# The role of zeatin and gibberellic acid in breaking of the abscisic acid — induced dormancy in *Triticale* caryopses

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#### Abstract

The investigations were conducted on the germinating embryos and the whole caryopses of Triticale. During preimbibition and 24 hours germination caryopses were treated with abscisic acid (ABA), which produced 63% inhibition of embryo growth. Gibberellin-A (GA<sub>3</sub>) reversed the ABA effect in 18%, while zeatin in 22%. The clear synergic reaction was observed (36%) when both stimulators acted together. There was no significant effect of ABA, ABA and GA3, as well as ABA and zeatin on the synthesis of polyribosomal RNA in the initial period of germination of excised embryos. However, during 24 hours germination of whole caryopses ABA caused a two--fold decrease in <sup>3</sup>H-uridine incorporation into the total fraction of embryonic ribosomes. While the incorporation of <sup>14</sup>C-aminoacid mixture into ribosomal proteins was even three-fold lower. Effect of GA3 and zeatin on breaking of the ABA-induced "dormancy" was studied. It was confirmed that the higher polyribosome contribution to the sum total of ribosomes the more intensive synthesis of ribosomal proteins. No higher <sup>3</sup>H-uridine incorporation into polyribosomal fraction was observed. From the results it may be inferred that in the initial period of germination of Triticale caryopses regulation of protein biosynthesis occurs rather at the translation than transcription level.

Key words: germination, abscisic acid, gibberellin, cytokinin, Triticale

## INTRODUCTION

There are many concepts and theories on the complex mechanisms of dormancy. According to them dormancy stage results from: 1) the presence of inhibitors in some parts of the seed (Molisch 1922, Wareing 1965); 2) the limited oxygen uptake due to the presence of seed coats, which is followed by higher inside temperature (Thornton 1935, Crocker 1948, Vegis 1964, Roborts 1969); 3) the action of active and inactive forms

of phytochrome (Wesson and Wareing 1969, Kivilaan and Bandurski

of phytochrome (Wesson and Wareing 1969, Kivilaan and Bandurski 1973). However, the majority of research workers believes that the basic mechanism of the dormancy control and induction lies in the action of plant growth regulators varied in time and place (Wareing and Saunders 1971, Khan 1971, 1977, Villiers 1972, Bewley and Black 1982).

According to Amen (1968) seed dormancy results from the particular ratio of the growth inhibitors to the growth stimulators. Also Khan (1971, 1977, 1980) has formed the model of seed germination and dormancy based upon the interaction of phytohormones. Given it, it may be inferred that ABA plays a main role in the induction of seed dormancy, while cytokinins and gibberellins—in the process of dormancy release. ABA also plays an important role in the regulation of growth and development of plant tissues (Addicot and Lyon 1969, Milborrow 1974). There are many papers on the inhibiting effect of ABA on the synthesis of various nucleic acids in plant tissues (Jacobsen 1977, Jacobsen and Higgins nucleic acids in plant tissues (Jacobsen 1977, Jacobsen and Higgins 1978a). Whether the effect is direct or indirect is not always clear. The paper presents results of the studies on ABA effect on germination-in-duced synthesis of the ribosomal fraction in the whole *Triticale* caryopses and embryos excised from them. The interaction between ABA and growth stimulators has also been analyzed.

## MATERIAL AND METHODS

The investigations were conducted on *Triticale* caryopses of MT-3 generation. The caryopses were harvested at full ripeness in 1982 from the investigation plots of Institute of Plant Biology, Agricultural-Technical Academy, Olsztyn.

Caryopses were dry-stored for 4 months. Then washed with tap water and placed in 1% solution of sodium hypochloride for 3 minutes. Sterilized caryopses were washed with sterile water and their surface dried. Next, sterile material was subjected to 12 hours imbibition at 2°C (preimbibition). In some samples, pointed-out earlier, preimbibition was conducted in the presence of phytohormones.  $GA_3$  and ABA (isomer mixture) were supplied by the Sigma firm, zeatin and 3-indoleacetic acid by the Calbiochem firm. The concentration of every phytohormone solution, used in the analysis, equaled  $1 \times 10^{-5}$  M. Hence from many results it could be concluded that during the seed germination phytohormone solutions were the most active at this concentration (Poulson and Beevers 1970, Sussex 1975, Walbot et al. 1975, Takaiwa and Tanifuji 1978).

