Journal of Agricultural Sciences
Vol. 46, No 1, 2001
Pages 1-16

UDC: 633.15:588.144.4
Original scientific paper

INVESTIGATION OF MECHANISM OF LEAF GROWTH INHIBITION IN MAIZE

Zorica Jovanović*

Abstract: The mechanism of leaf growth inhibition was investigated in eight maize genotypes differing in drought resistance and maturity groups. In controlled conditions the effects of drought, nitrogen deficiency, pH and ABA on leaf growth were investigated. In soil drying experiment measurements of water potential and its components and leaf growth and development parameters were carried out. The same parameters of leaf growth and development were measured in nitrogen deficiency experiment, while leaf growth was measured in pH and ABA experiments. In field experiment measurement parameters of plant growth and productivity were done.

Obtained results pointed out that hydraulic and chemical signaling regulated the leaf growth under drought conditions. Drought decreased leaf growth in all genotypes and resistant lines from both maturity groups showed faster leaf development. Water deficit affected cell production and elongation with significant genotypic differences. A similar phenomenon was observed with nitrogen deficiency. Effect of alkalization of "artificial xylem sap" and application of exogenous ABA (10^{-6} and 10^{-8} M) on reduction of leaf growth was more expressed in susceptible line. Analysis of growth and productivity in field conditions showed that drought had smaller effect on inhibition of leaf growth in resistant genotypes, which had consequences on the yield of these plants.

Key words: leaf, growth, productivity, maize, drought, nitrogen deficiency, pH, ABA.

---

* Dr Zorica Jovanović, Assistant, Faculty of Agriculture, 11081 Belgrade-Zemun, Nemanjina 6, FR Yugoslavia

This paper is a shortened version of the PhD thesis defended on October 27, 2000 at the Faculty of Agriculture, University of Belgrade, Belgrade-Zemun.

Introduction

Leaf growth is one of the very important determinants of plant productivity. Yield or dry matter production for different crops is closely related to the interception of photosynthetically active radiation (Monteith and Elston, 1983), which itself is a direct function of leaf development. Therefore, there is much interest in the understanding of leaf growth and development, especially under unfavorable environmental conditions. According to Christiansen (1982), drought is one of the most frequent stress factors which limits crop production. One of the most sensitive processes to drought is leaf growth (Hsiao, 1973) and water deficits result in reduced rate of leaf development and leaf area expansion. Decreasing of leaf growth is one of the earliest effects of nitrogen deficiency and similar effect can be induced by exogenously applied hormone abscisic acid (ABA).

The convential view of drought is that soil drying induces restriction of water supply that caused a reduction of water and turgor potential and leaf growth (Hsiao, 1973). However, many results indicated that leaf growth could be reduced without any changes in leaf water status and that these changes in leaf growth are more linked with changes in soil water status. A number of experiments in control and field conditions have shown that roots are primary sensors of soil drying and producers of chemical signals. Experiment done by Zhang and Davies (1990) confirmed that this chemical signal is a stress hormone ABA. ABA is produced in root in the response to soil drying and transported to the shoots via xylem and causes stomatal closure and reduced leaf area. As an additional signal in the plant response to soil drying can be changes in concentrations of other hormones (cytokinins) and mineral composition and pH of xylem (Dodd et al., 1996). Recently, it has been shown that increasing of pH of xylem sap is a drought signal that reduces leaf growth through ABA-dependent mechanism (Bacon et al., 1998).

Leaf growth pattern in plants from family Poaceae (commonly known as grasses) is primarily unidirectional with basal meristem that produces parallel files of cells. Therefore, grass leaf with developmental gradient of cells presents useful experimental system for the study of cellular and spatial parameters of growth (Schnyder et al., 1990).

The vegetative growth period of grasses is characterized by the successive appearance of leaves. The interval of the time between the appearance of successive leaves on stem is phyllochron and it is influenced by genetics and environmental factors (Rickman and Klepper, 1995). Thus, any factor that affects leaf growth would also affect the phyllochron and finally has effect on leaf area and plant productivity.

Analysis of plant growth and productivity based on monitoring of parameters like RLER, RGR, NAR and LAR could help to understanding growth pattern

during the plant development, as well as the influence of different environmental and genotypic factors (C r a m e r et al., 1994). Also, it is still questionable which factors determine RGR as a most significant indicator of plant growth and productivity. Recent results indicated that the higher RGR of fast growing species was associated with a rapid leaf elongation and leaf appearance (G r o e n e v e l d et al., 1998).

The aim of the present PhD thesis was to investigate the mechanism of maize leaf growth inhibition under stress conditions (drought, nitrogen deficiency, pH and interaction pH with ABA) and to identify possible genotypic variation in the response of different maize genotypes.

Material and Methods

For these investigations, eight genotypes differing in drought resistance and maturity groups were used: early maturing lines (Polj-17 - drought resistant and F-2 - drought susceptible), late maturing lines (ILB 84 - resistant and B 73 - susceptible), hybrids from early, medium and late maturing group (ZPTC 260, NSSC 420, ZPSC 677) and population from late maturing group (DTP). Inhibition of leaf growth was investigated in controlled and field conditions. In controlled conditions the effects of drought, nitrogen deficiency, pH and ABA on leaf growth were investigated.

