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PHOTOSYNTHETIC PROPERTIES OF ERECT LEAF MAIZE INBRED LINES AS THE EFFICIENT PHOTO-MODEL IN BREEDING AND SEED PRODUCTION

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The initial idea of this study was a hypothesis that erect leaf maize inbred lines were characterised by properties of an efficient photo-model and that as such were very desirable in increasing the number of plants per area unit (plant density) in the process of contemporary selection and seed production. The application of a non-invasive bioluminescence-photosynthetic method, suitable for the efficiency estimation of the photo-model, verified the hypothesis. Obtained photosynthetic properties of observed erect leaf maize inbred lines were based on the effects and characteristics of thermal processes of delayed chlorophyll fluorescence occurring in their thylakoid membranes. The temperature dependence of the delayed chlorophyll fluorescence intensity, phase transitions (critical temperatures) in the thylakoid membranes and activation energy are the principal parameters of the thermal processes. Based on obtained photosynthetic properties it is possible to select erect leaf maize inbred lines that are resistant and tolerant to high and very high temperatures, as well as, to drought. They could be good and efficient photo-models wherewith

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the further improvement of the modern breeding and seed production is achieved.

Key words: maize inbred line, erect leaves, photo-model, photosynthetic and thermal processes, thylakoid membrane, conformational and functional changes, thermal and photosynthetic properties, delayed chlorophyll fluorescence

INTRODUCTION

This study regards two evident facts from the most recent history of maize selection and breeding. The first one is with a positive sign, based on results of maize breeding that has been very intensively developing during the last 50 years. As a result of such an activity, approximately 1,000 grain and silage maize hybrids were developed (DUVICK, 1984; TRIFUNOVIĆ, 1986; IVANOVIĆ *et al.*, 1995). Regardless of such an extraordinary success in maize breeding, eagerness and enthusiasm of the total research has not been slowing down. The search for new methods and exact approaches in the enrichment and completion of the research within maize breeding was continued. The other fact with a negative sign is related to the interrelation between photosynthesis and maize breeding. Although it is evident that photosynthetic processes are very spread, highly productive in their intensity, very complex in their nature, and vastly studied in their scientific actuality, their application in maize breeding is still insignificant. Such a state is probably a consequence of the existence of several functional interrelations that unify conformational and dynamic changes within chloroplasts and their thylakoid membranes, on the one hand, and effects of environmental stress factors on them, on the other hand.

Delayed chlorophyll fluorescence (DF) can be phenomenologically described as an occurrence of luminescence (bioluminescence) within the red range of the visible spectrum produced by plant systems: bacteria, algae and higher plants (maize) immediately after their intermittent illumination (RADENOVIĆ, 1992; 1994; 1997). DF was discovered by STREHLER and ARNOLD (1951). Important studies, especially those of the last 20 years (JURSINIC, 1986; VESELOVSKI and VESELOVA, 1990; MARKOVIĆ *et al.*, 1993; 1996) revealed the direct connection between DF and photosynthetic processes, in which DF was considered an unavoidable indicator - a susceptible "probe" for experimental photosynthetic and bioluminescence studies (RADENOVIĆ *et al.*, 1994a; 1994b; RADENOVIĆ and JEREMIĆ, 1996; MARKOVIĆ *et al.*, 1987; 1999).

The objective of the present study was to determine general and photosynthetic properties of erect leaf maize inbred lines, as an efficient photo-model, by the application of the non-invasive photosynthetic and bioluminescence method in maize breeding and seed production (RADENOVIĆ *et al.*, 2000; 2001a; 2001b; 2002a; 2002b), and thereby to contribute to more exact and rational proceeding of the contemporary process of breeding and seed production.

MATERIAL AND METHODS

The material selected for this study was composed of 16 non-related maize inbred lines of different origin (local and introduced) and different duration of the growing season (FAO maturity groups ranging from 100 to 800). Furthermore, all selected erect leaf maize inbred lines were yellow-seeded, but differed in the kernel type (from the real dent to typical flint kernels). Erect leaves are their essential property.

