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Simulation of Quantitative Characters by Genes with Biochemically Definable Action. III. The Components of Genetic Effects in the Inheritance of Anthocyanins in *Matthiola incana R. Br.*[1,2]

S. JANA and W. SEYFFERT

Institut für Biologie der Universität Tübingen, Lehrstuhl für Genetik, Tübingen (BRD)

Summary. In a self-pollinated plant species, *Matthiola incana* R. Br., six groups of isogenic lines were developed which were ideally suited for investigating the properties of individual genes controlling a quantitative character. Each group consisted of four homozygous parents for two alleles at each of the two loci in a common genetic background. A complete 4 × 4 diallel cross was obtained in each group. Because of the identical genetic background each diallel set could be considered as a genetic system of two loci. The biochemical functions of the alleles at each locus modifying the structure of the anthocyanin molecule were known. The phenotypes of the nine possible genotypes were qualitatively distinguishable by their flower colour differences. A quantitative measure of the phenotypic value associated with a genotype is the concentration of anthocyanins in flower tissues. In these simplified genetic systems, the nine phenotypic values could be expressed in terms of nine biometrical quantities, eight of which are attributable to the genetic effects of the alleles at the two loci under consideration. An unique solution of the set of nine equations in nine unknowns provided direct estimates of the parameters specifying additive, dominance and epistatic effects. Thus the effects of individual genes in a well-defined genetic background could be estimated by the use of a simple additive genetic model. An extension of the model provided estimates of the genetic parameters in different years and genetic backgrounds.

Dominance was found to be the most important type of gene action in the inheritance of anthocyanin content in the flower tissues of *M. incana*. There was considerable epistasis, but the effect was very unstable over years and genetic backgrounds. The relative magnitude of additive effect was most stable. Heterosis was observed and was found to be largely due to dominance and additive × dominance interactions.

Introduction

The standard biometrical techniques employed in the analysis of quantitatively inherited characters are based on partioning of variances and covariances of non-segregating and segregating populations into genetic components such as additive and dominance, and non-genetic component such as environment, and its interaction with the genotype. Cockerham (1954) extended the variance component method of analysis to include deviations due to epistasis. Anderson and Kempthorne (1954) developed the factorial gene model and by applying to experimental data they found that epistasis could be an important factor for inbreeding depression. By using the generation means method Hayman (1958) observed widespread occurrence of epistasis in plant populations and showed that epistasis could be as important as additive and dominance components of genetic variation. Since in the study of quantitatively inherited characters one is usually confronted with the situations allowing for estimation of the collective effects of an unknown number of genes at an unknown number of loci, the estimates of epistatic variance represent the average or statistical interactions among genes. Besides, the subdivision of sum of squares for genotypes into various orthogonal components leads to the overestimation of the contribution of additive and underestimation of the role of epistasis (Jana, 1971). Seyffert (1966) described an additive genetic model by which the effects due to the actions and interactions of individual genes can be directly estimated in an ideal condition of common genetic background and well-defined two-gene system. The model can be extended to three or more loci and the geometrically increasing number of parameters can be readily estimated on a computer.

The Model

The model was described in detail in a previous paper of this series (Seyffert, 1966). Following is a brief review:

Consider a population of a diploid species where the individuals are genetically identical except for a pair of unlinked loci, say I/i and J/j, each of which has only two alleles. The phenotypes of the nine possible genotypes can be completely described in terms of nine biometrical parameters:

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[2] Research supported by Deutsche Forschungsgemeinschaft.

Genotype	Phenotype	Description
$IIJJ$	22	$Y + a_i + a_j + aa_{ij}$
$IIJj$	21	$Y + a_i + d_j + ad_{ij}$
$IIjj$	20	$Y + a_i - a_j - aa_{ij}$
$IiJJ$	12	$Y + d_i + a_j + da_{ij}$
$IiJj$	11	$Y + d_i + d_j + dd_{ij}$
$Iijj$	10	$Y + d_i - a_j - da_{ij}$
$iiJJ$	02	$Y - a_i + a_j - aa_{ij}$
$iiJj$	01	$Y - a_i + d_j - ad_{ij}$
$iijj$	00	$Y - a_i - a_j + aa_{ij}$