Drought experiment

Seeds of these genotypes were germinated on moist paper for 72^h and uniform seedlings planted in pots with soil. Plants were grown in a growth cabinet where photoperiod was 14^h, light intensity at level of the plants was $200\ \mu mol m^{-2}s^{-1}$, temperature 25/18°C and relative humidity 70%. Plants were watered daily and shortly before the emergence of the third leaf, half the plants were selected and water withheld from them. Ten plants were selected randomly for all measurements.

Leaf water potential was measured by pressure chamber method (S c h o l a n d e r et al., 1965). Osmotic potential was measured in the same leaf sample by crioscopic method and turgor potential was calculated as a difference between leaf water potential and osmotic potential. Length of the third leaf was measured daily and leaf elongation rate (LER) was calculated. Phyllochron present inverse value of leaf appearance rate that was calculated as the slope of a linear regression Haun index vs. time (K l e p p e r et al., 1982). Growth in the leaf elongation zone in the day of maximal leaf growth was measured by parameters of cell elongation and production: cell elongation rate, duration of elongation, cell flux out from zone and number of cells in cell division zone (V o l o n e c and N e l s o n, 1981).

Nitrogen deficiency experiment

In this experiment we used genotypes that have been previously classified as "low LER" (line F-2) and "high LER" (hybrid ZPSC 677) according to the measurements of leaf growth parameters done in both control and drought conditions. Uniform seedlings were planted in pots with perlite and grown in a growth cabinet under same conditions as in the experiment with drought. Plants were watered daily with nutrient solutions with nitrogen and nitrogen-deficient solution (H e w i t t, 1966). The pH value of both nutrient solutions was adjusted at 4.9 with 1M HCl.

Leaf elongation bioassay

For leaf elongation bioassay (M u n n s, 1992) we used the same genotypes as in the experiment with nitrogen deficiency to investigate the effect of different pH of "artificial xylem sap" with and without exogenous ABA (10^{-6} M and 10^{-8} M). Plants were grown in pots with perlite to induce the extension of the subcrown internode. Plants at the third leaf stage on the day of maximal leaf growth were transferred to a vial with "artificial xylem sap" (W i l k i n s o n and D a v i e s, 1997). The pH of solution was corrected to the appropriate pH (5-7) with HCl or KOH and ABA was added to give final concentrations of 10^{-6} M and 10^{-8} M. The vials with plants were left in a growth cabinet and the length of the third leaf was measured.

Field experiment

The genotypes used for the assay were late maturing lines ILB 84 and B 73, and population DTP provided by Maize Research Institute, Zemun Polje. Trial was carried out on chernozem soil in the irrigated and rainfed field and measurements were done on the plants during vegetation season 1996 and 1997.

The samples for measuring the parameters of growth and production were taken in different stages of maize development. We used the following parameters (H u n t, 1982): relative leaf expansion rate (RLER), relative growth rate (RGR) and net assimilation (NAR). At the end of vegetation period measurements of yield parameters were done.

For all these measurements 5-10 plants per treatment were used, except for measurements of yield components in the field conditions (30 plants). Experimental data were discriminated using unpaired T-tests in program Sigma Plot Windows Version 1.0 (Jandel Scientific, Erkhart, Germany).

Results and Discussion

Drought experiment

Effect of drought on maize leaf growth was investigated in two different experimental systems. In the first experiment plants were exposed to drought and correlation of parameters of water regime and leaf growth were monitored, although in the second experiment leaf growth process under drought conditions was investigated.

Analysis of correlative relationship between total and turgor potential as parameters of water regime and LER as a parameter of leaf growth during drought conditions is presented in Figure 1. Obtained results showed that in early lines Polj-17 and F-2 and hybrid NSSC 420 reduction of LER followed changes in total and turgor potential, and pointed out that the leaf growth of these genotypes was regulated by leaf water status (hydraulic signaling). However, in the hybrid ZPTC 260 reduction of leaf growth started before changes of parameters of water regime, which indicated that this genotype had a chemical signaling regulation mechanism. Similar genotypic differences in leaf growth responses to drought were found in other plant species (P u l i g a et al., 1996).

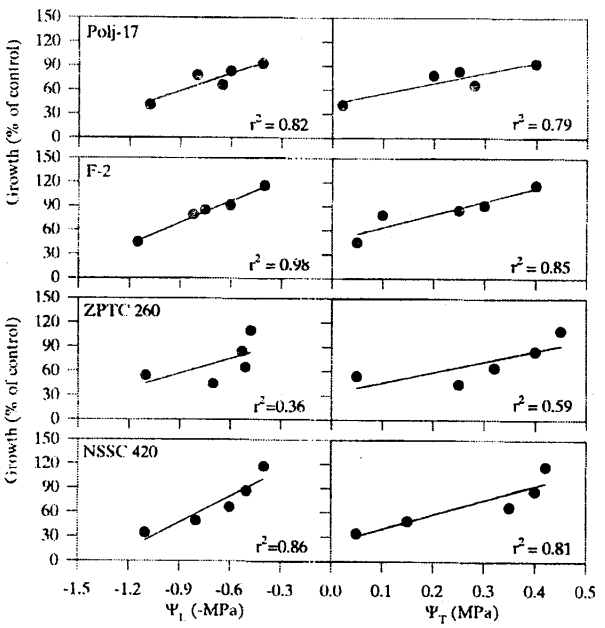

Fig.1. - Correlative relationship between water and turgor potential and leaf growth in investigated maize genotypes Polj-17, F-2, ZPTC 260 and NSSC 420

