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The role of photosynthetic pigments in the leaf of maize inbred lines in improving photosynthetic efficiency

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Abstract

Methods of absorption and Raman spectroscopy were applied in this study to analyze functions and amounts of photosynthetic pigments in the leaf of maize inbred lines (M1-3-3Sdms, ZPPL186, and ZPPL225). Absorption spectroscopy was used to determine the dynamics of biosynthesis of chlorophyll a, chlorophyll b, and carotenoids. Raman spectroscopy was used to present the dynamics of biosynthesis of carotenoids and other compounds in terms of origin and kinetic form of the formation of spectra with all spectral bands. Organic molecules and compounds causing the formation of certain spectral bands in the Raman spectrum (carotenoids, phosphates, glycogen, amid III, and others) were determined. Conformational and functional changes of photosynthetic pigments in the leaves of the maize inbred lines, which occur due to changes in the ratio (quotient), were analyzed. The ratios (quotients) obtained indicate different contributions of valence oscillations of their chemical bonds, which inevitably alter the conformation of molecules and compounds. The results presented for the overall study point to minor biogenic differences among the maize inbred lines under study.

Key words: maize inbred line, leaf, chlorophyll, carotenoid, Raman spectrum

Introduction

In higher plants, the photosynthetic apparatus encompasses two types of chlorophyll: chlorophyll a and chlorophyll b. Their role is to absorb the energy of sunlight and convert it into the energy of chemical processes and bonds (Rys, 2014). The almost identical role of photosynthetic pigments regarding the transfer of solar energy into the leaf and the photosynthetic apparatus has been presented in the monograph dedicated to the connection of the processes caused by delayed chlorophyll fluorescence, photosynthesis, and maize breeding (Radenović, 2013).

Carotenoids in higher plants are divided into two major classes: the class of carotenoinds and the class of xantophylls (Adar, 2017). Carotenoids are molecules of tetraterpenes (linear or cyclic form) consisting of the carbon nucleus and hydrogen, while xantophylls contain an oxygen atom (Sajilata et al., 2008). Xanthophylls have an important role in the structure of the photosynthetic apparatus. The first function refers to the absorption of light energy and the transfer of absorbed energy to chlorophyll in the photosynthetic reaction centre. The second function refers to the protection of the system by deactivating the triplet state of chlorophyll, utilisation of active forms of oxygen. The third function refers to the regulation based on the ability of □ (beta) carotene to regulate membrane microviscosity by epoxidation and de-epoxidation of xanthophylls in the thylakoid membrane (Максимов et al., 1996; Jahns et al. 2009). Carotenoids are predominantly in the all-trans configuration, except for carotenoids of the reaction centre, where the C15-cis configuration is activated (Robert, 2004).

There are several methods used to analyse the functions, roles, and amounts of carotenoids. However, a prominent place is occupied by the method of Raman spectroscopy, with a special study of oscillation occurrence of chemical bonds of organic molecules. Raman spectroscopy provides a possibility of studying the impacts of high temperatures, drought, and stress on vital functions of the leaf (Macernis et al., 2014); or on the application of the origin of a spectral band with forward or backward movement (Radenović et al., 1998a). Such processes occur due to the effects of laser radiation in the Raman spectrometer. Under such conditions, different shapes of spectral bands occur in the Raman spectra that change their kinetic form or shift to one or the other side of the wavenumber (cm-1) (Radenović et al., 1998b, Arteni et al., 2015).

Absorption spectroscopy techniques were used to study the quantitative average content of chlorophyll a, chlorophyll b, carotenes, and xanthophyll in the leaf of maize inbred lines (Radenović et al., 2022). These techniques provide the measurement of the light absorption coefficient in characteristic peaks (absorption maxima) of pigments (chlorophyll a, chlorophyll b, and all carotenoids). This coefficient, proportional to the quantitative content of pigments dissolved in 100% acetone, has been presented in the manuscripts written by Bulda et al. (2008), Журавская et al. (2011), and Ilioaia et al. (2011). The main feature of the Raman spectrum with spectral bands is that it shows structural changes in organic molecules from the carotenoid class. All structural changes inevitably lead to numerous physiological changes in several processes. Any stress that occurs in plants is usually followed by conformational changes in organic molecules (Kornilina, 2012).

