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Genetically based differences in photochemical activities of isolated maize (*Zea mays* L.) mesophyll chloroplasts

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Abstract

Photochemical activity of isolated mesophyll chloroplasts was measured as Hill reaction activity (HRA) and photosystem 1 (PS1) activity in three diallel crosses of maize (*Zea mays* L.) inbred lines and F_1 hybrids. Statistically significant differences between genotypes together with positive heterotic effect in F_1 generation were found for both traits studied. These differences were more pronounced when HRA or PS1 activity was expressed per leaf area unit or dry matter unit compared to the expression per chlorophyll content unit. Analysis of variance showed that both the genetic and non-genetic components of variation in the photochemical activity of isolated mesophyll chloroplasts are present in all three diallel crosses examined. The positive heterosis in F_1 hybrids probably arises from non-additive genetic effects of a positive dominance type. Additive genetic effects were also statistically highly significant. We found no differences between reciprocal crosses.

Additional key words: diallel cross, genetic analysis, heterosis, Hill reaction activity, photosystem 1.

Introduction

The inheritance of many morphological, anatomical and physiological traits has been studied for many years with the aim to improve crop productivity. Although the

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Abbreviations: Chl - chlorophyll; CCU - chlorophyll content unit; DCMU - 3-(3',4'-dichlorophenyl)-1,1-dimethylurea; DCPIP - 2,6-dichlorophenolindophenol; HRA - Hill reaction activity; LAU - leaf area unit; LDM – leaf dry matter unit; PAR - photosynthetically active radiation; PS - photosystem.

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relationship between productivity and photosynthetic potential of plants has not yet been fully determined (Nelson 1988, Medrano and Vadell 1993, for review see Evans 1993), photosynthesis is probably one of the limiting factors which influence the yield (*e.g.*, Avratovščuková 1977, Nasyrov 1978, Gifford and Jenkins 1982, Bansal *et al.* 1993, Ishii 1993, Aliev *et al.* 1996). Photochemical activity of isolated chloroplasts is one of the components of the photosynthetic traits complex. It is often expressed as the activity of photosystem (PS) 1 or 2 or as the rate of photophosphorylation. The efficiency of primary photochemical reactions that occur in suspensions of isolated chloroplasts under irradiation and are coupled with reduction of artificial electron acceptor is called Hill reaction activity (HRA) (Hill 1939).

Genetic variation in photochemical activity of isolated chloroplasts has already been found for many agronomically important crops. According to Miflin and Hageman (1966), several inbreds and hybrids of maize (*Zea mays* L.) differ significantly in this trait, and positive heterosis in F_1 generation has often been observed (Ovchinnikova and Yakovlev 1974, Yakovlev and Ovchinnikova 1975, Makovec 1975, Kočová 1986, 1992a). Higher photochemical activity of isolated chloroplasts has been found for interspecific (Azizkhodyayev *et al.* 1975) and intraspecific hybrids of cotton (*Gossypium* sp.) compared to the parent lines (Krasichkova and Giller 1979, Krasichkova *et al.* 1989). Cotton as well as wheat and other cereals are also characterised by a positive correlation between photochemical activity of chloroplasts and some components of productivity or total yield (Gavrilenko *et al.* 1974, Volodarskiï *et al.* 1980, Nasyrov 1982). Statistically significant differences in photochemical activity of chloroplasts in wheat (*Triticum* sp.) have been found among some species with different ploidy levels (Mogileva *et al.* 1976, Zelenskiï *et al.* 1978, Hieke 1983, Bansal *et al.* 1991, Bansal *et al.* 1993) and among several cultivars of one species (Zelenskiï *et al.* 1979). In contrast to this, Barta and Hodges (1970), who studied HRA in two winter and one spring cultivars of *T. aestivum* L., have not reported any such differences. Burkey (1994) found genetic variation in photosynthetic electron transport in barley (*Hordeum* sp.). HRA differences among soybean (*Glycine max* L.) genotypes have been observed by Curtis *et al.* (1969), Watanabe (1973), Du *et al.* (1982), and Burkey *et al.* (1996). Kočová (1992b) reports similar differences for sugar-beet (*Beta vulgaris* L.) and Makovec (1975) for tobacco (*Nicotiana tabacum* L.). The genotypic variability in photochemical activity of chloroplasts isolated from tomato leaves has been studied, *e.g.*, by Synková *et al.* (1997).

