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RADMILA STIKIĆ, SOFIJA PEKIĆ, ZORICA JOVANOVIĆ, LORA LJUBOJEVIĆ, LJILJANA PROKIĆ

GENOTYPIC DIFFERENCES IN THE RESPONSE OF MAIZE TO EXOGENOUS ABSCISIC ACID

Faculty of Agriculture, University of Belgrade, Belgrade, Jugoslavia

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Effect of ABA on root and shoot growth and stomatal conductance was investigated in maize lines, selected for ABA content, using two different systems. In the first experiment seedlings were grown in Petri dishes with ABA added in substrate (1 and 10 mmol m^{-3}). Results from this experiment showed that exogenously applied ABA inhibited growth of both coleoptile and root but depending on concentration and genotype. The biggest effect of ABA treatment on root to shoot ratio was evidenced in high-ABA parent line Polj-17 being 1.6 fold bigger than in low-ABA parent F-2. Those differences between progeny lines 167 B1 (high-ABA) and 83 A5 (low-ABA) were less expressed. In the second experiment solution of synthetic (±) ABA was fed to part of the root in aim to manipulate xylem and leaf ABA content without changes in plant water relations. These results showed that the increase in endogenous ABA content (xylem and leaf) reduced leaf elongation rate (LER) and stomatal conductance in all investigated lines. These results also showed existence of genotype differences in sensitivity to ABA and proved that the most sensitive reaction to ABA had high-ABA parental line Polj-17 in both experimental systems.

Key words: Maize *(Zea mays* L.), abscisic acid (ABA), genetic variation, different sensitivity to ABA

Ključne reči: Kukuruz *(Zea mays* L.), abscisinska kiselina (ABA), genetsko variranje, različita osetljvost na ABA

INTRODUCTION

Many results indicate that plant growth is the most sensitive plant process to water stress, especially in the initial phases when water deficit induces drop in turgor pressure demonstrating that leaf growth could be reduced without any changes in the leaf water status (Michelena & Boyer, 1982; Passioura, 1988; Saab & Sharp, 1989; Gowing et al., 1990). It become evident that changes in root environment modify, not only amount of water moving from root to shoot (hydraulic signal), but also the production of some chemicals (non hydraulic signal). Research of the nature of this chemical proved that development of water deficit sensed by root system induces production of abscisic acid (ABA) as a signal molecule (Davies et al., 1987; Zhang, Shurr & Davies, 1987). Moving through transpiration stream into leaves, ABA markedly influences the growth and development of shoot (Trewavas & Jones, 1991). Recent studies have provided evidence that the effect of exogenously applied ABA induces leaf growth inhibition (Zhang & Davies, 1990 a, b).

It is well know that different kinds of stresses (drought, low and high temperature, salt, nutrients and waterlogging) increase ABA content in the leaves. Increasing ABA content leads to many changes in plant physiology, which in general, make the plant better adapted to environmental stresses (Quarrie, 1991). Selection on the basis of ABA accumulation capacity was done with a spring wheat genotypes. Field trials with plants from this selection program showed that high- ABA genotypes significantly outyilded low-ABA genotypes in a water limited conditions (Innes, Blackwell & Quarrie, 1984). A similar selection programe has been carried out with maize to produce recombinant inbred lines having significantly different leaf ABA content under field conditions (Pekić & Quarrie, 1988). For the parental lines in this selection programe (Polj 17 and F-2) it has been previously shown to differ consistently in the responses of a range of traits to drought stress under both cabinet and field conditions (Pekić & Quarrie, 1987; Quarrie, 1991). These response include ABA content and yield: Polj 17 contents more ABA and is more drought resistant than F-2. Recent measurement done with progeny plants didn't prove such marked differences in the field conditions, except at flowering time (Pekić et al., 1995). Therefore, it is still missing enough information to give reliable picture about physiological consequences of genetic variation in ABA content. However, investigation of this problem is in a progress and preliminary results indicate that there are differences in rooting behaviour amongst genotypes. Therefore to elicit response of those plants comparable to that caused by root sourced ABA in drying soil, we repeated Zhang's and Davies's (1990a) ABA feeding maize roots experiment. The aim of this experiment was to determine whether genetic variation in leaf ABA content was reflected in growth and stomatal responses to externally applied ABA.