The reference point Y in the above descriptions is a constant component of all the phenotypes representing the contribution of the genes which are not segregating in the population and the effects of the non-heritable factors. According to the present model, it is the arithmetic mean of the phenotypes associated with the homozygous genotypes, 1/4 (22 + 20 + 02 + 00), the reference-basis from which the effects of the alleles at the I/i and J/j loci are described as positive or negative increments. The quantities a_i, a_j, d_i and d_j denote additive effect of I/i, additive effect of J/j, dominance effect of I/i and dominance effect of J/j, respectively. The interaction components, homozygous phase at I/i with homozygous phase at J/j, homozygous (I/i) with heterozygous (J/j), heterozygous (I/i) with homozygous (J/j) and heterozygous (I/i) with heterozygous (J/j) are represented as aa_{ij}, ad_{ij}, da_{ij} and dd_{ij}, respectively. The descriptions of the nine phenotypes as linear combinations of the relevant parameters provide a system of nine linear equations in nine unknowns. By systematic elimination following unique solutions for the parameters are derived:

$$\begin{bmatrix} Y \\ a_i \\ a_j \\ d_i \\ d_j \\ aa_{ij} \\ ad_{ij} \\ da_{ij} \\ dd_{ij} \end{bmatrix} = \frac{1}{4} \begin{bmatrix} 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 & 0 & -1 & 0 & -1 \\ 1 & 0 & -1 & 0 & 0 & 0 & 1 & 0 & -1 \\ -1 & 0 & -1 & 2 & 0 & 2 & -1 & 0 & -1 \\ -1 & 2 & -1 & 0 & 0 & 0 & -1 & 2 & -1 \\ 1 & 0 & -1 & 0 & 0 & 0 & -1 & 0 & 1 \\ -1 & 2 & -1 & 0 & 0 & 0 & 1 & -2 & 1 \\ -1 & 0 & 1 & 2 & 0 & -2 & -1 & 0 & 1 \\ 1 & -2 & 1 & -2 & 4 & -2 & 1 & -2 & 1 \end{bmatrix} \times \begin{bmatrix} 22 \\ 21 \\ 20 \\ 12 \\ 11 \\ 10 \\ 02 \\ 01 \\ 00 \end{bmatrix} \quad (A)$$

Parameters — Coefficients — Phenotypes (P)

When the variances of the estimates of the mean phenotypic values are known, the approximate variances of the estimates of the parameters are calculated as:

$$\begin{bmatrix} V_y \\ V_{a_i} \\ V_{a_j} \\ V_{d_i} \\ V_{d_j} \\ V_{aa_{ij}} \\ V_{ad_{ij}} \\ V_{da_{ij}} \\ V_{dd_{ij}} \end{bmatrix} = \frac{1}{16} \begin{bmatrix} 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 4 & 0 & 4 & 1 & 0 & 1 \\ 1 & 4 & 1 & 0 & 0 & 0 & 1 & 4 & 1 \\ 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 1 \\ 1 & 4 & 1 & 0 & 0 & 0 & 1 & 4 & 1 \\ 1 & 0 & 1 & 4 & 0 & 4 & 1 & 0 & 1 \\ 1 & 4 & 1 & 4 & 16 & 4 & 1 & 4 & 1 \end{bmatrix} \times \begin{bmatrix} V_{22} \\ V_{21} \\ V_{20} \\ V_{12} \\ V_{11} \\ V_{10} \\ V_{02} \\ V_{01} \\ V_{00} \end{bmatrix} \quad (B)$$

Variances — Coefficients — Variances of phenotypes

The estimater of the parameters can be summed, ignoring their signs, to specify three types of gene actions in a two -locus system as

additive, $A = |a_i| + |a_j|$
dominance, $D = |d_i| + |d_j|$
interaction, $I = |aa_{ij}| + |ad_{ij}| + |da_{ij}| + |dd_{ij}|$.

Having pooled into three major groups representing additive (A), dominance (D) and interaction (I) effects, the relative magnitude of the three types of genetic effects can be calculated either as percentage of the total genetic effect at the ith and jth loci ($G = A + D + I$) or as the ratios, D/A and I/A. The D/A ratio is comparable to Mather's dominance ratio, but unlike $\sqrt{H/D}$, the former ratio measures the average degree of dominance even in the presence of nonallelic gene interactions. The I/A ratio is an average measurement of nonallelic interactions between the I/i and J/j loci, relative to their additive effects. The approximate variances of the ratios are:

$$\mathrm{Var}\,(D/A) = \left[\frac{\delta(D/A)}{\delta D}\right]^2 \mathrm{Var}\,(D) + \left[\frac{\delta(D/A)}{\delta A}\right]^2 \mathrm{Var}\,(A)$$
$$= \frac{\mathrm{Var}(D)}{D^2} + \frac{D^2\,\mathrm{Var}(A)}{A^4}$$

$$\mathrm{Var}\,(I/A) = \left[\frac{\delta(I/A)}{\delta I}\right]^2 \mathrm{Var}\,(I) + \left[\frac{\delta(I/A)}{\delta A}\right]^2 \mathrm{Var}\,(A)$$
$$= \left[\frac{I}{A}\right]^2 \left[\frac{\mathrm{Var}(I)}{I^2} + \frac{\mathrm{Var}(A)}{A^2}\right]$$

ignoring the covariance terms.