The drought effect on the leaf growth parameters of investigated genotypes is presented in Table 1. In the control conditions highest leaf elongation rate was found in hybrid ZPCS 677 and lowest in drought susceptible line F-2. Investigation of parameters of leaf growth showed that drought decreased leaf elongation rate (LER) in all maize genotypes. Decreasing LER during developing drought was also observed in other species (B a c o n, 1998).

T a b. 1. - Effect of drought on parameters of leaf growth and development

Genotype	LER (cm/day)		Phyllochron (day/leaf)	
	Control	Drought	Control	Drought
Polj-17	3.07	1.93	7.7	7.1
F-2	2.38	1.34	8.3	12.5
ILB 84	3.50	3.00	7.7	6.7
B 73	3.36	2.81	7.7	9.1
ZPTC 260	4.20	3.74	7.1	7.7
NSSC 420	3.79	3.10	6.2	8.3
ZPSC 677	5.16	2.93	7.1	10
DTP	4.30	3.29	5.9	6.2

Comparison between genotypes showed that highest reduction in LER and consequently on leaf area was observed in late maturing hybrid ZPSC 677 and lowest reduction in early maturing hybrid ZPTC 260.

Results of leaf development (Tab. 1) showed that in control conditions early maturing line F-2 had slowest, although late population DTP the highest leaf development. Comparison between genotypes showed that drought had a slowing effect on leaf development, which caused increasing of phyllochron. Similar results were observed in sugar beet (M i l f o r d et al., 1985). The highest increase for phyllochron was measured in the drought susceptible line F-2 (50% of control). In drought conditions resistant lines from both maturity group (Polj-17 and ILB 84) showed faster leaf development, which could be an adaptive drought mechanism (T u r n e r, 1979).

A measurement of parameters of cell elongation and cell production was presented on Table 2. Our results demonstrated that drought affected both cell elongation and cell division with significant genotypic differences. Drought caused significant decreasing in cell density in the cell division zone in some genotypes. Cell flux out from growth zone and cell elongation rate were also decreased in drought conditions, while duration of cell elongation increased in the most investigated genotypes.

The leaf elongation rate is a function of length of the elongation zone and segmental elongation rate of position within the zone. These parameters also depend on the rate of epidermal cell production, cell elongation rate and duration of elongation of individual cells (M a c A d a m et al., 1989). Our results also

showed that decrease of leaf elongation rate is a result of decreasing of segmental elongation rate, cell length and length of the elongation zone (data are not presented). Similar effect has been reported in leaves of other species (D u r a n d et al., 1995).

T a b. 2. - Parameters of cell production and elongation under drought conditions

Genotype	Number of cells in the cell division zone		Flux of cells (cell/day)		Duration of elongation (day)		Cell elongation rate (µm/day)	
	Control	Drought	Control	Drought	Control	Drought	Control	Drought
Polj-17	248	180***	179	118***	2.84	2.79	56.03	52.91
F-2	218	216	134	83***	4.41	7.08***	37.28	20.76***
ILB 84	257	215	201	168*	3.06	2.37**	53.61	69.00**
B 73	256	265	207	172*	2.28	2.62	65.83	61.59
ZPTC 260	261	209***	246	227	2.25	2.34	71.02	63.57
NSSC 420	206	189**	199	167*	2.56	3.92**	67.58	44.73***
ZPSC 677	234	245	346	179***	3.06	4.57**	64.77	33.25***
DTP	253	254	226	195	2.56	2.28	70.55	69.93

*, **, *** indicate the level of significance ($P < 0.05$, $P < 0.01$ and $P < 0.001$ respectively)

Obtained results also pointed out that drought effect in resistant lines and early maturing hybrid was more expressed in cell division, in susceptible lines, late maturing hybrid and population DTP in cell elongation, while in medium maturing hybrid drought affected both cell division and cell elongation.

Nitrogen deficiency experiment

Effect of nitrogen deficiency on third maize leaf growth was presented in Table 3. These results showed that nitrogen deficiency reduce leaf elongation rate (LER) in both investigated genotypes, which is reflected on leaf length and area. Similar results were observed in other species (P a l m e r, 1996).

