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RELATIONSHIPS OF STAY GREEN TRAIT IN MAIZE

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Genetic variation for stay green character has been exploited in maize improvement mainly in the light of selecting high yielding rather then typical stay green genotypes. Stay green is an indicator of good plant health later in the season, reduced progressive senescence, tolerance to post-flowering drought and stalk lodging, what ensure superiority of stay green genotypes in comparison to non-stay green ones, especially in drought conditions. The objective of the study was to examine relationship of stay green trait with some vegetative characters in two genetically broad based maize populations. The most consistent correlations with stay green were established for leaf and stalk water content, which has been confirmed by path-coefficient analysis.

Key words: maize, stay-green, correlation, path analysis

INTRODUCTION

Genetic variation for stay green character has been exploited in maize improvement more in the light of selecting high yielding then typical stay green

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genotypes. A genotype can be considered to characterize by stay-green trait if the contribution of green plant tissue area to the total plant area is above the population average, and its grain moisture is lower or equal to the population average (BEKAVAC *et al*., 1998). If a genotype's stay-green and grain moisture are both higher than the population average, it is not considered to be a stay-green genotype but a genotype with longer vegetation.

The superiority of modern maize hybrids compared to those of preceding breeding eras is associated with improvement of resistance to lodging, reduction of dropped ears, extended grain-filling period, improved late season plant health or stay green, reduction of tassel size and a tendency for upright leaves (CAVALIERI and SMITH, 1985; MEGHJI *et al*., 1984). Non stay-green genotypes start losing the green color of their leaves approximately 30 days after anthesis, while the stay-green ones do not show similar process until physiological maturity (SWANK *et al*., 1982; CRAFT-BRANDNER *et al*., 1984). Although competitive and environmental factors are clearly associated with leaf senescence, this process is genetically controlled. Regarding to their expression during leaf development, genes with functions in senescence can be divided into four groups (HOWARD and SMART, 1993).

Several traits, such as increased water and chlorophyll content in leaves at physiological maturity, water and sucrose content in stalks at grain fill, water content in husks and cobs, and higher grain protein content are tightly connected with delayed senescence (GENTINATTA *et al*., 1986). Stay-green is an indicator of good plant health later in the season (CROSBIE, 1982; MEGHJI *et al*., 1984), reduced progressive senescence (MCBEE, 1984), tolerance to post-flowering drought and stalk lodging (ROSENOW and CLARK, 1981). Due to these reasons, stay-green genotypes are often superior to non stay-green ones, especially in drought conditions.

Most papers that have been published in this regard dealt with relationships between stay green and grain yield, while data dealing with relationships of stay green and other traits are relatively scarce. The aim of this study was to determine correlations and direct and indirect effects of some vegetative traits on stay-green.

MATERIALS AND METHODS

Two genetically broad-based maize populations (NS Syn 88/12 and NS Syn 88/14) have been chosen for the study. These populations were developed at the Institute of Field and Vegetable Crops in Novi Sad by crossing U.S. Corn Belt lines with Yugoslavian domestic germplasm. Five cycles of mass selection has been conducted for adaptation. The S_1 progenies were produced in the 1996 breeding nursery by selfing random S_0 plants. At harvesting, 95 ears (S_1 families) per population were randomly chosen (the only criterion was sufficient seed supply). Independent field experiments with 80 S_1 families were set up for each population in four environments (Novi Sad and Srbobran, Yugoslavia, in 1997 and 1998). Each experiment was arranged as an incomplete block design with replicates in sets (Hallauer and Miranda, 1988). The 80 entries of each population were evaluated in 4 sets and each set consisted of 20 S_1 families, tested in two replications at the density of 63500 plants ha^{-1}.

Data were collected for stay-green (SG), anthesis-silking interval (ASI), stalk water content (SW), leaf water content (LW), and grain moisture (GM). Stay-green was estimated once, immediately prior to harvesting using a scale from 1 to 10, where 1 represents a genotype with less than 10% of green plant tissue area and 10 one with 90%-100% (WALULU *et al*., 1994). Anthesis-silking interval (in days) equaled the difference between mid pollination and mid silking. Stalk and leaf water content (%) was calculated after oven-drying the plant material at 105°C to the constant mass. Grain moisture (%) was calculated from a grain sample weighting 300 g that was taken at harvest and oven-dried. Stay-green, anthesis-silking interval and grain moisture were determined taking into account all plants per plot, while the estimation of stalk and leaf water content were carried out on ten randomly chosen competitive plants.