Although numerous studies deal with the intraspecific variation of this trait, their authors seldom identified the genetic mechanisms participating in its inheritance. Characterisation of such mechanisms can help to better understand the basis for high photosynthetic efficiency. However, photosynthesis is also closely connected with many morphological and physiological traits, *e.g.*, dry matter, specific leaf area, leaf area ratio, stomatal resistance. The way in which photosynthetic characteristics are expressed can affect the range of intraspecific differences and even the relationship between genotypes. The aim of this work is to analyse individual components of genetic variation in the photochemical activity of isolated mesophyll chloroplasts in three diallel crosses of maize and to compare the effects of different types of expression (per units of leaf area, dry matter, or chlorophyll content) on the results of genetic analysis.

Materials and methods

The photochemical activity of isolated mesophyll chloroplasts was analysed in three diallel crosses of maize (*Zea mays* L.) inbred lines and their F_1 hybrids: Diallel I (inbred lines CE777, CE508, A677, F564), Diallel II (CE777, CE813, CE819, CE829), and Diallel III (CE777, 2013, 2023, CE704, CE810) during the years 1994-1997. The parent lines differed in both yield and photosynthetic characteristics and their hybrids showed a positive heterotic effect. Seeds were obtained from the Maize Breeding Station in Čejč (Czech Republic). They were sown at the end of April to low dishes with soil and placed in a glass-covered hot-bed. After approximately three weeks of growth they were transplanted to the experimental field of the Department of Genetics and Microbiology, Faculty of Science, Charles University, Prague. Each genotype was represented by 13-18 plants grown in a randomised plot with two replicates. The distance between rows was 70 cm, between plants in rows 50 cm. Standard agrotechnical procedures were used and no fertiliser was applied during the experimental seasons.

Each diallel cross was at first analysed as a complete diallel, *i.e.*, containing all reciprocal hybrids (Diallels I and II in 1994, Diallel III in 1997). Diallel III was analysed also as an incomplete diallel cross (without genotypes CE777×2023, 2013×CE704, and CE810×2023) in 1996. The absence of statistically significant differences between reciprocal hybrids enabled us to reduce Diallels I and II to one half, and to further increase the number of plants for each genotype in 1995 and 1996. During these experiments, each genotype was represented by two replicates of two independent plant groups. The experiments were made from the end of June to the beginning of August: in 1994 for 10 d, in 1995 for 16 d, in 1996 for 9 d, and in 1997 for 16 d.

Photochemical activity of isolated mesophyll chloroplasts was usually measured as Hill reaction activity (HRA). The activity of PS1 was measured in 1996 and 1997. The assimilation tissue samples were taken at 07:00 h of summer time from the middle part of the leaf blade of the fourth or the fifth leaf counting from the vegetative top. To get a sufficient amount of the leaf tissue we usually needed 8-10 plants. 2-3 g of this tissue were immediately immersed in 40 cm^3 of isolation medium (0.4 M sucrose, 0.05 M $MgCl_2$, 0.05 M Tris-HCl, pH 7.0) and homogenised for 18 s in *Thurmix 302* homogeniser (*MPW*, Poland; maximum rotations). The homogenate was then filtered through 8 layers of gauze and the filtrate centrifuged at 1000×*g* for 10 min. The resulting pellet was resuspended in a small volume (approx. 1 cm^3) of resuspension medium (0.4 M sucrose, 0.006 M $MgCl_2$, 40 % glycerol, 0.05 M Tris-HCl, pH 7.0) and the suspensions were stored in a dark and cool place till the measurements. To obtain chloroplasts with maximum activity, each of the above steps was performed at 0-4 °C. The chlorophyll (Chl) content was determined spectrophotometrically in 80 % aqueous acetone (Porra *et al.* 1989). The final concentration of Chl (*a*+*b*) in the suspensions of isolated chloroplasts was about 1-2 kg m^{-3}.