Table 1 presents the survey of all 16 studied erect leaf maize inbred lines. Photosynthetic properties of only three dent erect leaf maize inbred lines of FAO 600 (ZPLA 84, ZPLA 1134 and ZPLA 1641), were discussed in the present study. The studied inbreds were grown in the experimental field of the Maize Research Institute, Zemun Polje. During July and August, maize plants were brought from the field to the laboratory during morning hours (between 7 am and 8 am). Plants, when sampled in the field, were transversely cut in the ground internode. In the laboratory, plants were internode lengthwise placed in water. Prior to the bioluminescence experiment the plants were kept under the black ball glass for two hours. A segment of ear intact leaves was taken from such plants and placed into a chamber of the phosphoroscope (Fig. 1) and kept (in dark) for at least 15 minutes, and then DF was measured.

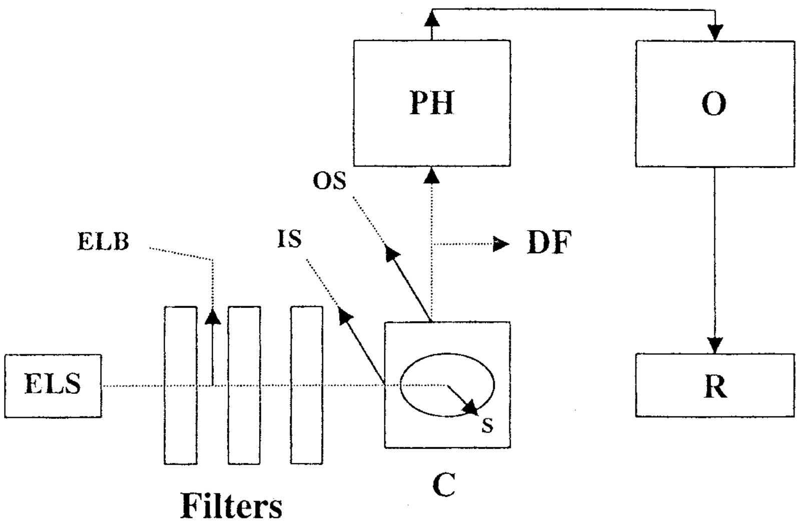

Figure 1. Experimental setup of the method and measuring equipment for delayed chlorophyll fluorescence: C - dark chamber with a sample stand; S - sample (leaf segment), filters, ELS - excitation light source, PH - photo-multiplier; O - oscilloscope, R - printer, ELB - excitation light beam, DF - luminescent light, IS - input chamber slot, OS - output chamber slot

The non-invasive photosynthetic bioluminescence method used to measure DF is presented in Fig. 1. This block scheme of the bioluminescence method was developed at the Maize Research Institute, Zemun Polje. Measurements of changes in DF intensities were performed after a method that had been both, in principle and details, described in previous papers RADENOVIĆ (1992; 1994; 1997), RADENOVIĆ *et al.* (2001a; 2001b; 2002a; 2002b), MARKOVIĆ *et al.* (1969).

RESULTS

The results of photosynthetic properties of erect leaf maize inbred lines, as optimal photo-models, are presented through the following five sections.

The measure of an angle and leaf area of erect leaf maize inbred lines. A specially designed protractor was used to measure the angle between lines of the position of each leaf and the position of the erect leaf maize inbred plants. Results on the measures of angles (ranging from 31.5° to 34°) between ear leaf position and the plant position, as well as, average leaf areas are presented in Table 1. It is clear that the leaf area has no properties that would particularly characterise the studied erect leaf maize inbred lines (Table 1).

Table 1. Ear leaf angle and leaf area of studied erect leaf maize inbred lines

Ordinal number of inbred lines	Designation of inbred lines	Angle between ear leaf and stalk	Ear leaf area (cm^2)
1	ZP LA 69	33.84°	5553.88
2	**ZP LA 84**	**32.96°**	**5695.07**
3	ZP LA 101	32.50°	5660.10
4	ZP LA 116	32.10°	4896.20
5	ZP LA 146	31.53°	4719.47
6	ZP LA 236	31.96°	4808.26
7	ZP LA 270	32.20°	5112.18
8	ZP LA 327	31.88°	4788.30
9	ZP LA 409	31.86°	4660.36
10	ZP LA 466	32.60°	4780.16
11	ZP LA 567	31.86°	4590.18
12	ZP LA 933	33.51°	4460.12
13	**ZP LA 1134**	**31.42°**	**4607.63**
14	ZP LA 1612	31.84°	4880.60
15	**ZP LA 1641**	**31.94°**	**4910.80**
16	ZP LA 1758	31.90°	4856.87