Analyses for all traits were calculated on the basis of plot mean data. Estimates of genetic variance for each trait were calculated from the combined analysis of variance. Genetic correlations between traits were calculated as the covariance between traits divided by the square root of the product of the corresponding individual trait variances. The set of correlation coefficients was subjected to path-coefficient analysis, and direct and indirect effects were estimated according to the method of symmetric correlation matrix proposed by Edwards (1979). The level of significance of the path coefficients ($b'_{yi} = p_{yi}$) was calculated via the standard error of regression coefficients (S'_{bi}) by the following equation:

$$S_{b'_i} = \sqrt{\frac{1 - R^2{}_{yi}}{(n-k-1)(1-R^2{}_i)}}$$

Where y and i represent dependent and independent variables, respectively (i=1,2,3,...,k); n and k are the number of genotypes and the number of independent variables, respectively;

$$R_i^2 = 1 - \frac{1}{r'_i}$$

Where r'_i represent the diagonal of the inverse correlation matrix.
F values are calculated by equation:

$$F_{b'_i} = \left(\frac{b'_i}{S_{b'_i}} \right)^2,$$

and critical values are read for (1) and (n-k-1) degrees of freedom.

RESULTS

Analysis of variance (not shown) combined across four environments indicated that environment had large effect on all of the studied traits. The differences were caused by climatic differences in growing seasons between 1997 and 1998. Highly significant mean squares for families within the sets were found for all of the traits in both populations.

The populations examined here differed significantly in the average values of grain moisture and slightly in the average values of stalk and leaf water content. Higher mean values for all traits were obtained in the population NS Syn 88/12, except in the case of leaf water content (Table1).

Table 1. Mean values (± SE) of the traits in the populations NS Syn 88/12 and NS Syn 88/14

Populations	SG (1-10)	ASI (days)	SW (%)	LW (%)	GM (%)
NS Syn 88/12	2.73 ± 0.073	2.94 ± 0.054	54.85 ± 0.341	15.82 ± 0.295	24.98 ± 0.064
NS Syn 88/14	2.59 ± 0.068	2.21 ± 0.051	51.24 ± 0.413	18.53 ± 0.262	20.06 ± 0.064

There was no evident similarity in the values of genetic correlations in these populations. Highly significant positive association existed between stay-green from one side and stalk and leaf water content, and grain moisture from the other side. Very strong and highly significant correlations were found among stalk water content, leaf water content, and grain moisture in both populations. At the same time, the highest discrepancy was found for correlation between stay-green and anthesis-silking interval. Genetic correlation between these two traits was strong and highly significant in the population NS Syn 88/12 (r_g = 0.491**), while the association between the same traits in the population NS Syn 88/14 was weak and insignificant (r_g = 0.171) (Table 2).

Table 2. Genetic correlations in the population NS Syn 88/12 (above diagonal) and in NS Syn 88/14 (below diagonal)

Traits		SW (%)	LW (%)	GM (%)	ASI (days)	SG (1-10)
1. SW	r_g		0.801**	0.812**	0.408**	0.881**
2. LW	r_g	0.676**		0.671**	0.376**	0.865**
3. GM	r_g	0.717**	0.823**		0.621**	0.809**
4. ASI	r_g	0.191	0.052	-0.043		0.491**
5. SG	r_g	0.821**	0.900**	0.806**	0.171	

** Significant at the 0.01 probability level.

Path coefficient analysis was conducted to obtain further information about interrelationships between traits. This method involves a procedure of partitioning correlation coefficients into direct effects (unidirectional pathways) and indirect effects (through alternate pathways). The direct effects obtained in the path coefficient analysis indicated that stay-green depended mainly upon leaf water content, followed by stalk water content. The influence of grain moisture on stay-green was low but significant (p_{3y} = 0.193*) in the population NS Syn 88/12 and negligible in the population NS Syn 88/14. Stay-green was not affected by the anthesis-silking interval (Table 3).

The indirect effects of the examined traits on stay-green were, in general slight, except the indirect effects of stalk water content via leaf water content in the population NS Syn 88/14. In both populations, the indirect effects of grain moisture via stalk and leaf water content exceeded its direct effects.

Table 3. Path coefficient analysis for stay-green in the populations NS Syn 88/12 and NS Syn88/14

