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EFFECT OF PLANT DENSITY ON AGRONOMIC TRAITS AND PHOTOSYNTHETIC PERFORMANCE IN THE MAIZE IBM POPULATION

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SUMMARY

Photosynthesis is a vital process in plant physiology. Performance index is an indicator of plant vitality and is used as a main parameter in chlorophyll fluorescence measurements. Plant density is an important factor in maize production that can affect grain yield. Objective of this paper was to estimate the effect of plant density on agronomic traits and photosynthetic efficiency in the maize IBM population. The results showed a decrease in grain yield per plant basis (20 plants per plot) in higher plant density (normal density - 3.88 kg per plot, high density - 2.95 kg per plot) and an increase in grain yield per unit area (yield/ha) in higher plant density (normal density - 11.03 t ha^{-1}, high density - 13.64 t ha^{-1}). Performance index was decreased in higher plant density (normal density - 5.31, high density - 4.95). Statistical analysis showed highly significant effect ($p<0.001$) of density on performance index and highly significant effects ($p<0.001$) of plant density and genotype on maize yield. Low positive correlation was observed between grain yield per plot and performance index ($r = 0.36$, $p<0.001$).

Key-words: plant density, photosynthetic performance, maize, yield

INTRODUCTION

Plant density is an important factor in crop production that can significantly affect grain yield. One of the main tasks in maize production is finding the optimum plant density where the negative effects of competition between plants will not result in significant yield reduction. Optimum plant density in maize for high grain yield in Croatia is from 55,000 to 80,000 plants per hectare for hybrids in FAO groups 700 to 200, respectively (Pucarić et al., 1997). Recently, Gonzalo et al. (2010) investigated plant density-related traits in the late maize population of 186 intermated recombinant inbred lines (IRILs) derived from the cross of inbred lines B73 and Mo17 (IBM population) to elucidate the genetic basis of plant response to density in maize considering moderate (50 000 plants per hectare) and high (100 000 plants per hectare) plant densities.

Increased plant density unavoidably increases mutual plant shading which causes depression in photosynthesis and greater competition for water and nutrients (Sangoi, 2001; Marchiori et al., 2014). Photosynthesis is one of the most explored mechanisms in plant physiology as well as an indicator of adverse conditions which can affect photosynthetic efficiency and various molecular mechanisms (Horváth et al., 1998; Perreault et al., 2011). It can be indirectly measured through the fluorescence of chlorophyll *a* (Strasser et al., 2000). Analysis of the clorophyll fluorescence increase, known as JIP test (Strasser and Strasser, 1995) is widely used for assessment of plant reaction to various types of stress conditions (Appenroth et al., 2001; Hermans et al., 2003). Index of the photosynthetic efficiency or performance index (PI), as an indicator of plant vitality is the most sensitive parameter of JIP test which takes into account all main photochemical processes. Performance index (PI) is defined as a ratio of functional PSII events leading to electron transport within photosynthesis and the energy lost from photosynthetic electron transport (Strasser et al., 1999; 2000). As shown in the research of Reddy and Strasser (2000), chlorophyll fluorescence analysis is suitable for research in bioenergetic descrip-

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tion of cultivars in normal and stress induced conditions as well as for estimation of vitality and stress in different cultivars and subsequently their reaction to stress factors. Since photosynthesis is the basis of yield formation it is very important to know at which plant densities it is significantly affected. Objective of this study was to estimate the effect of plant density on some agronomic traits and photosynthetic efficiency in the maize IBM population.

MATERIAL AND METHODS

Field trial was set up on location (Osijek), using incomplete block design. Germplasm used in this trial was developed from the known public inbred lines B73 and Mo17, which were intermated into IBM population (Intermated B73 and Mo17 or IRILs). Seeds of IRILs (Coe et al., 2002; Lee et al., 2002) of the IBM population had been received from the Maize Genetic COOP Stock Center in Urbana, Illinois, USA. Total of 80 IRILs were planted in two adjacent experiments with different plant densities (normal density 57000 plants per hectare and high density 95000 plants per hectare). Due to insufficient number of plants one IRIL was omitted from chlorophyll *a* fluorescence measurements. Plot sizes of normal and high density experiments were 3.5 m^2 and 2.1 m^2, respectively with 20 plants per plot on both densities. Standard fertilization and cultivation practices for maize were applied.