Suppose we have two independent measurements of each of the nine phenotypes, one from environment e_1 and the other from environment e_2, then these eighteen values can be expressed in terms of 18 parameters giving 18 linear equations in 18 unknowns. The Gaussian elimination and simplification give the unique solutions for the parameters (see p. 331 above).

Note that the parameters Y, a_i and a_i etc. can be estimated independently from each environment. A sufficient estimate of a parameter is then the arithmetic mean of the two estimates. For example, an average estimate of a_i is $\frac{1}{2}(a_{i.1} + a_{i.2})$, where $a_{i.1}$ and $a_{i.2}$ are two independent estimates of a_i in the environments e_1 and e_2, respectively, which is identical to the solutions given in (C). The average difference between the two estimates, $\frac{1}{2}(a_{i.1} - a_{i.2})$, is a measure of the environmental variation in additive effect at the ith locus, represented as $a_i e$ in (C).

$$\begin{bmatrix} Y \\ a_i \\ a_j \\ d_i \\ d_j \\ aa_{ij} \\ ad_{ij} \\ da_{ij} \\ dd_{ij} \\ Ye \\ a_ie \\ a_je \\ d_ie \\ d_je \\ aa_{ij}e \\ ad_{ij}e \\ da_{ij}e \\ dd_{ij}e \end{bmatrix} = \frac{1}{8} \begin{bmatrix} 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 1 & 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 1 \\ 1 & 0 & 1 & 0 & 0 & 0 & -1 & 0 & -1 & 1 & 0 & 1 & 0 & 0 & 0 & -1 & 0 & -1 \\ 1 & 0 & -1 & 0 & 0 & 0 & 1 & 0 & -1 & 1 & 0 & -1 & 0 & 0 & 0 & 1 & 0 & -1 \\ -1 & 0 & -1 & 2 & 0 & 2 & -1 & 0 & -1 & -1 & 0 & -1 & 2 & 0 & 2 & -1 & 0 & -1 \\ -1 & 2 & -1 & 0 & 0 & 0 & -1 & 2 & -1 & -1 & 2 & -1 & 0 & 0 & 0 & -1 & 2 & -1 \\ 1 & 0 & -1 & 0 & 0 & 0 & -1 & 0 & 1 & 1 & 0 & -1 & 0 & 0 & 0 & -1 & 0 & 1 \\ -1 & 2 & -1 & 0 & 0 & 0 & 1 & -2 & 1 & -1 & 2 & -1 & 0 & 0 & 0 & 1 & -2 & 1 \\ -1 & 0 & 1 & 2 & 0 & -2 & -1 & 0 & 1 & -1 & 0 & 1 & 2 & 0 & -2 & -1 & 0 & 1 \\ 1 & -2 & 1 & -2 & 4 & -2 & 1 & -2 & 1 & 1 & -2 & 1 & -2 & 4 & -2 & 1 & -2 & 1 \\ 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 1 & -1 & 0 & -1 & 0 & 0 & 0 & -1 & 0 & -1 \\ 1 & 0 & 1 & 0 & 0 & 0 & -1 & 0 & -1 & -1 & 0 & -1 & 0 & 0 & 0 & 1 & 0 & 1 \\ 1 & 0 & -1 & 0 & 0 & 0 & 1 & 0 & -1 & -1 & 0 & 1 & 0 & 0 & 0 & -1 & 0 & 1 \\ -1 & 0 & -1 & 2 & 0 & 2 & -1 & 0 & -1 & 1 & 0 & 1 & -2 & 0 & -2 & 1 & 0 & 1 \\ -1 & 2 & -1 & 0 & 0 & 0 & -1 & 2 & -1 & 1 & -2 & 1 & 0 & 0 & 0 & 1 & -2 & 1 \\ 1 & 0 & -1 & 0 & 0 & 0 & -1 & 0 & 1 & -1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & -1 \\ -1 & 2 & -1 & 0 & 0 & 0 & 1 & -2 & 1 & 1 & -2 & 1 & 0 & 0 & 0 & -1 & 2 & -1 \\ -1 & 0 & 1 & 2 & 0 & -2 & -1 & 0 & 1 & 1 & 0 & -1 & -2 & 0 & 2 & 1 & 0 & -1 \\ 1 & -2 & 1 & -2 & 4 & -2 & 1 & -2 & 1 & -1 & 2 & -1 & 4 & -4 & 2 & -1 & 2 & -1 \end{bmatrix} \times \begin{bmatrix} 22.2 \\ 21.2 \\ 20.2 \\ 12.2 \\ 11.2 \\ 10.2 \\ 02.2 \\ 01.2 \\ 00.2 \\ 22.1 \\ 21.1 \\ 20.1 \\ 12.1 \\ 11.1 \\ 10.1 \\ 02.1 \\ 01.1 \\ 00.1 \end{bmatrix} \quad (C)$$

