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Genetic analysis of photosynthesis and productivity in corn

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Summary. The genetic relationships among different inbred stocks of corn with respect to different indices of photosynthetic efficiency and plant productivity was assessed by means of diallel graphs. The salient feature of the current study was "apparent overdominance" for some important indices of photosynthetic efficiency, viz. photosynthetic rate/unit leaf area (at the silking stage), total chlorophyll content and chlorophyll a content, as well as for total dry matter production and economic yield. The results could be explained in terms of complementary gene action and the multiplicative effects of the sub-components that comprise these traits. However, complete dominance was recorded for photosynthetic rate (at the grain filling period), leaf area/plant, number of leaves/plant, number of leaves above the ear, ratio of chlorophyll a/b and harvest index. In the majority of cases graphic analysis was possible only when a number of epistatic parents were omitted from the analysis. Although the position of the array points for different indices of photosynthetic efficiency was consistent across the years, the ontogenetic and seasonal differences in the genetic behaviour of parents, meaning thereby, different loci being active at different stages and seasons, was apparent. The same was true for the epistatic parents. Non-allelic interaction of the genes rather than the non-random distribution of the genes among the parents seemed to be the most common cause of disturbance in the W_r/V_r relationship.

Inbred stock MG 115 was identified to be the most promising because it embodied an efficient photosynthetic machinery by virtue of increasing the number of alleles for a majority of the indices of photosynthetic efficiency, thereby enabling it to register the highest biological productivity and economic yield. Further, inbred stocks MG 138, MG 121, and MG 125 were also promising for different photosynthetic parameters.

Key words: Photosynthetic efficiency – Corn – Gene action – Diallel graph

Introduction

In recent decades the urgent propensity of improving total biomass in different crop plants has been attributed primarily to the vertical ceiling imposed on photosynthate partitioning (Swaminathan 1986; Jain 1986; Austin 1989). Therefore, future increments in yield potential will have to bank heavily on improving biomass productivity, hitherto unaffected by selection. An improvement in photosynthesis and an increase in a general tolerance to reduced photosynthesis (Edmeads and Tollenar 1988) are imperative in sustaining the current trend of production.

There exists, however, an internecine record of evidence for a direct relationship between leaf photosynthetic rate and grain yield or biomass production (Nelson 1988; Sarkar et al. 1991). Nevertheless, there are sufficient grounds for undertaking genetic investigations on photosynthetic efficiency in relation to plant productivity for obvious reasons.

The in vitro genetic control of photosynthetic efficiency has been studied employing various forms of statistical genetic analyses (Wilson and Cooper 1969 in *Lolium;* Crosbie et al. 1978; Albergoni et al. 1983 in maize; Hobbs and Mahon 1985 in peas; van de Dijk 1987 in tomato), and in none of these studies was the photosynthetic efficiency monitored in vivo under field condi-

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tions with the diallel graph technique for genetic determination.

The research discussed in this paper therefore had the objective of obtaining an overall picture of the genetic control of some important indices of photosynthetic efficiency with the help of diallel crossing. Six and eight inbred stocks of corn with variable photosynthetic activity [selected from a previous study, Mehta et al. 1989] were studied for 2 years (1985 and 1986).

Materials and methods

The experiments for the present investigations were conducted for 2 years (1985 and 1986) and involved the diallel analysis of 6 and 8 inbred lines of maize, respectively, with respect to different components of photosynthetic efficiency. The inbred lines were selected on the basis of seedling photosynthetic rates after the preliminary screening of 46 inbred lines (Mehta et al. 1989) in a greenhouse. Two inbred lines, each representing high, medium and low classes of photosynthetic rate, were chosen randomly and crossed in all possible combinations with 6 lines in the winter of 1984–1985 at the Maize Research Station, Amberpet Farm, Hyderabad (South India). The diallel set so developed was designated as "diallel 1985" and tested for performance during the summer of 1985 at New Delhi. A second diallel set (8 × 8) involving the same 6 inbred lines plus 2 more inbred lines representing the high and low category (Table 1) was developed during the winter of 1985–1986 at Hyderabad and designated as "diallel 1986". The diallel set so developed was grown in a trial during the summer of 1986 at New Delhi. All the inbred lines were developed by the Maize Genetics Section following four to six selfings of the breeders' inbred lines obtained from the All India Coordinated Maize Improvement Project and other sources. While selecting the parents for making crosses we made a deliberate effort to choose only among parents of a similar maturity group. The peak photosynthetic rate is attained early in early maturing lines, while in late maturing ones this plateau is reached later. This factor might complicate such investigations to some extent, however the effect of differential silking (43–57 days) was minimised as much as possibly in such a way that it was possible to obtain some representative plants of each entry at the silking stage for recording the observations. Moreover, the observations on photosynthetic efficiency were completed in a single day for each replication. It took 3 days to complete the observations of a complete set.

Table 1. Pedigree, family code and the class of seedling photosynthetic rate of the inbred lines involved in the present investigation

Seedling number	Inbred pedigree	Original source	Seedling photosynthetic performance
1.	MG 121 (6717-1)	D-32	High
2.	MG 138 (6618)	Eto 81	High
3.	MG 115 (6702 A)	Pioneer 440	Medium
4.	MG 103	Pant 77AD 608	Medium
5.	MG 114 (6701)	A-2077	Low
6.	MG 111 (6696-2)	B-49	Low
7.	MG 125 (6930-B-1)	(EH 2310 × Y42) PSC7IC	High
8.	MG 132 (6627)	D-36	Low

In each trial, the F_1s along with the parents were planted in randomised complete block design with three replications. Each experimental plot consisted of three 5-m-long rows with a row to row spacing of 0.75 m and plant to plant distance of 0.25 m. The experimental area was bordered on either side with an early maturing composite. Standard culture practices were followed. Data were collected on the following attributes of photosynthetic efficiency.

Photosynthetic rate/unit leaf area

The photosynthetic rate was measured at the grain-filling stage in 1985, however in 1986 it was measured at the silking stage (the genetic potential for photosynthetic rate was ideally expressed at this stage) with the help of a battery-operated LCA-2 model of an Infra Red Gas Analyser (IRGA) [Analytical Development Co (ADC), UK] especially designated to measure Co_2 (ADC, LCA-2 instruction manual). The sample leaf consisted of the leaf subtending the ear, which received incident photosynthetic photon flux density (PPFD) of 1,600–2,000 μmol m^{-2} s^{-1}. The measurements were made on a clear and cloudless day between 9.30 and 11.30 A.M. Three plants/replication were selected at random from each entry, and one replication was completed in a single day. The IRGA was run on differential mode where the difference between the CO_2 fraction of the input air to a leaf chamber and the corresponding output is measured. This differential reading therefore was the fixation of carbon dioxide by the enclosed leaf. Taking into account the flow rate of the air and the leaf area enclosed in the chamber, the rate of photosynthesis was calculated by the formula:

$$F_{CO_2} = \frac{(f)(\Delta CO_2)}{A}$$

where:

F_{CO_2} = rate of carbon dioxide assimilation (μl CO_2 cm^{-2} min^{-1} subsequently expressed as mg CO_2 dm^{-2} h^{-1})

f = flow rate of air (ml min^{-1})

A = leaf area (cm^2)

ΔCO_2 = difference in CO_2 concentration before and after passage through the leaf chamber (μl l^{-1})

Leaf area/plant (dm^2), number of leaves/plant and number of leaves above the ear. Leaf area was recorded with the help of a LICOR leaf-area meter model 3,100. Five plants from each plot were picked randomly at the grain-filling period (when no further increase in leaf area was expected), and all the leaves were clipped with scissors, wrapped in polythylene sheets and brought quickly to the laboratory for leaf-area estimations. In 1985 the number of leaves was the number of green leaves per plant at the time of counting, while in 1986 the number of leaves and the number of leaves above the ear were computed by counting the number of nodes on the corn stalks on a plot mean basis.

Total chlorophyll content, chlorophyll a, chlorophyll b and ratio of chlorophyll a/b. The chlorophyll content was determined at the silking (1985) and vegetative (1986) stages according to the standard procedure of Arnon (1949).

Biological yield (g). Biological yield was recorded at the time of harvesting and comprised the whole plant dry weight of the aerial portion; the average of five plants per plot. The fallen leaves were not included in expressing biological yield.

Grain yield (g). Grain yield was recorded on the basis of 15 plants/plot and standardised at 15% grain moisture immediately after harvesting.

Harvest index. The harvest index was expressed as the ratio of grain yield to total biological yield.