The HRA was measured polarographically using Clark type electrode (*Theta '90*, Czech Republic), as the amount of oxygen formed in the suspensions of isolated chloroplasts irradiated by "white light" (170 W m^{-2} PAR) after the addition of the artificial electron-acceptor (final concentration 7 mM $K_3[Fe(CN)_6]$). The chamber for oxygen evolution measurement was made according to Bartoš *et al.* (1975) and the reaction medium was identical with the isolation medium. The activity of PS1 was similarly measured as the amount of oxygen consumed by the chloroplasts' suspensions using *Hansatech* (U.K.) system with oxygen electrode. The system was irradiated by red radiation emitting diodes (wavelength 660 nm), total irradiance was 162 W m^{-2}. In this case, the reaction medium consisted of 0.4 M sucrose, 0.05 M phosphate buffer, pH 6.5. We used 0.15 mM reduced DCPIP as artificial electron donor, 0.1 mM methylviologen as an artificial electron acceptor, and 0.1 mM DCMU as inhibitor of PS2 activity. A minimum amount of crystalline catalase, 1 mM sodium ascorbate, and 0.5 mM NH_4Cl was also added. Fresh solutions of ascorbate and methylviologen were prepared for each experimental day. The reaction mixtures were stirred by a magnetic stirrer and a constant temperature of 25 °C was maintained during all measurements. Each sample was measured two to four times. The values were expressed per unit of leaf area (LAU), leaf dry matter (LDM), or Chl content (CCU). The average values characterising each genotype on each experimental day were used for the genetic analysis. Hayman's (1954) analysis of variance was applied to determine the individual components of genetic variation. This method enabled us to separate of the additive and non-additive genetic effects. When analysing the complete diallel, the effects of reciprocal crosses were introduced as another component of genetic variation. All calculations were done using an ADC computer program (*Version 3.0, RKS*).

Results

The mean values of both HRA and PS1 activity of individual maize genotypes slightly differed between experimental seasons, but the relationship between genotypes remained approximately the same in all three diallel crosses studied during the years 1994-1997. The analysis of variance revealed statistically significant differences in photochemical activity of isolated mesophyll chloroplasts between inbreds and their F_1 hybrids. These differences were more pronounced in Diallels I and III compared to the Diallel II, and could be noted especially if HRA or PS1 activity was expressed per LAU or CCU.

The F_1 hybrids of Diallel III usually showed a high heterotic effect in both HRA and PS1 activity (Table 1). The highest HRA values were found for CE777×CE810 in both experimental seasons; the only exception was in 1997 when parent line CE777 exceeded this genotype in HRA per CCU. The other hybrids with high HRA above could also be noted for high PS1 activity, the highest values of this trait were usually recorded for 2023×CE810.

Table 1. The average heterosis in F_1 hybrids (calculated as the percent of the mid-parent value) for Hill reaction activity (HRA) and PS1 activity analysed in three diallel crosses of maize during the years 1994-1997 and calculated per leaf area (LAU), leaf dry matter (LDM), and chlorophyll content (CCU) units.

Diallel cross	Year	Expression per LAU	Expression per LDM	Expression per CCU
HRA				
Diallel I	1994	109.46	102.65	96.97
	1995	116.70	106.47	95.20
Diallel II	1994	113.03	99.90	95.81
	1995	109.15	107.01	99.19
	1996	119.84	108.39	102.80
Diallel III	1996	129.82	114.69	108.73
	1997	131.54	124.30	108.69
PS1 activity				
Diallel III	1996	130.83	122.50	106.55
	1997	137.92	132.52	113.50

The character of parents-hybrids relationship in Diallels I and II depended on the way of HRA expression (Table 1). A positive heterosis in F_1 generation of Diallel I was observed when HRA was expressed per LAU or LDM. The highest HRA values among genotypes of this diallel cross were found in the hybrid CE508×CE777, which was exceeded by the parent line CE777 in 1994 when calculated per LDM. However, individual hybrids usually did not exceed their parental mean in HRA per CCU and the highest photochemical activity of isolated mesophyll chloroplasts was displayed here by CE777. In the case of Diallel II, the differences between inbred lines and their F_1 hybrids were even less marked. A positive heterotic effect in HRA per LAU was found for hybrids in all three experimental seasons, and the situation was similar for HRA per LDM, but the differences were mostly statistically insignificant. High values of HRA among F_1 hybrids were recorded in CE777×CE813, CE777×CE819, and CE813×CE819, whereas CE777 showed the highest photochemical activity among parent lines. If HRA was expressed per CCU, the hybrids usually did not show higher photochemical activity of isolated mesophyll chloroplasts compared to their parental mean.

The analysis of variance showed high variability in photochemical activity of mesophyll chloroplasts due to genotypic differences. Further dissection of genetic variation showed both additive and non-additive genetic effects of high significance in each diallel cross and each experimental season when HRA was expressed per LAU (Table 2). The additive component of variation was statistically significant also for the other types of HRA expression. However, as regards non-additive genetic

Table 2. Statistical significance (*p* values) of individual components of variation in Hill reaction activity (HRA) analysed in three diallel crosses of maize (Diallel I, II, III) during the years 1994-1997 and calculated per leaf area (LAU), dry matter (LDM), and chlorophyll content (CCU) units.