Chlorophyll *a* fluorescence measurements were done in the field in July (10^{th}-17^{th} 2013), during tasselling when the maize plant was particularly stress sensitive. During the growing season deviations in the amount of rainfall occurred in March (203% more than normal) and in June (72% less than normal). Deviations from mean monthly temperatures took place in March (1.8°C warmer than normal), July (1.8°C warmer than normal) and August (2.6°C warmer than normal). Measurements were conducted in the morning not later than 10 a.m. due to midday depression of photosynthesis. Before measurements, leaves were dark adapted for 30 minutes using dark adaption leaf clips. After dark adaptation chlorophyll *a* fluorescence was measured using Handy-PEA fluorimeter (Plant Efficiency Analyser, Hansatech Instruments Ltd, Great Britain). Fluorescence was measured on ear leaves in four replications per genotype. By dark adapting the leaves before measurement plastoquinone is completely reduced and reaction centers are opened hence providing conditions for minimum fluorescence intensity measurement F_0. Polyphasic rise in fluorescence is induced by high intensity (3200 $\mu mol_{PHOTONS} m^{-2} s^{-1}$) red saturation light (maximum at 650 nm) pulse. Fluorimeter measures changes in chlorophyll fluorescence by 1 s, starting 50 μs after the pulse. Obtained data was analyzed using JIP test which outputs biophysical changes that quantify the flow of energy through PSII (Strasser et al., 2004).

Two-way analysis of variance for grain yield per hectare and performance index (PI) and phenotypic parameters was performed using 'R' statistical software (R Core Team, 2013). Pearson´s correlation coefficient was also calculated to check for important correlations between main traits.

RESULTS AND DISCUSSION

Mean values of all phenotypic parameters except barren plants (fertile plants, ears per plant, ears per plot, grain yield per plot), as well as performance index (PI), were higher in normal density (Table 1), whereas grain yield per hectare (calculated parameter) and barrenness were higher in high density. From Table 1 it can be seen that performance index (PI) was lower in higher density indicating that plants were stressed and the same decreasing trend is noticeable in grain weight per plot (and also in other measured parameters, except for barren plants). After calculating grain yield per hectare, yields were higher in high density suggesting that lower yields per plant basis (20 plants per plot) in high density would be compensated by larger number of plants per hectare. In general, yield per hectare in normal density was 19% lower than yield in high density.

Table 1. Yield, performance index and phenotypic parameters of two different plant densities averaged across 79 IRIL-s of IBM maize population

Tablica 1. Srednje vrijednosti prinosa, indeksa učinkovitosti i ostalih fenotipskih parametara 79 rekombinantnih inbred linija iz IBM populacije pri dvije različite gustoće sjetve

Density Gustoća	**Fertile plants ± SE** *Fertilne biljke*	**Barren plants ± SE** *Jalove biljke*	**Ears per plant ± SE** *Klipova po biljci*	**Ears per plot ± SE** *Klipova po parceli*
Normal *Normalna*	14.83 ± 0.31	1.11 ± 0.11	1.41 ± 0.02	20.75 ± 0.40
High *Visoka*	12.84 ± 0.29	1.33 ± 0.10	1.35 ± 0.03	17.07 ± 0.46

Density Gustoća	**Grain yield per plot** *Prinos zrna po parceli* **(kg) ± SE**	**Performance index** *Indeks učinkovitosti* **(PI) ± SE**	**Grain yield** *Prinos zrna* **(t ha⁻¹) ± SE**
Normal *Normalna*	3.88 ± 0.06	5.31 ± 0.07	11.03 ± 0.30
High *Visoka*	2.95 ± 0.07	4.95 ± 0.05	13.64 ± 0.21

According to the analysis of variance, all sources of variation were highly significant ($p<0.001$) for performance index, grain yield per plot and grain yield, except the effect of genotype on performance index, which was not significant at $p<0.05$ level (although it was significant at $p<0.1$ level). Highly significant effects of density and genotype were observed on the number of fertile plants and ears per plot while the effect of density on ears per plant was not significant. Although the number of barren plants was slightly higher in high density, the effect of density and genotype were not significant (Table 2).