The aim of this study was to present the application of absorption and Raman spectroscopy methods, including all procedural details in terms of the technique and operating conditions that were necessary to determine the amounts of photosynthetic pigments, as well as to discover the conformational characteristics of organic molecules in the functional groups contained in leaves of the maize inbred lines observed.

Material and Methods

Maize inbred lines, M1-3-3Sdms, ZPPL186, and ZPPL255, developed at the Maize Research Institute, Zemun Polje, Belgrade, Serbia, were used in the study. After sowing inbred lines (10 seeds each), germinated seeds were grown under 16 : 8 light : dark photoperiod at relative air humidity of 75%. Maize plants were grown until the appearance of the third leaf. This when they are most suitable for these experimental investigations. It was possible to use leaves at different ages. The first leaf was 14 days old, the second leaf 20 days old, and the third leaf was 25 days old. The average values of all three leaves were taken for experimental measurements in this study. The third leaf was used to register the Raman spectrum of chlorophyll a, chlorophyll b, and carotenoids in the leaves of the maize inbred lines. It was also used to determine the average amounts of chlorophyll and carotenoids by absorption spectroscopy.

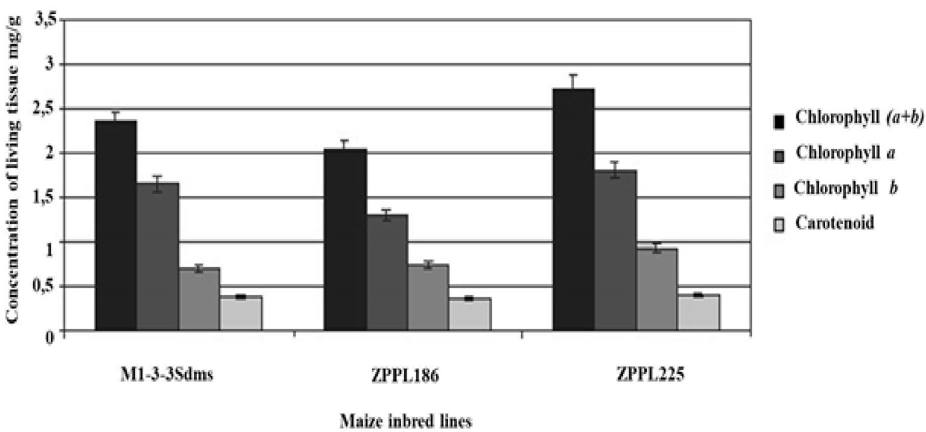
Raman spectroscopy was used to study conformational changes in organic molecules. The carotenoids in the leaves of the maize inbred lines were studied by the Raman microspectroscopy method that included the application of the Renishow spectrometer microscope with excitation of □ = 532 nm. A fragment of a leaf blade of the maize inbred line was placed on a sample carrier/ holder and exposed to laser radiation (5mW) for 10 seconds, after which the Raman spectrum with all spectral bands was registered.

The WiRE - version 3.3 software was used for the primary processing of Raman spectra, while the Origin programme package - version 8.1 was used for detailed processing of these spectra. Absorption spectrometry methods were used to observe photosynthetic pigments in the leaves of the maize inbred lines. The experimental material consisted of samples that were tested by using the Shimadzu UV-mini 1240 spectrophotometer (the single beam photometric system). The spectral band width was 5 nm, wavelength accuracy was ± 0.1 nm for the experiment duration. Photometric accuracy of this spectrophotometer ranged from ± 0.003 to 0.005 Abs.