Parameters of thermal processes of the delayed chlorophyll fluorescence in the studied erect leaf maize inbred lines. The detailed study on thermal processes of chlorophyll DF was performed on eight selected erect leaf maize inbred lines including the stated three inbreds: ZPLA 84, ZPLA 1134 and ZPLA 1641 (Table 2). These processes are characterised by time parameters in regard to the duration of conventionally sampled segments: a, b, c, d, e, f and g on the thermal curve of chlorophyll DF (Figure 2). The results on time parameters of the chlorophyll DF thermal curve for the stated segments are presented in Table 2.

Table 2. Duration (in seconds) of segments on the thermal curve of delayed chlorophyll fluorescence for erect leaf maize inbred lines *

Segments of thermal curve	Segment designation	ERECT LEAF MAIZE INBRED LINES								Temperature range for establishing thermal curve (°C)
		LA 69	**LA 84**	LA 116	LA 146	LA 409	LA 933	**LA 1134**	**LA 1641**	
Stationary level of DF intensity	a	> 180	**> 180**	> 180	> 180	> 180	> 180	**> 180**	**> 180**	25-60
Initial increase of DF intensity	b	450	**438**	450	336	546	480	**498**	**360**	25-60
Linear increase of DF intensity	c	120	**150**	162	198	150	156	**138**	**184**	25-60
Maximum level of DF intensity	d	36	**60**	42	54	48	48	**36**	**30**	25-60
Linear decrease of DF intensity	e	126	**132**	120	162	120	150	**186**	**150**	25-60
Decelerated decrease of DF intensity	f	78	**168**	366	432	384	300	**168**	**156**	25-60
Minimum level of DF intensity	g	144	**132**	84	24	18	12	/	**84**	25-60

* Examine together with Fig. 2.

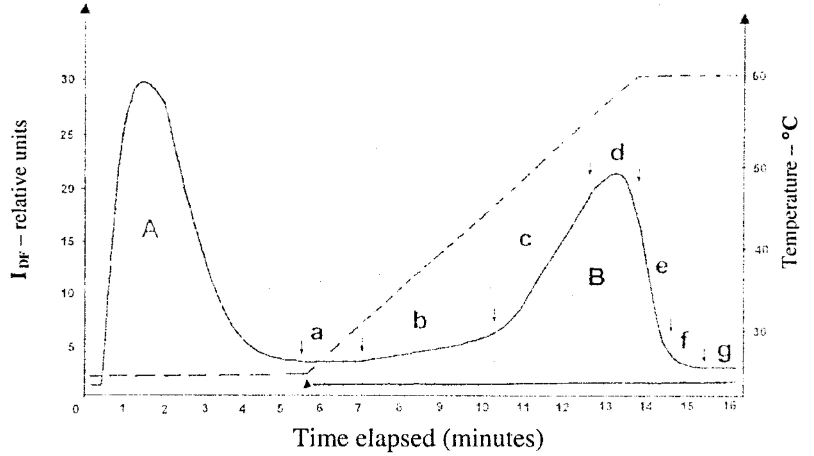

Fig. 2. Schematic presentation of typical changes of chlorophyll DF intensities on the intact leaf of the observed maize inbred lines (solid line) and changes of temperatures (dashed line): curve A indicates induction processes of chlorophyll DF, while curve B encompasses thermal processes of chlorophyll DF. Segments on the thermal curve (a, b, c, d, e, f, g) are interception points in which conformational and functional changes in the thylakoid membrane occur

The temperature dependence of the delayed chlorophyll fluorescence intensity for the thylakoid membrane of the erect leaf maize inbred lines. Figures 3a, 3b and 3c present the changes of the intensity of the stationary DF level in the function of temperatures ranging from 25°C to 60°C for the observed selected erect leaf maize inbred lines: ZPLA 84, ZPLA 1134 and ZPLA 1641.

The Arrhenius plot for the determination of conformational changes in the thylakoid membrane of the erect leaf maize inbred lines. Figures 4a, 4b and 4c, present results of conformational changes that occurred in the thylakoid membrane of the selected erect leaf maize inbred lines. These changes were caused by the temperature impact on the intact leaf segment of the studied erect leaf maize inbred lines: ZPLA 84, ZPLA 1134 and ZPLA 1641.