Since our previous experiments (Stikić *et al.,* 1991) based on techniques developed by Sharp et al., (1988) revealed differencesinin root and shoot growth rates at low water potential between parental lines, we, also, wished to test for genetic variation of growth responses to ABA at the seedlings stage in the progeny.

MATERIALS AND METHODS

Genotypes

The genotypes of maize *(Zea mays* L.) used for this work consisted of the inbred lines Polj 17 (high-ABA) and F-2 (low-ABA) and progeny from the cross between Polj 17 and F-2: high-ABA line 167 B_1 and low-ABA 83 A_5. The two inbred parental lines had previously been shown to differ by up to four-fold in leaf ABA content under field conditions (Pekić & Quarrie, 1988). The recombinant lines were classified into high-ABA and low-ABA lines according to leaf ABA content in the F4 generation. The difference in leaf ABA content means between these two populations and, also, between high and low ABA lines used in this work is about four times (Pekić et al., 1995).

Experiment with young seedlings

Seeds were germinated in wet vermiculite in dark at 25°C. Ten seedlings of each genotype with radicles 3 cm long were placed into plastic Petri dishes (diameter 12 cm) with vermiculite saturated with water (control) and different (±) ABA solutions (1 and 10 mmolm^{-3}). Petri dishes were sealed with plastic sheets, placed vertically into dark at 25°C for 28^h. Coleoptile and root length was quickly recorded at dim green light by marking the lid of the Petri dish.

ABA-feeding experiment with plants in 3 leaf stage

Seeds of investigated lines were germinated in John Innes No 2 compost in a greenhouse, with temperature varying between 22-28°C (day) and 12-15°C (night). At the one leaf-stage were selected for uniformity and transferred in the growth cabinet, where they remained under the constant conditions (day and night temperatures 25 and 18°C, PAR 200 mmol m^{-2}s^{-1} and photoperiod 16^h). In these conditions plant were grown until three-leaf stage, and than transferred (with attached soil) into 80 mm diameter pots from which the bottom were removed and replaced with a piece of plastic mesh (5 mm diameter holes). Pots were inserted into plastic beakers which were blackened and contained 100 cm^3 Hogland's nutrient solution. Plants remained in these conditions (approximately 10 days) until substantial amount of roots (about 20% of the whole mass) was established outside the pot and dangling in the nutrient solution.

ABA-feeding was done with a following ABA concentrations: 10, 50 and 100 mmol m^{-3} (synthetic (±) ABA, Lancaster Synthesis, Morecambe, UK) previously shown to affect growth and stomatal conductance in maize leaves (Zhang & Davies, 1990a). Starting 3 days before and continuing 2 days after ABA-feeding, length of two elongating leaves on each intact plant was measured (by ruler) every 24^h. At the same time (10^h) measurements of conductance of the abaxial leaf surface were done with a porometer (AP-4 Delta T Devices LTD). Xylem exudates and leaf ABA samples were collected after 48^h of ABA-feeding from the youngest mature leaves. Xylem exudate was collected after shoots were detopped as have been described by Zhang and Davies (1990a). After freeze drying ABA content was measured by RIA test (Quarrie et al., 1988). For each treatment 4-5 plants per genotype were used. Growth rate and conductance were calculated as a means of two leaves per plant. Because of the variation in the leaf elongation rate (LER) and stomatal conductance (gs) among genotypes these results are presented as percentages of control values. These percentages were calculated differently for LER and stomatal conductance. Leaf elongation rate is presented as percentage of the elongation rate before treatments were given. Control values used in these calculations were the average rates of leaf growth during whole experimental period, while control values for stomatal conductance were from measurements done last day of experiment (48^h after ABA feeding).

