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Studies on the mechanism which prevents germination of unripe *Triticale* caryopses

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Abstract

Triticale (MT-3) caryopses were collected at three developmental stages (milk, milk-wax, and full ripeness i.e. 25, 39, 53 days after flowering) and germinated for 72 hours. The highest polyribosome contribution to the sum total of ribosomes, as well as, the highest ^{3}H-uridine incorporation into the total ribosomal fraction of embryos (seedlings) were found at full ripeness, lower — at milk ripeness, and the lowest at milk-wax ripeness. Treatment of caryopses with gibberellin-A_3 (GA_3) and benzyloadenine (BA) caused an increase in the percentage of embryonic polyribosomes in caryopses which were collected at milk and full ripeness. Whereas the significant increase in ^{3}H-uridine incorporation into the total ribosomal fractions of embryos (seedlings) was observed only during the germination of the least ripe caryopses. This was characteristic of samples with caryopses at milk ripeness treated with BA, or BA and GA_3 together. The studies proved that the mechanism which prevents the germination of unripe *Triticale* cyryopses and the formation of polyribosomes which were germination-induced, originated at the final stage of grain development, before its full ripeness.

Key werds: polyribosome formation, development germination, Triricale, dormancy

INTRODUCTION

The period of formation and development of cereal caryopses can be divided into three stages (Grzesiuk 1967, Weidner 1982): 1) the basic endosperm development (embryo still at the pre-embryonic stage beginning of reserve storage in endosperm) sometimes termed green ripeness stage; 2) the basic embryo development (intensive reserve storage in endosperm) — milk

ripeness stage; 3) the highest reserve storage and caryopse ripening (tissue dehydration, caryopse transiton to the state of dormancy) — wax and full ripeness stages. Earlier formation of endosperm tissues leads to embryo development. Hence, endosperm serves as a main and direct source of nutrients for an embryo during embryogenesis and germination.

Embryo development can be divided into two phases: initial morphogenesis and maturation. During morophogenesis embryo structures are produced by embryo cell divisions. While during maturation no further cell divisions occur. Then enzymes and structures are synthetized, which enable an embryo to be well adapted to desiccation dormancy and germination. This division is characteristic not only of cereal caryopses, but also of other seeds (Dure 1975, Long et al. 1981). For example the final cell number in pea embryo is attained during the first half of seed formation, whereas in *Phaseolus vulgaris* — when embryo dry mass equals only one--sixth of its final value (Dure 1975).

For practice it is realy important, especially in respect of yield and harvest term, to know at what stage of ripeness the grain is the heaviest and what it results from. Seed ripeness can be assessed on the basis of its water, or dry mass contents, It is assumed that the seed contains more than 50% of water at milk ripness, 50-25% of water — at wax ripeness, and less than 25% of water — at full ripeness.

Grain shrivelling and wax sprouting in ears result in serious obstacles in the cultivation of varieties of *Triticale*, the synthetic hybrid between *Triticum* (wheat) and *Secale* (rye) which are in use in agriculture. The reason of shrivelling is not known yet. Cytological research (Bennett 1977) shows that anomalies in the initial cell divisions cause aberrations in the cells nuclei, which affect further endosperm development. The relations between sprouting, α-amylase activity and caryopse shrivelling have been also analyzed (Klassen et al. 1971. Dedio et al. 1975). It seems that in *Triticale* caryopses the regulation of development and sprouting, as well as, α-amylase synthesis depend upon the equilibrium of endogenous phytohormones. Many studies on changes in the endogenous level of phytohormones in the course of ripening and development of cereal caryopses have shown the control role of cytokinins, gibberellins, and abscisic acid (Wheeler 1972, Goldbach and Michael 1976, King 1976, Radley 1976, 1979, King et al. 1979). In this paper, in aim to get more data on the subject, the research into transcriptional activity and polyribosome formation has been undertaken. The former has been analyzed on the basis of ^{3}H-uridine incoporation into the total ribosomal fraction. The analysis has been conducted on the embryos during 3 days germination of freshly collected *Triticale* caryopses at the stages of milk, milk-wax, and full ripeness. The effects of GA_3 and BA on the synthesis of the total ribosomal fraction and formation of polyribosomes have been also studied.