Results and Discussion

Quantitatively determined content of photosynthetic pigments in the leaf of the maize inbred lines

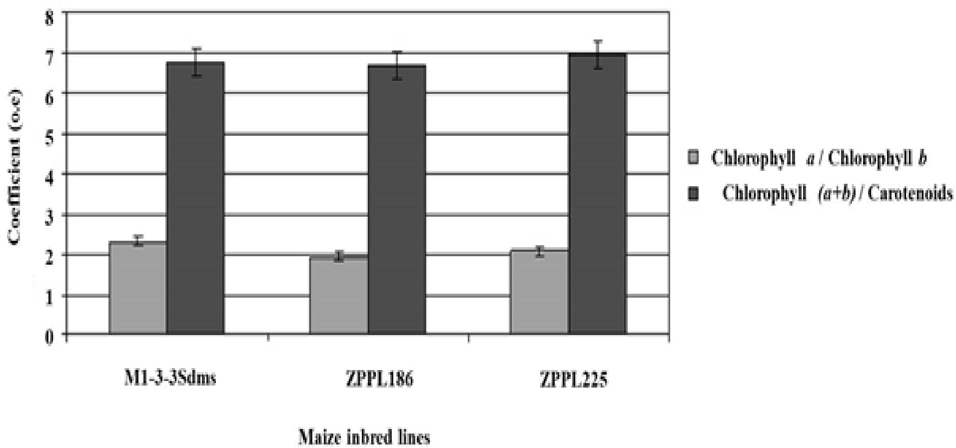
Histogram 1 shows the average concentrations of photosynthetic pigments studied in the leaves of the maize inbred lines. The highest content of photosynthetic pigments was found in the leaves of ZPPL225. A slightly lower and the lowest contents of photosynthetic pigments were detected in the leaves M1-3-3Sdms and ZPPL186, respectively. Also, the highest amount of total chlorophyll of 2.73 mg/g was recorded in the ZPPL225 inbred line. The carotenoid contents were fairly uniform, but the highest one of 0.40 mg/g was determined in the ZPPL225 inbred line.



Histogram 1. The quantitatively determined content of photosynthetic pigments in the maize leaf

Concentration ratio of photosynthetic pigments in the leaf of the maize inbred lines

The ratio (quotients) of chlorophyll a, chlorophyll b, chlorophyll a+b, and carotenoids are shown in Histogram 2. The highest values have been determined for the ZPPL225 inbred line, though the differences among inbreds were small.



Histogram 2. Changes in the ratio (quotient) of concentrations: chlorophyll a/ chlorophyll b and the sum of concentrations of chlorophyll (a+b)/ concentrations of carotenoids in the leaf of the maize inbred lines

Resonance Raman spectrum registered on the leaf segments of the maize inbred lines

A typical/ characteristic resonance Raman spectrum (Figure 1) has been registered on the third leaf segment of the maize inbred lines studied. Spectral bands appeared within 960 cm^{-1}, 1004 cm^{-1}, 1156cm^{-1}, 1188cm^{-1}, 1245cm^{-1}, and 1520 cm^{-1} ranges. Figure 1 shows the existence of spectral bands with higher intensity amplitudes, namely 1520cm^{-1}, 1156cm^{-1}, and 1004cm^{-1} and spectral bands with low intensity amplitudes, i.e., 960cm^{-1}, 1188cm^{-1}, and 1245cm^{-1}.

A spectral band at 960cm^{-1} (or 962cm^{-1}), 1004 cm^{-1} (or 1026cm^{-1}), 1188cm^{-1} (or 1118cm^{-1}), 1245cm^{-1} (or 1206cm^{-1}), and 1520 cm^{-1} was caused by phosphates, glycogen, phosphates, amide III, and carotenoids, respectively.