RESULTS

Experiment with young seedlings

Tab. 1 illustrates the effect of two treatments on coleoptile shoot and root growth in four genotypes based on calculation of the growth rate in percentage of the growth rate in control plants and root to shoot length ratio. Results show that in all genotypes: a) ABA inhibited growth of both organs, b) effect of both concentrations was more expressed on coleoptile than on root growth (especially in parental line Polj 17), and c) effect of the higher ABA concentration was more expressed and, consenquently, induced increase in root to shoot ratio. The biggest effect of ABA treatment on root to shoot ratio was evidented in high-ABA parent (the increase of 1.2 and 1.6 fold for two ABA treatments in comparison to control). Genotipic differences in growth responses to ABA were more expressed between high and low-ABA parents, comparing to high and low-ABA lines. Thus root/shoot ratios at lower and higher ABA concentration were 0.7 and 1.6 times bigger in line Polj 17 comparing to F-2.

Tab. 1. – Effects of ABA on young seedlings shoot and root growth rate (in % of controls) and root to shoot ratio (R/S) based upon seedlings lengths in investigated maize lines

	ABA (mmol/m^3)	Polj-17	F-2	$167B_1$	$83A_5$
	0	100 ± 16	100 ± 14	100 ± 19	100 ± 14
Shoot	1	78 ± 18	96 ± 8	89 ± 16	83 ± 11
	10	52 ± 14	80 ± 11	79 ± 16	81 ± 10
	0	-100 ± 8	-100 ± 13	- 100 ± 9	- 100 ± 14
Root	1	- 92 ± 18	- 101 ± 20	- 90 ± 19	- 88 ± 12
	10	- 82 ± 9	- 92 ± 18	- 86 ± 15	- 78 ± 11
	0	1.755	1.473	2.514	1.889
R/S	1	2.058	1.385	2.198	2.029
	10	2.755	1.692	2.617	1.824

Experiment with ABA-fed root

The effect of ABA-feeding on leaf elongation rate (LER), stomatal conductance and xylem and leaf ABA content are presented on tab. 2. Values of LER were expressed as percentages of the rate before treatments because measurements of this parameter showed that there were marked differences in growth habit between investigated lines. Thus, growth rate in controlled condition varied in a range of 1.28 (line F-2) to 2.2 cm per 24^h (line 167 B_1). Similarly variation of stomatal conductance values under control conditions was between 58.7 (line 167 B_1) and 73.6 mmol $m^{-2}s^{-1}$ (line 83

A_5). Expressing those results in relative, instead absolute values, allowed to distinguish the effect of applied ABA and genotipic differences between investigated lines.

Tab. 2. – Effects of ABA feeding on leaf elongation rate (LER), stomatal conductance (Gs), leaf ABA content and xylem ABA content in investigated maize lines

	ABA (mmol/m3)	Polj-17	F-2	167 B_1	83A_5
LER (% of control)	0	100 ± 11	100 ± 6	100 ± 6	100 ± 4
	10	70 ± 8	72 ± 6	71 ± 9	69 ± 9
	50	55 ± 6	62 ± 12	57 ± 11	61 ± 7
	100	49 ± 5	43 ± 5	52 ± 9	61 ± 5
Gs (% of control)	0	100 ± 12	100 ± 12	100 ± 8	100 ± 4
	10	61 ± 8	48 ± 4	55 ± 11	71 ± 11
	50	55 ± 7	47 ± 7	52 ± 8	48 ± 12
	100	43 ± 4	36 ± 5	51 ± 7	35 ± 5
Leaf ABA (nmol/gdw)	0	1.55 ± 0.3	1.29 ± 0.2	1.21 ± 0.1	1.46 ± 0.3
	10	1.89 ± 0.1	1.93 ± 0.4	3.91 ± 0.7	3.23 ± 0.6
	50	2.27 ± 0.5	2.21 ± 0.1	4.19 ± 0.2	4.33 ± 0.4
	100	6.82 ± 0.7	3.33 ± 0.4	6.80 ± 1.0	5.78 ± 0.4
Xylem ABA (μmol/m^3)	0	9.30 ± 0.7	11.39 ± 2.0	5.96 ± 0.9	4.90 ± 0.7
	10	14.92 ± 3.0	26.70 ± 5.0	98.20 ± 23.0	25.40 ± 3.0
	50	25.10 ± 4.0	37.60 ± 6.0	116.23 ± 25.0	50.84 ± 4.0
	100	131.66 ± 9.0	137.30 ± 23.0	140.40 ± 20.0	161.07 ± 26.0