T a b. 3. - Effect of nitrogen deficiency on parameters of leaf growth and development

Genotype	LER (cm/day)		Phyllochron (day/leaf)	
	+N	-N	+N	-N
F-2	2.14	1.63	10.0	12.5
ZPSC 677	3.02	2.23	9.1	10.0

Under nitrogen deficiency, leaf development of both maize genotypes (Tab. 3) was slower comparing to control, which as a result in increasing of phyllochron for both genotypes, especially in line F-2. Results of M c C u l l o u g h et al., (1994) for maize genotypes confirmed effect of nitrogen on leaf appearance rate and phyllochron. Similar phenomena were obtained with other crops, where

Longnecker et al., (1993) showed that stronger nitrogen deficit had a slowing effect on leaf appearance rate in wheat.

T a b. 4. - Effect of nitrogen deficiency on parameters of cell production and elongation

Genotype	Number of cells in the cell division zone		Flux of cells (cell/day)		Duration of elongation (day)		Cell elongation rate (μm/day)	
	+N	-N	+N	-N	+N	-N	+N	-N
F-2	228	220	109	81***	4.50	3.83**	39.65	49.68***
ZPSC 677	211	210	165	124**	1.37	1.95***	125.82	83.21***

, * indicate the level of significance ($P < 0.01$ and $P < 0.001$ respectively)

Analysis of cell elongation and cell production in nitrogen deficiency conditions is presented in Table 4. Results showed that deficiency of nitrogen affected both cell elongation and cell division with significant genotypic differences. Nitrogen deficiency decrease cell flux out from growth zone for both genotypes and had different effect on cell elongation rate. This caused increasing of the duration of elongation in hybrid ZPSC 677, while in line F-2 decreasing of the time needed for cell to pass growth zone was found. The leaf growth analysis showed that in these conditions in line F-2 cell division was more affected, although in hybrid ZPSC 677 the cell elongation. Similar results were obtained by other authors (Fricke et al., 1997).

The pH and exogenous ABA experiments

Investigation of the effect of different pH of "artificial xylem sap" on leaf growth is presented in Figure 2. Results show that maximal leaf growth for both genotypes was found at pH 6. Alkalization of "artificial xylem sap" significantly reduced leaf length in line F-2 (by 36% comparing to maximal value at pH 6) and in hybrid ZPSC 677 (by 10%). Bacon et al., (1998) found in barley similar correlation between increasing of pH xylem sap and the reduction of LER.

Reduction of LER at alkaline pH could be the result of change in activity of ATP-pump that is involved in auxin-stimulated acidification of cell wall growth (Cleland, 1991). It is well known that auxins also control the activity of cell wall enzymes - expansyns, which is involved in cell expansion. These enzymes are highly pH dependent and showed reduced activity at alkaline pH (McQueen - Mason, 1995), which suggests that water deficit reduced leaf growth via effect of pH on expansyns.

Exogenous application of ABA (10^{-6} and 10^{-8} M) had different effect on investigated genotypes. In line F-2 application of ABA caused significant decreasing of leaf growth at all applied pH and showed highest reduction at pH 6

(60%) comparing to control. However, higher ABA concentration (10^{-6} M) didn't show significantly different effect than lower ABA concentration (10^{-8} M). On the contrary, results for hybrid ZPSC 677 showed a significant ABA concentration effect. In this genotype the interaction of 10^{-6} M ABA and pH 5 and 7 had a higher reducing effect on leaf growth than interaction of 10^{-8} M ABA and pH.

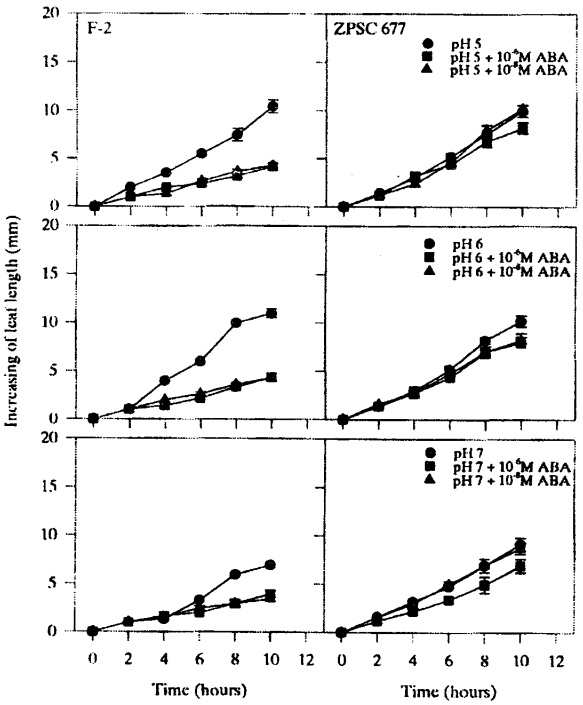

Fig.2. - Effect of pH and ABA on leaf growth maize genotypes F-2 and ZPSC 677

Results of leaf elongation bioassay with wheat and barley plants (M u n n s, 1992) showed that exogenous application of 10^{-8} M ABA had no effect on reduction, while 10^{-6} M and higher concentrations caused significant leaf growth reduction. Investigation of the effect of ABA on the growth of 36 wheat cultivars (B l u m and S i n m e n a, 1995) showed significant genotypic variation. According to M u n n s and C r a m e r, (1996) one of the reasons for this kind of response is possibility that some of the endogenous factors may have influence on different sensitivity of tissue to xylem ABA and leaf growth response.