Parameters — Coefficients — Phenotypes

The variances of the estimates of parameters in (*C*) are calculated as usual as the sums of the variances of the components appearing in their respective solutions. For example, the approximate variance of di is:

$$V_{d_i} = \frac{1}{64}(V_{22.2} + V_{20.2} + 4\,V_{12.2} + 4\,V_{10.2} + V_{02.2} + + V_{00.2} + V_{22.1} + V_{20.1} + 4\,V_{12.1} + + 4\,V_{10.1} + V_{02.1} + V_{00.1})$$

ignoring the covariance terms.

When the genetic effects of the same pair of loci are evaluated in the same environment, but in two genetic backgrounds, say, b_1 and b_2, the situation is analogous to that involving two environments described above. In the present context, the parameters specifying interactions of the genetic effects with background may be denoted as Yb, $a_i\,b$ and $a_j\,b$ etc.

The model can be extended to more than two loci and environments. With n loci, each having two alleles, there are $3^n - 1$ components specifying the genetic effects at the loci, of which there are n additive, n dominance and $3^n - 2n - 1$ epistatic types. With the increasing number of loci, soon the number of parameters to be estimated becomes too large and the experiment grows to a prohibitive size. Thus the usefulness of the model would be most certainly restricted to the simple genetic systems consisting of a relatively small number of loci.

Materials and Methods

In a self-pollinated plant species, *Matthiola incana* R. Br., experimental materials were developed which satisfied the following conditions essential for the use of the linear combination model described in the previous section:

1. Common genetic background,
2. Two alleles at each locus,
3. No lethal or deleterious effects of the alleles,
4. Diploid segregation,
5. Availability of all genotypes by controlled crosses and the possibility of estimating the phenotypic values associated with them, and
6. Assessment of the effects of genes in such a way that the results are comparable to those of conventional biometrical methods.

The materials and the methods of determining anthocyanin concentration in plant tissues were described by Seyffert (1971). With regard to the basic colour factors, e^+/e, g^+/g and f^+/f, all materials included in the present studies were of the genotype, $e^+e^+g^+g^+f^+f^+$. The genotype of an individual which is not otherwise mentioned in this paper is homozygous and identical to other members of the group. Following six groups were studied:

Group Number	Genetic background	Loci under investigation	Genotype of the parents
I	$l^+l^+uud^+d^+$	b^+/b, v^+/v	$b^+b^+v^+v^+$ $b^+b^+v\ v$ $b\ b\ v^+v^+$ $b\ b\ v\ v$
II	$l^+l^+u^+u^+dd$	b^+/b, v^+/v	$b^+b^+v^+v^+$ $b^+b^+v\ v$ $b\ b\ v^+v^+$ $b\ b\ v\ v$
III	$b^+b^+lld^+d^+$	u^+/u, v^+/v	$u^+u^+v^+v^+$ $u^+u^+v\ v$ $u\ u\ v^+v^+$ $u\ u\ v\ v$
IV	bbu^+u^+dd	l^+/l, v^+/v	$l^+l^+v^+v^+$ $l^+l^+v\ v$ $l\ l\ v^+v^+$ $l\ l\ v\ v$
V	$b^+b^+uud^+d^+$	l^+/l, v^+/v	$l^+l^+v^+v^+$ $l^+l^+v\ v$ $l\ l\ v^+v^+$ $l\ l\ v\ v$
VI	$uuvvd^+d^+$	b^+/b, l^+/l	$b^+b^+l^+l^+$ $b^+b^+l\ l$ $b\ b\ l^+l^+$ $b\ b\ l\ l$

The quantitative character under investigation was the concentration of anthocyanins in petals produced by the genes, e^+, g^+ and f^+ and modified by the alleles at the loci b^+/b, l^+/l, u^+/u, v^+/v and d^+/d. The extinction or optical density of the anthocyanin extracts of the flower tissues was continuously recorded at wave-lengths between 400 and 600 mμ in a Zeiss RPQ 2 spectrophotometer. The height of the anthocyanin peak which is at wavelengths between 500 and 530 mμ for *M. incana*, represents the total anthocyanin content in sufficient approximation, and therefore, was considered as a metri-

cal character controlled by the genes with biochemically definable actions.