The ABA treatment caused decrease in a leaf growth and stomatal conductance in all investigated lines and this effect was proportional to ABA concentration in feeding solution. For example, 100 mmol m^{-3} ABA induced LER and stomatal reduction varying in different genotypes between 43-61% and 35-51% respectively.

Xylem and leaf ABA content increased with increasing concentration of applied ABA indicating that those changes were sufficient to account for observed changes in LER and gs. Maximal values of xylem ABA estimated in 100 mmol m^{-3} ABA solution were ranging from 6 to 140 mmol m^{-3} (line 167 B_1) and from 49-161 mmol m^{-3} (line 83 A_5). Variation between investigated lines was also expressed on the leaf ABA content since these values varying between 1.3 to 3.3 nmol g DW^{-1} (line F-2) and from 1.2 to 6.8 nmol g DW^{-1} (line 167 B_1). Comparing to xylem ABA increase (mean increase 20 fold) those changes were less expressed in all investigated lines (mean increase 4 fold).

Relationship between LER versus the xylem and leaf ABA content is presented on Fig. 1. (A and B). From these figures it can be seen that LER declined as xylem and leaf ABA concentration increased. However, points corresponding to different genotypes indicated different growth response to ABA. In the leaves of the parental lines Polj 17 and F-2 the response of LER to both xylem and leaf ABA had a biphasic character. Initial increase (up to cca 30 mmol m^{-3}) of xylem ABA was followed by a fast reduction of LER until a plateau of approximately 60% of LER was reached. When the values of stomatal conductance were plotted against xylem and leaf ABA content similar graph to LER was obtained (Fig. 2A and B). This figure also confirmed genotipic differences in stomatal sensitivity to both xylem and leaf ABA content. Data also showed that, not only LER but, also, stomata of high-ABA parental line had the most sensitive response to xylem ABA.