Preimbibed caryopses were germinated in darkness at  $21\text{-}22^{\circ}\text{C}$  at constant humidity and in the presence of chloramphenicol ( $10\,\mu\text{g}\cdot\text{cm}^{-3}$ ) and phytohormones under the study. 5-<sup>3</sup>H-uridine (radioactivity concentration — 0.4 MBq·cm<sup>-3</sup> and specific activity — 765 GBq·mM<sup>-1</sup>) and <sup>14</sup>C-aminoacid mi-

xture (activity—0.4 MBq·cm<sup>-3</sup> and specific activity—1.295 MBq·mA<sup>14</sup>C<sup>-1</sup>). Radioactive precursors were supplied by the Chemapol UVVVR firm (Czechoslovakia). The embryos were excised from caryopses after 24 hours germination. The process was carried-out in ice. Next, the embryo surface was washed clean of the remainder of unmetabolised procursors and dried. Embryos were stored in the closed dishes at  $-25^{\circ}$ C, ready for the further analyses.

Embryos were excised also after preimbibition, as well as, preimbition and 16 hours germination of grains in the presence of phytohormones. Next they were germinated for 2 h in the presence of chloramphenicol  $(10 \, \mu g \cdot cm^{-3})$ , 5-3H-uridine  $(0.8 \, MBq \cdot cm^{-3})$  and phytohormones. After incubation embryos were throughly washed and their germination arrested by sample freezing at  $+25^{\circ}C$ .

Polyribosomes were isolated from Triticale embryos, such as monosomes according to the Davies's method (Davies et al. 1972). Hence, approx. 2 g plant material were homogenized in buffer "A" (0.2 M sucrose, 200 mM Tris-HCl, pH 8.5, 30 mM MgCl<sub>2</sub>, 60 mM KCl). The homogenate was centrifuged at 29 000 × g in "Janetzki" centrifuge. Supernatant was placed in the 65-Ti rotor tube on 4 cm<sup>3</sup> layer of 1.5 M sucrose in buffer "B" (40 mM Tris-HCl, pH 8.5, 10 mM MgCl<sub>2</sub> 20 mM KCl) and centrifuged in the Spince L-3-40 ultracentrifuge at 95 000 × g for 90 minutes. Polyribosome and monosome sediment (about 1 mg) was suspended in 1 cm3 of buffer "B" and overlaid on the sucrose linear gradient. Gradient had been prepared in buffer "C" (20 mM Tris-HCl, pH 8.5, 10 mM MgCl<sub>2</sub>, 20 mM KCl) a day before and stored in cool. It consisted of four sucrose concentrations: 500 mg·cm<sup>-3</sup> — 1.8 cm<sup>3</sup>, 375 mg·cm<sup>-3</sup> — 3.8 cm<sup>3</sup>, 250 mg·cm<sup>-3</sup> — 3.8 cm<sup>3</sup>, and 125 mg·cm<sup>-3</sup> — 1.8 cm<sup>3</sup>. Polyribosomes were fractioned by ultracentrifugation at 122 000×g in SW-41 Ti rotor for 75 minutes. Polyribosome isolation and fractioning were conducted at 0-4°C. After centrifugation test tube contents (13 cm<sup>3</sup>) were divided by a means of crane and their extinctions were measured at 260 nm. Radioactivity was measured by the Fl-100C scintillation counter, manufactured by the Beckman firm. To each 1 cm<sup>3</sup> of sample 10 cm<sup>3</sup> of "Tritosol" (efficiency for  $^3H - 47\%$ , for  $^{14}C - 87\%$ ) were added as a scientillator (Fricke 1973). In aim to assess the amount of ribosomes it was assumed that extinction of 1% solution of ribosomes, measured in cuvette with the optical pathway of 1 cm, at wavelength of 260 nm equaled  $E_{1\%}^{1 \text{ cm}} = 135$  (Gualerzi and Cammarano 1969).

Inhibiting ABA effect on the embryo growth, as well as 3-indoleacetic acid,  $GA_3$ , zeatin,  $GA_3$  and zeatin mixture reversal of this action were also studied during 24 hours grain germination. Samples were collected every 3 h. The fresh mass increment was treated as a measure of the embryo growth. Results were given in terms of average fresh mass of an embryo.

