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The effect of ABA and AMO-1618 on the preharvest sprouting of triticale caryopses

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Abstract

The experiments were conducted on developing triticale var. Grado caryopses. Treatment of freshly gathered, unripe triticale caryopses with abscisic acid (ABA) decreased their precocious germination throughout the entire period of development and ripening. The more mature the embryos that were germinated, the lower the inhibition by ABA. This indicates that the sensitivity of the embryo to ABA decreases during the course of caryopsis development and that the role that this hormone can play in the prevention of spouting in ears during the final stages of maturation, is limited. A known inhibitor of gibberellin synthesis, the retardant AMO-1618, was also tested in these experiments. This compound caused the reduction of germination capability only in the initial stages of development of triticale caryopses. Its most visible effect was noted during the germination of caryopses collected 30 days after flowering. The effect of this compound on the precocious germination of isolated embryos also decreased as the degree of maturity of these embryos increased. In the opinion of this author, this is connected with the fact that intense gibberellin synthesis and accumulation occurs only in the early stages of caryopsis development.

Key words: triticale, precocious germination, AMO-1618, abscisic acid

INTRODUCTION

Sprouting in cereals causes very high losses. It decreases the consumption and fodder value of caryopses and disqualifies them as industrial and seed grain. The level of dormancy of cereal cyryopses determines the tendency of grain to precociously germinate. It has been found that the longer

and deeper the dormancy of grain, the less probable it is that it will precociously germinate (Mazurek 1975). Most authors tend to accept the concept that, in addition to the physical effect of seed coats, a basic mechanism of control of the onset and completion of dormancy is the differentiated, in time and place, action of various growth regulators (Wareing and Saunders 1971, Villiers 1972, Khan 1977, Bewley and Black 1982, King 1982).

In previous studies (Weidner 1984a, b) it was found that cytokinins stimulate the preharvest sprouting of triticale caryopses at a different point in their development than do gibberellins. In this study, the effect of exogenous abscisic acid and another known inhibitor of gibberellin synthesis, AMO-1618, on the precocious germination of triticale caryopses and isolated embryos during development was examined.

MATERIAL AND METHODS

The studies were conducted in 1985 on triticale var. Grado caryopses supplied by the Plant Cultivation Station in Choryń. This variety was cultivated on the experimental plots of the Department of Plant Physiology and Biochemistry of the ATA in Olsztyn. The period of development and ripening of the caryopses lasted 58 days. During that time, the dry weight and water contents were determined in the caryopses and embryos. During development and ripening, starting from the 23rd day after flowering, 6 samples of caryopses were taken at 7 day intervals. The freshly collected caryopses were isolated from the ears by hand under sterile conditions. Immediately after isolation, the caryopses were subjected to germination in cylinders, in the dark at 21-22°C for 14 days. Germination was conducted in water (control), in two concentrations of abscisic acid, 10^{-6} and 10^{-5} M (Sigma, USA) and in a solution of AMO-1618 (2-isopropyl-4-dimethyl--amino-5-methylphenyl-1-piperidinecarboxylate methyl chloride) at a concentration of 3×10^{-4} M (Serva, FRG). After the set time of germination, the percentage of germinated caryopses and the average dry weight of seedlings, shoot lenght, length of the longest root and number of roots per seedling were determined. The obtained results were supplemented with the calculation of the standard deviation.

The second part of the study was on the germination of isolated embryos on agar with glucose according to the method of Johnston and Stern (1957). Four samples of embryos were taken for this. The embryos were isolated (under sterile conditions) from caryopses collected 23, 30, 37 and 58 days after flowering. ABA to the final concentration of 10^{-6} M

and 10^{-5} M and AMO-1618 to 3×10^{-4} M were added to the appropriate agar substrata. In these experiments, in addition to controls, so-called washing-out of samples was used. The embryos that were intended to be used in the washing-out trials were first subjected to an hour-long washing in sterile, aerated water in order to remove inhibitors of germination. The germination of isolated embryos was conducted at a temperature of 21-22°C for 12 days. Observations on the number of germinating embryos were done initially every 6, then every 24 hrs. An embryo was considered to have germinated if the length of its radical attained 2 mm.