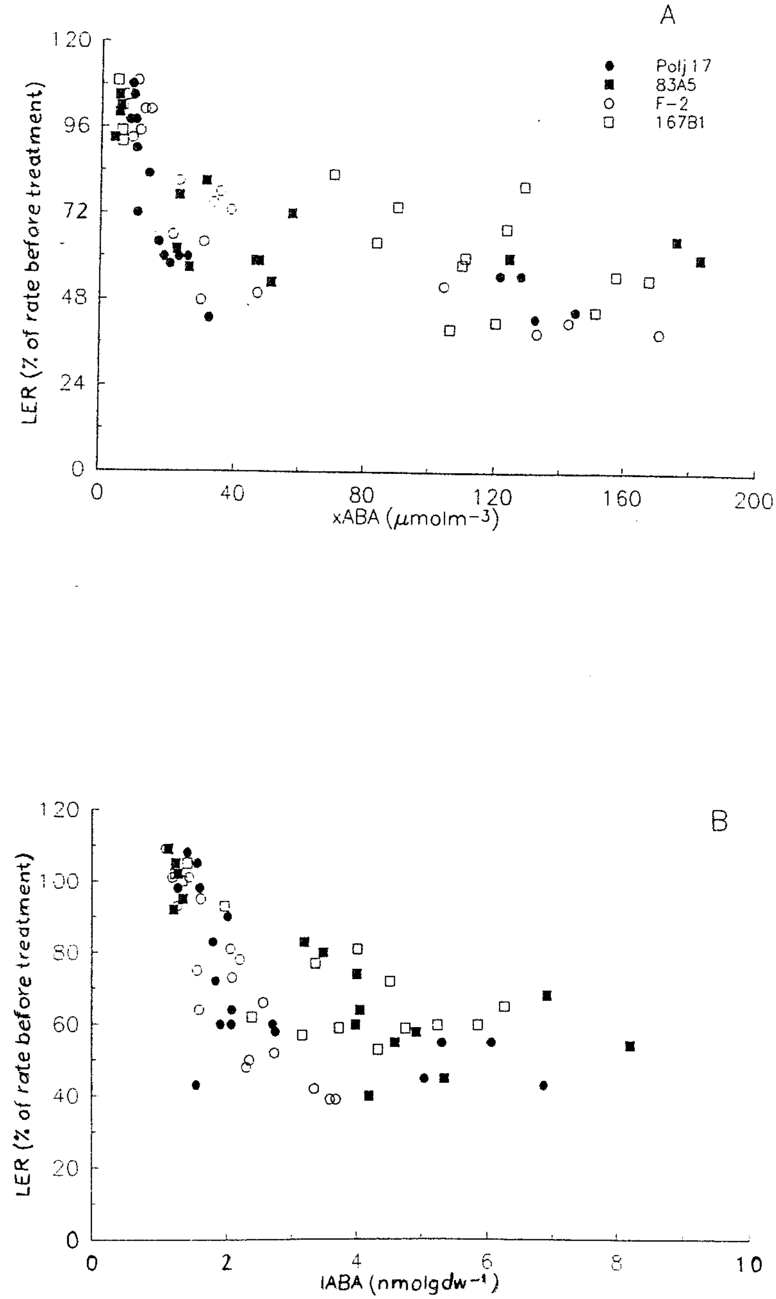

Fig. 1. – Relationship of leaf elongation rate (LER) to xylem (A) and leaf ABA content (B) in investigated maize lines Polj 17 (•), F-2 (O), 167 B1 (□), and 83A5 (■). Each point represents coupled values corresponding to one leaf

