vernalized wheat such a maximum was not observed. This does not exclude the role of PQ played in the transition of plants to reproduction, although a similar dynamics of α -T earlier permitted to point out the role of α -T in replacing thermo- and photoinduction (7, 10, 15, 36).

When analyzing the accumulation of lipoquinones in the particular leaves it was possible to determine the maximum falling on the flowering period of wheat applied to each leaf or, if it was the result obtained from the analyses of all leaves. Each leaf reaches the maximum of accumulation of lipoquinones in the stage of its full development, and even in the initial phases of becoming yellow.

This would coincide with the regularity for α -T found Both and Hobson-Frohock (14), verified by Baszyński and Ożga (8), that its level depends on the rate of plant growth. This can be observed till the time when degradation processes begin to dominate over those of synthesis. Thus the behaviour of lipoquinones would resemble the dynamics of α -T, which can be interpreted by the structural similarity of these compounds, their biosynthesis and their joint occurrence in chloroplasts. The maximum accumulation of lipoquinones in various leaves falls on different developmental stages of wheat. It can be distinctly noticed when comparing the distribution of lipoquinones in the 3rd and 5th leaves of vernalized wheat.

The data of the total content of lipoquinones in the plant give fuller evidence of the synthesis being inhibited after the flowering period. The total balance of the compounds studied, comprising both the above-ground portions and the ripening grain, does not indicate their possible synthesis after flowering. In this stage of plant development the membranes of chloroplasts undergo degradation, whereas these subchloroplastic structures are indispensable for the synthesis of lipoquinones (9, 11, 12, 34).

It is difficult to explain the impossibility to find PQC in leaves of vernalized and non-vernalized wheat in the first stages of development, particularly in the light of Barr's and Crane's studies (5). According to these authors, PQC appears immediately after exposing etiolated leaves to light. The appearance of PQC is accompanied by vanishing PQB, and PQC, therefore, should also occur in the first developmental stages of wheat.

In vernalized wheat PQB appeared only by the end of ontogenesis, and solely in the 5th and 6th leaves, and in the ear and ripening grain. It was not in the leaves of non-vernalized wheat.

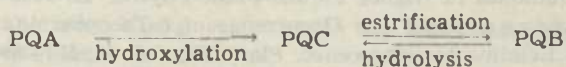
When comparing the dynamics of α -T and α -TQ in ontogenesis of vernalized and non-vernalized wheat, it was shown that the level of both compounds was higher in vernalized wheat. A distinct concentration of these compounds was found to exist in the flowering period of wheat. These facts are in agreement with the hypothesis set up earlier (6, 39) that the transition of plants to reproduction depends on the action of α -T. This hypothesis was confirmed by studies of several authors (7, 8, 10, 15, 36).

There is, however, lack of evidence which would indicate the role of α -TQ in the transition of plants to reproduction. It could be assumed from the results obtained that α -TQ plays a similar role as that of α -T. As it was shown, the highest α -TQ level occurred in the flowering period. The easiness of α -T to oxidize to α -TQ (the second redox-system in chloroplasts besides plastoquinones) could explain the role of α -TQ in flowering. It was however, found by Griffiths and Threlfall and Goodwin (26) that α -TQ cannot be formed α -T, but later studies of Bucke (17) pointed to the possibility of such conversion. The increase in α -TQ by the end of ontogenesis can be interpreted by the increase of oxidation processes. Bar and Arntzen (4) found δ -TQ in ageing leaves of maple and tobacco, and they reported that the appearance of δ -TQ resulted in oxidation of δ -T. Oxidation processes could be then characteristic of chloroplasts undergoing degeneration with age.

Positive correlation between the content of vit. K_1 and chlorophyll was observed. This quinone, as it is known, is connected with chloroplasts, and strictly speaking, with their lamellar structure. Chlorophyll synthesis

was not observed to be followed by an addition synthesis of vit. K₁. Tendille et al. (45) found that the content of vit. K₁ and chlorophyll remained at the same level.

The studies on the dynamics of plastoquinones in wheat grains showed that as their ripening advanced the content of PQA and PQC decreased, and PQB appeared in the phase of wax ripening. If we assumed that PQB increases with maturing of kernels, and, as it was shown by Barr and Crane (3), disappears as soon as the germinating seeds are exposed to light (and PQC appears), PQB could be considered as an emergency form found in seeds. If the loss of PQB was correlated with the appearance of PQC and conversely, the possibility of the following correlations between the homologues of plastoquinones in plant ontogenesis could be assumed:



In the final stages of ontogenesis (ripening phases of grain) the balance would be shifted to the right, whereas in the processes of seed germination and greening of etiolated seedlings — to the left. The elucidation of this assumption is being studied.