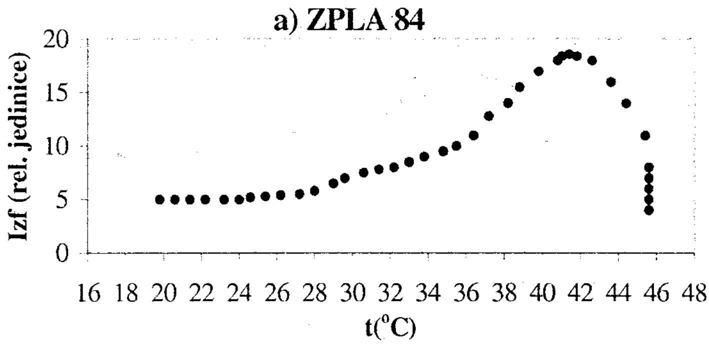

Fig. 3a.

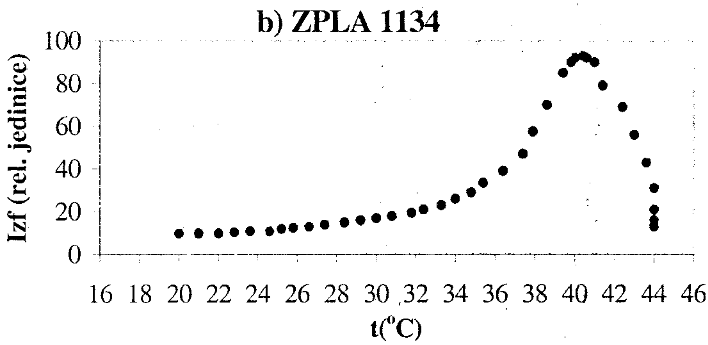

Fig. 3b.

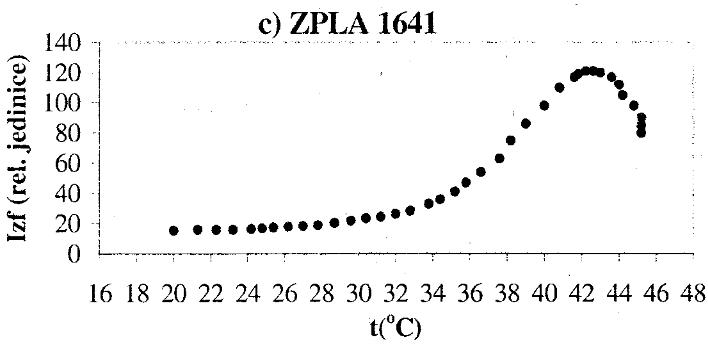

Fig. 3c.

Fig. 3a, 3b, 3c. Changes of the intensity of the stationary chlorophyll DF level in dependence on temperatures in the thylakoid membrane of the intact leaf of the erect leaf maize inbred lines: a) ZPLA 84, b) ZPLA 1134, c) ZPLA 1641

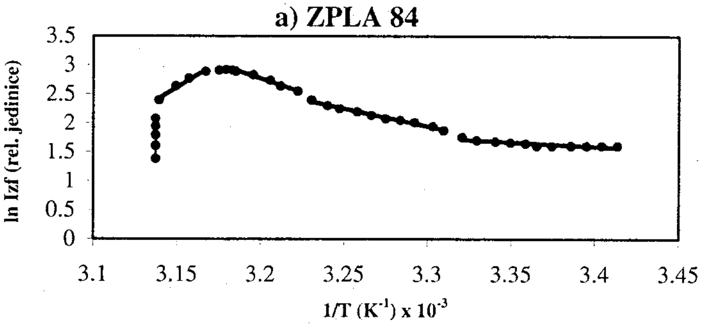

Fig. 4a.

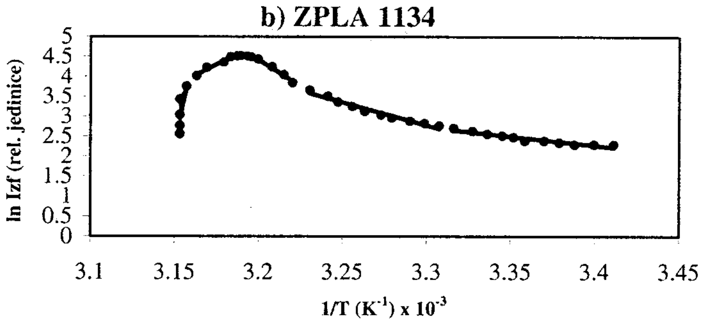

Fig. 4b.