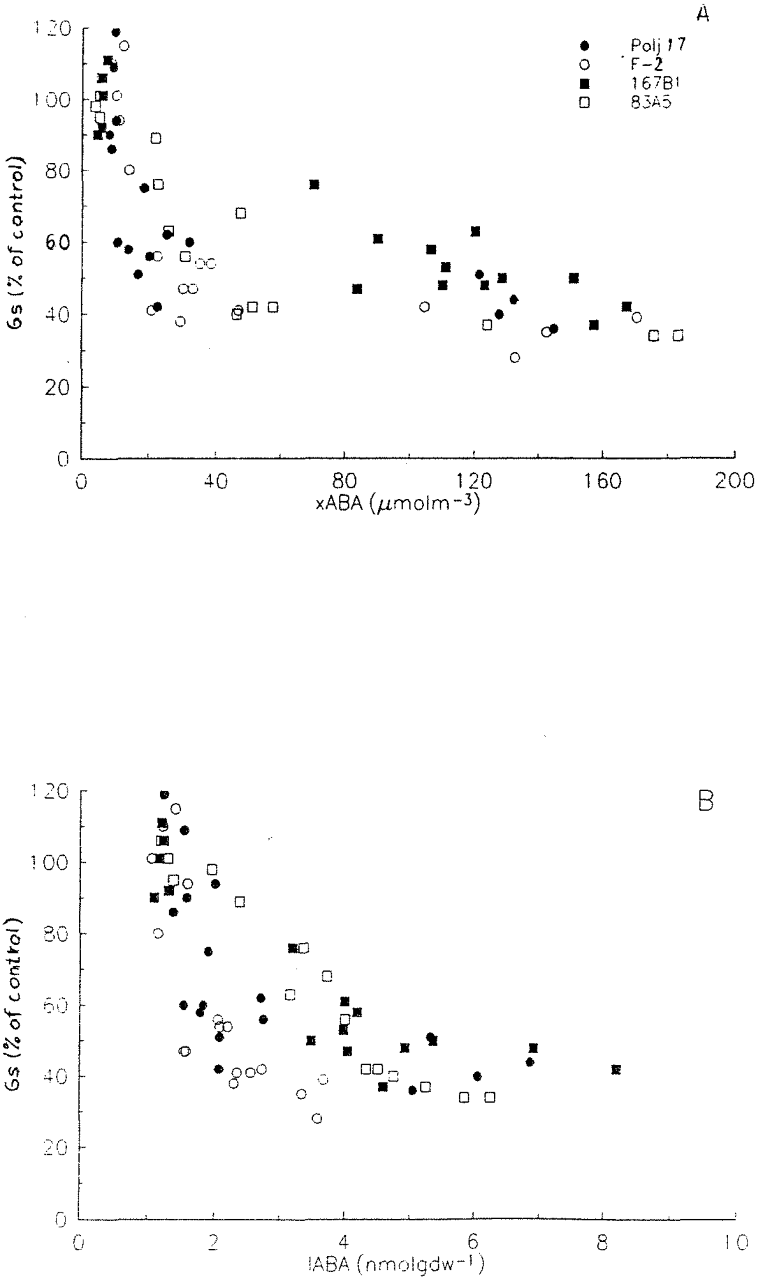

Fig. 2. – Relationship of stomatal conductance (Gs) to xylem (A) and leaf ABA content (B) in investigated maize lines Polj 17 (•), F-2 (O), 167B1 (□), and 83A5 (■). Each point represents coupled values corresponding to one leaf

Comparison of linear regression lines (Tab. 3) for this initial phase between 2 parental lines showed that slopes of LER vs xylem ABA was 2.531 in line Polj 17 and 1.261 for line F-2, while correlation coefficients were similar (0.895** and 0.802**). Differneces in slopes for LER vs leaf ABA between parental lines were less expressed (26.88 for Polj 17 and 31.25 for F-2), while correlation coefficient was more significant in line F-2 (0.80**) than in line Polj 17 (0.58*). The decline of LER vs xylem or leaf ABA in the leaves of progeny lines was more gradual comparing to parental lines and linear for the whole range of ABA values (correlation coefficient varying between 0.76** and 0.86**). Comparison of slopes for both regression (LER vs, xABA and LER vs lABA) showed that high-ABA line had smaller slope of LER vs xylem ABA (0.32) than low-ABA line (0.77) while there was no significant difference in the slopes of LER vs leaf ABA.

Tab. 3. – Correlation coefficients (r) and slopes (a) of linear regressions in maize lines

	Polj-17	F-2	$167B_1$	$83A_5$
LER vs xABA				
r	0.89**	0.80**	0.86**	0.80**
a	2.53	1.26	0.32	0.77
LER vs lABA				
r	0.58*	0.80**	0.79**	0.76**
a	26.88	31.25	8.25	8.36
Gs vs xABA				
r	0.64*	0.82**	0.94**	0.77**
a	2.02	1.87	0.39	0.35
Gs vs lABA				
r	0.59*	0.77**	0.85**	0.96**
a	30.64	43.85	10.09	15.79

*and **indicate the level of significance of correlation coefficient (at $P_{0.05}$ and $_{0.01}$ respectively)