#### RESULTS

For the first 6 h of the germination the effect of the used phytohormones was small. Only in the samples of caryopses, which were imbibed and germinated in the presence of ABA slightly lower embryo mass was observed (Fig. 1). For the next hours of germination (6-24 h) phytohormone effect was more pronounced and the gradual embryo growth occurred. ABA, present during imbibition and 24 hours germination, caused 63% inhibition of embryo growth. Partial reversal of the ABA inhibiting influence was noticed when

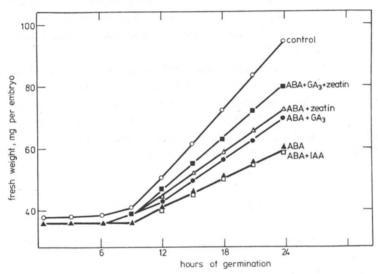


Fig. 1. Zeatin, GA<sub>3</sub>, IAA, as well as, GA<sub>3</sub> and zeatin mixture reversal of ABA inhibiting effect on the *Triticale* embryo growth during 24 hours caryopse germination. Germination was preceded by 12 hours imbibition at +2°C in the presence of the same phytohormones

GA<sub>3</sub> and zeatin were added. Gibberellic acid led to approx. 18% and zeatin—to approx. 22% stimulation of embryo growth. When GA<sub>3</sub> and zeatin acted together inversal of the ABA inhibiting effect in 36% was observed after 24 hours grain germination. In spite of this clear synergic reaction the complete reversal of the ABA inhibiting effect could not be attained. No counteraction of 3-indoleacetic acid (IAA) on the ABA-induced inhibition of embryo growth was observed (Fig. 1).

Figures 2 and 3 show sedimentation profiles of polyribosomes isolated from *Triticale* caryopses after their 2 hours germination and 16 hours of grain germination followed by 2 hours embryo germination respectively. Excised embryos were germinated in the presence of <sup>3</sup>H-uridine. Already in the initial period of germination ABA inhibiting effect on the formation of embryonic polyribosomes and its patrial reversal by growth stimulators

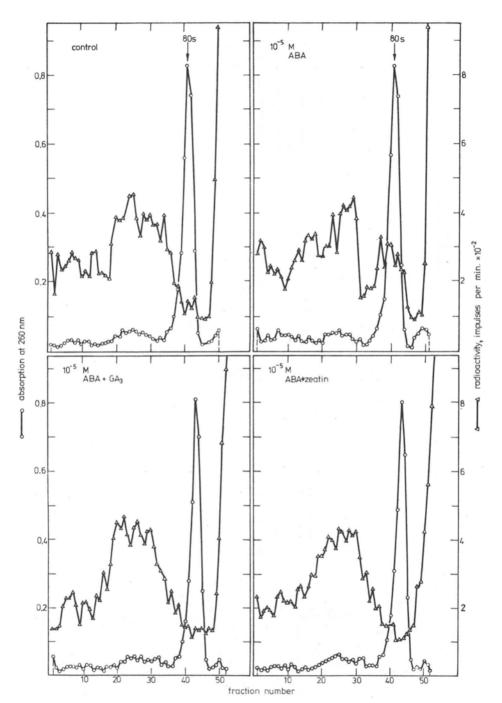


Fig. 2. Sedimentation profiles of polyribosomes (in 12.5-50% sucrose gradient) isolated from *Triticale* embryos. Embryos were excised from caryopses after preimbibition in the presence of phytohormones. Next, they were germinated for 2 h in the presence of <sup>3</sup>H-uridine (0.8 MBq·cm<sup>-3</sup>) and chloramphenicol (10 µg·cm<sup>-3</sup>) in all samples, as well as, ABA, ABA and GA<sub>3</sub>, ABA and zeatin in some samples, pointed-out earlier. Arrow indicates monosome fraction (80 S)