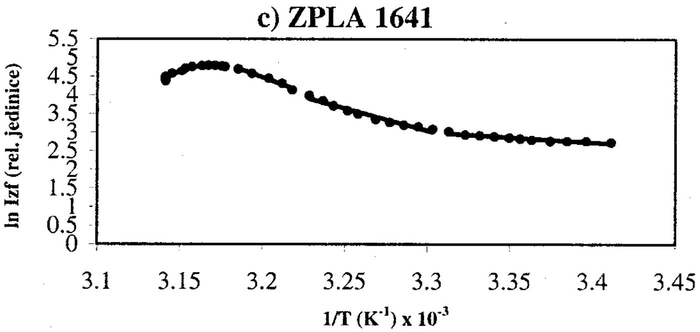

Fig. 4c.

Fig. 4a, 4b, 4c. Arrhenius plot for a change of logarithm of the intensity of chlorophyll DF in dependence on reciprocal values of temperatures on the thylakoid membrane of the erect leaf maize inbred lines: a) ZPLA 84, b) ZPLA 1134, c) ZPLA 1641

Table 3. Activation energies and temperatures of phase transitions in the thylakoid membrane of the studied erect leaf maize inbred lines

ZP LA 84		ZP LA 1134		ZP LA 1641	
Ea (kJ mol^{-1})	$t_{p.t.}$ (°C)	Ea (kJ mol^{-1})	$t_{p.t.}$ (°C)	Ea (kJ mol^{-1})	$t_{p.t.}$ (°C)
/	28.2	/	28.81	/	28.71
12.69	36.3	28.23	36.5	51.65	37.02
50.52	40.7	62.88	39.2	129.92	40.82
79.77	41.8	175.98	41.92	181.76	42.21
0.009	/	1.15	/	/	/

Activation energies and critical temperatures in the thylakoid membrane of the erect leaf maize inbred lines. Activation energies and temperatures of phase transitions (critical temperatures) in the thylakoid membrane of the studied erect leaf maize inbred lines (ZPLA 84, ZPLA 1134 and ZPLA 1641) are presented in Table 4.

DISCUSSION

The second half of the 20th century, as already mentioned, will be remembered, recognised and hardly excelled by a great success achieved in maize breeding and seed production. This almost spontaneous and grand activity was characterised by its expanded and complex breeding and seed production programme. The aim was clear and concrete - to obtain yield of newly developed maize hybrids as high as possible and to provide sufficient quantities of seed of high quality. The number of plants per area unit has been growing since 1980. This trend in maize breeding was referred to as a "plant density" programme and most directly affected the further yield increase. In addition, a subprogramme on breeding of erect leaf maize inbred lines was established. In pursuance of our hypothesis it was considered that these inbreds were the closest to the proposed photo-model. These two subprogrammes in maize breeding and seed production were not only complement, but they have also been expanded. Their implementation in the wide-scale production led to new results in maize breeding and seed production. In such a way, new hybrids with high grain and silage yields were developed (KOJIĆ, 1993; IVANOVIĆ *et al.*, 1992; 1995; TRIFUNOVIĆ, 1986; DUVICK, 1984).

Considering the stated, the initiation and broadening up of the maize breeding programme of the Maize Research Institute, Zemun Polje, with erect leaf maize inbred lines was quite expected. The group of 16 erect leaf maize inbred lines, including inbreds: ZPLA 84, ZPLA 1134 and ZPLA 1641, that were objectives of the present study, was in fact an attempt to achieve set goal and to confirm the proposed hypothesis.

It was necessary to photosynthetically characterise in detail the erect leaf maize inbred lines (Table 1). For that purpose, the non-invasive photosyntheticbioluminiscence method was applied (RADENOVIĆ *et al.*, 2001a; 2001b; 2002a; 2002b). The application of this programme provides the characterisation of the observed erect leaf maize inbred lines in relation to their resistance to both, increased and high temperatures and drought.