The photosynthetic phenomenon is regulated by the chloroplast genome, more explicitly by key carboxylating enzyme (ribulose biophosphate carboxylase, (E.C. 4.4.1.39) partly encoded by it. Yet the reciprocal differences for photosynthetic rate have been extensively ruled out (Crosbie et al. 1978; Mahon and Hobbs 1981; van de Dijk 1987; Austin 1989), hence only half-diallel crosses (F_1s and their parents) were attempted and analysed following Hayman's (1954) analysis. This analysis makes several assumptions that must be satisfied if this technique is to be considered appropriate for a given data set. In the absence of information directly related to these assumptions, the appropriateness of Hayman's analysis (1954) was considered by means of two tests: (1) Z^2-test and (2) regression of covariance (W_r) on variance (V_r) and testing the regression coefficient (b) against unity and zero. The significant deviation of the regression coefficient against unity and also the non-significant difference of b from zero suggested the failure of the hypothesis. Thus W_r-V_r values were plotted against array means, and the interacting lines deleted one by one and the reduced diallels re-analysed until a perfect rectilinear relationship between Wr and Vr was established.

Results

1. *Analysis of means*

Genetic investigations on a number of important traits associated with photosynthetic efficiency were undertaken for 6 and 8 inbred lines of corn in 1985 and 1986, respectively (Table 2). The initial classification and ranking of the inbred lines on the basis of photosynthetic efficiency (i.e. high, medium and low) was radically altered when such estimates were made at the grain-filling stage (1985) or silking stage (1986). At the silking stage (1986) high photosynthetic efficiency was maintained in entries, 1, 3 and 7 whereas low rates were displayed in 4, 5, 6 and 8, thus establishing sharp differences for low and high categories for photosynthetic rate. Line number 2, which at the seedling stage had been earlier classified in the high category (Table 1), fell into the low category at silking, while the medium category was completely obliterated. At the grain-filling stage (1985), however, such differences were not so pronounced; nevertheless, diallel entries showed significant differences from each other ($P < 0.05$) Table 2. Similarly, for all of the other traits except number of leaves/plant significant differences among the parents ($P < 0.01$) were recorded ($P = 0.05$) in 1985.

The mean of the F_1s (single crosses) and their respective standard errors are presented in Tables 3 (1985) and 4 (1986). The estimates of average heterosis were computed (Table 5) and found to be significant for photosynthetic rate, leaf area/plant, number of leaves/plant, chlorophyll a content, biological yield and grain yield in both years. This indicates substantial differences between the parental and F_1 means. Non significant heterosis was

Table 2. The mean or parents entering the diallel cross averaged over blocks

Character	Year	Mean of parents								$SE_{(m)}$	LSD
		1	2	3	4	5	6	7	8		
Photosynthetic rate	1985	14.2	22.7	20.3	15.9	18.9	11.8			1.2	1.7
(mg CO_2 dm^{-2} h^{-1}	1986	50.2	15.5	62.1	23.0	20.3	21.7	38.0	24.2	5.7	8.0
Leaf area/plant (dm^2)	1985	13.3	15.0	13.0	4.5	8.5	5.9			0.8	1.1
	1986	28.3	34.6	33.6	26.9	20.2	19.6	33.9	24.2	1.74	2.5
No. of leaves/plant	1985	10.9	11.8	11.1	10.3	10.3	10.3			0.6	0.9
	1986	13.7	12.7	13.3	12.6	12.3	12.3	14.3	13.5	0.5	0.7
No. of leaves above the ear	1985	5.5	4.8	5.7	5.0	4.6	3.6			0.5	0.7
	1986	6.5	5.3	5.5	6.5	4.9	4.9	6.2	5.5	0.3	0.4
Total chlorophyll content	1985	123.7	154.9	152.4	167.5	126.8	110.7			12.5	17.7
(mg/100 mg fresh weight)	1986	142.8	155.9	199.0	161.7	150.2	114.4	148.0	22.8	4.7	9.8
Chlorophyll a	1985	78.9	93.2	87.4	85.3	80.8	69.5			3.2	4.5
(mg/100 g fresh weight)	1986	97.0	124.7	135.8	98.1	96.2	72.4	93.9	144.2	8.5	12.1
Chlorophyll b	1985	55.7	63.0	55.6	62.6	56.7	38.9			4.1	5.8
(mg/100 g fresh weight)	1986	55.9	54.8	76.5	61.2	53.9	46.1	52.7	88.5	6.4	9.1
Ratio of chlorophyll a/b	1985	1.4	1.5	1.6	1.4	1.4	1.7			0.1	0.1
	1986	1.7	2.3	1.8	1.6	1.8	1.6	1.8	1.6	0.1	0.1
Biological yield/plant (g)	1985	129.7	221.3	230.0	119.3	91.0	109.0			5.2	7.3
	1986	126.0	225.3	256.0	117.6	78.7	107.3	245.7	239.0	7.9	11.2
Grain yield/plant (g)	1985	33.7	54.2	66.3	44.4	21.3	35.3			5.2	7.3
	1986	32.5	54.9	74.0	44.1	19.4	35.9	86.9	55.6	6.2	8.8
Harvest index	1985	25.5	21.3	34.4	32.4	18.4	33.6			2.4	3.3
	1986	23.2	21.2	32.0	32.7	19.0	33.6	28.1	19.5	3.1	4.3

Table 3. The mean of F_1 (single crosses) averaged over blocks in 1985

Cross	Photo-synthetic rate	Leaf area/ plant	No. of leaves/ plant	Leaves above the ear	Total Chloro-phyll content	Chloro-phyll a content	Choro-phyll b content	Ratio of Chlo-rophyll a/b	Biological yield/plant	Grain yield/plant	Harvest index
1×2	17.8	22.3	12.2	4.9	127.5	76.9	55.5	1.4	227.7	72.1	19.9
1×3	19.1	19.5	11.3	5.2	147.2	75.1	56.8	1.3	277.0	84.0	16.9
1×4	11.4	16.7	11.3	4.8	143.0	77.8	56.8	1.4	216.7	84.6	13.9
1×5	21.8	19.2	10.9	5.4	154.2	84.4	56.5	1.5	240.7	72.9	22.6
1×6	22.1	22.7	11.8	4.9	118.6	61.5	43.1	1.4	214.0	88.3	21.5
2×3	23.6	19.6	11.0	4.7	121.6	76.0	45.6	1.7	213.7	78.4	21.3
2×4	17.3	12.4	10.8	4.8	120.6	75.1	55.4	1.3	281.0	90.7	19.3
2×5	20.6	22.9	11.7	5.1	150.2	85.1	58.0	1.5	261.3	70.0	17.1
2×6	22.2	18.3	11.5	4.9	138.7	86.7	45.1	1.9	229.3	82.8	16.4
3×4	23.9	24.9	11.1	4.7	116.2	78.0	67.5	1.1	270.3	64.9	12.5
3×5	19.7	21.6	11.1	4.8	136.3	77.5	49.8	1.6	235.0	78.3	18.1
3×6	22.3	13.3	11.4	5.1	107.6	62.4	41.7	1.5	232.0	95.0	19.8
4×5	19.0	14.5	10.7	4.9	143.9	81.2	60.7	1.3	229.7	81.1	16.3
4×6	15.1	8.4	10.5	4.4	140.1	84.7	56.1	1.5	192.3	62.3	15.5
5×6	11.5	17.9	11.5	4.7	146.5	89.3	65.6	1.4	169.0	67.6	17.1
$SE_{(m)}$	1.6	1.0	0.7	0.3	10.7	2.7	2.7	0.1	7.5	5.1	2.3
LSD	2.3	1.5	1.0	0.4	15.1	3.8	3.9	0.1	10.5	7.2	3.2