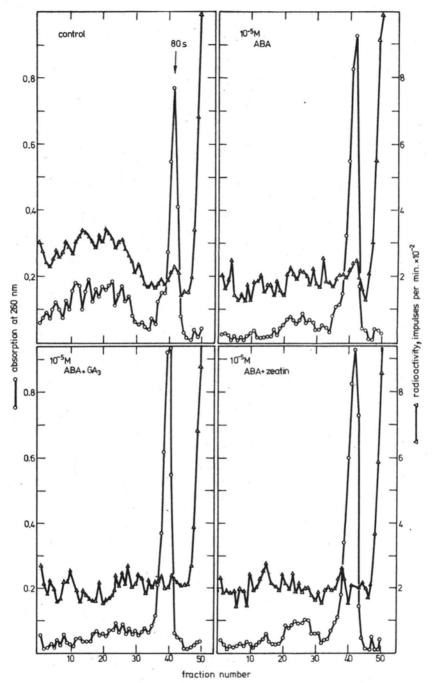


Fig. 3. Sedimentation profiles of polyribosomes (in 12.5-50· sucrose gradient) isolated from *Triticale* embryos. Caryopses were imbibed (12h at  $+ 2^{\circ}$ C) and germinated (16 h) in water and in the presence of appropriate phytohormones. Next, embryos were excised and germinated (16-18 h) in the presence of <sup>3</sup>H-uridine (0.8 MBq·cm<sup>-3</sup>) and chloramphenicol (10  $\mu$ g·cm<sup>-3</sup>), as well as, ABA, ABA and GA<sub>3</sub>, ABA and zeatin. Arrow indicates monosome fraction (80 S)

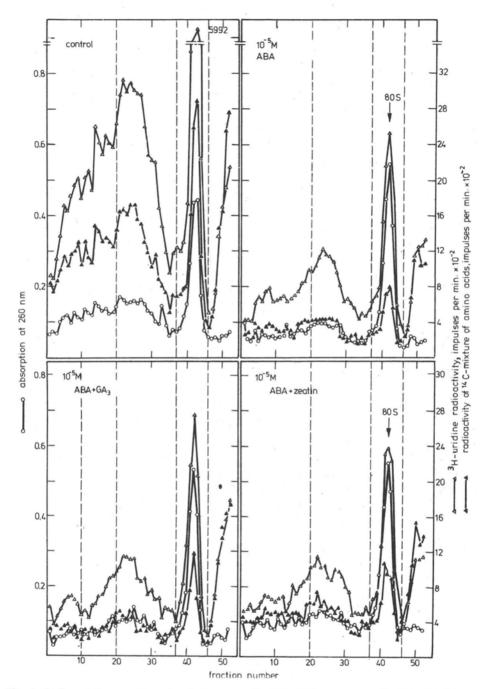


Fig. 4. Sedimentation profiles of polyribosomes (in 12.5-50% sucrose gradient) isolated from *Triticale* embryos. Caryopses were preimbibed and germinated in the presence of ABA, ABA and GA<sub>3</sub>, ABA and zeatin, and in water. Next embryos were excised. Caryopses were germinated in the presence of additional radioactive precursors: <sup>3</sup>H-uridine (0.4 MBq·cm<sup>-3</sup>), <sup>14</sup>C-aminoacid mixture (0.4 MBq·cm<sup>-3</sup>) and chloramphenicol (10 μg·cm<sup>-3</sup>). Broken line separates fractions of large polyribosomes, small polyribosomes and monosomes

Table 1

Differences in the formation of embryonic polyribosomes in *Triticale* caryopses after 2, 18, and 24 hours germination of caryopses. Every grain was preimbibed at low temperature. Preimbibition and germination were conducted in the presence of the same phytohormones

Treatment				Germination time							
	2 h			18 h			24 h				
	P/T	LP/T	LP/P	P/T	LP/T	PL/P	P/T	LP/T	PL/P		
Control	31.6	16.9	53.5	60.3	32.5	51.8	67.1	33.6	53.1		
ABA	21.3	9.3	41.7	32.4	12.3	40.9	47.2	26.0	54.8		
$ABA + GA_3$	29.1	15.7	53.8 -	50.0	25.7	49.3	52.3	27.5	52.7		
ABA +zeatin	29.3	15.8	53.8	53.9	27.3	50.6	55.4	29.6	53.5		

T — total absorbing material (polyribosomes plus monosomes plus ribosomal sub-units). LP — large polyribosomes (material sedimenting faster than monosomes). Figure 4 illustrates polyribosome division into fractions.

was observed (Table 1). As in the case of embryo growth zeatin was more active than GA<sub>3</sub> in reversal of the ABA inhibiting effect on polyribosome formation. On the other hand, in samples where <sup>3</sup>H-uridine was present no significant effect of ABA, ABA and GA<sub>3</sub> mixture, as well as ABA and

Table 2

<sup>3</sup>H-uridine and <sup>14</sup>C-aminoacid mixture incorporation into the polyribosomal fraction.