MATERIAL and METHODS

The investigations were conducted in 1983. The analyzed *Triticale* caryopses of MT-3 generation were cultivated on the investigation plots of Institute of Plant Biology of Agricultural-Technical Academy, Olsztyn. They were harvested 25, 39, and 53 days after flowering (i.e. at milk, milk-wax and full ripeness) at the average water contents in grains appropriately of 67.82, 49.02 and 20.90%. Cut-down ears were brought to the laboratory. Then caryopses were removed by hand from the middle part of the ear. Every 3 extreme top and bottom spikelets were thrown away. The grains were sterilized with 1% solution of sodium hypochloride and germinated under the sterile conditions. They were germinated for 72 h on the filter paper in Petri dishes at constant humidity and in darkness. During germination chloramphenicol (10 $\mu g \cdot cm^{-3}$) and 5-^{3}H-uridine (0.8 $MBq \cdot cm^{-3}$ and specific activity of 765 $GBq \cdot cm^{-3}$) were present in all samples, while N-^{6}BA, GA_3 and their mixture only in some samples pointed-out earlier. The concentrations of all the solutions of growth stimulators equaled 1×10^{-5} M. GA_3 and N-^{6}BA came from the Sigma firm, while ^{3}H-uridine from Chemapol UVVVR (Czechoslovakia). After the germination embryos were excised in ice. Their surface washed clean of the remainder of precursor which had not been metabolised and dried. Germination was arrested by freezing of samples at -25°C.

Embryonic polyribosomes and monosomes were isolated according to the Davies's method (Davies et al. 1972). Approximately 2 g of the plant material were homogenized in buffer "A" (0.2 M sucrose, 200 mM Tris-HCl, pH 8.5, 30 mM $MgCl_2$, 60 mM KCl). The homogenate was centrifuged at 29 000 × g in the "Janetzki" centrifuge. Next the supernatant was transferred to the 65 Ti rotor test tube on the 4 cm^3 layer of 1.5 M sucrose in buffer "B" (40 mM Tris-HCl, pH 8.5, 10 mM $MgCl_2$, 20 mM KCl) and centrifuged in the Spinco L-3-40 ultracentrifuge at 95 000 × g for 90 minutes. The sediment of polyribosomes and monosomes was suspended in 1 cm^3 of buffer "B" and overlaid on the linear sucrose gradient. The gradient had been prepared on buffer "C" (20 mM Tris-HCl, pH 8.5, 10 mM $MgCl_2$, 20 mM KCl) the day before and kept in cold. It consisted of 4 different sucrose concentrations: 500 $mg \cdot cm^{-3}$ — 1.8 cm^3, 375 $mg \cdot cm^{-3}$ — 3.8 cm^3, 250 $mg \cdot cm^{-3}$ — 3.8 cm^3, and 125 $mg \cdot cm^{-3}$ — 1.8 cm^3. Polyribosomes were fractioned through ultracentrifugation at 122 000 × g in SW-41 Ti rotor for 75 minutes. The whole analysis was conducted at 0-4°C. Next, tube contents (13 cm^3) were divided into layers by a means of crane and the extinction of every layer was measured at 260 nm. Radioactivity was measured by a means of Fl 100 C scientillation counter, manufactured by Beckman. 10 cm^3 of "Tritosol", acting as a scintillator, were added to 1 cm^3 of sample (Fricke 1973).

Caryopses harvested 25 and 39 days after flowering i.e. at milk and milk-wax ripeness were also subjected to the germination in ears. Ears, which were cut down with the parts of stems, were bounded up (100 specimens each bunch). Their surface was sterilized. Finally they were placed in a glass chamber at 21-22°C and at high relative humidity of 98%. Stem ends were immersed in water and in GA_3, N-^{6}BA, or their mixture. Caryopses were collected after 14 days of germination under the sterile conditions in day light. Next the percentage of germinating caryopses was determined.