A separate problem to be solved is, whether estrification reactions take place in ripening grain or ready-formed PQB is transported from leaves. The alternative is supported by the appearance of PQB in top leaves at the end of ontogenesis.

The qualitative composition of tocopherols of wheat grain agrees with the earlier data of Green (24). Their behaviour during grain ripening corresponds with the conviction based on detailed studies of Baszyński (6) that ripening is followed by the increase in mono- and dimethyl-derivatives due to demethylation of trimethyl-derivatives.

CONCLUSIONS

1. It was found that the composition of plastid lipoquinones of wheat leaves corresponds to the pattern found for higher plants.
2. Leaves of non-vernalized wheat did not contain PQB.
3. It was shown that the content of lipoquinones expressed in terms of the unit of chlorophyll mass did not indicate proper changes of lipoquinones in ontogenesis of plants. The content of dry matter is a better fudicaal point.
4. The content of lipoquinones depends on the developmental stages of wheat. The maximum accumulation takes place in the flowering stage.

5. In the individual leaves the highest accumulation of lipoquinones is connected with the optimal development of the leaf and its physiological function.

6. In the process of kernels' maturation the content of PQA and PQC decreases, but that of PQB increases. α -TQ and vit. K₁ are not detectable.

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STRESZCZENIE

Celem pracy było: 1) zbadanie dynamiki lipochinonów plastydowych w ontogenezie pszenicy ozimej; 2) prześledzenie dystrybucji tych związków w liściach poszczególnych pięter w określonych stadiach rozwoju pszenicy; 3) ustalenie składu i ilości lipochinonów w ziarnie pszenicy w trakcie jego dojrzewania.

Badania prowadzono w latach 1970 i 1971 na pszenicy ozimej odm. Dańkowska biała jaryzowanej i niejaryzowanej. Oznaczano zawartość

lipochinonów PQA, PQB, PQC, α -T, α -TQ oraz wit. K₁ w określonych stadiach rozwoju pszenicy.

Wykazano, że skład lipochinonów plastydowych liści pszenicy odpowiada składowi innych dotychczas zbadanych roślin wyższych. W liściach pszenicy niejaryzowanej nie stwierdzono PQB. Maksymalna akumulacja lipochinonów (z wyjątkiem wit. K₁) przypada na okres kwitnienia. W liściach poszczególnych piętrowości zawartość lipochinonów zależy od rozwoju liścia i jego sprawności fizjologicznej. Ponadto wykazano, że wyrażanie zawartości lipochinonów na jednostkę masy chlorofilu, szczególnie w końcowych stadiach ontogenezy, nie ujawnia właściwej dynamiki lipochinonów. Odpowiedniejszym punktem odniesienia jest zawartość suchej masy.

W procesie dojrzewania ziarniaków pszenicy zmniejsza się zawartość PQA i PQC, natomiast PQB wzrasta. α -TQ i wit. K₁ nie zostały wykryte.

РЕЗЮМЕ

Цель работы: 1) исследование динамики пластидовых липохинонов в онтогенезе озимой пшеницы; 2) рассмотрение дистрибуции этих соединений в листьях отдельных этажей в определенных стадиях развития пшеницы; 3) установление состава и количества липохинонов в зерне пшеницы во время его созревания.

Опыты велись в 1970 и 1971 годах на яризированной и не яризированной озимой пшенице сорта Даньковская белая. Определили содержание липохинонов PQA, PQB, PQC, α -T, α -TQ, а также витамина K₁ в определенных стадиях развития пшеницы.

Доказали, что состав пластидовых липохинонов листьев пшеницы отвечает составу других, исследованных до сих пор высших растений. В листьях не яризированной пшеницы не констатировали PQB. Максимальная аккумуляция липохинонов (за исключением витамина K₁) происходит во время цветения. В листьях отдельных этажей содержание липохинонов зависит от развития листа и его функциональной физиологической способности. Кроме того установлено, что выражение содержания липохинонов на единицу массы хлорофила, особенно в последних стадиях онтогенеза, не выявляет характерной динамики липохинонов. Более подходящим исходным пунктом является содержание сухой массы.

В процессе созревания зерновок пшеницы понижается содержание PQA и PQC, а PQB растет. α -TQ и витамин K₁ не были выявлены.