Table 4. The mean of F_1 (single crosses) averaged over blocks in 1986

Cross	Photo-synthetic rate	Leaf area/ plant	No. of leaves/ plant	Leaves above the ear	Total Chloro-phyll content	Chloro-phyll a content	Choro-phyll b content	Ratio of Chlo-rophyll a/b	Biological yield/plant	Grain yield/plant	Harvest index
1×2	61.1	35.3	13.5	5.9	204.4	117.6	80.2	1.5	248.3	72.9	25.6
1×3	55.4	40.8	15.5	6.3	233.4	139.9	96.5	1.4	276.7	80.8	25.5
1×4	65.2	38.2	14.6	6.6	249.3	143.6	99.8	1.4	223.3	77.6	30.3
1×5	53.0	39.7	15.1	5.5	216.7	130.6	80.8	1.6	251.0	75.6	16.9
1×6	62.5	46.0	14.6	6.5	205.1	135.4	76.4	1.8	227.3	91.8	35.1
1×7	56.1	25.9	13.2	5.5	197.6	116.7	76.0	1.6	198.7	45.9	20.1
1×8	43.3	44.0	15.3	6.3	263.6	160.7	89.7	1.8	214.3	70.4	28.6
2×3	57.0	33.1	14.1	4.5	112.2	108.9	67.2	1.6	235.7	81.1	27.4
2×4	45.3	32.8	14.3	6.5	217.3	131.8	87.2	1.5	321.7	100.3	25.7
2×5	53.9	38.5	14.1	5.4	205.5	118.6	72.1	1.6	276.0	75.3	18.3
2×6	56.7	39.2	13.1	5.4	161.0	92.8	57.5	1.6	246.0	89.8	31.8
2×7	52.5	35.0	14.7	5.6	133.7	93.6	55.5	1.7	214.7	47.1	19.0
2×8	55.3	33.9	14.4	5.7	201.0	128.8	78.2	1.6	203.3	67.7	29.0
3×4	47.2	33.3	14.0	6.1	183.8	116.1	67.9	1.7	238.3	51.8	18.9
3×5	55.1	39.0	13.7	5.4	167.8	107.5	60.5	1.8	201.3	93.4	25.8
3×6	64.9	41.8	13.9	5.6	187.2	122.5	49.1	2.5	230.7	94.6	25.8
3×7	19.3	42.3	14.1	5.3	275.1	128.6	79.3	1.6	290.3	94.2	28.3
3×8	65.4	41.1	14.2	5.6	233.8	141.0	92.8	1.5	271.3	87.9	28.2
4×5	57.4	28.4	13.4	5.2	213.9	138.0	82.3	1.7	224.0	78.5	30.6
4×6	49.7	26.3	13.3	5.6	250.7	112.3	92.7	1.2	176.7	62.2	43.7
4×7	59.6	29.6	14.2	5.6	201.7	121.0	77.1	1.4	223.3	78.1	30.5
4×8	63.9	31.8	15.3	6.6	238.7	156.7	98.7	1.6	273.0	95.0	30.3
5×6	71.6	31.9	13.7	5.3	180.2	122.6	67.7	1.8	178.7	63.4	32.6
5×7	48.8	28.0	13.2	5.1	147.0	89.4	58.3	1.5	226.3	68.8	26.5
5×8	61.2	28.8	13.5	5.1	206.6	122.5	70.8	1.7	230.7	80.7	30.5
6×7	49.8	27.0	13.6	4.4	172.5	132.3	61.9	2.1	229.7	65.1	24.8
6×8	10.0	35.6	13.4	5.3	189.0	109.0	74.2	1.5	255.0	75.7	25.8
7×8	45.5	41.8	14.4	4.6	217.4	128.1	73.6	1.7	230.7	74.6	28.2
$SE_{(m)}$	4.8	2.1	0.4	0.3	9.8	6.5	3.5	0.1	14.8	11.7	3.0
LSD	6.7	2.9	0.6	0.4	13.8	9.2	5.0	0.1	20.9	16.6	4.3

Table 5. Generation means ($\bar{P}$, $\bar{F}_1$), average heterosis and coefficient of variation (CV) for different photosynthetic traits and productivity potential

Characters	Year	$\bar{P}$	$\bar{F}_1$	$\frac{\bar{F}_1 - \bar{P}}{\bar{P}} \times 100$ (%)	CV
Photosynthetic rate	1985	17.3	19.2	11.0**	6.9
	1986	31.9	53.1	66.4**	8.8
Leaf area/plant	1985	10.0	18.3	83.0**	5.2
	1986	28.1	35.3	25.6**	5.2
No. of leaves/plant	1985	10.8	11.2	3.7**	5.6
	1986	13.1	14.1	7.6**	2.9
Leaves above the ear	1985	4.9	4.9	–	6.2
	1986	5.6	5.6	–	4.2
Total chlorophyll content	1985	139.3	134.2	−3.7 NS	6.6
	1986	162.1	204.0	25.8**	4.1
Chlorophyll a content	1985	82.5	78.1	5.3**	2.9
	1986	107.8	123.8	14.8**	5.0
Chlorophyll b content	1985	55.4	54.3	−2.0 NS	4.6
	1986	61.2	75.9	24.0**	5.0
Ratio chlorophyll a/b	1985	1.5	1.5	–	4.4
	1986	1.8	1.6	−11.1**	4.4
Biological yield/plant	1985	150.0	232.6	55.1**	2.7
	1986	174.5	236.3	35.4**	5.4
Grain yield/plant	1985	42.9	78.2	82.3**	6.0
	1986	50.4	76.4	51.6**	13.3
Harvest index	1985	27.6	28.2	0.6 NS	6.7
	1986	26.2	27.3	4.2 NS	9.9

** $P<0.01$; NS, not significant

observed for number of leaves above the ear and harvest index in both years, thereby implying no difference among the parents and their hybrids. In 1985 non-significant heterosis was noticed for chlorophyll content and chlorophyll b content.

2. *Analysis of V_r and W_r*

Variances (V_r) and parent-progeny covariances (W_r) of individual arrays over replications and reciprocal crosses were used to calculate 6 and 8 V_r, W_r values in the 1985 and 1986 seasons, respectively. The linear regression of W_r on V_r was tested for significance ($b \neq 0$) and for deviation from unity ($b \neq 1$) by the usual *t*-tests. A simple genetic explanation of the data on an additive-dominance model was sought after testing it for epistasis and non-random distribution of the genes among parents. In the majority of cases the failure of the additive-dominance model could be attributed to the disturbance caused by the epistatic parent. The elimination of such arrays and the subsequent analysis of 5×5 and 7×7 diallels in 1985 and 1986, respectively, helped restore the desired rectilinear relationship. In some instances more than one parent had to be deleted to salvage as much genetic information as possible; in each instance $W_r - V_r$ differences of arrays were tested for their non-significance, thereby enabling the explanation of results as per diallel theory.

2.1. Photosynthetic rate. The W_r/V_r graph calculated from the means over replications yielded a poor regression in both seasons (Fig. 1, Ai, Bi). Systematic elimination of individual arrays and the subsequent analysis of the remaining data revealed that array number 1 and 4 were the most offending in the 1985 and 1986 seasons, respectively. Satisfactory improvements in establishing the rectilinear relationship were made in 1985 ($b = 0.684 \pm 0.018$ and 1986 (0.999 ± 0.167) (Fig. 1, Aii, Bii). The position of the array points along the regression graph indicated that parents 2 and 3 in 1985 and parents 1 and 7 in 1986 had most of the dominant alleles for higher photosynthetic rate. Array 5 embodied an equal distribution of dominant and recessive alleles in either season. There was a complete reversal of array points along the regression graph with respect to arrays 2 and 3, which showed the excess of dominant alleles in 1985. In 1986, however, the former registered an excess of recessive alleles while the latter had an equal distribution of dominant and recessive alleles.

The W_r/V_r graph almost traversed through the origin in 1985 indicating complete dominance for higher photosynthetic rate at the grain-filling stage, while in 1986 it

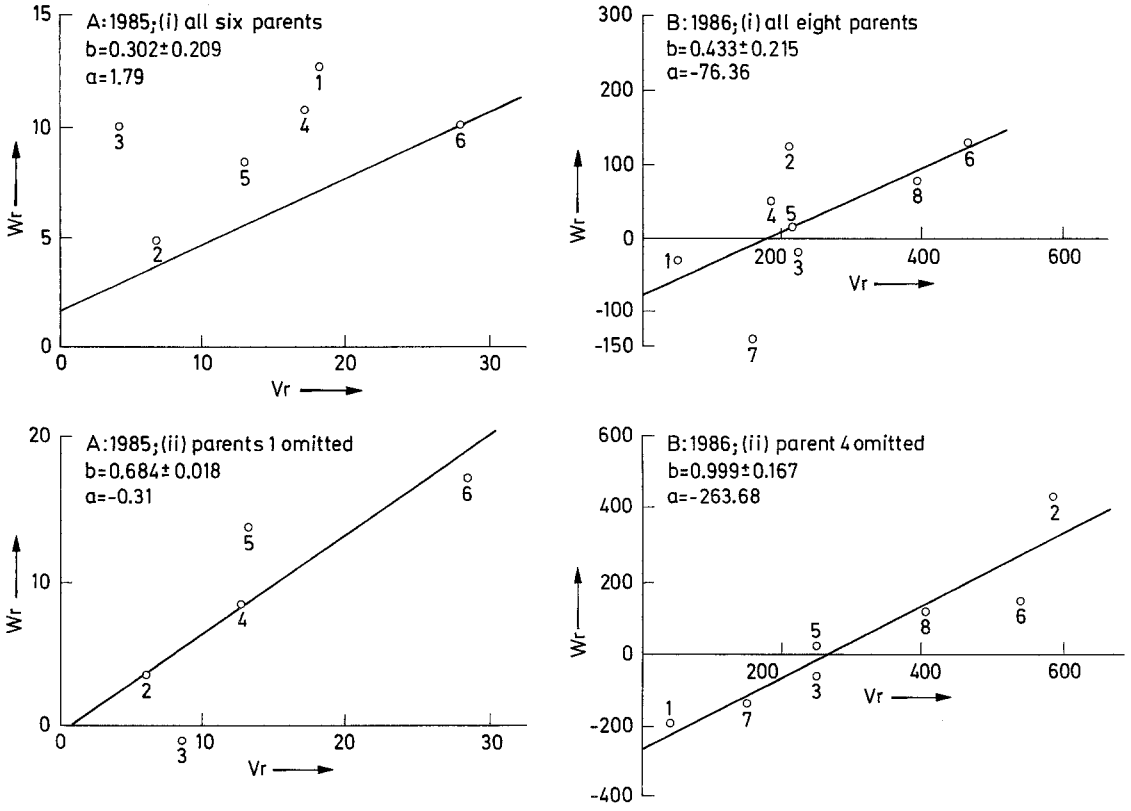

Fig. 1. The regression of W_r on V_r for photosynthetic rate

passed well below the point of origin indicating positive overdominance at silking stage.