The diallel cross of the four homozygous parents in each group was grown in the experimental nursery in Tübingen in 1965 and 1966 without replication. A freshly opened flower was taken from each cross in each 4×4 diallel set on a sampling date for measuring its anthocyanin content. The sixteen samples, each of which represented one of the sixteen possible matings in a diallel cross, were drawn on the same day. Five such samples were taken in 1965 and 16 in 1966, distributed over the entire flowering period of *M. incana* between June and August. The average of five or 16 extinction values was used for the estimation of the components of genetic effect in a group. Thus any variation due to the environmental differences among the days of sampling must have been confounded with the sampling errors.

Results

Table 1 contains the estimated mean extinction values associated with the nine genotypes in each group. These values were substituted in the phenotype vector P in (A) and the direct estimates of the nine parameters were obtained. The eight components of genetic effect attributed to a pair of loci in each group are deviations from their respective reference point Y, either in positive or negative direction as indicated by their signs (Table 2). The standard errors of the estimates of parameters are the square roots of the respective variances calculated as in (B). The estimates of the phenotypic means and consequently the estimates of the parameters have large standard errors. Since each observation was taken on a different day, it is very likely that the standard errors are inflated due to the environmental fluctuations on the days of sampling. Furthermore, it can be seen from (B) that some components like *d*'s and *dd*'s would have larger standard errors than *a*'s and *aa*'s merely because of the larger magnitude and/or number of the non-zero coefficients in their linear equations. It is evident from Table 2 that additive and additive $\times$ additive components have the smallest standard errors, whereas the estimates of dominance $\times$ dominance interactions have the largest standard errors in all cases.

A real difficulty arises, in performing a statistical test of significance of the estimates of genetic parameters. An approximate test of significance is given by the comparison of the absolute value of an estimate of parameter with twice its standard error. However, in the present studies, the upward bias due to the

Table 1. *The mean extinction values associated with nine genotypes and their standard errors (S.E.) in each group. All observed extinction values were multiplied by 10^3 prior to estimation of arithmetic means and their standard errors. The mean extinction values in 1965 und 1966 are averages of five and sixteen observations, respectively*

Genetic background: $l^+l^+uud^+d^+$					$l^+l^+u^+u^+dd$					$b^+b^+lld^+d^+$				
Loci studied: b^+/b, v^+/v					b^+/b, v^+/v					u^+/u, v^+/v				
Year:	1965		1966			1965		1966			1965		1966	
Genotype	Mean	S.E.	Mean	S.E.	Genotype	Mean	S.E.	Mean	S.E.	Genotype	Mean	S. E.	Mean	S. E.
bbvv	238.2	16.19	327.5	20.28	*bbvv*	745.4	110.54	929.4	34.15	*uuvv*	385.6	49.91	333.8	16.97
bb+v	283.7	16.69	296.5	10.20	*bb+v*	781.0	76.67	1054.4	36.40	*uu+v*	420.2	31.46	475.9	16.88
bb++	250.8	24.52	302.7	24.52	*bb++*	813.4	73.72	1032.9	51.97	*uu++*	511.4	77.70	525.7	24.36
+bvv	472.4	11.65	489.7	12.98	*+bvv*	785.5	85.74	1154.1	49.68	*+uvv*	388.5	27.65	448.8	16.65
+b+v	491.1	16.67	512.4	11.35	*+b+v*	1072.5	49.87	1136.4	39.72	*+u+v*	540.1	12.62	459.7	16.72
+b++	541.0	7.75	485.7	14.80	*+b++*	1171.5	51.78	1131.9	28.72	*+u++*	604.8	22.80	581.3	22.65
++vv	377.0	15.23	436.6	16.33	*++vv*	1021.0	117.17	1094.8	36.83	*++vv*	509.4	55.23	488.3	15.82
+++v	580.5	30.93	532.6	10.62	*+++v*	883.3	83.00	1199.5	42.20	*+++v*	593.3	24.27	595.6	18.99
++++	452.4	14.98	537.5	21.16	*++++*	864.8	13.96	1139.9	33.17	*++++*	467.4	23.92	536.9	31.95