DISCUSSION

The results presented in this paper confirmed that exogenous ABA treatment can modify growth both of the seedling and leaves and to change stomatal reaction in different maize lines. Our results for relative root and shoot growth response of young seedlings can be compared to data obtained in experiment with plants at similar stage of development grown at low water potentials (Stikić et al., 1991). Thus, mean elongation rate for roots grown in ABA solution was about 1.33 mm h^{-1} what is similar to root growth rate found by Stikić et al., (1991) at different water potentials: 1.2 mm h^{-1} at -0.0025 MPa and 0.6 mm h^{-1} at -0.52 MPa. From the results of Saab et al. (1990) differences in ABA content in the root and shoot may be expected to affect relative growth rates under growth conditions. Measurements of endogenous ABA content in roots and shoots of several maize lines (among them Polj 17 and F-2) in experiment done by Stikić et al. (1991) revealed genotipic differences in root and shoot growth responses to endogenous ABA. In only few genotypes under certain drought treatments, both root growth and shoot growth responded to ABA as suggested by Saab et al. (1990) leading to the conclusion that genotypes may differ in the sensitivity to ABA. Genotipic variability in growth responses to exogenous ABA presented in this paper confirms that possibility. Thus, the most striking effect of ABA on line Polj 17, in comparison to F-2 and other lines can be attributed to its greatest sensitivity to ABA if we assume that endogenous ABA content do not differ from F-2 according to data from similar experiment (Stikić et al., 1991).

Experiments done in the field and laboratory conditions have proved that feeding of ABA to the part of an intact plant may be a convenient way to manipulate endogenous ABA content and monitor physiological consequences (Zhang & Davies, 1990a; Tardieu, Zhang & Davies, 1993). Experiments done by Zhang & Davies (1990a) provided evidence that increased ABA content in xylem sap of ABA-fed maize plants was root sourced and responsible for restriction of leaf growth and stomatal closure. Taking the results of these experiments as a reference for the results obtained from our ABA feeding we can confirm large genotipic differences in LER and gs response to applied ABA. For example 60% of gs reduction in Zhang and Davies's (1990a) experiment (done with John Innes F1 maize hybrid) was accompanied by an increase in xylem ABA content of aproximately 60 mmol m^{-3}. Data from our experiment (Fig. 2A) showed that for similar gs reduction xylem ABA concentration varyed between genotypes in a range of 11 to 90 mmol m^{-3}. Different stomatal sensitivity to xylem ABA have been proved in several studies and led to a model of stomatal behaviour in which the effect of xylem ABA is mediated by leaf water status (Tardieu & Davies, 1993). However, in the ABA-feeding experiments the xylem ABA mimics the root signal in drying soil and affects shoots independently from the effects of leaf water status. Thus, observed differences in stomatal sensitivity of our lines could not to be due to water potential differences. Wolf, Jeschke and Hartung (1990) studding long distance transport of ABA have shown that part of ABA could be exported via phloem to the roots and than reciculated to the aerial parts of the plants. However, investigation of effect of girdling on ABA export from the leaves of parental lines Polj 17 and F-2 their progeny didn't prove differences in phloem ABA transport (Pekić et al., 1995). Differences found by measurements of some leaf anatomical characteristics, such as xylem vessel area, between parental lines (Ristić & Cass, 1991) and their progeny (our unpublished data) inderectly indicate possible genotipic differences in hydraulic conductivity of transpiration stream. Differences in chemical composition of xylem sap (ion content and pH) can also alter sensitivity of stomata to ABA as have been proposed by Shurr and Golan (1990). Zhang and Davies (1990a) results indicated that leaf ABA showed a relatively insensitive response (compared to xylem ABA content) to applied ABA. Similarly to Zhang's and Davies's data (1990a) our results indicate that feeding plants with 100 mmol m^{-3} ABA solution increase ABA content in the leaves maximally up to 6 fold, and in the xylem sap up to 30 fold.

Results of Gowing, Jones and Davies (1993) indicated that conductance of cherry leaves fed by ABA in pulses was more influenced by the amount of ABA entering the leaf than by absolute xylem ABA concentration. This indicates that stomata perceive a local concentration or apoplastic ABA content which is in dynamic equilibrium between the rate of ABA arrived via xylem and rate of ABA removal by partitioning into cells as a consequence of pH gradients (Hartung & Slovik, 1991).