Investigations with ABA-deficient barley mutants (B a c o n et al., 1998) showed that changes of pH of "artificial xylem sap" had no effect on leaf growth

and also they demonstrated that alcaline pH without ABA can not reduce leaf growth. Therefore, they pointed out that changes of pH have no direct effect on the activity of cell wall enzymes.

Comparisons of inhibition in leaf growth in ABA vs. pH experiment with results obtained in experiments with drought and nitrogen deficiency showed higher reduction of leaf growth for line F-2 than for hybrid ZPSC 677. It is difficult to explain increased sensitivity of line F-2 to ABA. Since previous investigations with line F-2 showed that drought and interaction of nitrogen deficiency vs. ABA caused high accumulation of ABA in the proximal part of elongation zone (S t i k i ć et al., 1998), it could be presumed that such accumulation of ABA increased the sensitivity of this genotype to ABA and as a consequence the inhibition of leaf growth was higher.

Field experiment

Analysis of parameters of plant growth and productivity in field conditions is presented in Tables 5 and 6. Results of our measurements showed that highest value of relative leaf expansion rate (RLER) was found in the vegetative stage of ontogenesis, especially in population DTP. Also, drought resistant genotype ILB 84 had higher value of RLER than drought susceptible line B 73.

T a b. 5. - Parameters of plant productivity of population of DTP in irrigated and rainfed field

Stage of ontogenesys	RLER (cm^2/cm^2 d)		RGR (g/g day)		NAR (g/m^2 day)	
	Irrigated field	Rainfed field	Irrigated field	Rainfed field	Irrigated field	Rainfed field
			1996			
vegetative stage	0.085	0.099	0.142	0.143	11.59	10.98
vegetative stage - flowering stage	0.018	0.015	0.043	0.052	6.72	8.73
flowering stage - milky stage	0.003	0.001	0.041	0.042	13.50	17.13
			1997			
vegetative stage	0.046	0.046	0.070	0.065	9.00	6.61
vegetative stage - flowering stage	0.008	0.006	0.014	0.022	2.64	3.36
flowering stage - milky stage	0.009	0.002	0.030	0.040	8.65	12.02

Leaf expansion is very a sensitive process to water deficit and may have significant influence on maize yield (S o b r a d o, 1987). However, inhibition of leaf growth under drought conditions could be an adaptive mechanism, which helped the plants to survive in unfavorable environmental conditions (B l u m, 1988).

T a b. 6. - Parameters of plant productivity of lines ILB 84 and B 73 in irrigated and rainfed field

Stage of ontogenesys	RLER (cm^2/cm^2 d)		RGR (g/g day)		NAR (g/m^2 day)	
	Irrigated field	Rainfed field	Irrigated field	Rainfed field	Irrigated field	Rainfed field
				ILB 84		
vegetative stage	0.055	0.052	0.081	0.082	9.53	10.95
vegetative stage - flowering stage	0.002	0.006	0.020	0.020	5.41	3.97
flowering stage – milky stage	0.0003	0.006	0.014	0.010	2.36	2.51
				B 73		
vegetative stage	0.045	0.045	0.074	0.068	9.76	7.74
vegetative stage - flowering stage	0.006	0.008	0.005	0.023	1.11	4.17
flowering stage - milky stage	0.011	0.006	0.011	0.017	2.06	4.05

Obtained results show highest value of relative growth rate (RGR) in vegetative stage and after this phase RGR declined until the end of the season. Similar trend in ontogenetic decline during the development of plants was observed in experiment with other species (D e l g a d o and M e d r a n o, 1991). Our results also show that drought increased of RGR could be significant for higher accumulation of dry matter for population DTP and line B73 whose data are not showed. S i m a n e et al., (1993) investigated genotypic differences in RGR between different wheat cultivars. They found that drought resistant cultivars in favorable period of the growing season had a high RGR (being fast-growing), although during stress conditions had a low RGR (being low-growing). Opposite trend was found with susceptible cultivars. These results are similar with ours.

Net assimilation (NAR) presents a rate of increase of dry matter per unit leaf area and indicates the photosynthetic capacity of crops. Our measurements show that population DTP in both investigated years had two NAR maximum, the first in the vegetative stage and second in period between flowering and milky stage. However, late maturing lines had one maximum in the vegetative stage of development. Drought increased NAR in population DTP and drought susceptible line B 73 and caused higher accumulation of dry matter. E c k (1986) showed that NAR was high during the phase of intensive leaf growth period when carbon was mainly used for production of leaves, and during and after flowering phase, where the distribution of photosynthates to development of reproductive organs took place.

Analysis of yield parameters (Tab. 7) for population DTP grown in 1996 showed statistic significant increasing in ear weight and kernel in the rainfed field, and absence of significant differences for plants grown in 1997.

Measurements of the same parameters done with late maturing lines (Tab. 8) showed that in line B 73 drought significantly decreased ear length, number of kernel/ear, ear weight and weight of 1000 kernels.