Genetic background: bbu^+u^+dd					$b^+b^+uud^+d^+$					$uuvvd^+d^+$				
Loci studied: l^+/l, v^+/v					l^+/l, v^+/v					b^+/b, l^+/l				
Year:	1965		1966			1965		1966			1965		1966	
Genotype	Mean	S.E.	Mean	S.E.	Genotype	Mean	S.E.	Mean	S.E.	Genotype	Mean	S.E.	Mean	S.E.
llvv	525.0	53.78	540.0	16.05	*llvv*	385.6	49.91	333.8	16.97	*bbll*	164.6	11.34	232.1	10.60
ll+v	637.5	19.31	724.5	23.98	*ll+v*	420.2	31.46	475.9	16.88	*bb+l*	227.1	7.37	294.5	8.27
ll++	718.2	41.37	708.2	45.19	*ll++*	511.4	77.70	525.7	24.36	*bb++*	238.2	16.69	327.5	20.28
+lvv	580.4	115.83	1105.4	37.14	*+lvv*	379.6	27.20	417.6	13.10	*+bll*	373.7	8.72	432.6	14.23
+l+v	930.5	52.76	1088.7	31.92	*+l+v*	503.1	13.90	494.0	10.75	*+b+l*	479.0	20.50	451.7	11.92
+l++	1049.5	61.72	1036.2	28.49	*+l++*	588.3	21.88	564.6	15.93	*+b++*	472.4	11.50	489.7	12.98
++vv	745.4	110.54	929.4	34.15	*++vv*	377.0	15.23	436.6	16.33	*++ll*	385.6	49.91	333.8	16.97
+++v	781.0	76.67	1054.4	35.40	*+++v*	580.5	30.93	532.6	10.62	*+++l*	379.6	27.20	417.6	13.10
++++	813.4	73.72	1032.9	51.97	*++++*	452.4	14.98	537.5	21.16	*++++*	377.0	15.23	436.6	16.33

Table 2. *The estimate of parameters and their respective standard errors (S.E.) for the six genetic systems in Matthiola incana in years 1965 and 1966*

Genetic background: $l^+l^+uud^+d^+$					$l^+l^+u^+u^+dd$				$b^+b^+lld^+d^+$				
Year:	1965		1966		1965		1966			1965		1966	
Parameter	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Parameter	Estimate	S.E.	Estimate	S.E.
y	329.6	9.1	401.1	10.4	861.1	44.4	1049.2	19.9	y	468.5	27.6	471.1	11.6
a_b	85.1	9.1	86.0	10.4	81.7	44.4	68.1	19.9	a_u	19.9	27.6	41.4	11.6
a_v	22.0	9.1	19.0	10.4	−22.0	44.4	37.1	19.9	a_v	20.9	27.6	60.1	11.6
d_b	177.1	11.5	86.6	14.3	117.3	66.9	93.7	34.9	d_u	28.2	32.9	43.9	18.2
d_v	102.5	19.8	13.5	12.7	−29.0	69.0	77.7	34.2	d_v	38.3	34.0	64.6	17.2
aa_{bv}	15.7	9.1	31.4	10.4	−56.0	44.4	−14.6	19.9	aa_{uv}	−41.9	27.6	−35.8	11.6
ad_{bv}	63.3	19.8	32.1	12.7	−30.6	69.0	4.5	34.2	ad_{uv}	66.6	34.0	18.4	17.2
da_{bv}	12.3	11.5	−21.0	14.3	215.0	66.9	−48.2	34.9	da_{uv}	87.2	32.9	6.1	18.2
dd_{bv}	−118.0	26.5	11.2	19.7	123.0	98.8	−84.3	59.8	dd_{uv}	5.2	40.4	−19.9	27.8

Genetic background: bbu^+u^+dd					$b^+b^+uud^+d^+$				$uuvvd^+d^+$				
Year:	1965		1966		1965		1966			1965		1966	
Parameter	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Parameter	Estimate	S.E.	Estimate	S.E.
y	700.5	37.3	802.6	19.6	431.6	23.7	458.4	10.0	y	291.3	14.0	332.5	8.2
a_l	78.9	37.3	178.5	19.6	−16.9	23.7	28.6	10.0	a_b	89.9	14.0	52.7	8.2
a_v	65.3	37.3	67.9	19.6	50.3	23.7	73.2	10.0	a_l	16.2	14.0	49.5	8.2
d_l	114.4	75.5	268.2	27.9	53.2	29.4	32.7	14.3	d_b	131.7	15.5	128.6	12.6
d_v	8.7	54.3	86.8	29.3	68.7	32.4	45.9	14.1	d_l	12.0	19.9	23.6	11.3
aa_{lv}	−31.3	37.3	−16.2	19.6	−12.6	23.7	−22.7	10.0	aa_{bl}	−20.5	14.0	1.8	8.2
ad_{lv}	−7.2	54.3	−13.6	29.3	97.0	32.4	−0.3	14.1	ad_{bl}	−13.7	19.9	8.9	11.3
da_{lv}	169.2	75.5	−102.5	27.9	54.0	29.4	0.3	14.3	da_{bl}	33.1	15.5	−20.9	12.6
dd_{lv}	106.8	100.2	−68.9	49.3	−49.6	39.3	−43.0	20.5	dd_{bl}	44.0	29.3	−33.1	19.0

