stresses in two strains of maize

Comparative studies on the hormonal patterns as possible indicators of different

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ABSTRACT

Seed of two pure strains of Maize (G4 and Rg11) were treated with gamma rays (60 Gy) or Na-azide (0.001 M) as physical and chemical mutagens, respectively, for possible induction of mutations that might be useful in enhancing their tolerance against drought. Two different irrigation systems were applied to both strains, normal irrigation and drought stress. Under normal irrigation, auxins and cytokinins were likely the main factors in alliance with growth, so that Rg11 plants with relatively enhanced levels maintained a higher growth rate. Under drought stress, these hormones showed minor changes in both strains. Abscisic acid appeared likely to play a major part in the response, since an enhanced level was displayed in G4 plants that exhibited higher ability to cope with drought stress. Similar trends were also generally shown with respect to the changes concomitant with gamma irradiation and Na-azide treatment.

Keywords: Maize, gamma rays, drought, auxins, cytokinins, Abscisic acid

INTRODUCTION

Physical and chemical mutations were used in several crop species to induce variation in quantitative and qualitative traits. Ionizing radiation is known to induce alterations to morphological and physiological processes in plants, and can produce modifications of the DNA bases (Arouma *et al.* 1989a,b). The growth habits and physiological properties of plants may differ markedly under stressful conditions (Bray *et al.* 2000). In this connection, growth hormones have long been known to be important as starting or mediating signal transduction cascades in plants, where the components of the underlying cellular machinery have been identified and characterized (Trewavas 2000). Certain mutations can simultaneously influence one or more of the plant hormones, thus altering the response to many environmental stresses including drought (Ghassemian *et al.* 2000). Crozier *et al.* (2000) also mentioned that changes in hormone concentrations and tissue sensitivity mediate a whole range of developmental processes, many of which involve interaction with stressful environmental factors.

Abscisic acid (ABA) is the most studied plant hormone under water stress. Thus, higher amounts of ABA were recorded in leaves of drought-stressed maize (Jia & Zhang 2000) and wheat (Chandrasekar *et al.* 2000) than in those of corresponding unstressed plants. Many authors studied the mechanism of ABA action at low water potentials (e.g. Papova, 2000). Generally it has been concluded that ABA appears likely to act via

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multiple pathways including rapid closure of stomata and by slower changes in gene expression.

Other growth hormones have also been studied under adaptation to water stress. Thus, Polevoi & Polevoi (1992) determined the highest free IAA and ABA content in the root zone of maize. There was a positive relationship between cell meristematic activity and the levels of zeatin and zeatin riboside. The ratios of these hormones were assumed to be responsible of the maintenance of primary root elongation and retarded shoot growth under water stress.

Studies of the effect of mutagens on plant hormones have mostly used gamma (y) rays. Thus Staikov et al. (1985) concluded that a low dose of gamma rays (1000 R) enhanced the level and activity of IAA and GA3 in pea seeds. Uppal & Maherchandani (1988) and Arora et al. (1989) mentioned that GA3 could reduce the cytological damage induced by γ rays in wheat seeds. The latter authors interpreted the effect of GA3 as enhancing peroxidase activity for elimination of the chromosome-damaging peroxide radicals formed during irradiation. They also added that GA3 could promote repair processes. Rabie et al. (1996) also showed that y rays at low doses (1, 2, and 4 K rad) enhanced auxins, gibberellins, and cytokinins, and reduced ABA levels. A reverse sequence was observed on application of higher doses (8 and 10 K rad). Momiyama et al. (1999) concluded that inhibited elongation of maize coleoptiles in response to y irradiation could be ascribed to attenuated IAA levels, as a result of modulation of IA A biosynthesis or catabolism. Furthermore, a γ-ray-induced mutant of Catharenthus roseus was rendered resistant to water stress (Rai et al. 2001). The authors found that under water restriction, ABA content in the leaves of this mutant was approximately 500fold higher than in leaves of the wild type.

The present work uses maize because it is an important human animal food source, and there is a great need in Egypt to narrow the gap between cereal crop production and consumption. Gamma irradiation and Na-azide were used as mutagenic agents for triggering drought tolerance under inadequate irrigation. The growth responses and drought tolerance of the treated plants were also studied (see Hamid-Eldin, 2004). In this work, identifying the responses of endogenous hormones in the plants encountering drought stress was the main target. For this purpose, two pure strains of maize G4 and Rg11 were used.

MATERIALS AND METHODS

Seeds of two pure strains of maize, G4 and Rg11, were obtained from the Maize Research Department, Institute of Field Crop Research, Agriculture Research Center, Ministry of Agriculture, Giza, Egypt. Dry grains of the two strains were irradiated with 60 gray γ rays. For application of Na-azide treatment, seeds (dry unirradiated) were soaked in 0.001M solution for 6 hours, and then washed thoroughly with tap water before sowing. Lots of untreated grains were used as controls.