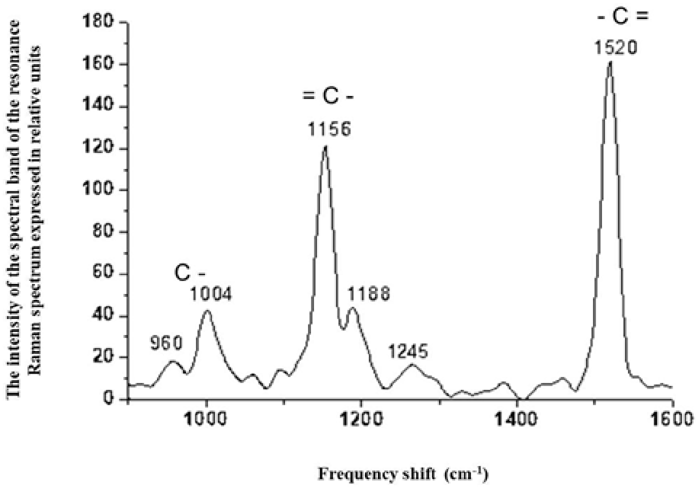


Figure 1. Raman spectrum of the leaves of the maize inbred lines studied

Changes in the ratio (quotient) of the intensity of the amplitudes of spectral bands of the Raman spectrum for all third leaves of the maize inbred lines

The ratios of the intensity of amplitudes of spectral bands of the Raman spectrum are presented in the order of their registration in the wavenumber range from 400 to 1600 cm^{-1} (Table 1). The I_{960} / I_{1004} ratio characterizes the proportion of the formation of a new shape of the conformation of molecules or compounds (Radenović, 1994). The I_{1004} / I_{1156} ratio characterizes the proportion of valence oscillations of the $C - C$ methyl radicals in relation to the valence oscillations of $= C - C =$ bonds (Henry et al., 2004; Radenović et al., 2021b). The I_{1156} / I_{1188} ratio characterizes the proportion of valence oscillations of carbon in the carotenoid molecule. The I_{1156} / I_{1245} and I_{1245} / I_{1520} ratios characterize the proportion of valence oscillations of unknown compounds.

In addition, the following ratios (quotients) are presented: the I_{1520} / I_{1156} ratio characterizes the proportion of valence oscillations of double $-C = C -$ bonds, in relation to single $= C - C =$, while the I_{1004} / I_{1520} ratio characterizes the proportion of valence oscillations of $C - C$ methyl group according to $-C = C -$ bonds. The presentation of all the results stated was done by analogy with the oscillation of transients in the induction processes of delayed chlorophyll fluorescence in the leaf of the maize inbred lines (Radenović et al., 2010).

Tab. 1. Changes in the ratio (quotient) of the intensity of amplitudes of spectral bands of the Raman spectrum of maize inbred line leaves.

Ratio of the intensity of amplitudes of spectral bands	Maize inbred lines (relative ratio)		
	M1-3-3Sdms	ZPPL186	ZPPL225
960 / 1004	0.357 ± 0.017	0.331 ± 0.018	0.37 ±± 0.019
1004 / 1156	0.110 ± 0.005	0.114 ±± 0.006	0.134 ± 0.007
1188 / 1156	0.282 ± 0.014	0.332 ±± 0.017	0.353 ± 0.015
1004 / 1520	0.286 ± 0.014	0.271 ±± 0.014	0.296 ± 0.015
1520 / 1156	1.197 ±± 0.060	1.179 ± 0.059	1.218 ± 0.061

Overlaps of the resonance Raman spectrum with all spectral bands

Figure 2 shows the overlap of the spectral bands of the Raman spectrum for the maize inbred lines studied in the full range from 900 to 1600 cm-1 (A) and the complete overlap of a spectral band of the Raman spectrum with the maximum intensity in the range of 1520 cm-1 (B).