Pathway	NS Syn 88/12	NS Syn88/14
Stalk water content → Stay-green		
Direct effect, p_{1y}	0.357**	0.358**
Indirect effect via leaf water, $r_{12}p_{y2}$	0.340	0.418
Indirect effect via grain moisture, $r_{13}p_{y3}$	0.157	0.030
Indirect effect via anthesis-silking interval, $r_{14}p_{y4}$	0.027	0.010
Leaf water content → Stay-green		
Direct effect, p_{2y}	0.424**	0.619**
Indirect effect via stalk water, $r_{21}p_{y1}$	0.286	0.242
Indirect effect via grain moisture, $r_{23}p_{y3}$	0.130	0.033
Indirect effect via anthesis-silking interval, $r_{24}p_{y4}$	0.025	0.004
Grain moisture → Stay-green		
Direct effect, p_{3y}	0.193*	0.043
Indirect effect via stalk water, $r_{31}p_{y1}$	0.290	0.257
Indirect effect via leaf water, $r_{32}p_{y2}$	0.285	0.510
Indirect effect via anthesis-silking interval, $r_{34}p_{y4}$	0.041	-0.003
Anthesis-silking interval → Stay-green		
Direct effect, p_{4y}	0.065	0.072
Indirect effect via stalk water, $r_{41}p_{y1}$	0.146	0.068
Indirect effect via leaf water, $r_{42}p_{y2}$	0.160	0.032
Indirect effect via grain moisture, $r_{43}p_{y3}$	0.120	-0.002
Coefficient of determination, R^2	0.870	0.898

*,** Significant at the 0.05 and 0.01 probability level, respectively.

DISCUSSION

The mean values of the examined traits differed due to specific genetic background of the populations, and their specific respond to environmental factors. Considerably higher grain moisture in the population NS Syn 88/12 indicates that these two populations differ with respect to maturity, so the appearance of a different degree of association among traits was expected.

Several interesting relationships can be observed from the Table 2. One of the most important to a maize breeder is that between stay-green and stalk water content. Due to negative correlation between stalk water content and plant lodging (IVANOVIĆ, 1982, ĐORĐEVIĆ, 1994), it's possible to indirectly improve stalk resistance to lodging by selecting stay-green genotypes. The highly significant correlation was found between leaf water content and stay-green in both populations. This association is not unexpected since it appears reasonable that presence of water in leaves is ultimately request for physiological activity of plant canopy. Similar results reported BEKAVAC *et al*., (1995). Stalk water content is an important trait that determines the stay-green character, but judging on the basis of correlation coefficients it is of the same importance as leaf water content. Nevertheless, path coefficient analysis undoubtedly revealed more importance of leaf water content, especially in the population NS Syn 88/14. The discrepancy between some of the results obtained by correlation and path coefficient analyses arises from the fact that correlation simply identifies mutual association between traits irrespective of causation, but path coefficient analysis specifies the causes and measures their relative importance (DEWEY and LU, 1959).

Strong correlation between stay-green and grain moisture in both populations could be a problem in practical breeding programs since the population improvement for stay-green can bring changes in maturity. Direct effect of grain moisture on stay-green in the population NS Syn 88/12 was significant, but this effect were much weaker than was to be expected on the basis of correlation analysis in both populations. A small and insignificant direct effect of grain moisture on stay green in the population NS Syn 88/14 indicate possibility to improve stay-green in maize populations regardless of the length of vegetation.

The correlation coefficients showed significant relation between the anthesis-silking interval and stay-green in the population NS Syn 88/12, and low and insignificant in the population NS Syn 88/14. The usefulness of path coefficient analysis is evident here. When the indirect effects are removed from the correlation coefficients by path analysis, direct effects reveal that anthesis-silking interval had no influence on stay-green.

Both, the correlation and path coefficient analysis carried out in this paper divulged that leaf followed by stalk water content are of primary importance to stay green. Analysis of the effects of some other traits, such as activity of different enzymes, chlorophyll or sugar content on stay-green, would be of great help to obtain a more complex picture of maize traits and their relationships. Although the traits studied here represent the traits of interest in many applied breeding programs, they don't require complicated and time-consuming lab procedure, and data for these traits could be easily obtained from routine trial analysis.

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MEĐUZAVISNOST STAY GREEN SVOJSTVA KUKURUZA

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Izvod

Genetička varijabilnost populacija kukuruza za stay green svojstvo je u praktičnom oplemenjivanju korišćena više u svetlu selekcionisanja prinosnijih nego tipičnih stay green genotipova. Stay green je indikator dobrog zdravstvenog stanja biljaka u kasnijim fazama vegetacije, redukovanog progresivnog starenja, tolerantnosti na sušu i tolerantnosti prema poleganju, što obezbeđuje superiornost sray green genotipova u poređenju sa genotipovima koji ne poseduju ovo svojstvo (non-stay green). Ova superiornost posebno dolazi do izražaja u sušnim uslovima. Cilj rada bio je da se ispitaju međusobni odnosi stay green-a i nekoliko vegetativnih svojstava u dve sintetičke populacije kukuruza. Korelacionom i path koeficijent analizom ustanovljeno je da se stay green nalazi u najkonzistenetnijim međusobnim odnosima sa sadržajem vode u listu i sadržajem vode u stablu.

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