2.2. Leaf area per plant. The regression coefficient of W_r and V_r established a satisfactory rectilinear relationship in 1985 (Fig. 2, Ai) but a poor one in 1986. Upon the elimination of array 1, (which incidentally had the largest $W_r - V_r$ value) a satisfactory graphical situation was etrieved ($b = 0.709 \pm 0.240$; Fig. 2, Bii). However, the best fit into unit linear regression was obtained with the elimination of parents 1 and 6 ($b = 0.766 \pm 0.173$; Fig. 2, Biii). The scatter of array points along the regression graph indicates the concentration of dominant genes in parents 2 and 3 in each season. The nature of the genes was profoundly influenced by seasonal effects in entries 4 and 5: the former showed a preponderance of recessive alleles in the first season while in 1986 it manifested a preponderance of dominant alleles; similarly array 5, which had an equal proportion of dominant and recessive alleles in 1985, displayed the highest proportion of recessive alleles in 1986. That seasonal effects were also clearly evident was indicated by the fact that the arrays 1 and 6, which were highly epistatic in 1986, behaved benignly in 1985, the former embodying the largest proportion of dominant alleles and the latter on excess of recessive alleles. The W_r intercept did not deviate from zero in any of the seasons indicating a complete dominance for higher leaf area per plant.

2.3. Number of leaves per plant. A satisfactory rectilinear relationship was obtained with all 6 parents in 1985 (Fig. 3, Ai) but in the 1986 season, the best fit into unit linear regression was achieved upon eliminating arays 1, 5 and 8 jointly ($b = 0.767 \pm 0.118$; Fig. 3, Biii). The distribution of array points along the regression line showed that array 3 was the richest in dominant alleles for both years, while array 4 embodied a slight excess of dominant alleles in 1985 while in 1986 dominant and recessive alleles were equally preponderant. Similarly, array 2 displayed an equal proportion of dominant and recessive alleles in 1985 while in 1986 it registered the highest proportion of recessive alleles. The regression line passed through the origin in both years, establishing the complete dominance for higher number of leaves.

2.4. Number of leaves above the ear. In 1985 the W_r, V_r regression involving all 6 parents revealed a perfect rectilinear relationship ($b = 1.249 \pm 0.187$; Fig. 4, Ai), but in 1986 a satisfactory graphical situation was only obtained upon joint elimination of arrays 5 and 7 ($b = 0.943 \pm 0.224$; Fig. 4, Biii). Array 2 embodied most of the dominant alleles for higher number of leaves above

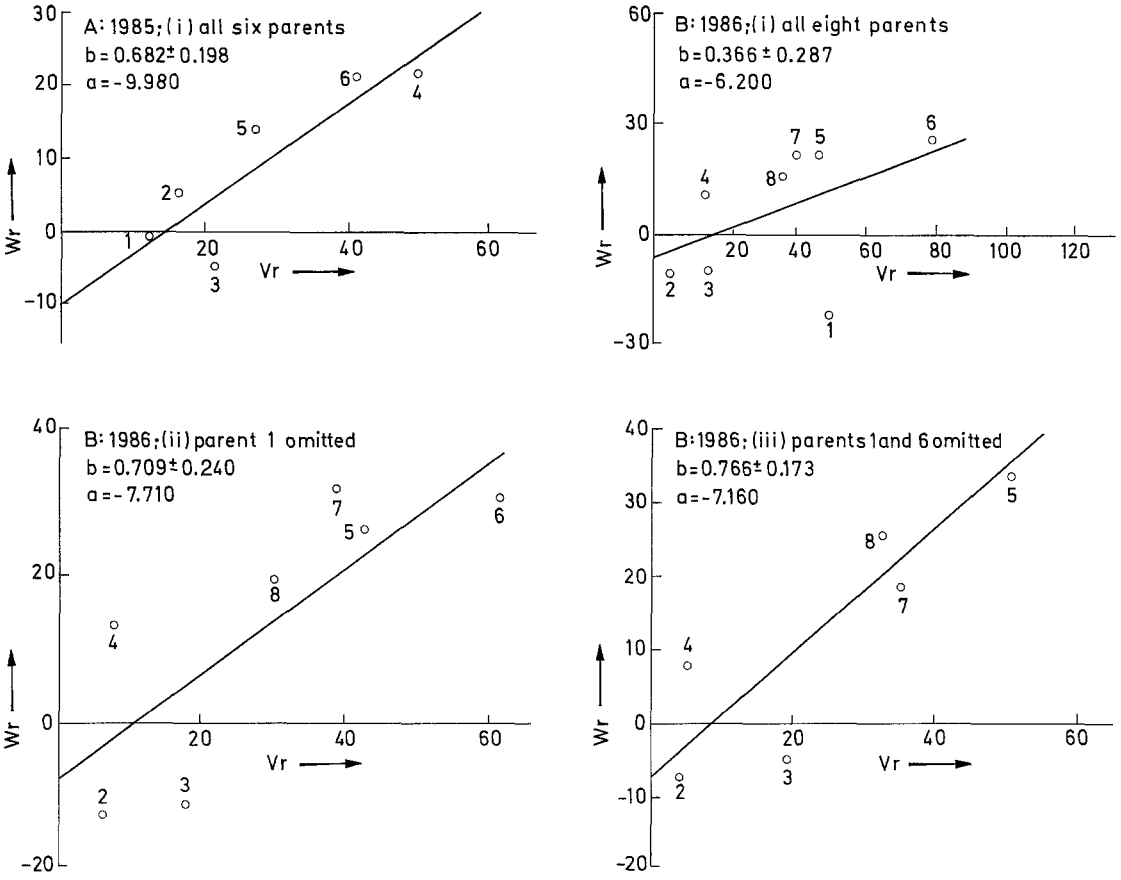

Fig. 2. The regression of W_r on V_r for leaf area per plant

the ear in each season. Array 3, which contained a slight excess of recessive alleles in 1985, had a clear excess of recessive alleles in 1986. Correspondingly, array 1, which contained a slight edge in dominant alleles in 1985, had a clear excess of dominant alleles in 1986. The W_r intercept did not deviate from zero within the sampling limits, thereby establishing a complete dominance for higher number of leaves above the ear.

2.5. Total chlorophyll content. The regression coefficient of W_r/V_r for total chlorophyll content in both the years was non-significant (Fig. 5, Ai and Bi). The systematic elimination of individual array and the subsequent analysis of 5×5 diallel sets in 1985 identified the array 4 to be the disturbing parent to achieve a satisfactory graphic situation. The arrays 2 and 5 embodied most of the dominant alleles, while 3 had the preponderance of recessive alleles. On the contrary, in 1986 season, the elimination of individual arrays and the analysis of resulting 7×7 diallel sets failed to resolve the discrepancy (Fig. 5, Bii). Further, the pairwise elimination of arrays in all possible combinations failed to rectify the anomalies. However, the most satisfactory graphic analysis was possible upon the joint elimination of three arrays viz., 3, 6 and 8 (Fig. 5, Biii). The spread of array points along the regression line revealed that the arrays 1, 5 and 2 were rich in recessive alleles. The regression line traversed well below the point of origin in both the years indicating overdominance.

2.6 Chlorophyll a. The graphic analysis for chlorophyll a was marred by array 6 which in maintaining a substantial difference in $W_r - V_r$ caused the slope of the regression line to drop significantly from the expected value of unity in each season. The removal of array 6 led to a tremendous improvement in retrieving a satisfactory rectilinear graphical relationship between W_r and V_r (Fig. 6, Aii, Bii). However, among the non-epistatic parents there was a complete reversal of array points along the regression graph. In the 1985 season, arrays 5, 1 and 4 had most of the dominant alleles while array 2 embodied most of the recessive alleles. Array 3 contained an equal distribution of dominant and recessive alleles in each season. The negative W_r intercept implied overdominance in both years.