RESULTS

The sum total of ribosomes isolated from embryos (seedlings) after 72 hours germination of freshly collected *Triticale* caryopses consisted mainly of two fractions: polysomes and monosomes (Figs. 1, 2, 3), whereas ribosomal subunits were rare (2-8%). Within polysomes large polysomes were distinguished (test tubs 1-29 in the figures). Polysome contribution to the sum total of embryonic ribosomes depended upon the ripeness of a germinated seed. After 3 days germination of the freshly collected cyryopses polysome percentage amounted to 56% in the initial period of milk ripeness, it was 41% at milk-wax ripeness and 62% — at full ripeness. Growth stimulators present during the germination caused an increase in the polysome percentage in embryos (seedlings) in caryopses collected at milk and full ripeness (Table 1). BA was slighty more active than GA_3. The joint effect of BA and GA_3 mixture produced more intensive polysome formation than the single action of each of them. Caryopses collected at milk-wax ripeness were insensitive to the action of GA_3 and BA within the range of used concentrations (Fig. 2, Table 2). After 3 days germination their embryos contained also the least polysomes.

During the germination of freshly harvested *Triticale* caryopses the course of the process of ^{3}H-uridine incorporation into the total embryonic fraction of ribosomes was similar to the course of polyribosome formation. The highest incorporation of the radioactive precursor occurred in the embryos excised from the grains harvested at full ripeness, lower — at milk ripeness, and the lowest at the milk-wax ripeness (Figs. 1, 2, 3, Table 2). Significant increase in the transcriptional activity caused by the action of growth stimulators on the synthesis of polyribosomal RNA took place only during the germination of the least ripe caryopses. In caryopses at milk ripeness significant increase in the incorporation of radioactive precursor was caused by BA, as well as, BA and GA_3 together (Fig. 1, Table 2), in spite of the differences in radioactivity of individual fractions of polyribosomal RNA.

The author (Weidner 1984) carried-out detailed studies on the phytohormone regulation of germination of *Triticale* caryopses. This paper contains