RESULTS

The content of water in caryopses determines to a large extent the metabolic activity of both endosperm and embryo tissues. It can be seen from the data presented on Fig. 1 that in the initial phase of development

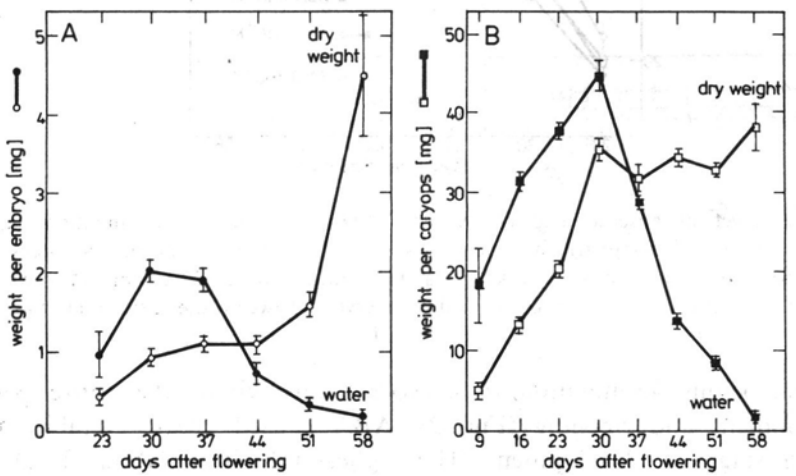

Fig. 1. The dry weight and water contents of embryos (A) and whole triticale caryopses (B) during development and ripening. The data on the figure represent the mean values of 5 determinations. Standard deviation is marked by vertical bars

(milk ripeness) the content of water in the embryos and entire caryopses increased quickly up to 30 days after flowering, then underwent a sharp decline. The dry weight content of the embryos increased during the entire period of development. This increase was very swift from the 44th day after flowering. The dry weight content of the caryopses increased to 30 days after flowering, then remained practically constant.

The results of the experiments on the germination of unripe, freshly

collected triticale caryopses are presented on Fig. 2. It results from these data that as the caryopses develop and mature, their germination capability increases. The largest increase in the number of germinating caryopses was seen up to 30 days after flowering (to about 60%). Between the 30th and 37th days after flowering, the increase in the germination capacity was somewhat checked, after which it slowly grew to when full ripeness was attained, where the germination capacity of the control sample was over 80%.

Treatment of unripe caryopses with abscisic acid (ABA) caused a decrease

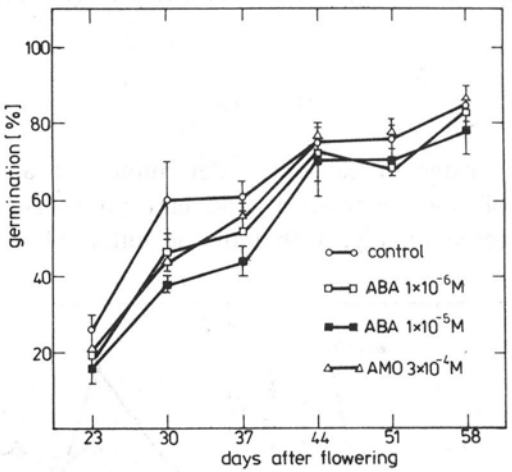

Fig. 2. The effect of abscisic acid (ABA) and AMO-1618 on the germination capacity of developing and ripening triticale caryopses. Freshly collected, unripe caryopses were subjected to germination in the dark, at a temperature of 21-22°C for 14 days. The samples of caryopses were collected in 7-day intervals between the 23rd and 58th days after flowering

of the precocious germination of caryopses throughout the entire period of development and ripening (Fig. 2). ABA caused greater inhibition in the earlier stages of development. The highest inhibition (about 37%) was found between the 30th and 37th days after flowering in the samples treated with 10^{-5} M ABA.