2.7. Chlorophyll b. It was not possible to make any genetic interpretations by means of the diallel graph since

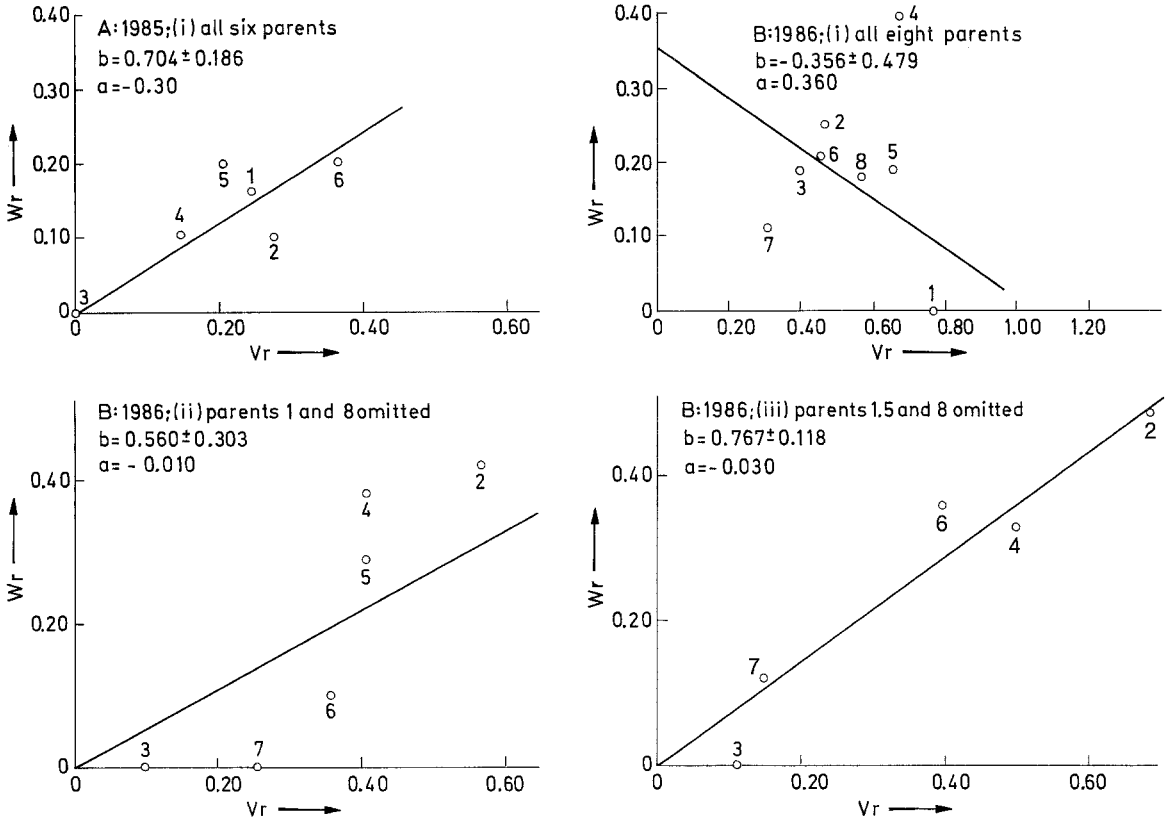

Fig. 3. The regression of W_r on V_r for number of leaves

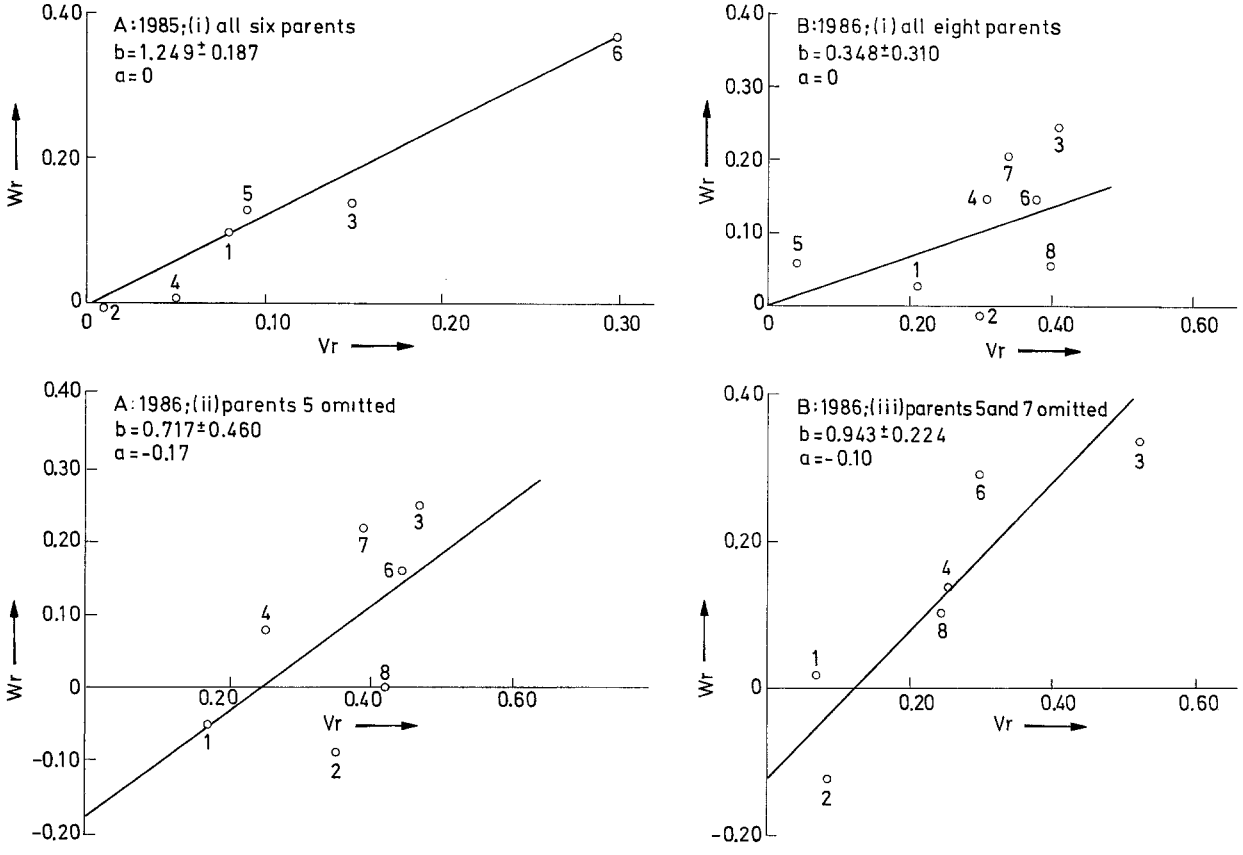

Fig. 4. The regression of W_r on V_r for number of leaves above the ear

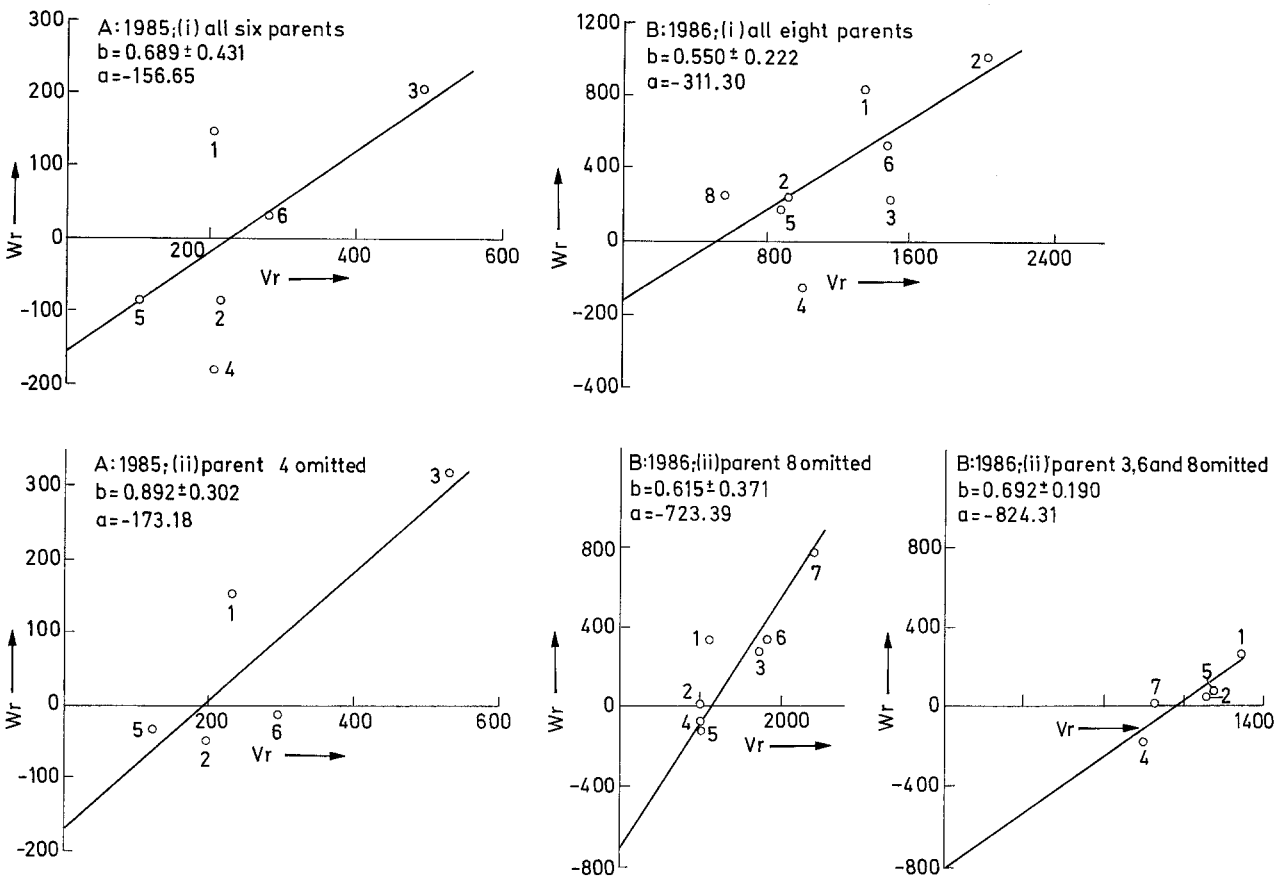

Fig. 5. The regression of W_r on V_r for total chlorophyll content

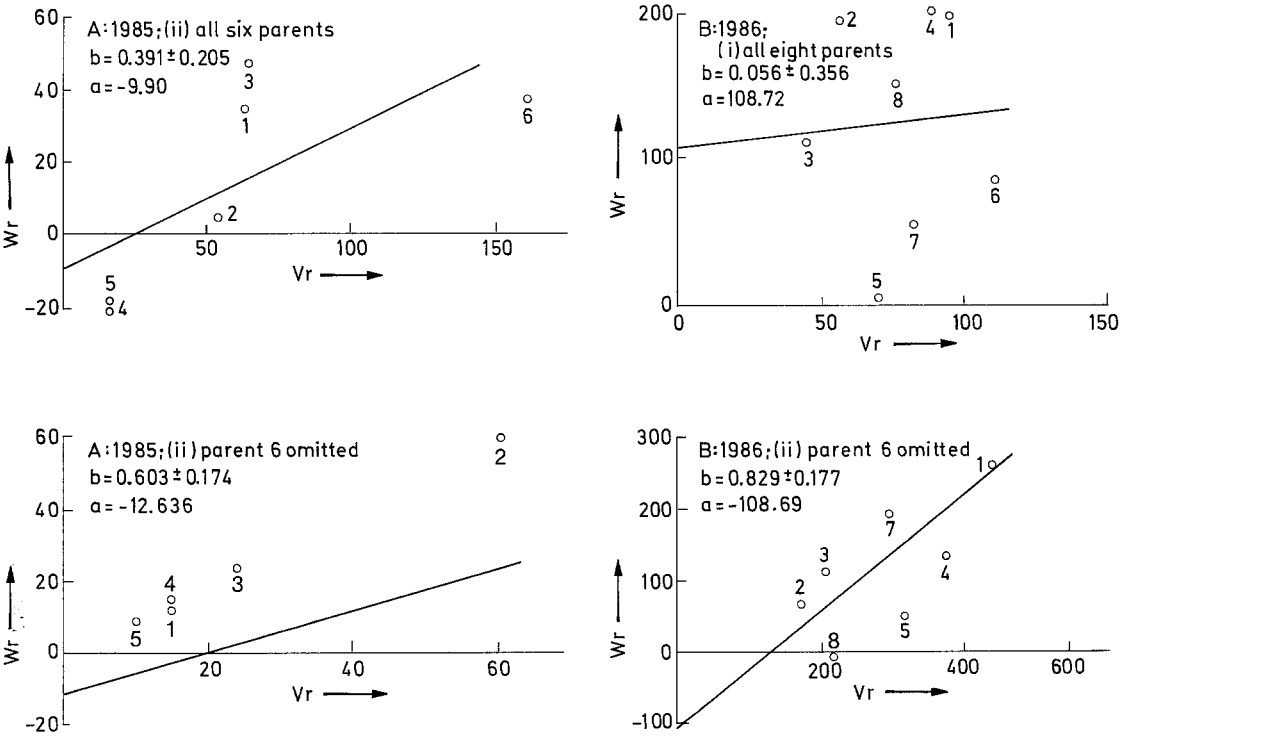

Fig. 6. The regression of W_r on V_r for chlorophyll a content

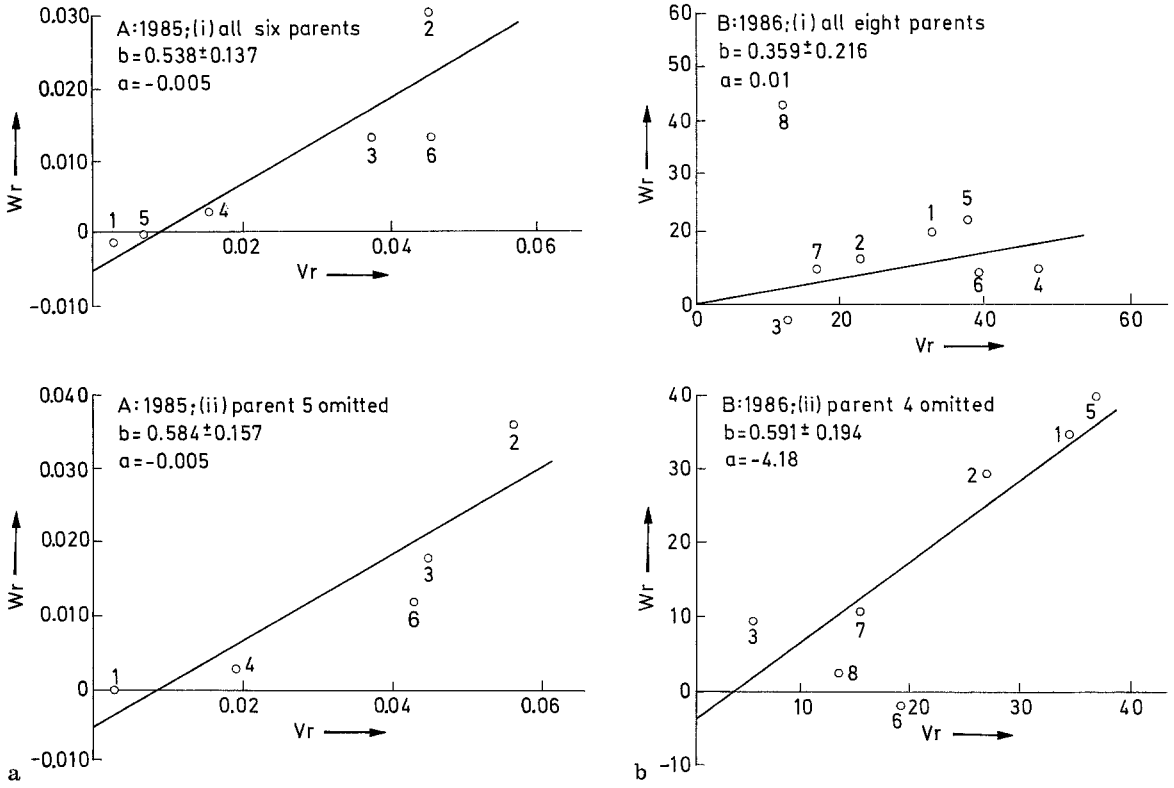

Fig. 7. **a** The regression of W_r on V_r for chlorophyll a/b and **b** the regression W_r on V_r for harvest index

the systematic elimination of one, two or even three arrays at a time failed to rectify the anomalies, in either year, indicating the failure of one or more of the assumptions underlying the diallel analysis.

2.8. Ratio of chlorophyll a/b. The results of graphic analysis were amenable to the genetic explanation in the 1985 season only by deleting array 5; thereby restoring a satisfactory rectilinear relationship between W_r, V_r (Fig. 7a, Aii). Array 1 had the highest proportion of dominant genes while array 4 had a slight edge in dominant alleles. Array 2 embodied the most evident preponderance of recessive alleles followed by arrays 3 and 6. The W_r/V_r regression line passed almost through the origin, indicating complete dominance.