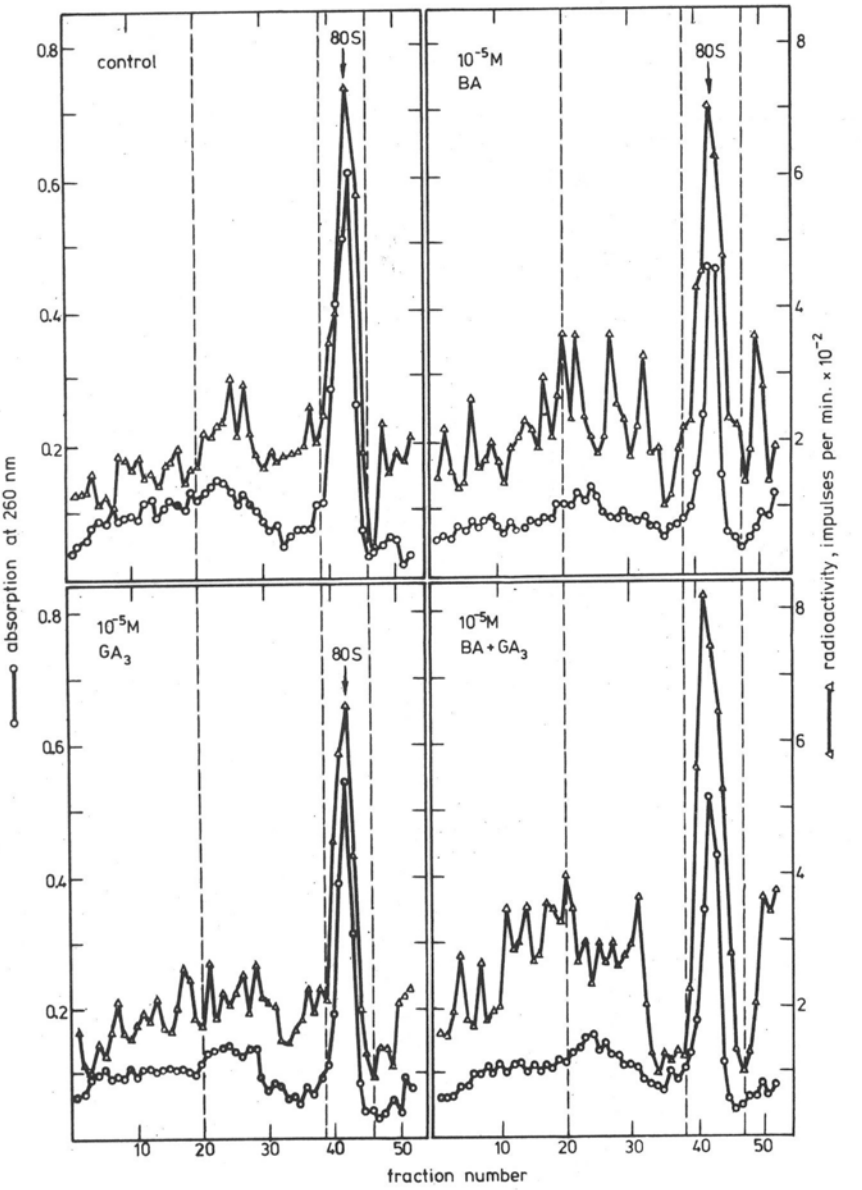

Fig. 1. Profiles of polyribosome sedimentation (in 12.5-50% sucrose gradient). Polyribosomes were isolated from *Triticale* embryos after 72 hours germination of unstored grains harvested at milk ripeness (25 days after flowering). The seeds were germinated in the presence of 5-^{3}H-uridine (0.8 MBq·cm^{-1}) and chloramphenicol (10 μg·cm^{-3}) in all the samples, as well as, BA, GA_3 and their mixture in some samples, pointed-out earlier. Broken line separates fractions of large polyribosomes, small polyribosomes and monosomes. Arrow indicates monosome fractions (80 S)

Table 1

Differences in the formation of embryonic polyribosomes in *Triticale* caryopses after 72 hours germination of unstored grains harvested at milk, milk-wax, and full ripeness (25, 39 and 53 days after flowering). Seeds were garminated in water, as well as, BA, GA_3 and their mixture. Polyribosomes were fractioned through centrifugation

Treatment	Stage of ripeness								
	milk			milk-wax			full		
	P/T	LP/T	LP/P	P/T	LP/T	LP/P	P/T	LP/T	LP/P
Control	56.1	27.6	49.2	41.2	22.6	53.6	62.0	28.3	45.6
GA_3	65.2	30.7	47.2	40.9	19.7	48.4	73.9	30.8	41.7
BA	66.1	22.6	34.2	41.3	23.9	57.9	78.5	23.6	30.0
BA + GA_3	64.9	28.5	44.8	41.8	19.4	46.2	82.9	25.8	31.1