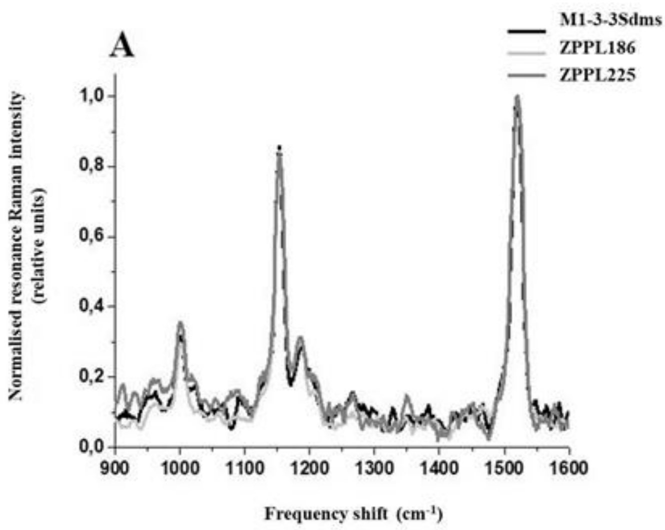


Fig. 2A. - Characteristic resonance Raman spectrum of the leaves of the maize inbred lines studied in the form of a smaller or a larger overlap in the full range from 900 to 1600 cm^{-1} (A), normalized to the value of the most intense spectral band with a peak of 1520 cm^{-1}

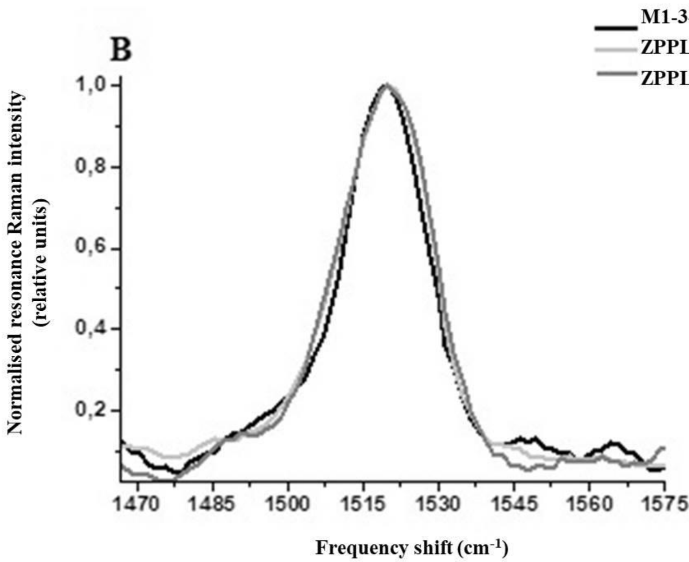


Fig. 2B. - Characteristic resonance Raman spectrum of the leaves of the maize inbred lines studied and overlaps for the spectral band at 1520 cm^{-1}

It is desirable to analyze the Raman spectrum with all spectral bands for the maize inbred lines studied (M1-3-3Sdms, ZPPL186, and ZPPL225) in the range from 400 to 1600 cm^{-1}. It was established that the Raman spectra of maize leaf chloroplasts within this range are characterized by high-amplitude bands of carotenoids and low-amplitude bands of cellulose molecules (bands at 1095 cm^{-1} and 1477 cm^{-1} correspond to valence oscillations of S – O – S bonds and N – S – H groups of atoms of cellulose molecules, respectively) (Radenović et al., 2021a).