T a b. 7. - Components of yield of population DTP in irrigated and rainfed field

Parameters	1996		1997	
	Irrigated field	Rainfed field	Irrigated field	Rainfed field
Ear length (cm)	17.55	17.90	19.25	18.87
Row number/ear	15.93	16.42	16.00	15.40
Grain number/row	32.55	33.67	37.60	38.00
Ear weight (g)	184.87	214.60*	230.31	240.65
Kernel weight (g)	158.49	183.85 *	192.49	200.42
Weight of 1000 kernel (g)	327.21	346.04	375.70	381.50

* indicate the level of significance (P < 0.05 respectively)

T a b. 8. - Components of yield lines ILB 84 and B 73 in irrigated and rainfed field

Parameters	ILB 84		B 73	
	Irrigated field	Rainfed field	Irrigated field	Rainfed field
Ear length (cm)	13.53	13.22	13.53	12.25***
Row number/ear	16.18	16.00	17.20	17.14
Grain number/row	20.54	21.47	26.45	21.36***
Ear weight (g)	107.25	101.68	113.08	84.68***
Kernel weight (g)	84.69	81.34	89.54	68.95**
Weight of 1000 kernel (g)	327.66	299.86	252.52	254.42

, * indicate the level of significance (P < 0.01 and P < 0.001 respectively)

Investigation of N e S m i t h and R i t c h i e (1992) showed that drought in the reproductive phase had the greatest effect on yield. In the vegetative phase drought induced reduction in maize yield as a result of stomatal closure and smaller CO_2 uptake, although in grain filling phase due to reduced assimilate translocation (B r e v e d a n and H o d g e s, 1973).

Results of our investigations show that highest value of RLER in the period of intensive leaf growth was found for population DTP (1996) and drought resistant line ILB 84. Comparison between genotypes show that drought resistant line ILB 84 have higher RLER and weight of 1000 kernels than susceptible line B 73. Analysis of growth and productivity in rainfed field show that drought had smaller effect on inhibition of leaf growth in population DTP and resistant line ILB 4, which had consequences on the yield of these plants.

S o b r a d o (1990) showed that maize cultivars with higher leaf growth in the drought conditions maintain turgor through osmotic adjustment and have higher potential for photosynthesis, although C r o s s (1991) found that relative leaf expansion rate is in positive correlation with maize yield. These results indicate that selection of genotypes with higher leaf and stem growth and increased capacity for osmoregulation could improve water status of plants and consequently increase yield (B o l a n o s et al., 1993).

Conclusion

Obtained results point out that the leaf growth of early lines (Polj-17 and F-2) and hybrid NSSC 420 in the drought conditions was regulated by leaf water status (hydraulic signaling), although the leaf growth from hybrid ZPTC 260 had a chemical signaling regulation mechanism.

Investigation of parameters of leaf growth show that drought decreased leaf elongation rate (LER), appearance and leaf development in all genotypes, although these effects were more expressed in line F-2 and hybrid ZPSC 677. In drought conditions resistant lines from both maturity group showed faster leaf development, which could be an adaptive drought mechanism. These results also suggest that leaf growth analysis can be used as a convenient assay for screening genotypic differences in drought reactions.

Measurements of parameters of cell elongation and cell production in the elongation zone demonstrated that drought affected both processes with significant genotypic differences. These results show that drought effect in resistant lines and early maturing hybrid was more expressed on cell division, in susceptible lines, late maturing hybrid and population DTP on cell elongation, while in medium maturing hybrid drought affected both cell division and cell elongation.

Deficiency of nitrogen caused inhibition of leaf growth and development especially in line F-2. The leaf growth analysis show that in these conditions in line F-2 cell division was more affected, although in hybrid ZPSC 677 the cell elongation.

Effect of alkalization of "artificial xylem sap" and application of exogenous ABA (10^{-6} and 10^{-8} M) on reduction of leaf growth was more expressed in line F-2 than in hybrid ZPSC 677.

Analysis of plant growth and productivity based on monitoring of parameters like RLER, RGR and NAR could help to understanding growth pattern during the plant development, as well as the influence of different environmental and genotypic factors. Our results show that drought had smaller effect on inhibition of leaf growth in population DTP and resistant line ILB 4, which had consequences on the yield of these plants.

REFERENCES

1. B a c o n, M. A. (1998): The control of leaf extension in *Lolium temulentum* L. and *Hordeum vulgare* L. growing in drying soil. Ph.D. thesis. University of Lancaster, Lancaster, UK.
2. B a c o n, M. A., W i l k i n s o n, S., D a v i e s, W. J. (1998): pH-regulated leaf cell expansion in droughted plants is abscisic acid dependent. Plant Physiology, 118, 1507-1515.
3. B l u m, A. (1988): in "Plant Breeding for Stress Environments", CRC Press Boca Raton, Florida.