T — total absorbing material (polyribosomes plus monosomes plus ribosomal sub-units). LP — large polyribosomes (material sedimenting faster than septamers). P — polyribosomes (material sedimenting faster than monosomes). Polyribosomes division into fraction is shown in Figures.

Table 2

^{3}H-uridine incorporation into embryonic polyribosomal fraction in *Triticale* caryopses after 72 hours germination. Freshly harvested caryopses were germinated at milk, milk-wax and full ripeness in the presence of 5-^{3}H-uridine (0.8 MBq·cm^{-3}) in all the samples, as well as, BA, GA_3 and their mixture in some samples, pointed-out earlier. After the germination embryos were excised and the total ribosomal fraction isolated from them

Stage of ripeness	Treatment	cpm·1 mg^{-1} of polyribosomal RNA fraction			
		T	LP	P	M
Milk	control	32697	29879	31679	23200
	GA_3	32671	30931	31594	23983
	BA	45076	57255	43431	30000
	BA +GA_3	48243	52900	45985	32750
Milk-wax	control	25142	28246	28694	19532
	GA_3	25631	28341	28931	19362
	BA	26094	28831	29863	19698
	BA +GA_3	25923	28632	29043	19460
Full	control	60004	56381	59381	53500
	GA_3	60247	54141	59213	60836
	BA	60372	67515	59187	59327
	BA +GA_3	61038	55231	59589	66492

M — mono-somes; T, LP, P as in Table 1.