Actually, the temperature dependence of DF in studied erect leaf maize inbred lines is, to a certain extent, characterised only by the typical points on the thermal curve (Figure 2). The first typical point occurred in the contact of a segment **a** and a segment **b** and it was related to the lowest critical temperature at which the initial change of the DF intensity was observed. The second typical point occurred in the contact of the segment **b** and a segment **c** and it was related to a linear monotony and the angle of the increasing part of the DF intensity. During the duration of this typical point, evident conformational changes of the thylakoid membrane occurred. The third typical point reflected a smaller or greater rotundity of DF intensity peaks. The "breaking" conformational changes occurred in two interception points of the segments **c** and **d** and the segments **d** and **e**. The fourth typical point was related to the linear monotony and the inclination angle of the declining part of the DF intensity. This segment bore the last conformational changes that had occurred in the thylakoid membrane. These changes can hardly be described as characters of functioning of a living leaf segment. The typical points designated with **f** and **g** almost had no physiological role.

The observed typical points (Figure 2) can be considered as points that characterise erect leaf maize inbred lines, especially as these points are also points of possible conformational changes in the thylakoid membranes. This statement is in accordance with literature data (VUČINIĆ *et al.*, 1982; RADENOVIĆ, 1992; 1994; RADENOVIĆ *et al.*, 2001a; 2001b; 2002a; 2002b; MARKOVIĆ *et al.*, 1987).

All critical temperatures (phase transitions) at which even the slightest conformational changes occurred in the thylakoid membranes of studied erect leaf maize inbred lines were determined by the Arrhenius criterion and the linearisation of the DF temperature dependence. The value of critical temperatures (°C), their frequency and intermediate distance characterise erect leaf maize inbred lines in relation to their resistance and adaptation to increased and high temperatures. The Arrhenius criterion is based on the existence of straight lines. Each Arrhenius straight line represents its activation energy (Ea). The interception point of two straight lines is determined by a critical temperature. Each critical temperature follows a certain value of the activation energy and then is followed by another value of the activation energy (RADENOVIĆ, 1985; 1997; MARKOVIĆ *et al.*, 1993; 1996; RADENOVIĆ *et al.*, 2000; 2001a; 2001b; 2002a; 2002b). Results of the values of activation energies in the inclining and declining part of the thermal curve are explained by lower or greater conformational changes that occur in the molecules of the thylakoid membranes with the temperature increase. Due to such changes these molecules become more reactive and thereby gain the additional energy that is used in the recombining process of DF occurrence (Table 3).

This study was an attempt to show that there were erect leaf maize inbred lines with the properties of the efficient photo-model and that such properties were very desirable in the process of contemporary selection and seed production.

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FOTOSINTETIČKE KARAKTERISTIKE USPRAVNIH LISTOVA SAMOOPLODNIH LINIJA KUKURUZA KAO EFIKASAN FOTO-MODEL U OPLEMENJIVANJU I SEMENSKOJ PROIZVODNJI

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Izvod

Početna ideja za ovaj rad je bila hipoteza da su uspravni listovi samooplodnih linija kukuruza karakteristični za efikasan foto-model i da su kao takvi veoma poželjni u povećanju broja biljaka po jedinici površine (gustina biljaka) u procesima savremenog oplemenjivanja i semenske proizvodnje. Primena neinvazivne bioluminiscencne fotosintetičke metode, pogodne za efikasnu ocenu modela, potvrdila je hipotezu. Dobijene fotositetičke karakteristike posmatranih uspravnih listova samooplodnih linija kukuruza su zasnovane na efektu i karakteristikama termalnih procesa odložene fluorescencije hlorofila, koji se pojavljuje na njihovim tilakoidnim membranama. Temperaturna zavisnost intenziteta odložene hlorofilne fluorescencije, fazni prelaz (kritična temperatura) u tilakoidnim membranama i aktivaciona energija su glavni parametri termalnih procesa. Na osnovu dobijenih fotosintetičkih karakteristika, moguće je izabrati samooplodne linije kukuruza uspravnih listova, koje su otporne i tolerantne na visoke i vrlo visoke temperature, kao i na sušu. One mogu biti efikasan fotomodel, za postizanje poboljšanja modernog oplemenjivanja i semenske proizvodnje.

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