2.9. Harvest index. The diallel data of 1985 could not be explained by a simple additive-dominance model because of non-fulfilment of the diallel assumptions. In 1986 array 4 was found out to be the most disruptive parent, and its elimination helped restore the satisfactory rectilinear relationship of unit slope between W_r/V_r for the remaining arrays (Fig. 7b, Bii). Array 3 embodied the highest proportion of dominant alleles followed by arrays 8, 7 and 6, and array 5 showed the other extreme, being preponderant in recessive alleles, followed by arrays 1 and 2. The W_r intercept did no deviate from zero, implying complete dominant gene action.

2.10. Biological yield. The diallel analysis of the 1985 season revealed a near perfect rectilinear relationship of unit slope between W_r, V_r (Fig. 8, Ai). However in 1986 a satisfactory graphic analysis was dependent upon the omission of arrays 1 and 2 simultaneously ($b = 0.839 \pm 0.240$; Fig. 8, Biii). Array 3 was fairly rich in dominant alleles for increased biomass production, while arrays 4 and 5 embodied more of the recessive alleles in both seasons. Array 2 was close to array 3 in number of dominant alleles in the first season but became epistatic in the second season. The striking discontinuity of the distribution of array points in each year enabled us to identify three broad groups in the 1985 season, (1) one containing a higher proportion of dominant alleles (arrays 2, 3); (2) one containing a higher proportion of recessive alleles (arrays 4, 5); (3) one containing an equal proportion of dominant and recessive alleles (arrays 1, 6). However, in 1986 the last group was not recorded, and the distribution of the array points was distinctly confined to dominant (3, 7, 8) and recessive (4, 5 and 6) groups. Therefore, the pattern of genetic diversity could be viewed as one of large inter-group and small intra-group differences.

In the 1985 season, the W_r intercept was negative but in 1986 it passed almost through the origin within the sampling limits giving a general inference of overdominance and complete dominance, respectively, for increased biomass production.

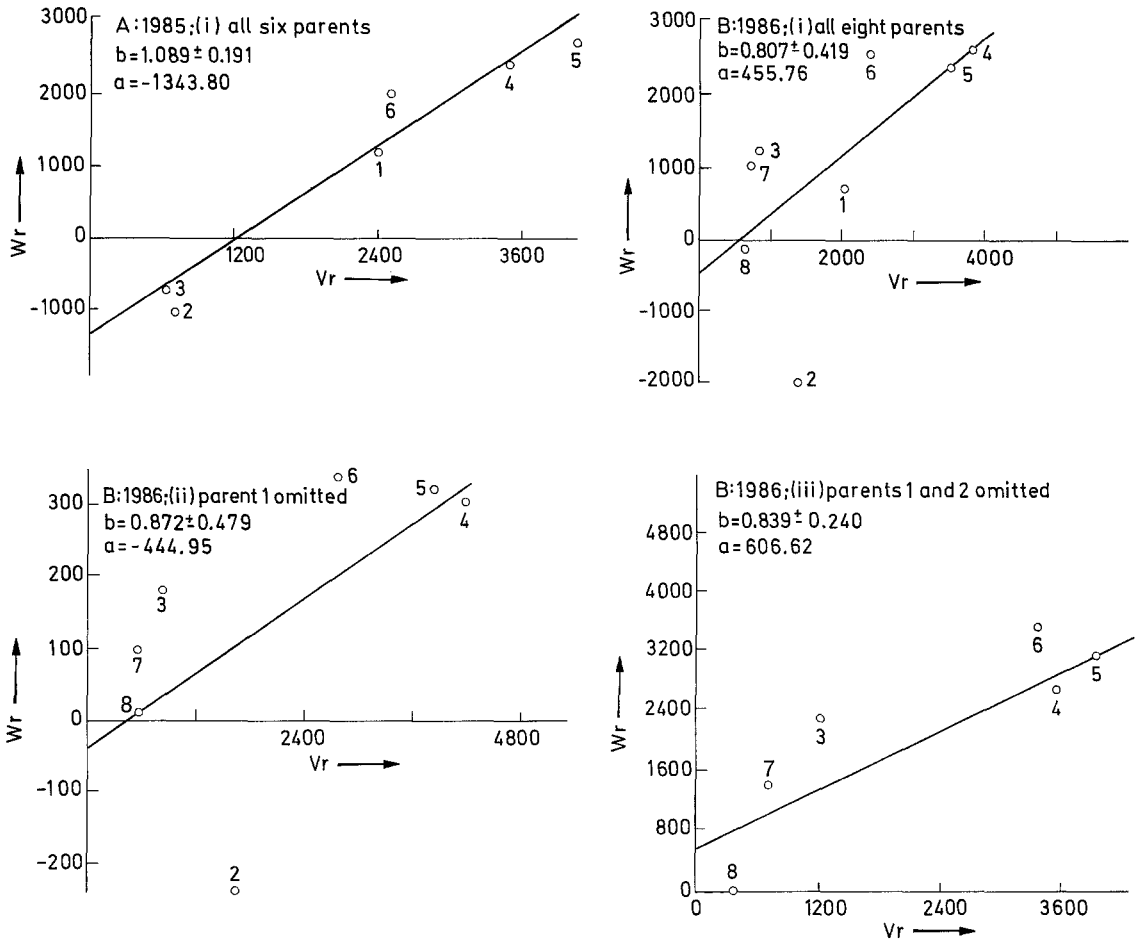

Fig. 8. The regression of W_r on V_r for biological yield

2.11. Grain yield per plant. The graphic analysis of variance covariance for grain yield fitted into a satisfactory linear regression of unit slope in 1985 (Fig. 9, Ai). In the 1986 season, diallel analysis revealed array 7 to be the most offending and its elimination resulted into a regression coefficient that did not differ from unity (Fig. 9, Bii). The scatter of array points was almost similar in both seasons. Arrays 2 and 3 embodied a high proportion of dominant alleles, while arrays 5 and 6 were preponderant in recessive alleles. Arrays 1 and 4 embodied an equal proportion of dominant and recessive alleles.

The W_r intercept being negative in both seasons revealed overdominance gene action for increasing grain yield per plant.

Discussion

There are no known instances where genetic improvements in crop yield can be traced back to improved photosynthesis. Nor are there many clear instances where the selection for leaf photosynthesis has increased crop yield (Nelson 1988). The frequent lack of correlation between leaf photosynthesis and yield is certainly not encouraging, nevertheless leaf photosynthesis is expected to be directly related to biomass productivity and yield.

The topic has been broached comprehensively by Zelitch (1982), Austin (1989) and Sarkar et al. (1991), indicating that the scenario is not that gloomy. The often cited absence of correlation between photosynthesis and yield should not be a deterrent to clarification of the anomalies. As scientific knowledge and technology monitoring the components of photosynthetic efficiency improves, one should be able to locate the critical rate-limiting factors in each instance and thereby overcome the barriers to future improvements. Thus, studies addressing the genetic architecture of leaf photosynthetisis must be sustained.

The research discussed in this article involved the assessment of genetic relationships among different inbred lines of maize with respect to plant productivity and photosynthetic efficiency by means of regression graph of covariance (W_r) and variance (V_r) of arrays in diallelic crosses. A simple genetic explanation as envisaged in the theory was sought whenever the rectilinearity between W_r and V_r appeared to have been achieved. The technique