Table 3

Percent of sprouting in different stages of ripeness of *Triticale* caryopses in ears. Ears were collected, with the stem parts, at milk and milk-wax ripeness (25 and 39 days after flowering). Stem ends were immersed in water (control), as well as in GA_3 and BA and their mixture. Seeds were germinated for 14 days at 21-22 °C, in day light and at high humidity (approx. 98%)

Treatment	Stage of ripeness	
	milk	milk-wax
Control	5.6	14.5
GA_3	8.4	49.0
BA	18.9	13.9
BA +GA_3	16.4	45.8

only data on 14 days germination of unripe *Triticale* caryopses in ears and the effects of GA_3, BA and their mixture on the seed sprouting. In the initial period of milk ripeness BA induces premature germination better than GA_3 (Table 3). On the contrary, at milk-wax ripeness BA did not affect germination, whereas GA_3 stimulated it highly.

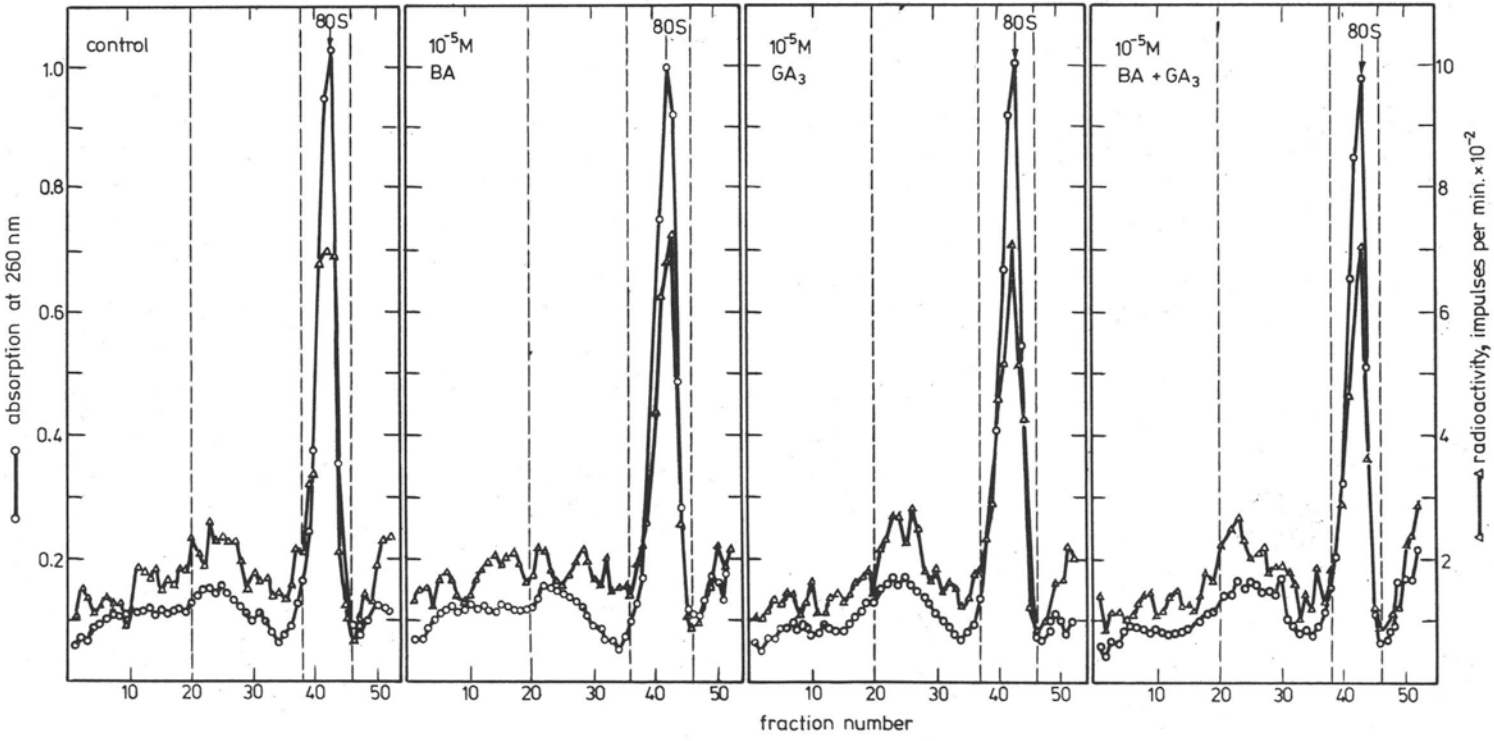

Fig. 2. Profiles of polyribosome sedimentation (in 12.5-50% sucrose gradient). Polyribosomes were isolated from *Triticale* embryos after 72 hours germination of unstored grains harvested at milk-wax ripeness (39 days after flowering). The seeds were germinated in the presence of 5-^{3}H-uridine (0.8 MBq·cm^{-3}) and chloramphenicol (10 μg·cm^{-3}) in all the samples, as well as, BA, GA_3 and their mixture in some samples, pointed-out earlier. Broken line separates fractions of large polyribosomes, small polyribosomes and monosomes. Arrow indicates monosome fractions (80 S)