The seeds treated with either γ rays or Na-azide, and those of the control were sown in a randomized complete-block experiment with two replications. The experiment was conducted under two different irrigation conditions. The first was normally irrigated every 10 days after germination, and the other was subjected to drought stress by irrigating every 20 days after germination.

Leaf samples for extraction of the different hormones were taken after 50 days from sowing. For this purpose the first fully expanded youngest leaves (from the top) were taken. Extraction, methylation and estimation of acidic hormone fraction (IAA, GA3, and ABA) were done following the method of Vogel (1975), as adopted by Guinn et al.

(1986). The method of extraction of cytokinins was similar to that used with the acidic hormones. Estimation of the different cytokinin fractions was carried out by HPLC, using an ODS hypersil C18 column as described by Müller (1986). The different data of acidic hormones and cytokinin fractions were given automatically by software programs connected to the apparatus.

RESULTS AND DISCUSSION

The values measured by HPLC of the endogenous concentrations of different phytohormones in 50-day-old plants of the maize strains G4 and RG11 are shown in Table 1 for auxin (IAA), gibberellin (GA3), and ABA. The results of cytokinins (benzyladenine, zeatin, zeatin riboside, and total cytokinins) are presented in Table 2. These results are devoted to plants resulting from seeds treated with γ rays (60 Gy) or sodium azide (0.001M) and subjected to normal irrigation or to drought stress. Seeds of the control were not treated, but were irrigated either normally or subjected to drought.

Table 1 shows that the concentrations of IAA and total cytokinins are markedly higher in RG11 than G4 plants of the normally irrigated controls. The increase of cytokinins in the strain RG11 was mainly attributed to a markedly higher concentration of zeatin riboside: zeatin was lower and benzyladenine was comparable to corresponding value in the G4 strain. The relatively higher levels of auxin and cytokinins in strain RG11 than G4 agrees with our previous results (Hamid-Eldin, 2004), which indicated that RG11 exhibited markedly enhanced growth rates and biomass production. Auxin and cytokinin are known to have a spectrum of diverse physiological activities, including the control of cell division and enlargement as well as diametric growth (Cleland, 1999). A recent area of research, in this respect is the interference of both hormones with the orientation of microtubules in the cell cytoskeleton, in a way relevant to genetically determined growth (Baluska *et al.* 1999).

Table 1 also shows more or less comparable levels of ABA and a lower content of GA3 in the control plants (normally irrigated) of strain RG11, as compared with corresponding plants of G4. Inspired by sharing biosynthetic origins of both GA3 and ABA in the terpenoid biosynthesis pathway (Crozier *et al.* 2000), a reverse correlation of their concentrations might be assumed. Thus, ABA was found to influence the accumulation or operation of gibberellins (Benson *et al.* 1990).

Under drought conditions, the plants of the control (seeds untreated) of both strains showed enhanced levels of IAA and a comparatively slight increase of total cytokinins, as compared with corresponding control plants under normal irrigation. Different responses were shown in the two strains with respect to the concentrations of GA3 and ABA. Thus in G4 there was a decrease of GA3 and an increase of ABA in response to drought, but in RG11 both ABA and GA3 decreased. In general, there is considerable evidence that ABA increases during most stresses, particularly water deficit (Bray *et al.* 2000). There is also evidence that exogenous treatment with ABA may induce changes similar to those caused by drought and some other stresses (Shen & Ho 1999, Kim *et al.* 2003). Molecular studies further reveal that ABA is involved with the transcriptional response to dehydration by inducing, for example, proteins such as the late-embryogenesis-abundant proteins with water deficit in vegetative tissue (Cuming 1999), phospholipase-D involved in plant responses to various forms of osmotic stress, and recently discovered novel drought-responsive genes and transcription factors (Bartels & Salamini 2001).

We have shown (Hamid Eldin 2004) that the growth parameters and biomass productivity of the strain G4 were only slightly changed under the influence of drought from corresponding normally irrigated plants, but a substantial drop was observed with the

RG11 plants. This indicated that the strain G4 is rather drought tolerant, whereas RG11 is sensitive. This might be further supported by the fact that RG11 has a higher ABA content than G4 when both were grown under normal irrigation condition (Table 1). Others have shown that stress-tolerant species have lower contents of ABA than sensitive species (He & Cramer 1996). Therefore it might be concluded that the relative drought-sensitivity of RG11 is associated or even caused by its higher ABA content than the tolerant strain G4, under normal irrigation conditions. Under conditions of water stress, RG11 may be unable to elevate ABA levels to the threshold required to achieve adaptation to the drought signal.