The application of Raman spectroscopy within the range of 400-1600 cm^{-1} can also provide the analysis of the conformation of carotenoid molecules in chloroplasts. The 1520 cm^{-1} spectral bands in the Raman spectra are attributed to the valance oscillations of $C = C$ bonds. On the other hand, the 1156 cm^{-1} bands in carotenoid molecules are assigned to the valence oscillations characteristic for the $C - C$ bond, which is in agreement with the study carried out by Krimmer et al. (2019). It happens that the 1520 cm^{-1} spectral bands shift in the range of high frequencies, which causes the conversion of the all-tans to the cis configuration in the carotenoid molecules. The closer a cis position of the bond is to the centre of the molecule, the greater the shift of the 1520 cm^{-1} spectral band is. The double cis configuration shifts the 1520 cm^{-1} spectral band even further to a high frequency side (Robert, 2004). In the case of the trans-conformation of double bonds in the carotenoid molecule, the 1156 cm^{-1} band changes and acquires two pronounced arms: one at 1188 cm-1 and the other at 1245 cm^{-1}. Based on the results obtained by the analysis of the Raman spectra of carotenoids, it can be concluded that there have been no conformational changes in $-C = C -$ bonds in the carotenoid molecules of the maize leaves under study. However, these molecules have double conjugated bonds and methyl groups that also contribute to the position of spectral bands in the range from 400 to 1600 cm^{-1} of the Raman spectrum. The 1004 cm^{-1} band corresponds to valence oscillations of the side methyl group $C - CH_3$ (Robert, 2004). The spectral band at approximately 960 cm-1 has been characterized by $C - H$ valence oscillations beyond the in-plane $C - C$ bond, while the increase in the intensity of this band has been observed when the configuration of the organic molecule has been disturbed. A greater amount of pigment attributed to protein has led to less pronounced twisting beyond the plane between carbon atoms C11 and C12, and the band intensity indicated in the range of the Raman spectrum has been a consequence. It has been assumed that the spectral band at around 1188 cm^{-1} (Figure 1) causes changes in the position of C16 methyl in the *all-trans* configuration (Andreeva et al., 2011).

In the analysis of the Raman spectrum of carotenoids, normalization has been performed based on the size of the peaks, choosing, as a rule, a range of constant amplitudes whose change during the process has been minimal. According to the Raman spectrum obtained, the carotenoids in chloroplasts can be in different conformational states in different maize inbred lines. It has been found that the ratio intensity of characteristic spectral bands of the Raman spectra of carotenoids in the leaf of inbred lines are not the same. The contribution of the Raman spectrum and its spectral bands is reflected in conformational changes of photosynthetic pigments, particularly in the structure of carotenoid molecules. It depends on the examined inbred line of maize. Figure 2B shows the peaks of the spectral bands and the relationships between the inbred lines, i.e., M1-3-3Sdms, ZPPL186, and ZPPL225. The I_{1520} / I_{1156} ratio characterizes the polyene chain length of carotenoids, and the value of this ratio (quotient) has varied from 1.179 in the inbred M1-3-3Sdms to 1.218 in the inbred ZPPL225. The polyene chain length conformation of the carotenoid molecule in chloroplasts of the maize leaves under study has been in 15-trans form. With this conformation of the molecule in the range of 1155 cm-1 of the Raman spectrum, there has been one inflection point at 1190 cm^{-1}. The I960/I1006 ratio has been minimum in the carotenoids in chloroplasts of leaves of ZPPL186, indicating a minor conformational change caused by the rotation of carotenoid molecules outside the plane of the polyene chain or by the absence of such changes. During the test, significant changes in the valence oscillations of the methyl group have been detected. This refers to the following intensity ratios: I_{1004} / I_{1156}, I_{1004} / I_{1520}, and

I_{1156} / I_{1190}. In the spatial orientation of the atoms in the plane, there have also been certain minor changes in the I_{960} / I_{1004} ratio. The carotenoid molecule in ZPPL186 has been characterized by more pronounced vibrations of the side CH_3 group. It is known that carotenoid bound to protein complexes collects light to the photosystem II, and is characterized by the intensive spectral band at 960 cm^{-1} in the Raman spectrum, which particularly differs in the amplitude from bands at 1156 and 1004 cm^{-1}. Moreover, it has also been observed that the amplitude of the band at 960 cm^{-1} of the carotenoid Raman spectrum has been significantly smaller than amplitudes of the spectral bands at 1156 and 1004 cm^{-1}, and that it does not differ in different lines in the chloroplast Raman spectrum, which probably indicates the absence of protein-lipid interactions (Radenović et al., 2021a; Radenović et al., 2021b).

All maize inbred lines studied were predominantly in *trans* conformation, because the Raman spectra did not show bands characteristic of the *cis* isomers in the so-called fingerprint region, nor significant shifts of two spectral bands (1520 cm^{-1} and 1156 cm^{-1}) appeared. Differences in the studied maize inbred lines were associated with changes in the conformation of the carotenoid molecules in chloroplasts, but not in cellulose molecules. In two samples (M1-3-3Sdms and ZPPL186) the carotenoid molecules were in 15-*trans* shape with the different polyene chain confirmation. The experiments have shown that there was no dependence of the molecule configuration on the pigment concentrations in the leaves of the maize inbred lines studied. However, those differences that were established among maize inbred lines were probably caused by their genetic nature.