Polyribosomes were isolated from embryos after 24 hours germination of intact caryopses in the presence of phytohormones under study

	cmp·1 μg <sup>-1</sup> polyribosomal fraction										
Treatment		<sup>3</sup> H inco	rporation	<sup>14</sup> C incorporation							
	T	LP	P	M	T		P	М			
Control	279	209	188	137	184	124	105	71			
ABA	137	40	60	44	63	16	26	16			
$ABA + GA_3$	136	40	59	45	66	16	27	23			
ABA + zeatin	134	38	58	43	79	20	33	24			

M - monosomes; T. LP. P as in Table I.

zeatin mixture on the synthesis of polyribosomal RNA was found in the first 2 h of germination and from 16 to 18 h. Similar results were obtained for samples with the radioactive precursor during 46 hours grain germination and 2 hours germination of the excised seedlings (data unpublished). In all the studies on polyribosomal RNA synthesis in excised embryos (0-2 h, 16-18 h, 46-48 h) in the control, as well as, in samples treated with ABA and stimulators specific radioactivities (cpm·1 mg<sup>-1</sup> RNA) were almost identical after the specified time of germination.

The results were strickingly different when embryos were germinated in intact grains for 24 h in the presence of <sup>3</sup>H-uridine, <sup>14</sup>C-aminoacid mixture and phytohormones (Fig. 4, Table 2). ABA caused then nearly two-fold decrease in the polyribosomal RNA synthesis in embryos (on the basis of <sup>3</sup>H-uridne incorporation) and nearly three-fold decrease in the ribosomal protein synthesis (on the basis of <sup>14</sup>C-aminoacid mixture incorporation). During germination of the intact caryopses, as in the excised embryos, ABA action also resulted in a significant decrease in the polyribosome contribution to the total ribosomal fraction. After 24 hours grain germination polyribosome contribution to the sum total of embryonic ribosomes was in the presence of ABA — 47.2% and in the control — 67.1%. When the grains were germinated in the presence of inhibitor and GA3, as well as zeatin an increase in the polyribosome contribution to the total ribosomal fraction amounted to 52.3% and 55.4% respectively. ABA caused also significant changes within small and large polyribosomes (Table 1). From the obtained results it could be also determined that the higher polyribosome contribution to the sum total of ribosomes the higher ribosomal protein synthesis.

Interaction of ABA and GA<sub>3</sub> led to the enhanced ribosomal protein synthesis mainly within monosome fraction. Zeatin reversal was stronger and occurred in all the fractions obtained through ultracentrifugation (Fig. 4, Table 2). However, no enhanced transcriptional activity (on the basis of <sup>3</sup>H-uridine incorporation) associated with GA<sub>3</sub> and zeatin reversal of ABA inhibiting effect was observed during germination of *Triticale* caryopses.

# DISCUSSION

ABA prevents the starting of the germination process through physiological blocking. Its molecular character is still unknown. It is generally assumed that ABA action lies in the disturbance in mRNA synthesis, posttranscriptional modification, or translation (Dure 1975, Fountain and Bewley 1976, Walton 1977, 1980, Jacobsen and Higgins 1978a,b, Galli et al. 1979). In the samples treated with ABA water uptake in swelling embryos is lower already during preimbibition (Fig. 1). Schopfer et al. (1979) have found that during germination ABA prevents embryo development in a reversible way and its action consists in the inhibition of water uptake, which is associated with embryo growth. According to the authors mentioned above ABA inhibiting action lies more in the regulation of embryonic tissue water uptake, than in the regulation of gene activity. However, differences in water uptake, which were observed in this study during imbibition of embryos, between caryopses which were and were not treated with ABA were relatively small.