Table 1 shows that seed treatment with either y irradiation or Na-azide caused an obvious decrease of IAA, GA3, and ABA in both strains when irrigated normally, as compared with their corresponding control. On the other hand, γ irradiation or Na-azide treatment enhanced the total cytokinin levels over those of corresponding controls, particularly in RG11. In this respect, Na-azide was more effective than γ irradiation in both strains. The decrease of auxin in response to y irradiation was also recorded by Momiyama et al. (1999), who ascribed temporal inhibition of maize coleoptile elongation to a reduction of IAA in the tips. However, modulations of endogenous phytohormone levels as a result of y irradiation are not consistent, but generally show different trends depending on the applied dose (Rabie et al. 1996). In the present work, the recorded increase in cytokinin levels (particularly zeatin riboside) in response to γ irradiation and Na-azide treatments may be caused by the induced enhancement of cell division by such mutagenic agents. This might explain albeit indirectly the reduced levels of IAA in the treated plants. We may tentatively suggest on the basis of recent molecular evidence that induced elevation of cytokinins, primarily zeatin and its derivatives 9-ribosylzeatin and 9ribosylzeatin 5'- phosphate, not only reduce the size of the endogenous IAA pool but also lower the rate of IAA turnover (Bray et al. 2000).

Under drought conditions, treatment with γ irradiation and Na-azide in the G4 strain resulted in an obvious attenuation of the levels of IAA and ABA and a slight decrease in that of GA3, as compared with corresponding control (Table 1). Here, Na-azide was more effective than γ irradiation. In RG11, on the other hand, γ irradiation generally induced a marked decrease of IAA, whereby levels of GA3 and ABA were increased, as compared to corresponding control levels under drought conditions. Under drought condition, both strains (G4 and RG11) showed a generally elevated total cytokinin concentration when seeds were treated with γ irradiation or Na-azide.

Another point of certain interest is the possible role of reactive oxygen species (ROS) in the γ-irradiated and Na-azide treated plants, in relation to their hormone levels. According to Rodriguez et al. (2002), ROS in the elongation zone of maize leaves are necessary for leaf extension. A certain level of particularly H₂O₂ may be necessary for leaf elongation: the authors gave evidence that H₂O₂ resulted mainly from spontaneous dismutation of O². This could be proved by the use of Na-azide (NaN₃), on the bases that it inhibits apoplastic Cu-Zn superoxide dismutase and peroxidases (Ogawa et al. 1997), which would consequently lead to increased O₂ accumulation. Ionizing radiations (Shirley et al. 1992) and UV are also known to enhance ROS and induction of flavonoid biosynthesis (Kliebenstein et al. 2002). On the other hand, Schopfer et al. (2001) showed that 'OH scavengers could inhibit auxin-induced elongation growth, and that gibberellins and ABA could control the release of ROS-intermediates (superoxide radicals, hydrogen peroxide, and hydroxyl radicals). Thus, it might be concluded that there is possible crosstalk between growth hormones and both y irradiation and Na-azide, which determines growth rate under normal and stressful conditions. However, this suggestion needs further work.

In conclusion, endogenous hormone levels and their balance are predicted to interfere with a plant's ability to adjust metabolically in response to drought. It seems likely that under normal irrigation conditions, auxins, gibberellins and cytokinins may be the main determinants of growth, so that RG11 plants maintain higher growth rates than G4 plants. Under drought stress, although changes in the growth-stimulating hormones exhibit a similar trend as that under adequate water, the G4 gene set seem to display ABA drought-induced signals that enable the plants to cope with drought.

This interpretation was further supported by our recent work (unpublished data) showing that under normal irrigation, the growth potential of RG11 plants is higher than that of G4, whereas under drought stress the latter showed better performance than the former. The higher potentiality of RG11 under adequate water supply and of G4 under limiting supply showed similar trends in the control and the treated plants. Our interpretation is supported by the results of many workers showing that increased concentrations of ABA are needed to express several water-deficit-induced genes; under normal conditions these genes can be induced by the exogenous application of ABA. Shen & Ho (1999) state that, under normal conditions, plants usually do not carry out overproduction of osmoprotectants, which need extra energy. Therefore naturally occurring ABA/stress-responsive 'molecular switches' would be valuable in driving the inducible expression of genes whose products are beneficial in plant tissues under stress.

Table 1: The concentrations of IAA, GA3 and ABA of 50-day-old of two strains (G4 and Rg11) of maize from seeds of the control (T0), or those treated with 60G γ rays (T1) or 0.001 M Na-azide (T2). Irrigation was either normal (N) every 10 days or under drought (D) every 20 days.