A known inhibitor of gibberellin biosynthesis, AMO-1618, was also used in these experiments. This compound caused a decrease in the germination capacity only in the initial stages of triticale caryopsis development. Its strongest effect was noted on the germination of caryopses collected 30 days after flowering.

The effects of ABA and AMO-1618 on the germination of isolated embryos of different ripeness are presented on Fig. 3. The embryos were isolated from caryopses at different stages of development. In these studies, in addition to controls, samples with washing-out were also used. Embryos in these samples were additionally subjected to one hour-long washing in

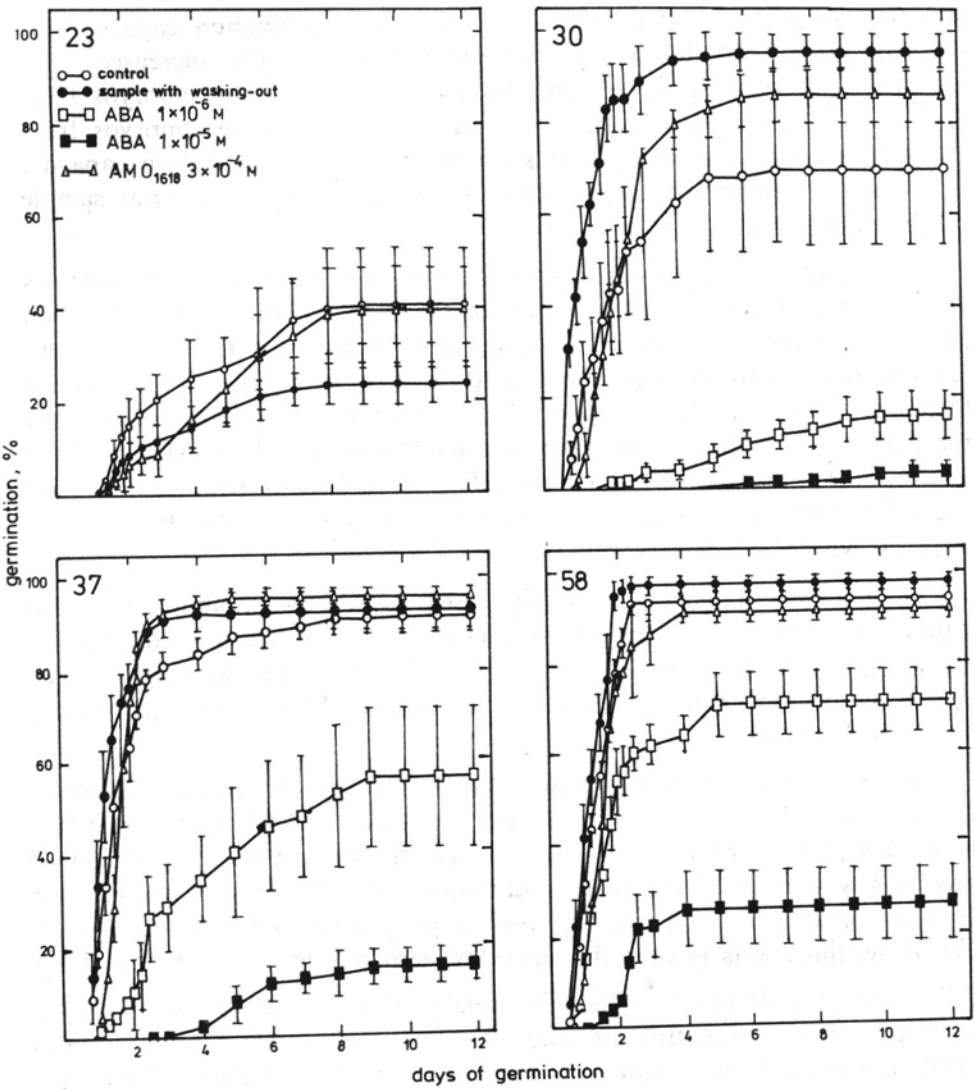

Fig. 3. The effect of abscisic acid (ABA) and AMO-1618 on the germination of isolated embryos from caryopses of different degrees of ripeness. The number in the upper corner of the each figure stands for the number of days after flowering on which samples of the caryopses were collected for study. The embryos were germinated according to the method of Johnston and Stern (1957), and a germinated embryo was considered to be one having a radical 2 mm long. Along with the control sample, a sample with washing-out was also used in this study. The embryos in this sample were additionally subjected to a one hour-long washing with aerated sterile water

aerated water. This was intended to remove germination inhibitors, synthesized in the caryopses during development. In all of the samples, with the exception of the first (embryos obtained from caryopses collected 23 days after flowering), washing-out enhanced both the germination capacity and the rate at which the number of germinated embryos increased. The greatest effect of washing out on germination was noted in embryos from caryopses collected 30 days after flowering. In this sample, embryos from the control (without washing-out) showed about 70% germination capacity, whereas the germination capcity of embryos from the washing-out sample reached about 95%.

ABA inhibited the germination of isolated embryos in all of the samples at both concentrations used. The use of the higher concentration (10^{-5} M) gave a stronger effect than the lower concentration (10^{-6} M). At both concentrations, ABA completely inhibited the germination of embryos isolated from caryopses collected 23 days after flowering. The more mature were the germinated embryos, the lower the inhibition caused by ABA, at both concentrations used (Fig. 3). In general, it should be concluded that ABA exerted a much greater influence on the germination of isolated embryos than on whole, intact caryopses.