The inhibiting effect of applied ABA on the growth of different plant parts is still contraversal. Quarrie and Jones (1977) in a study of the effect of exogenous ABA in wheat growth reported that reduction of a leaf size was a result of an inhibitory effect on both cell division and cell expansion. Results of Van Valkenburgh and Davies (1983) indicated that ABA reduced cell wall extensibility, possibly by inhibiting proton pumping throughout the plasmalemma into the apoplast (Chen & Kao, 1988). However, work of Munns and King (1988) refused that concept of ABA signal and proposed that, at least in wheat, drought induced increase in an another compound with antitranspirant activity. More recent results of Munns and Sharp (1993) suggested that ABA is responsible for only part of the regulation of leaf growth. They proposed that ABA moved in complexed form through the xylem (ABA-adduct) and that this form is physiologically ineffective and have to be metabolized in free form to affect some leaf processes.

In our ABA-feeding experiment the most sensitive growth and stomatal reaction to applied ABA was established for high-ABA parent Polj 17. For this line it has been previously shown to be resistant in many drought related traits comparing to other parental F-2 line (Pekić & Quarrie, 1978, 1988; Quarrie, 1991; Pekić et al., 1995). Root morphology also markedly differed between those lines both at the seedling (Stikić et al., 1991) and the maturity stage when the greater number of nodal roots produced by Polj 17 was associated with a significantly higher root pulling force than F-2 (Lebreton et al., 1995). Higher sensitivity of shoot growth and stomata to increased endogenous ABA may be an adaptive response, particularly in condition when mild stress induces synthesis of ABA as a root signal. Retardation of leaf area development and partial closure of stomata together with the increase of R/S ratio could be of some benefit in terms of water conservation. This „strategy" may allow Polj 17 to avoid or delay transition to more severe stress and to enable growth even at reduced rate. Such a hypothesis is supported by the field measurements of leaf area and plant height which indicate that effects of drought is less expressed in Polj 17 comparing to another lines (unpublished data). Since investigated lines differ markedly in leaf ABA content under field condition (Pekić et al., 1995), future work with ABA-fed plant under field conditions will provide further evidence on genotipic differences in sensitivity to ABA, their consequence for the overall drought response, and possible role of differential sensitivity to ABA as a regulatory mechanism of plant adaptation to water stress.

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Rezime

RADMILA STIKIĆ, SOFIJA PEKIĆ, ZORICA JOVANOVIĆ, LORA LJUBOJEVIĆ, LJILJANA PROKIĆ

GENOTIPSKE RAZLIKE U REAKCIJI KUKURUZA NA EGZOGENU ABSCISINSKU KISELINU

Poljoprivredni fakultet, Univerzitet u Beogradu, Beograd, Jugoslavija

U radu je ispitivan uticaj ABA na rastenje korena i izdanaka i na provodljivost stoma kod linija kukuruza selekcionisanih na sadržaj ABA u dva eksperimentalna sistema. Rezultati prvog ogleda sa mladim klijancima pokazali su da egzogeno dodata ABA inhibira rastenje i koleoptila i korena i to u različitoj meri zavisno od koncentracije i genotipa. U ogledu sa starijim biljkama (u fazi 3-eg lista) rastvor ABA je dodavan u deo korenovog sistema sa ciljem da se modifikuje sadržaj egzogene ABA u listu i ksilemu pri optimalnom vodnom režimu. Rezultati ovog ogleda su pokazali da je povećanje sadržaja ABA u listu-ksilemu dovelo do redukcije brzine rastenja lista i stomatalne provodljivosti kod svih linija, kao i da postoje genotipske razlike u osetljivosti ovih procesa na ABA. Najveća osetljivost na ABA konstatovana je kod linije Polj 17 u oba eksperimentalna sistema.