Source of variation	Diallel I		Diallel II			Diallel III	
	1994	1995	1994	1995	1996	1996	1997
HRA per LAU							
Additive gen. effect	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nonadditive gen. effect	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Reciprocal differences	0.482	-	0.224	-	-	0.000	0.397
Plant group	-	0.008	-	0.698	0.977	-	-
Experimental day	0.000	0.000	0.000	0.000	0.000	0.000	0.000
HRA per LDM							
Additive gen. effect	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Nonadditive gen. effect	0.054	0.009	0.491	0.003	0.000	0.004	0.150
Reciprocal differences	0.500	-	0.557	-	-	0.000	0.241
Plant group	-	0.320	-	0.482	0.847	-	-
Experimental day	0.000	0.000	0.002	0.000	0.000	0.000	0.001
HRA per CCU							
Additive gen. effect	0.012	0.000	0.000	0.000	0.000	0.000	0.000
Nonadditive gen. effect	0.050	0.000	0.502	0.000	0.000	0.159	0.000
Reciprocal differences	0.251	-	0.489	-	-	0.001	0.975
Plant group	-	0.147	-	0.000	0.844	-	-
Experimental day	0.000	0.000	0.002	0.000	0.000	0.000	0.000

effects, some slight differences were found. This component of genetic variation was statistically non-significant in Diallel II in the year 1994, but highly significant in 1995 and 1996. Similarly, the presence of non-additive genetic effects among genotypes of Diallel III was confirmed in 1997 but not in 1996 if HRA was expressed per CCU. High values of additive genetic effect were recorded for parent lines CE777 (all diallel crosses examined), CE508 (Diallel I), CE813 (Diallel II), and CE810 (Diallel III). The non-additive genetic effects were high in the hybrids CE508 ×A677 and F564×A677 of Diallel I, CE777×CE813 and CE813×CE829 of Diallel II, CE704×CE810 and 2013×2023 of Diallel III, and were usually of the positive dominance type. The absolute order of these genotypes slightly varied both with the way of HRA expression and individual years.

Inclusion of the reciprocal hybrids in the diallels during the experimental seasons 1994 and 1997 enabled us to examine the role of this component of genetic variation. As demonstrated by analysis of variance, this factor was statistically significant only in Diallel III in 1996. The effect of plant group on HRA examined in Diallels I and II during the years 1995 and 1996 was (with some exceptions) not found. The individual experimental days always exerted a highly significant effect upon HRA indifferent of its expression per LAU, LDM or CCU (Table 2).

Table 3. Statistical significance (*p* values) of individual components of variation in photosystem 1 activity (PS1) analysed in a diallel cross of maize (Diallel III) during the years 1996-1997 and calculated per leaf area (LAU), dry matter (LDM), and chlorophyll content (CCU) units.

Source of variation	PS1 per LAU		PS1 per LDM		PS1 per CCU	
	1996	1997	1996	1997	1996	1997
Additive gen. effect	0.044	0.000	0.056	0.000	0.032	0.000
Nonadditive gen. effect	0.002	0.000	0.077	0.000	0.058	0.000
Reciprocal differences	0.190	0.978	0.370	0.681	0.000	0.753
Experimental day	0.001	0.000	0.001	0.000	0.000	0.000

The genetic component of variation in PS1 activity examined in Diallel III included both additive and non-additive genetic effects; the later of positive dominance type (values not shown). The effect of reciprocal crosses was statistically not significant with the exception of the PS1 activity expressed per CCU during the experimental season 1996. Similar to HRA, the experimental days highly affected total variation in this trait, whereas the plant group did not (Table 3).

Discussion

The genetic analysis of various photosynthetic characteristics can substantially contribute to understanding the mechanisms of their inheritance and their use in the selection of genotypes with a high photosynthetic potential. The analysis of variance of a diallel cross is one of the possible approaches. On encountering significant genotypic differences in some trait, this method can be successfully used for the separation of genetic and environmental variation as well as of the individual components of genetic variation.