Table 2. Analysis of variance for performance index, grain yield and other traits

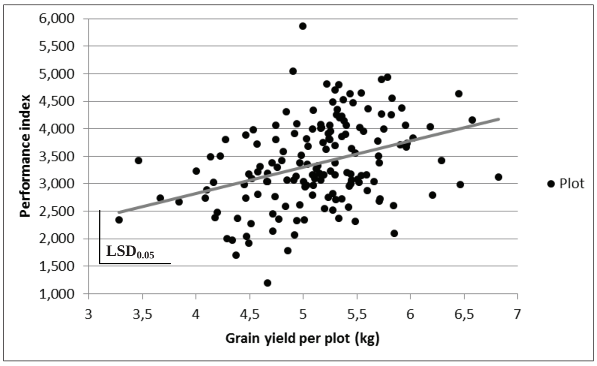
Tablica 2. Analiza varijance za indeks učinkovitosti, prinos zrna i ostala svojstva

Source of variation *Izvor variranja*	**df** *Stupnjevi slobode*	**F-value** / F-vrijednost			
		Fertile plants *Fertilne biljke*	**Barren plants** *Jalove biljke*	**Ears per plant** *Klipova po biljci*	**Ears per plot** *Klipova po parceli*
Genotype / *Genotip*	78	1.73**	0.78ns	2.09***	1.86**
Density / *Gustoća*	1	42.62***	1.94ns	2.71ns	68.33***
Source of variation *Izvor variranja*	**df** *Stupnjevi slobode*	**F-value** / F-vrijednost			
		Grain yield per plot (kg) *Prinos zrna po parceli (kg)*	**Performance index** *Indeks učinkovitosti*	**Grain yield (t ha⁻¹)** *Prinos zrna (t ha⁻¹)*	
Genotype / *Genotip*	78	2.41***	1.36ns	2.29***	
Density / *Gustoća*	1	183.43***	18.05***	84.74***	

***** Significant at 0.001 probability level** / **** Statistički značajno na razini značajnosti 0,001*

Correlation coefficient, averaged across densities, between performance index and grain weight per plot was positive with value of $r=0.36$ and significant at $p<0.001$ level (Graph 1). $LSD_{0.05}$ for performance index and grain weight per plot was 1.03 and 0.92, respectively. As shown by Kovačević et al. (2011), performance index can be interesting for screening due to its tendency to positively correlation with grain yield and its stability.

Results of this research show that higher plant density adversely affected grain yield per plant, but somewhat lower yields per plant in high density were compensated by larger number of plants per hectare resulting in higher yields on yield per hectare basis. These results are in accordance with Widdicombe and Thelen (2002) and Duvick (1996; 2005). According to Tollenaar and Lee (2002), maize grain yield per plant reduces with plant density increasing (or with the relative availability of resources per plant) but when density is increased from 1 plant m^{-2} to 7.9 plants m^{-2} grain yield per unit area increased from 4.5 to 12 t ha^{-1}. Duvick (1996) stated that yield per plant in non stressed low density (1 plant m^{-2}) environment has not changed in the past 70 years. The increase in yield is due to improved abiotic and biotic stress tolerance and increase in plant yield per unit area is due to constant adaptation of hybrids to higher plant densities providing more grain-bearing plants rather than more grain per plant.



Graph 1. Means of 79 IRILs for grain weight per plot and performance index with corresponding least significant differences at 0.05 probability level ($LSD_{0.05}$)

Grafikon 1. Srednje vrijednosti 79 IRIL za težinu zrna po parceli i indeks učinkovitosti s odgovarajućim najmanjim značajnim razlikama na 0,05 razini značajnosti ($LSD_{0,05}$)

Gonzalo et al. (2010) investigated the response of 186 B73 × Mo17 recombinant inbred lines (RILs) to low (50 000 plants ha^{-1}) and high (100 000 plants ha^{-1}) density. Evaluation of growth, development, and yield traits revealed significant increases of days to anthesis, ASI, final height and barrenness in high density. Number of ears per plant and yield per ear declined in high density, which is in accordance with our results (Table 1). Their results showed that evaluated traits are genetically controlled by multiple loci in their response to increasing density; in addition there was statistical evidence of epistatic interactions of these loci. Furthermore, loci were not dispersed throughout the genome but located on a small set of four regions making them suitable for marker-assisted selection.