The gibberellin biosynthesis inhibitor used, AMO-1618, inhibited the germination of isolated embryos of different degrees of ripeness during the initial stages of incubation. The influence of this compound on the germination of isolated embryos decreased as the ripeness of the germinating embryos increased.

Detailed analysis of the seedlings which grew from the triticale caryopses of different degrees of maturity in the presence of ABA and AMO-1618 is presented in Tables 1-4. Tables 1 presents the average dry weight of seedlings which grew from triticale caryopses after 14 days of germination. It was found that after the set period of germination, the dry weight of the seedlings was greater the riper the germinating caryopsis had been. ABA caused a decrease in the dry weight of the seedlings in all of the samples at both concentrations used. The higher (10^{-5} M) concentration of ABA caused greater inhibition of the development of the seedlings. AMO-1618 caused a decrease in the dry weight of seedlings in the first three samples — up to the 37th day after flowering.

It should be emphasized that ABA inhibited the precocious germination of all of the caryopses collected at all of the stages of development and ripening. This refers to both the germination capacity of the freshly collected caryopses and the dry weight of the seedlings which grew from them (Table 1), the length of their shoot part (Table 2), the length of the longest root (Table 3) and the number of roots (Table 4). On the

Table 1

The mean dry weight (mg) of seedlings grown from unripe triticale caryopses after 2 weeks of germination in the presence of abscisic acid (ABA) or AMO-1618

Combination / Number of days after flowering	Control	ABA, 1×10^{-6}M	ABA, 1×10^{-5}M	AMO-1618
23	3.95 ± 0.66	3.72 ± 0.61	2.76 ± 0.45	3.35 ± 0.16
30	6.83 ± 0.79	6.73 ± 0.69	4.56 ± 0.71	6.17 ± 0.44
37	7.11 ± 0.54	6.46 ± 0.77	4.47 ± 0.85	7.04 ± 0.75
44	8.54 ± 0.65	7.13 ± 0.57	4.20 ± 0.49	8.55 ± 0.36
51	9.13 ± 0.71	8.24 ± 1.12	3.21 ± 0.37	9.13 ± 0.29
58	9.33 ± 0.64	8.46 ± 0.80	3.85 ± 0.66	9.38 ± 0.64

During development, samples of caryopses were taken in weekly intervals (begining from the 23rd day after flowering). The data in the table are the mean values of 5 determinations with the standard deviation taken into account.