Conclusion

Quantities of photosynthetic pigments in the maize inbred lines observed were dissimilar. The highest concentration was detected in the inbred ZPPL225. Selection of maize inbred lines is performed according to the value of photosynthetic pigments in their leaves. The higher the concentration of these pigments is, the greater the capacity of the maize inbred to supply energy to the photosynthetic apparatus is.

Parameters of the Raman spectrum and its spectral bands for photosynthetic pigments have been recorded. The average quantities of photosynthetic pigments in leaves of the maize inbred lines studied have been determined for chlorophyll *a*, chlorophyll *b*, chlorophyll (*a* + *b*), and carotenoids. The origin (960cm-1, 1004cm^{-1}, 1156cm^{-1}, 1188cm-^{1}, 1245cm^{-1}, and 1520cm^{-1}) and kinetic form of all spectral bands of the Raman spectrum have been shown. The value of changes in the ratio (quotient) of the intensity of spectral bands of the Raman spectrum of leaves for each maize inbred studied has been established.

All spectral bands of the Raman spectrum caused by molecules and chemical compounds (phosphates, glycogen, amid III, carotenoids, and other compounds) have been presented. All spectral bands of the Raman spectrum where conformational changes of organic molecules or compounds occurred have been indicated: a change in the participation of chemical bonds (□C□CH_3, =C□C=, □C=C□), a change in the participation of valence oscillations of chemical bonds.

Our studies on the improvement of the photosynthetic efficiency in leaves of the maize inbred lines observed have been carried out during the developmental stage of grain filling with organic compounds. Main (top) leaves were active at this stage of the plant development – they had sufficient amounts of photosynthetic pigments and were able to transport solar energy into the photosynthetic structures of the leaf, due to which the expected grain yields of the maize inbred lines observed were achieved.

Other previously mentioned studies on the role and the function of photosynthetic pigments in the leaf and the photosynthetic apparatus contributed to the increase of overall knowledge about insufficiently studied processes within photosynthetic structures (chloroplasts, pigment-protein complexes, activities of antennas, and reaction centres), as a result of which efficient photosynthesis is achieved, and thereby higher grain yields of the maize inbred lines observed are obtained.

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The authors dedicate this paper to late Professor Mile R. Ivanović PhD, the most respected maize breeder in Serbia.

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Улога фотосинтетских пигмената у листу инбред линија кукуруза у повећавању ефикасности фотосинтезе

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Сажетак

У овом раду примењене су методе за апсорпциону и Раманову спектроскопију у изучавању функција и количина фотосинтетских пигмената у листу инбред линија кукуруза: M1-3-3Sdms, ZPPL186 и ZPPL225. Помоћу апсорпционе спектроскопије утврђена је динамика биосинтезе свих форми хлорофила: хлорофил a, хлорофил b, хлорофили *a* + *b* и каротеноида. Помоћу Раманове спектроскопије показана је динамика биосинтезе каротеноида и других једињења у погледу места и кинетичке форме настајања спектара са свим спектралним тракама. Утврђени су органски молекули и једињења који условљавају настајање појединих спектралних трака у Рамановом спектру (каротеноиди, фосфати, гликоген, амид III и други). Анализиране су структурне и функционалне промене фотосинтетских пигмената у листу инбред линија кукуруза до којих долази због промене односа (количника). Добијени односи (количници) указују на различите уделе валентних осцилација и њихових хемијских веза, што неминовно мења конформацију молекула и једињења. Изложени резултати указују на мање биогене разлике између проучаваних инбред линија кукуруза.

Кључне ријечи: инбред линија кукуруза, лист, хлорофил, каротеноид, Раманов спектар

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