4. B l u m, A., S i n m e n a, B. (1995): Isolation and characterisation of variant wheat cultivars for ABA sensitivity. Plant Cell Environment, 18, 77-83.
5. B o l a n o s, J., E d m e a d e s, G. O., M a r t i n e z, L. (1993): Eight cycles selection for drought tolerance in lowland tropical maize. III. Responses in drought-adaptive physiological and morphological traits. Field Crop Research, 31, 269-286.
6. B r e v e d a n, E. R., H o d g e s, H. F. (1973): Effects of moisture on ^{14}C translocation in corn (*Zea mays* L.) Plant Physiology, 65, 322-326.
7. C h r i s t i a n s e n, M. N. (1982): World environmental limitations to food and fiber culture. in: "Breeding Plants for Less Favorable Environments", eds. M.N. Christiansen and C.F. Lewis, Wiley Interscience, New York.
8. C l e l a n d, R. E. (1991): Auxin induced growth of *Avena* coleoptiles involves two mechanisms with different pH optima. Plant Physiology, 99, 1556-1561.
9. C r a m e r, G., A l b e r i c o, G. J., S c h d m i d t, C. (1994): Leaf expansion limits dry matter accumulation of salt-stressed maize. Australian Journal of Plant Physiology, 21, 663-674.
10. C r o s s, H. Z. (1991): Leaf expansion rate effects on yield and yield components in early-maturing maize. Crop Science, 31, 579-583.
11. D e l g a d o, E., M e d r a n o, H. (1991): Field performance and leaf characteristics of *Nicotiana tabacum* L. genotypes selected by low CO_2 survival. Photosynthetica, 25, 313-322.
12. D o d d, I. C., S t i k i ć, R., D a v i e s, W. J. (1996): Chemical regulation of gas exchange and growth in plants in drying soil in the field. Journal of Experimental Botany, 47, 1475-1490.
13. D u r a n d, J. E., O n i l l o n, B., S c h n y d e r, H., R a d e m a c h e r, I. (1995): Drought effects on cellular and spatial parameters of leaf growth in tall fescue. Journal of Experimantal Botany, 46, 1147-1155.
14. E c k, H. V. (1986): Effects of water deficits on yield, yield components, and water use efficiency of irrigated corn. Agronomy Journal, 78, 1035-1040.
15. F r i c k e, W., M c D o n a l d, A. J. S., M a t t s o n-D j o s, L. (1997): Why do leaves and leaf cells of N-limited barley elongate at reduced rates? Planta, 202, 522-530.
16. G r o e n e v e l d, H. W., B e r g k o t t e, M., L a m b e r s, H. (1998): Leaf growth in the fast-growing *Holcus lanatus* and the slow-growing *Deschampsia flexuosa*: tissue maturation. Journal of Experimental Botany, 49, 1509-1517.
17. H a u n, J. R. (1973): Visual quantification of wheat development. Agronomy Journal, 65, 116-119.
18. H e w i t t, E. J. (1966): Sand and water culture methods used in the study of plant nutrition. eds. Comm. Agri. Bur. Farn., Bucks, UK.
19. H s i a o, T.C. (1973): Plant responses to water stress. Annual Review of Plant Physiology, 24, 519-570.
20. H u n t, R. (1982): Plant growth curves. in: "The functional approach to growth analysis", Edward Arnold, London, UK.
21. K l e p p e r, B., R i c k m a n, R. W., P e t e r s o n, C. M. (1982): Quantitative characterization of vegetative development in small cereal grains. Agronomy Journal, 74, 789-792.
22. L o n g n e c k e r, N., K i r b y, E. J. M., R o b s o n, A. (1993): Leaf emergence, tiller growth, and apical development of nitrogen-deficient spring wheat. Crop Science, 33, 154-160.
23. M a c A d a m, J. W., V o l o n e c, J. J., N e l s o n, C. J. (1989): Effects of nitrogen on mesophyll cell division and epidermal cell elongation in tall fescue leaf blades. Plant Physiology, 89, 549-556.
24. M c C u l l o u g h, D. E., G i r a r d i n, P., M i h a j l o v i c, M., A g u i l e r a, A., T o l l e n a a r, M. (1994): Influence of N supply on development and dry matter accumulation of an old and new maize hybrid. Canadian Journal of Plant Sciences, 74, 471-477.
25. M c Q u e e n-M a s o n, S. (1995): Expansins and cell wall expansion. Journal of Experimental Botany, 46, 1639-1650.