Table 3. *The pooled estimates of three main types of gene action, expressed as percentage of the total genetic effect ascribable to the pair of loci under investigation. These percentages and the ratios D/A and I/A, are calculated from the absolute values of the estimates of parameters in Table 2.* $A = |a_i| + |a_j|$, $D = |d_i| + |d_j|$, $I = |aa_{ij}| + |ad_{ij}| + |da_{ij}| + |dd_{ij}|$, and $G = A + D + I$

Genetic background: $l^+l^+uud^+d^+$					$l^+l^+u^+u^+dd$				$b^+b^+lld^+d^+$				
Loci studied:	b^+/b,	v^+/v			b^+/b,	v^+/v			u^+/u,	v^+/v			
Year	1965		1966		1965		1966		1965		1966		
Parameter	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	
A (% of G)	17.97		34.90		15.38		24.57		13.27		34.98		
D (% of G)	46.90		33.27		21.69		40.03		21.57		37.36		
I (% of G)	35.13		31.83		62.93		35.40		65.16		27.66		
D/A	2.61	0.38	0.95	0.23	1.41	1.27	1.63	0.64	1.63	1.93	1.07	0.30	
I/A	1.96	0.41	0.91	0.31	4.09	2.86	1.44	0.85	4.91	4.97	0.79	0.41	

Genetic background: bbu^+u^+dd					$b^+b^+uud^+d^+$				$uuvvd^+d^+$				
Loci studied:	l^+/l,	v^+/v			l^+/l,	v^+/v			b^+/b,	l^+/l			
Year:	1965		1966		1965		1966		1965		1966		
Parameter	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	
A (% of G)	24.78		30.70		16.73		41.28		29.40		32.04		
D (% of G)	21.17		44.23		30.16		31.84		39.78		47.69		
I (% of G)	54.05		25.07		53.11		26.88		30.82		20.27		
D/A	0.85	0.72	1.44	0.24	1.80	1.11	0.77	0.22	1.35	0.35	1.49	0.24	
I/A	2.18	1.27	0.82	0.29	3.31	1.84	0.65	0.31	1.05	0.43	0.63	0.27	

confounded effect of the environmental variation is likely to conceal the real difference of a parameter from zero.

The pooled estimates of additive (A), dominance (D) and epistatic (I) effects expressed as percentages of the total genetic effects ($G = A + D + I$) of the pairs of loci are presented in Table 3. The ratios D/A and I/A in Table 3 measure average dominance and epistasis, respectively, relative to the additive effects of the genes. No consistent pattern in the relative importance of the three types of gene action can be seen from Table 3. Consider, for example, the first and the second groups, which represent the effects of the b^+/b and v^+/v loci in slightly different genetic backgrounds. In the $l^+l^+uud^+d^+$ background, dominance and epistasis were more important than additive effects in 1965, but were less in 1966. In the $l^+l^+u^+u^+dd$ background, although the relative magnitude of epistasis was much smaller in 1966, dominance and epistasis had larger contributions in both the years. Epistasis was found to be small in both years in group VI. Following general conclusions regarding the genetic structure of the quantitative inheritance of anthocyanins in *M. incana* are possible from the results presented Tables 2 and 3:

1. The reference point, Y, is greatly influenced by a slight change in the genetic background, but is less susceptible to the variation in environmental conditions. It may be mentioned here that the summer weather conditions in Tübingen in 1965 were quite different from that in 1966.

2. Dominance was most important in the genetic control of anthocyanin concentration in the flower tissues.

3. With the exception of group VI, the contribution of nonallelic interaction was considerable in 1965, but was much reduced in 1966.

4. There were marked variations between years or genetic backgrounds in the estimates of a parameter specifying a particular genetic effect at a locus.

The last conclusion suggests that the combined analyses over years and genetic backgrounds would provide additional useful information. The joint estimates of parameters over two years, given in Table 4 and summarized in Table 5, confirm the major role for dominance followed by epistasis and additive effects. These evaluations also reveal that the genetic effects vary appreciably with environmental changes from year to year. The average variations of the additive effects were smallest, whereas the interactions between years and epistatic components were most pronounced.

For two pairs of loci — b^+/b, v^+/v and l^+/l, v^+/v — it was possible to obtain average estimates of parameters over two slightly different genetic backgrounds (Table 6). The absolute values of these parameters are pooled into six major effects, and are expressed as the ratios of additive effects in Table 7. These results also indicate that dominance was the most important type of gene action for both pairs of loci. Epistasis played an important role in 1965, but had a greatly diminished role in 1966. There was least variation in additive effects with the changes in genetic backgrounds.