Table 2

The mean shoot length (mm) of seedlings grown from unripe triticale caryopses after 2 weeks o germination in the presence of abscisic acid (ABA) and AMO-1618

Combination / Number of days after flowering	Control	ABA, 1×10^{-6}M	ABA, 1×10^{-5}M	AMO-1618
23	82.12 ± 38.19	78.31 ± 46.51	45.57 ± 24.69	56.88 ± 33.47
30	102.60 ± 47.52	99.30 ± 53.09	54.96 ± 32.49	87.09 ± 46.03
37	108.50 ± 61.77	107.87 ± 62.95	35.46 ± 34.26	105.61 ± 67.58
44	135.78 ± 58.33	132.63 ± 64.14	56.09 ± 25.17	135.86 ± 64.34
51	138.65 ± 67.89	131.82 ± 58.96	33.67 ± 22.94	138.92 ± 63.74
58	145.08 ± 70.86	132.22 ± 55.44	63.56 ± 42.07	144.78 ± 57.54

The samples of caryopses were taken in weekly intervals during development. The data in the table are the mean values of 300 determinations with the standard deviation taken into account.

Table 3

The mean length of the longest root of seedlings (mm) grown from unripe triticale caryopses after 2 weeks of germination in the presence of abscisic acid (ABA) and AMO-1618

Combination / Number of days after flowering	Control	ABA, 1×10^{-6}M	ABA, 1×10^{-5}M	AMO-1618
23	93.01 ± 41.73	59.54 ± 23.13	57.90 ± 38.58	89.06 ± 44.80
30	117.09 ± 43.31	79.59 ± 35.72	65.86 ± 42.13	105.50 ± 50.44
37	122.64 ± 50.96	77.15 ± 40.89	63.92 ± 39.00	109.48 ± 53.04
44	130.61 ± 48.81	128.44 ± 44.44	88.76 ± 35.59	115.25 ± 42.35
51	137.12 ± 49.64	115.47 ± 46.50	79.69 ± 37.65	118.89 ± 42.95
58	144.11 ± 52.14	127.39 ± 52.29	79.74 ± 38.29	118.45 ± 41.30

During development, the caryopses were sampled weekly. The data in the table are the mean values of 300 determinations with the standard deviation taken into account.

Table 4

The mean number of roots of seedlings grown from unripe triticale caryopses after 2 weeks of germination in the presence of abscisic acid (ABA) and AMO-1618

Combination / Number of days after flowering	Control	ABA, 1×10^{-6} M	ABA, 1×10^{-5} M	AMO-1618
23	3.52 ± 1.24	3.49 ± 1.37	2.52 ± 1.03	3.17 ± 1.25
30	4.68 ± 1.31	4.57 ± 1.46	4.07 ± 1.54	4.43 ± 1.35
37	4.82 ± 1.32	4.69 ± 1.19	3.36 ± 1.45	3.63 ± 1.39
44	5.03 ± 1.02	5.01 ± 1.04	4.54 ± 1.28	5.06 ± 1.11
51	5.46 ± 1.12	5.39 ± 1.29	5.21 ± 1.29	5.41 ± 0.97
58	5.67 ± 1.14	5.52 ± 1.15	5.35 ± 1.16	5.61 ± 0.87

During development, the caryopses were sampled weekly. The data in the table are the mean values of 300 determinations, with the standard deviation taken into account.

other hand, AMO-1618 inhibited the germination of freshly collected unripe caryopses, mainly in the first stages of development, up to 37 days after flowering. An exception was in the case of only one seedling development index — the average length of the longest root (Table 3), where the retardant inhibited the elongation of the roots in all of the samples.

DISCUSSION

The data on the changes in the water and dry weight contents presented in the results of this study, are generally in agreement with the results of other authors working on the dynamics of water and organic substance accumulation in developing cereal carysopses (Ingle et al. 1965, Lityński 1977, Grzesiuk and Kulka 1981).