Cox (1996) reported 10-20% decrease in leaf CO_2 exchange rates in increasing plant densities (from 4.5 plants m^{-2} to 9 plants m^{-2}) and 40 % lower leaf area index in low density compensated by higher photosynthetic efficiency, but lower crop growth rates and dry matter. They concluded that in low plant density hybrids had 15% less grain yield and dry matter than in high plant density. Similarly, our results showed that grain yield (t ha^{-1}) was 19.1% higher in high density, although on plot basis (20 plants) yield was almost 24% lower in high density.

Dwyer and Tollenaar (1989) reported a decline in photosynthetic response in increasing plant density from 20 000 to 130 000 plants ha^{-1} and the decline was genotype dependent. Our results show a significant decline in photosynthetic performance in high density, but unlike in the aforementioned research it was not dependent on the genotype. With the increase of plant density available light in the canopy is reduced; plants exhibit photosynthetic acclimation to varying light intensity and have a reduced photosynthetic capacity in shaded environment. Concentration of RuBP decreases in plants grown in shaded environment and the decreases in RuBp/chlorophyll ratio have significant effects on sensitivity to photoinhibition. As a consequence shading also caused changes in metabolite concentration of the photosynthetic carbon reduction cycle (Seemann et al., 1987). In the research of Hashemi-Dezfouli and Herbert (1992) increased maize plant density (3, 7.5 and 12 plants m^{-2}) resulted in decrease of kernel number per ear and complete ear bareness, also tassel emergence was slightly delayed in increased density. They reported a decreased rate of apparent photosynthesis in higher density due to decreased PAR (photosynthetically active radiation) and decreased chlorophyll concentration in higher densities. Competition of plants for resources increases with increasing plant density and in the conditions when nutrients and water are not limiting factors solar radiation can become a factor that limits plant growth and development.

CONCLUSION

Increasing plant density from 57,000 plants ha^{-1} to 95,000 plants ha^{-1} resulted in a decrease of all measured parameters (fully developed plants, fertile plants, ears per plant, number of I. class and II. class ears, ears per plot, grain weight per plot and performance index). Correlation between performance index and grain weight per plot, although statistically significant, was weak (r=0.36). Decrease of performance index along with other measured parameters suggests that performance index measurements could detect plant density stress. Although plants in higher density were stressed (based on performance index and grain weight per plot) and had slightly lower yields per plant, yield per hectare in high density was actually higher due to larger number of plants per unit area.

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UTJECAJ GUSTOĆE SJETVE NA AGRONOMSKA SVOJSTVA I FOTOSINTETSKU UČINKOVITOST IBM POPULACIJE KUKURUZA

SAŽETAK

Fotosinteza je vitalni dio biljne fiziologije. Indeks fotosintetske učinkovitosti (eng. performance index) indikator je vitalnosti biljke i koristi se kao glavni parametar u mjerenju fluorescencije klorofila. Gustoća sklopa važan je faktor proizvodnje kukuruza, koji može utjecati na prinos zrna. Cilj ovoga istraživanja bio je procijeniti utjecaj gustoće sklopa na agronomska svojstva i fotosintetsku učinkovitost kod IBM populacije kukuruza. Rezultati su pokazali smanjenje prinosa zrna na osnovi jedne biljke (20 biljaka po parceli) u gušćem sklopu (manja gustoća sklopa – 3,88 kg po parceli, veća gustoća sklopa – 2,95 kg po parceli) i povećanje u prinosu zrna na osnovi prinosa po jedinici površine (prinos/ha) u gušćem sklopu (manja gustoća sklopa – 11,03 t ha^{-1}, veća gustoća sklopa 13,64 t ha^{-1}). Indeks fotosintetske učinkovitosti smanjio se s povećanjem gustoće sklopa (manja gustoća sklopa – 5,31, veća gustoća sklopa 4,95). Statističkom analizom utvrđen je značajan utjecaj ($p<0,001$) gustoće sklopa na indeks učinkovitosti fotosinteze i statistički značajni utjecaji ($p<0,001$) gustoće sklopa i genotipa na prinos zrna. Uočena je slaba pozitivna korelacija između prinosa zrna po parceli i indeksa učinkovitosti fotosinteze ($r=0.36$, $p<0,001$).

Ključne riječi: gustoća, fotosintetska učinkovitost, kukuruz, prinos

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