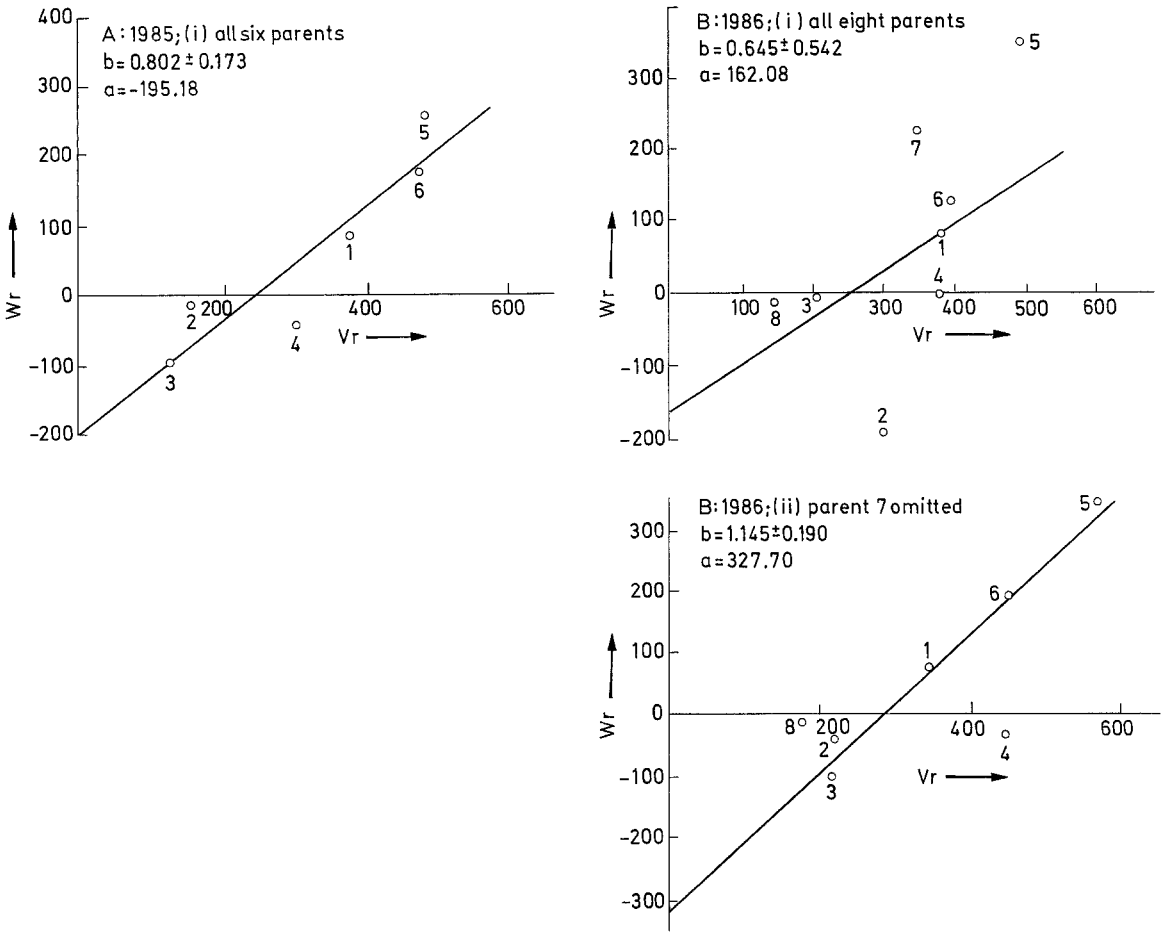

Fig. 9. The regression of W_r on V_r for grain yield

thus provided a reliable qualitative assay of the genetic relationships among the parents in diallel crosses.

With respect to the W_r/V_r graph, it must be pointed that gene dispersion and association may cause the graph to deviate from a straight line of unit linear regression in characteristic ways that have superficial similarities to the effects of complementary and duplicate interactions (Mather 1967; Coughtrey and Mather 1970). Such situations impose difficulties in discriminating between these phenomenon, which affect the rectilinearity of W_r/V_r relations. Also, the effect of duplicate interactions and gene associations may be minimal, causing no detectable departure from the expected linear regression of unit slope. Thus, a significant regression slope of unity may result in an inaccurate conclusion regarding the mode of inheritance of a metrical character. In addition, seasonal differences in the genetic control of a character have also been encountered. (Jinks 1956; Paroda and Hayes 1971; Riggs and Hayter 1972; Jana 1975). The results of the present study involving only the F_1s and parental values must, therefore, be considered with these possible limitations in mind.

A notable feature of the present investigation was the "apparent" overdominance for some important components of photosynthetic efficiency, which had a direct bearing on plant productivity. Overdominance in such cases could be attributed to the multiplicative effects of components that separately show simple Mendelian inheritance, thus overdominance being "apparent" in this sense (Duarte and Adams 1963; Sinha and Khanna-Chopra 1975; Gaudry et al. 1984). In the present situation total photosynthate production could be considered to be due to the result of multiplicative effects of photosynthetic rate per unit leaf area and total assimilatory leaf surface (Sinha et al. 1976; Khanna-Chopra 1982). The photosynthetic rate itself could be considered to be influenced by the interaction of several cellular traits, viz cell volume (Baer and Schrader 1985), mesophyll cell size (Dornhof and Shibles 1976) and chloroplast number (Molin et al. 1982), physiological attributes, viz stomatal resistance (Dornhof and Shibles 1976) and cellular CO_2 resistance (Nobel 1977), and lastly biochemical traits, viz pyruvate Pi dikinase (PPDK, EC.2.7.9.1), which catalyses the conversion of pyruvate to phosphoenolpyruvate

in mesophyll cells (Suguiyama and Hirayama 1983) and is the primary acceptor of CO_2 in the first carboxylation step of photosynthesis in C_4 plants, and ribulose-1, 5-bisphosphate carboxylase (RuBPCase, E.C. 4.1.1.39), which is responsible for carboxylation in bundle sheath cells (Buttery and Buzzell 1977; Baer and Schrader 1985). These cellular, physiological and biochemical traits, which participate in a complex interaction pathway where any one of them can be rate limiting, give the final manifestation of gas exchange in the form of the carbon dioxide exchange rate (CER), which was measured in the present study with the help of an infrared gas analyser.

The negative intercept of W_r in 1986 after elimination of the epistatic parents indicated overdominance gene action for the higher photosynthetic rate at the silking stage, while in 1985 complete dominance was noticed for higher photosynthetic rate at the grain-filling stage. The results are in close agreement with those of Avratovscukova (1983), Gaziyants (1983) and Gaziyants and Laiskhram (1986), who also monitored that positive overdominance was indicated with non-allelic gene interactions. The results also corroborate the conclusions of Fousova and Avratovscukova (1973), Crosbie et al. (1978) and Lutkov and Polyakova (1982) who in their genetical studies have recorded the dominance for higher photosynthetic rates. Under some exceptional cases some crosses will exhibit overdominance for low photosynthetic rate (Crosbie et al. 1978).

Thus, complementary gene action coupled with the multiplicative effect of the sub-components seems not only a plausible explanation but an unavoidable one when encountering overdominance for higher photosynthetic rates. The second dimension to total photosynthate production was total assimilatory surface. Thus, leaf area per plant depicted the complete dominance of increased leaf area. Nonetheless Gaziyants (1983) and Gaziyants and Laiskhram (1986) have recorded the overdominance of higher leaf surface area. According to this premise total assimilatory surface area could be a function of the total number of leaves and the size of the individual leaf. The total number of leaves in the present study showed complete dominance for increasing leaf number in both seasons. These results are in agreement with those of Stein (1956), Bonaparte (1977) and Rood and Major (1981). Besides, the number of leaves above the ear (which contributed directly to the economic sink) showed complete dominance for higher leaves in both years. The inheritance of photosynthetic pigments (total chlorophyll content and chlorophyll a) depicted overdominance for obvious reasons. However, the regression graph of chlorophyll a/b showed complete dominance in the 1985 season and holds some promise. The inheritance of biological yield (1985) and grain yield in both seasons could be explained by the multiplicative effects of the subcomponents with the final result of apparent overdominance gene action. Contrarily harvest index showed simple dominance gene action in 1986 where the graphical analysis was feasible.

Applied aspect

The scatter of array points along the regression line indicated that of all the entries inbred line MG 115 was the most promising as it embodied an increasing level of genes for most of the components of photosynthetic efficiency, thus enabling it to register the highest biological productivity and economic yield. The dominant alleles were notably preponderant with respect to photosynthetic rate, leaf area, number of leaves, chlorophyll a and harvest index (1986) in addition to the biological yield and grain yield. Further, promising inbred stocks have been identified for individual components of photosynthetic efficiency, viz photosynthetic rate (MG 121 and MG 132), leaf area per plant and number of leaves above the ear (MG 121 and MG 138), number of leaves (MG 125) in 1986, chlorophyll content (MG 114 and MG 138), chlorophyll a content (MG 114, MG 121, MG 103) in 1985 and chlorophyll a/b (MG 121 and MG 103).

Another significant assessment of the W_r/V_r graph was the complete reversal of the array positions along the regression line in the two crop seasons for MG 123, MG 138 and MG 114 for total chlorophyll content and MG 121, and MG 103 for chlorophyll a. This reversal of the array points along the regression line may be interpreted as different loci being active at different ontogenetic stages as well as seasons or as the reversal of the dominance effects at the loci that controlled these photosynthetic parameters among non-epistatic parents.

The parents causing the disturbances in the rectilinear relationship were not necessarily the same in each year, which points to seasonal differences in the epistatic effects of the parents. Further, the epistatic parents omitted in each case were not necessarily the ones corresponding to the maximum variances or the ones having the highest combining ability (not reported). As many as three parents disturbed the rectilinear relationship of W_r/V_r for number of leaves per plant (MG 121, MG 114 and MG 132) and total chlorophyll content (MG 115, MG 111 and MG 132) in the 1986 season; in 1985 the omission of only MG 103 from the graphic analysis corrected the discrepancy for total chlorophyll content, thereby enabling the data to be interpreted by a simple additive-dominance model. The fact that satisfactory regression graphs were obtained despite a drastic reduction in the number of parents entering the diallel table suggests that non-allelic interactions of the genes among the parents was the more common cause of the disturbance than non-random distribution of the genes among the parents.

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