The data obtained in this study on the germination of freshly collected unripe triticale var. Grado caryopses, is similar to that obtained for the triticale MT-3 strain (Weidner 1983, 1984a). The conducted study shows that the increase in germination capacity during development is not uniform. A quick increase in the germination capacity of cereal grains was observed in the initial period of development (milk ripeness). After this, a period of arrest or lowering was seen. It should be added that in earlier studies (Weidner 1983, 1984a) done on the MT-3 strain, a significant decrease in the germination capacity during the milk-wax stage was found. After the period of decreased germination capacity of the caryopses, a quick increase of this ability was observed lasting until the full ripeness stage was reached. The fall in the germination capacity during the milk-wax stage is, according to King (1976) caused by the peak accumulation of ABA in the grain — its concentration at this time in wheat rises 60-fold. Similar results have also been obtained in studies on triticale caryopses (King et al. 1979). These authors showed the strict interdependence between the increase in the ABA content in caryopses and the decrease in their germination capacity and ability to synthesize α-amylase. In another study on the formation of a mechanism preventing the germination of unripe caryopses (Weidner 1984b), freshly collected triticale (MT-3) caryopses from the three main development stages (milk ripeness, milk-wax and full) were allowed to germinate for 72 hours. The lowest polyribosome content as well ^{3}H-uridine incorporation into the total ribosome fraction was also shown by the embryos from the caryopses at the milk-wax ripeness stage. In this sample, in contrast to the samples collected at the remaining two stages, after 72 hours, no external signs of germination were observed.

A common characteristic of developing cereal caryopses is the high synthesis and activity of gibberellins and cytokinins during milk ripeness

(Wheeler 1972, Mounla and Michael 1973, Radley 1976), after which the intense accumulation of ABA during milk-wax ripeness takes place (King 1976, Radley 1976, Goldbach and Michael 1975, King et al. 1979). It is generally known that in mature cereal caryopses, GA_3 and ABA regulate germination and the synthesis of various enzymes, e.g. α-amylase. That is why it seems that changes in the accumulation of various phytohormones in caryopses during development also play a significant role in the regulation of dormancy. Confirmation of this can be the described phenomenon of unequal growth of the germination capacity of triticale caryopses.

It has been shown previously that the effect of various hormones depends to a large degree on the sensitivity of the system synthesizing enzymes (Weidner 1982). This sensitivity changes along with the changes of the physiological state of the tissues during the development of caryopses. Kinetin stimulated the precocious germination of triticale caryopses in the initial stages of development — up until the 30th day after flowering (Widner 1984a), whereas GA_3 stimulated the germination of wheat and triticale caryopses only in the second half of their development (Radley 1979, Weidner 1984a). The use of a strong inhibitor of gibberellin synthesis such as AMO-1618, brought about, however, a fall in precocious germination of triticale caryopses only in the first phase of their development (Fig. 2). It seems then, that the lack of stimulation of germination, during the first half of the development period, by exogenous gibberellin-A_3 observed in earlier studies can result from the fact of the large synthesis and presence of active endogenous gibberellins during this stage of development (Wheeler 1972, Radley 1976). Abscisic acid inhibited precocious germination during the entire period of development and ripening of caryopses. The effect of this hormone during the first phases of development was stronger, which in the opinion of this author, points to the greater sensitivity of tissues at this period to ABA. This opinion seems to be confirmed by the results of the experiments on isolated embryos (Fig. 3). They indicate that the sensitivity of embryo tissues to ABA change during development. The more mature that the embryos subjected to germination were, the weaker was the inhibition of germination by ABA at both concentrations.

In the experiments on the effect of AMO-1618 on the development of seedlings which grew from caryopses of different degrees of ripeness (presented in Tables 1-4), only the elongation of roots was highly inhibited in all of the studied samples. It should be added that Bode and Wild (1984), using another retardant — CCC (2-chloroethyl-trimethyl-ammonium chloride) — at a high concentration (10^{-2} M) found the immediate inhibition of the growth of roots and a strong inhibitory effect on the growth

of leaves in 11-day old wheat seedlings of the Kolibri variety. Similar results were also obtained by Wünsche (1970).