26. Milford, G. F. J., Pocock, T. O., Riley, J. (1985): An analysis of leaf growth in sugar beet. II. Leaf appearance in field crops. Ibid, 106, 173-185.
27. Monteith, J. L., Elston, J. (1983): Perfomance and productivity on foliage in the field. in: "The Growth and functitioning of leaves". eds. J. Dale and F. Milthorpe, Cambridge University Press, Cambridge, UK.
28. Munns, R. (1992): A leaf elongation assay detects an unknown growth inhibitor in xylem sap from wheat and barley. Australian Journal of Plant Physiology, 19, 127-135.
29. Munns, R., Cramer, G. R. (1996): Is co-ordination of leaf and root growth mediated by abscisic acid? Plant and Soil, 185, 33-49.
30. Ne Smith, D. S., Ritchie, J. T. (1992): Short- and long-term responses of corn to a pre-anthesis soil water deficit. Agronomy Journal, 84, 107-113.
31. Palmer, S. (1996): Leaf expansion - its inhibition at low nitrogen availability. Ph.D. thesis. University of Lancaster, Lancaster, UK.
32. Puliga, S., Vassana, C., Davies, W. J. (1996): Control of leaf growth of Mediterranean forages by chemical and hydraulic influences. Journal of Experimental Botany, 47, 529-537.
33. Rickman, R. W., Klepper, B. L. (1995): The phyllochron: where do we go in the future? Crop Science, 35, 44-49.
34. Schnyder, H., Seo, S., Rademacher, I. F., Kuhauch, W. (1990): Spatial distribution of growth rates and of epidermal cell lengths in the elongation zone during leaf development in *Lolium perenne* L. Planta, 18, 423-431.
35. Scholander, P. F., Hammel, H. T., Bradsteel, E. P., Hemmingsen, E. A. (1965): Sap pressure in vascular plants. Science, 148, 339-346.
36. Simane, B., Peacock, J. M., Struik, P. C. (1993): Differences in developmental plasticity and growth rate among drought-resistant and susceptible cultivars of durum wheat (*Triticum turgidum* L. var. *durum*). Plant and Soil, 157, 155-166.
37. Sobrado, M. A. (1987): Leaf rolling - A visual indicator of water deficit in corn. (*Zea mays* L.). Maydica, 32, 9-18.
38. Sobrado, M. A. (1990): Drought responses of tropical corn 2. Leaf expansion rate and water relation under controlled conditions. Maydica, 35, 227-234.
39. Stikić, R., Jovanović, Z., Prokić, Lj., Davies, W. J. (1998): Effect of drought, nitrogen deficiency and ABA on maize leaf growth. Bulgarian Journal of Plant Physiology, (Special issue), 228, FESPP Congress, Varna , Bulgaria.
40. Turner, N. C. (1979): Drought resistance and adaptation to water deficits in crop plants. in: "Stress Physiology in Crop Plants". eds. H. Musseland and R.H. Staples, Wiley, New York.
41. Volonec, J. J., Nelson, C. J. (1981): Cell dynamics in leaf meristems of contrasting tall fescue genotypes. Crop Science, 21, 381-385.
42. Wilkinson, S., Davies, W. J. (1997): Xylem sap increase: a drought signal received at the apoplastic face of the quard cell that involves the suppression of saturable abscisic acid uptake by the epidermal symplast. Plant Physiology, 113, 559-573.
43. Zhang, J., Davies, W. J. (1990): Does ABA in the xylem control the rate of leaf growth in soil-dried maize and sunflower plants? Journal of Experimental Botany, 41, 765-772.

Received January 31, 2001
Accepted March 27, 2001

PROUČAVANJE MEHANIZMA INHIBICIJE RASTENJA LISTOVA KUKURUZA

Zorica Jovanović*

Rezime

Mehanizam inhibicije rastenja listova ispitivan je kod osam genotipova kukuruza različite otpornosti na sušu i iz različitih grupa zrenja. U kontrolisanim uslovima ispitivan je efekat suše, nedostatka azota, pH i ABA na rastenje listova. U eksperimentu sa sušom urađena su merenja vodnog potencijala i njegovih komponenti i parametara rastenja i razvića lista. Isti parametri rastenja i razvića lista mereni su u eksperimentu sa nedostatkom azota, dok je rastenje lista mereno u eksperimentu sa pH i ABA. U poljskom eksperimentu mereni su parametri rastenja biljaka i produktivnosti.

Dobijeni rezultati pokazuju da hidraulička i hemijska signalizacija reguliše rastenje listova u uslovima suše. Suša smanjuje rastenje listova kod svih genotipova i otporne linije na sušu pokazuju brže lisno razviće. Vodni deficit utiče na produkciju i elongaciju ćelija sa značajnim genotipskim razlikama. Sličan fenomen je utvrđen pri nedostatku azota. Efekat alkalizacije rastvora "veštačkog ksilemskog soka" i aplikacije egzogene ABA (10^{-6} i 10^{-8} M) na redukciju rastenja listova više je izražen kod linije neotporne na sušu. Analiza rastenja i produktivnosti biljaka u poljskim uslovima pokazala je da je suša imala mali efekat na inhibiciju rastenja listova kod otpornih genotipova, što se odrazilo na prinos tih biljaka.

Primljeno 31. januara 2001.
Odobreno 27. marta 2001.

* Zorica Jovanović, asistent, Poljoprivredni fakultet, 11081 Beograd-Zemun, Nemanjina 6, SR Jugoslavija

Rad je skraćena verzija doktorske disertacije odbranjene 27. oktobra 2000. godine na Poljoprivrednom fakultetu u Zemunu, pred komisijom u sastavu: dr Radmila Stikić, redovni profesor, dr Ružica Džamić, redovni profesor, dr Ljubinka Ćulafić, redovni profesor, dr Nedeljko Nenadić, redovni profesor, dr Vlado Ličina, vanredni profesor.