It is often assumed that growth stimulator reversal of ABA inhibiting effect indicates that ABA acts upon nucleic acid biosynthesis. The studies on germination of pear embryos and elongation of bean embryonal axes have proved that cytokinin and gibberellin reversal of this inhibition is associated with an increase in the RNA synthesis (Khan and Heit 1969, Sussex et al. 1975). However, in the present studies on intact Triticale caryopses and embryos excised from them such a relation has not been observed. No increase in the polyribosomal RNA synthesis occurs with GA<sub>3</sub> and zeatin release of Triticale caryopses and embryos from the ABA--induced "dormancy". Moreover, in excised embryos ABA has not caused any decrease in the transcriptional activity. Yet, when intact caryopses were germinated for 24 h approx. two-fold decrease in the synthesis of embryonic polyribosomal RNA took place. As the results obtained are contradictory this phenomenon should be better analyzed. On the other hand, it is generally known that embryo excision stimulates the transcriptional process (Grzelczak and Buchowicz 1977).

A significant correlation between ABA-induced inhibition of the embryo growth and polyribosome formation has been observed. Also a clear in-

crease in the polyribosome contribution to the total fraction of embryonic ribosomes has been noticed during GA3 and zeatin reversal of ABA inhibiting effect. At that time enhanced synthesis of ribosomal proteins also occurs. The similar increase has been noted in the lettuce embryos, when they have been released from ABA-induced "dormancy" (Fountain and Bewley 1976). There is a close relationship between amount of polysomes and the total protein synthesis (Woodland 1974). It has been proved that the sprouts of high protein cereal varieties contain more polysomes than the sprouts of low protein varieties (Ching and Rynd 1978). All these facts indicate that ABA causes a decrease in the protein biosynthesis already in the earliest hours of germination. The other students have found that GA<sub>3</sub> stimulation of the polyribosome formation and protein biosynthesis takes place already in the initial period of lettuce seed germination, when an increase in RNA synthesis is undetectable (Fountain and Bewley 1976, Bewley and Black 1982). After 24 hours germination of intact Triticale caryopses in the samples treated with ABA <sup>3</sup>H-uridine incorporation into polyribosomes was two-fold lower. At the same time <sup>14</sup>C-aminoacid mixture incorporation decreased as many as three times. Hence, direct inhibitor action on the process of transcription is doubtful. From the results obtained it can be inferred that in the initial period of germination of Triticale caryopses phytohormone control of protein biosynthesis takes place more at the translation than transcription level.

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Działanie kwasu giberelowego i zeatyny w procesie znoszenia spoczynku indukowanego działaniem kwasu abscysynowego u ziarniaków Triticale

#### Streszczenie

Badania przeprowadzono na kiełkujących zarodkach i całych ziarniakach Triticale. Traktowanie ziarniaków kwasem abscysynowym (ABA) podczas preimibicji i 24 godz. kiełkowania spowodowało 63% inhibicję wzrostu zarodków. Częściowe odwrócenie wpływu ABA powodowała giberelina-A<sub>3</sub> (18%) oraz zeatyna (22%). Przy łącznym zastosowaniu obu stymulatorów. obserwowano wyraźną reakcję synergistyczną (36%). Nie stwierdzono istotnego wpływu ABA, mieszaniny ABA i GA3 oraz mieszaniny ABA i zeatyny na synteze polirybosomalnego RNA w pierwszych okresach kiełkowania izolowanych zarodków. Kwas abscysynowy powodował jednak ok. dwukrotne zmniejszenie wcielenia 3H-urydyny do ogólnej frakcji rybosomalnej zarodków, podczas 24 godzinnego kielkowania całych ziarniaków. W tym samym czasie stwierdzono, że wcielenie 14C-mieszaniny aminokwasów do białek rybosomalnych było około trzykrotnie mniejsze. W badaniach nad uwalnianiem ziarniaków z indukowanego kwasem abscysynowym "spoczynku" przez GA3 i zeatynę, stwierdzono że wraz ze wzrostem• udziału polirybosomów w ogólnej puli rybosomów wzrasta również synteza białek rybosomalnych. Nie stwierdzono natomiast wzmożonego wcielenia 3H-urydyny do frakcji polirybosomów. Uzyskane wyniki sugerują, że w początkowym okresie kiełkowania ziarniaków Triticale, regulacja biosyntezy białek przez fitohormony odbywa się raczej na pozimie translacji niż transkrypcii.