		IAA			GA ₃			ABA				
		Treatment										
Strain (S)	Irrigation (I)	T_0	T_1	T ₂	T ₀	T_1	T ₂	T ₀	T ₁	T ₂		
G4	N	441.2	114.8	150.6	1512.8	853.9	642.9	317.1	83.7	256.2		
	D	653.6	540.2	397.5	854.1	784.3	510.2	345.8	380.8	382.0		
Rg11	N	660.2	136.8	393.3	893.1	483.5	855.6	334.1	264.5	218.9		
	D	722.7	575.5	570.3	783.3	837.7	353.2	81.9	290.8	292.5		

Table 2a: The concentrations of Cytokinins(benzyl adinin, zeatin and zeatin riboside) of 50-day-old in two strains (G4 and Rg11) of maize from seeds of control (T0), or those treated with 60G γ rays (T1) or 0.001 M Na-azide (T2). Irrigation was either normal (N) every 10 days or under drought (D) every 20 days.

		Benzyladenin Zeatin				Zeatin riboside			Total Cytokinins				
		Treatment											
Strain (S)	Irrigation (I)	T_0	T ₁	T ₂	T_0	T ₁	T ₂	T_0	T ₁	T ₂	T_0	T ₁	T ₂
G4	N	217	101	284	832	822	1053	146	347	337	1195	1270	1674
	D	86	424	92	1029	1970	2520	170	412	308	1285	2806	2920
Rg11	N	213	213	375	526	928	1296	686	531	150	1425	1672	1821
	D	515	87	278	951	1846	1160	272	215	253	1738	2148	1691

Table 2b: The ratio of ABA / GA₃ concentration

		ABA / GA ratio						
		Treatments						
Strain (S)	Irrigation (I)	T_0	T ₁	T ₂				
G4	N	0.21	0.10	0.39				
	D	0.40	0.48	0.75				
Rg11	N	0.37	0.55	0.25				
	D	0.10	0.35	0.83				

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الملخص العربي

دراسة مقارنة على محتوى الهرمونات كدلالة على تحمل الإجهاد في سلالتين من الذرة الشامية

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قورنت مستويات اندول حمض الخليك (IAA) وحمض الجبريليك (GA3) و السايتوكاينينات: بنزايل أدنين وزياتين وزياتين رايبوسيد اضافة الى حمض الأبسسيك في سلانتين من الذرة هما G4 وRg11 لبيان امكانية الإستناد على محتواهما الهرموني لتقييم مقاومتهما النسبية للإجهاد. فقد تم قياس المحتوى الهرموني في النباتات المعرضة للجفاف و الناتجة عن بذور تمت معاملتها بأشعة جاما (٦٠ جـراى) أو صوديوم أزيد بتركيز ٠,٠٠١ مولار كعوامل مستحثة للطفرات. وقد أوضحت النتائج أنه تحت الظروف الطبيعية للرى تميزت نباتات السلالة Rg11 بمحتويات أعلى من اندول حمض الخليك والسايتوكينينات الكلية، مقارنة بمثيلاتها من نباتات السلالة G4. وقد عزيت التغيرات في السايتوكينينات الكلية الى الإختلاف في محتوى الزياتين رايبوسيد. وسجلت محتويات حمض الجبريليك انخفاضا في غالبية الحالات في نباتات السلالة Rg11 عن السلالة G4 و تجلت الإتجاهات المنكورة في جميع الهرمونات المشار اليها تحت الظروف الطبيعية للرى في نباتات المقارنة و النباتات الناتجة عن معاملة البذور في كلتا السلالتين. وفي حالة الجفاف لم يتضح ثمة اختلاف واضح في اتجاهات التغيرات في محتويات الهرمونات المذكورة آنفا عمائكر سابقا في حالة الري المعتاد. أما حمض الأبسيسيك فقد أظهر تغيرات مختلفة في حالتي توفر المصادر المائية للرى و الجفاف. ففي حالة الري المعتاد كانت معدلات حمض الأبسيسيك في نباتات السلالة Rg11 إما أعلى أو ذات تغير طفيف مقارنة بنباتات السلالة G4. أما تحت ظروف الجفاف فقد انعكس الوضع حيث ازداد معدل حمض الأبسيسيك بصورة واضحة في نباتات السلالة G4 عن Rg11. وقد انعكس ذلك على نسبة حمضى الأبسيسيك الى الجبريليك حيث أوضحت قيما أكثر انخفاضا في السلالة Rg11 عنها في السلالة G4. وقد انطبقت الخلاصة المذكورة على نباتات المقارنة والنباتات الناتجة عن معاملة البذور بأشعة جاما أو الصوديوم أزيد. وبناء على الأنماط الهرمونية الموضحة اقترح أن السلالة Rg11 أكثر ملائمة للزراعة عن G4 تحت ظروف الرى المعتاد بينما تبدو السلالة G4 أكثر قدرة على تحمل ظروف الجفاف.