The inbred lines and hybrids of maize which formed the analysed diallel crosses were selected on the basis of high heterotic effect observed in F_1 generation for some yield parameters. They differed in several photosynthetic characteristics, *e.g.*, dry matter content, rate of photosynthesis in leaf discs, Chl or carotenoid content, as well as in photochemical activity of isolated mesophyll chloroplasts. However, the differences in photochemical activity of isolated mesophyll chloroplasts, measured as HRA or activity of PS1, were not as prominent as in the rate of photosynthesis in leaf discs. F_1 hybrids usually showed a positive heterotic effect in both HRA and PS1 activity, the latter being more pronounced and the non-genetic variation in this characteristic smaller. This can arise, *e.g.*, from the greater stability of PS1 in suspensions of isolated chloroplasts or thylakoid membranes or from the greater phylogenetic age of this pigment-protein complex.

The range of genotypic differences also varied with the way HRA (or PS1 activity) was expressed. Photosynthesis is a complex process which depends on many morphological and physiological characteristics of plants. Leaf area and thickness, cell size and organisation, number of chloroplasts, content of photosynthetic pigments, proteins, and various photosynthates as well as many other factors which are often interconnected, strongly influence the photosynthetic capacity of a particular genotype (cf. Evans 1993). Thus, the intraspecific differences in a particular photosynthetic trait can become more (or less) pronounced depending on the type of its expression. From a plant geneticist's point of view it is perhaps more important that the relationship between genotypes can also change. In view of that, it is not surprising we found greater variability in photochemical activity of mesophyll chloroplasts isolated from maize leaves and positive heterotic effect in F_1 generation when HRA was expressed per LAU or LDM compared to CCU. The first two types of HRA expression take into consideration such important leaf parameters as leaf thickness or specific leaf area, which can (and do) differ among individual genotypes, and therefore better reflect conditions in the intact leaf.

Several environmental factors affect undoubtedly to a great extent the photosynthetic process. Though the studies on plants grown in field conditions suit the breeders' needs better, their results might be grossly misinterpreted. Large experimental sets are difficult to analyse in specific, defined conditions, especially if a need arises to analyse large number of plants—as it was in our case. The main part of total variation in HRA is caused by the fluctuation of experimental conditions which include both external factors (irradiance, air humidity, air temperature, *etc.*) as well as advancing ontogeny of plants. This conclusion agrees with the findings of Zelenskiï *et al.* (1978, 1979), Makovec (1975), Mogileva *et al.* (1976), and Kočová (1986, 1992a,b) both for maize and other plant species. The variation between individual plants of one genotype probably does not significantly contribute to the total variation in photochemical activity of mesophyll chloroplasts isolated from maize leaves. We did not find any statistically significant differences in HRA between genotypes of independent plant groups except for two cases in the year 1995: Diallel I (if HRA was expressed per leaf area unit) and Diallel II (if HRA was expressed per Chl content unit). However, this dissimilarity was found only during a few experimental days in some genotypes and was not detected for all types of HRA expression at the same time.

No reciprocal differences were observed with the exception of Diallel III in 1996. Our finding of statistically significant differences between reciprocal hybrids in this case can be probably attributed to the unbalanced experimental design (incomplete diallel set). The absence of maternal or paternal effects found by our study seems to support the opinion that cytoplasmic inheritance is not of much importance in the genetic determination of the photochemical activity of chloroplasts. Some authors, however, describe maternal effects as a component of the inheritance of this trait in maize (Ovchinnikova and Yakovlev 1974, Yakovlev and Ovchinnikova 1975) and cotton (Krasichkova and Giller 1979, Krasichkova *et al.* 1989). The relative importance of chloroplast genetic information in the determination of photosynthetic traits is therefore still far from being definitively answered.

As proved by the analysis of variance, both additive and non-additive components of genetic variation in photochemical activity of isolated mesophyll chloroplasts of maize are statistically highly significant. The high values of significance observed for the additive genetic effects support the opinion that such effects are most important among the mechanisms participating in the inheritance of HRA. The non-additive genetic effects play an important role in formation of the observed heterotic effect, because they are of a positive dominance type. Other authors, investigating the genetic mechanisms of inheritance of photosystem activities in maize, also report additive (Krebs *et al.* 1996) or both additive and non-additive genetic effects (Miflin and Hageman 1966) together with a positive heterotic effect in F_1 generation (Ovchinnikova and Yakovlev 1974, Makovec 1975, Yakovlev and Ovchinnikova 1975, Kočová 1986, 1992a). Makovec has also found some non-allelic interactions of an epistatic type. Our results bring further information about the genetic mechanisms involved in the inheritance of photochemical activity of mesophyll chloroplasts isolated from maize leaves. They also show the importance of the way in which this trait is expressed for the results of genetic analysis.

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