The greatest inhibitory effect of AMO-1618 was found in all of the samples during the initial period of germination of isolated embryos of various degrees of ripeness. As was previously shown (Weidner 1984a), the greatest promoting effect of gibberellin-GA_3 was also found in the first stages of germination of isolated embryos. It seems then, that both of these phenomena can be related to the fact that in the initial phase of germination, embryo growth occurs due to the elongation of cells, and only later, cell divisions begin to play a more important role (Weidner 1982). That is why the initial elongation of the embryo seems to be more sensitive to gibberellins. It should, however, be added that the studied system is, in this period, also sensitive to cytokinins (Weidner 1984a).

The embryos in cereal caryopses and other seeds contain, during certain periods of embryogenesis, high amounts of ABA (Radley 1979, King 1982, Ackerson 1984a, b). One of the effective ways of removing ABA and other inihibitors of germination from unripe embryos is washing them out with sterile water (Ackerson 1984a). A condition of success is, however, not injuring the embryos during the washing-out. The least mature embryos are the most vulnerable to this. The reduction of the germination capacity of embryos isolated from triticale caryopses, collected 23 days after flowering, in the washing-out test is, in the opinion of this author, connected with the embryos being damaged. Ackerson (1984b) found that the germination of isolated embryos is poor when they contain 4-16 $\mu g\ g^{-1}$ fresh weight ABA. When the ABA content in the embryos falls below 4 $\mu g\ g^{-1}$ fresh weight, germination abruptly increases. On the basis of the effectivity of washing-out, it can be concluded that the maximal ABA content is in triticale var. Grado embryos 30 days after flowering — during the period of maximal hydration of the embryo and caryopsis tissues. Similar results have also been obtained by King et al. (1979) in studies on developing triticale (6A190) caryopses, in which he determined the ABA content by gas chromatography. It also can be concluded from the presented data that triticale var. Grado caryopses collected 30 days after flowering (the period of development and ripening lasts 58 days) and subjected to germination react the most to treatment with both ABA and AMO-1618. This points to the strong reaction of caryopses to phytohormones in the middle period of their development (the milk-wax phase) and to the changing sensitivity of the tissues of the developing embryo and the whole caryopses to the presence of different types of growth regulators.

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Wpływ ABA i AMO-1618 na przedsprzętne porastanie ziarniaków triticale

Streszczenie

Badania przeprowadzono na rozwijających się ziarniakach triticale odmiany Grado. Traktowanie świeżo zebranych, niedojrzałych ziarniaków triticale kwasem abscysynowym (ABA) powodowało obniżenie przedwczesnego kiełkowania ziarniaków podczas całego okresu rozwoju i dojrzewania. Im bardziej dojrzałe zarodki poddawano kiełkowaniu, tym mniejszą inhibicję wywoływał ABA. Swiadczy to o malejącej wrażliwości zarodka na ABA w miarę postępującego rozwoju ziarna oraz o ograniczonej roli jaką może ten hormon odgrywać w zapobieganiu porastania ziarna w kłosach, w końcowych fazach dojrzewania. W badaniach zastosowano również znany inhibitor biosyntezy giberelin — retardant AMO-1618. Związek ten powodował zmniejszenie zdolności kiełkowania ziarna jedynie w początkowym okresie rozwoju ziarniaków triticale. Najsilniejsze jego działanie stwierdzono podczas kiełkowania ziarna zebranego 30 dni po kwitnieniu. Wpływ tego związku na przedwczesne kiełkowanie izolowanych zarodków również ulegał osłabieniu w miarę dojrzewania zarodków poddawanych kiełkowaniu. Zdaniem autora związane jest to z faktem intensywnej syntezy i akumulacji giberelin tylko we wczesnych fazach rozwoju ziarniaków.