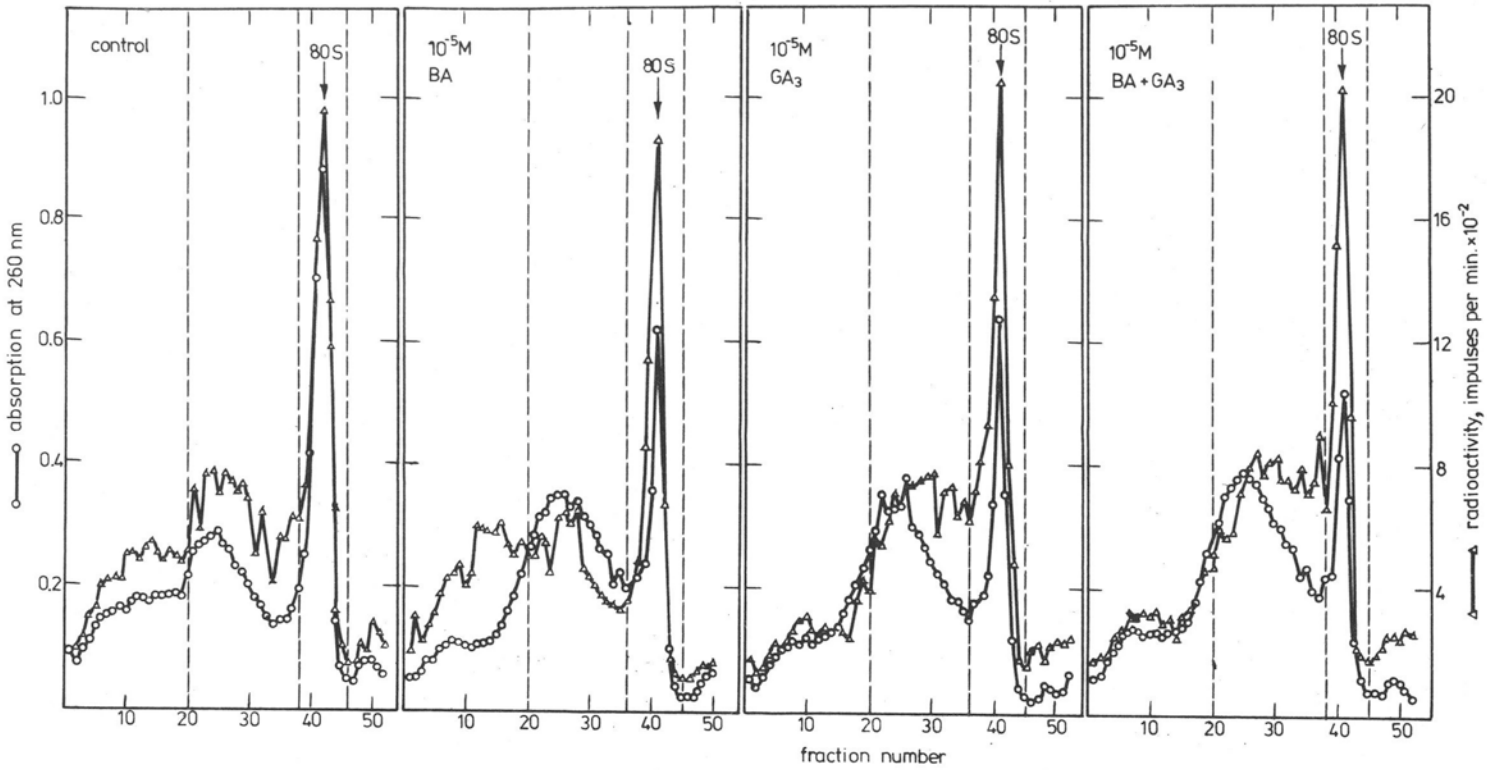

Fig. 3. Profiles of polyribosome sedimentation (in 12.5-50% sucrose gradient). Polyribosomes were isolated from *Triticale* caryopses after 72 hours germination of unstored grains harvested at full ripeness (53 days after flowering). The seeds were germinated in the presence of 5-^{3}H--uridine (0.8 MBq · cm^{-3}) and chloramphenicol (10 μg · cm^{-3}) in all the samples, as well as, BA, GA_3 and their mixture in some samples, pointed--out earlier. Broken line separates fractions of large polyribosomes, small polyribosomes and monosomes. Arrow indicates monosome fractions (80 S)

DISCUSSION

During the development and ripening of *Triticale* (MT-3) caryopses regular changes in the transcriptional activity of chromatin have been observed in embryos (Weidner and Wielgat 1984). Both, accessibility of DNA template and activity of RNA polymerases are high in the initial period of embryogenesis (20-30 days after flowering). Then they decrease (35-40 days) and increase in the final period of germination (60 days). King et al. (1979) have shown that abscisic acid (ABA) content in *Triticale* (GA 190) caryopses varies rapidly in the course of grain development and ripening. ABA concentration increases with the seed development. It attains its maximum value in the beginning of the second half of development and ripening period and then decreases rapidly. Moreover, both varieties i. e. MT-3 and GA 190 have many features in common, such as, seed shrivelling and short dermancy followed by the tendency to seed sprouting in the ear. Obtained results indicate that in the middle period of development higher ABA content in embryos may be associated with the lower transcriptional activity of chromatin. Also during 3 days germination of freshly harvested caryopses the lowest polysome contribution to the sum total of ribosomes, as well as, the lowest ^{3}H-uridine incorporation into the total embryonic fraction of ribosomes occured at milk-wax ripeness (Tables 1, 2). Data on the seedlings grown from the caryopses (in the presence of radioactive precursor), which were collected in the middle developmental phase, is also very interesting. Even when dormany was released (after several-months dry storage) the seedling contained polysomes and RNA of the lowest radioactivity (Weidner and Zalewski 1982, Weidner and Wielgat 1983, Weidner et al. 1984). According to the author it may be deduced that the fixation of some genome features which have originated during embryogenesis occurs.

From the results of the studies it may be proved that the mechanism which prevents precocious germination and formation of the germination-induced polysomes is formed at the stage of milk-wax ripeness i. e. before the seed is ripe. The synthesis of the embryonic polyribosomal RNA, discovered in caryopses at milk-wax ripeness is associated rather with the embryo development than seed germination. In the period under study (72 h) no external symptoms of the germination have been seen. Whereas when caryopses collected at milk and full ripeness were germinated the external germination symptoms have been observed. In the majority of them, in comparison with the caryopses collected at the same stages, but germinated after several-months dry storage, freshly collected caryopses of milk and full ripeness germinated significantly later (Weidner 1984). It seems that the processes of both grain development and germination overlap there. From results of several studies (Choiński and Trelease 1978, Sussex and Dale 1979, Dure et al. 1980) it may be concluded that in the pre-

cociously germinating embryos the synthesis of proteins characteristic of embryo maturity is arrested. Hence with changes in protein demands of developing seedlings significant qualitative changes within the population of newly formed mRNA occur. It has been determined that the concentrations of ABA which inhibit precocious germination of unripe embryos "*in vitro*" and those which occur in developing seeds are similar (Crouch and Sussex 1981, Long et al. 1981). Also high osmotic preasures of sucrose (0.2-0.3 M), or mannitol inhibit precocious embryo germination (Rappaport 1954). According to Sussex (1975) seed dormancy is initiated by the water stress followed by the significant and rapid increase in the ABA content through synthesis "*de novo*".

Growth stimulators do not affect polyribosome formation and ^{3}H-uridine incorporation in *Triticale* caryopses of milk-wax ripeness. It probably results from the high ABA concentration during that period. For example in wheat caryopses ABA content (mg/caryopse) increases nearly 60-fold in time from the beginning of development to the period of ABA maximum accumulation in seed (King 1976). The clear effect of both BA and GA_3 on the polysome formation has been noted for caryopses of milk, as well as, full ripeness. But only during germination of caryopses of milk ripeness the presence of BA, GA_3 and their mixture produces a significant increase in the ^{3}H-uridine incorporation into the total ribosomal fraction. This phenomenon should be further analyzed.

Studies on the seeds of viviparous plants can play an important role in the elucidation of complex control mechanisms of dormancy. These seeds are not dormant and there is no break in the embryo growth between the final stage of embryo development and the beginning of seed germination. However, from the preliminary studies on *Rhizophora mangle* seeds can be seen that in the excised seedlings ABA and BA do not affect neither ^{3}H-uridine incorporation into RNA, nor ^{3}H-aminoacids incorporation into proteins (Sussex 1975).

From the data on BA and GA_3 effect on germination of *Triticale* caryopses in ears, in day light (Table 3) it can be concluded that tendencies in the stimulation of germination process are similar to those confirmed earlier for freshly harvested caryopses, germinated on filter paper in darkness (Weidner 1984).

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Badania nad mechanizmem zapobiegającym kiełkowaniu niedojrzałych ziarniaków Triticale

Streszczenie

Ziarniaki *Triticale* (MT-3) zebrane w trzech etapach rozwoju (dojrzałość mleczna, mleczno-woskowa i pełna; 25, 39 i 53 dni po kwitnieniu) poddano 72 godzinnemu kiełkowaniu. Największy udział polirybosomów w ogólnej puli rybosomów, jak również, największe wcielanie ^{3}H-urydyny do ogólnej frakcji rybosomalnej zarodków (siewek), stwierdzono w pełnej dojrzałości morfologicznej ziarna, mniejsze w dojrzałości mlecznej, a najmniejsze w dojrzałości mleczno-woskowej. Traktowanie ziarniaków gibereliną-A_3 oraz benzyloadeniną powodowało wzrost procentowej zawartości polirybosomów w zarodkach ziarniaków zebranych w okresie dojrzałości mlecznej i pełnej. Istotne zwiększenie wcielania ^{3}H-urydyny do ogólnej frakcji rybosomalnej zarodków (siewek) obserwowano tylko podczas kiełkowania ziarniaków najmniej dojrzałych. Stymulację tę stwierdzono w próbach ziarniaków dojrzałości mlecznej traktowanych benzyloadeniną oraz benzyloadeniną i giberelinią-A_3 łącznie. Uzyskane wyniki badań dowodzą, że mechanizm, który zapobiega kiełkowaniu niedojrzałych ziarniaków *Triticale* oraz tworzenia się polirybosomów indukowanych kiełkowaniem powstaje w końcowym etapie rozwoju ziarna, przed jego pełną dojrzałością.