Discussion

In the commonly used methods of genetic analysis of quantitatively inherited characters, the total

Table 4. *The estimates of parameters as average of years 1965 and 1966. The last nine parameters in column 1 represent the variations of the parameters over the two years. The subcripts, i, and, j, refer to the first and the second locus, respectively, given at the top of each group*

Genetic background:	$l^+l^+uud^+d^+$		$l^+l^+u^+u^+dd$		$b^+b^+lld^+d^+$		bbu^+u^+dd		$b^+b^+uud^+d^+$		$uuvvd^+d^+$	
Loci studied:	b^+/b,	v^+/v	b^+/b,	v^+/v	u^+/u,	v^+/v	l^+/l,	v^+/v	l^+/l,	v^+/v	b^+/b,	l^+/l
Parameter	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.
y	365.3	6.9	955.2	24.3	469.8	14.9	751.6	21.1	455.0	12.9	311.9	8.1
a_i	85.5	6.9	74.9	24.3	30.7	14.9	128.7	21.1	5.9	12.9	71.3	8.1
a_j	20.5	6.9	7.6	24.3	40.5	14.9	66.6	21.1	61.7	12.9	32.9	8.1
d_i	131.9	9.2	105.6	37.8	36.0	18.8	191.3	40.2	42.6	16.4	130.2	10.0
d_j	58.0	11.8	24.4	38.5	51.5	19.0	47.8	30.9	57.3	17.7	17.8	11.4
aa_{ij}	23.6	6.9	−35.3	24.3	−38.9	14.9	−23.7	21.1	−17.7	12.9	− 9.4	8.1
ad_{ij}	47.7	11.8	−13.0	38.5	42.5	19.0	−10.4	30.9	48.3	17.7	2.4	11.4
da_{ij}	− 4.4	9.2	83.4	37.8	46.7	18.8	33.4	40.2	27.2	16.4	6.1	10.0
dd_{ij}	−53.4	16.5	19.3	57.7	− 7.4	24.5	19.0	56.3	−46.3	22.2	5.5	17.5
ye	35.7	6.9	94.0	24.3	1.4	14.9	51.1	21.1	13.4	12.9	20.6	8.1
a_ie	0.4	6.9	− 6.8	24.3	10.7	14.9	49.8	21.1	22.7	12.9	−18.6	8.1
a_je	− 1.5	6.9	29.6	24.3	19.6	14.9	1.3	21.1	11.5	12.9	16.6	8.1
d_ie	−45.2	9.2	−11.8	37.8	7.8	18.8	76.9	40.2	− 9.8	16.4	− 1.5	10.0
d_je	−44.5	11.8	53.3	38.5	13.5	19.0	39.0	30.9	−11.4	17.7	5.8	11.4
$aa_{ij}e$	7.9	6.9	20.7	24.3	3.1	14.9	7.6	21.1	− 5.0	12.9	11.2	8.1
$ad_{ij}e$	−15.6	11.8	17.5	38.5	−24.1	19.0	− 3.2	30.9	−48.0	17.7	11.3	11.4
$da_{ij}e$	−16.7	9.2	−131.6	37.8	−40.5	18.8	−134.3	40.2	−26.9	16.4	−27.0	10.0
$dd_{ij}e$	64.6	16.5	103.7	57.7	−12.6	24.5	− 87.8	56.3	3.3	22.2	−38.5	17.5

Table 5. *The estimates of parameters pooled into six main types of effects, summarized from the results presented in Table 4.* $Ae = |a_ie| + |a_je|$, $De = |d_ie| + |d_je|$, and $Ie = |aa_{ij}| + |ad_{ij}| + |da_{ij}| + |dd_{ij}|$

Genetic background:	$l^+l^+uud^+d^+$		$l^+l^+u^+u^+dd$		$b^+b^+lld^+d^+$		bbu^+u^+dd		$b^+b^+uud^+d^+$		$uuvvd^+d^+$	
Loci studied:	b^+/b,	v^+/v	b^+/b,	v^+/v	u^+/u,	v^+/v	l^+/l,	v^+/v	l^+/l,	v^+/v	b^+/b,	l^+/l
Parameter	Pooled Estimate	S.E.	Pooled Estimate	S.E.	Pooled Estimate	S.E.	Pooled Estimate	S.E.	Pooled Estimate	S.E.	Pooled Estimate	S.E.
A	106.0	9.8	82.5	34.4	71.2	21.1	195.3	29.8	67.6	18.2	104.2	11.5
D	189.9	14.9	130.0	53.9	87.5	26.8	239.1	50.7	99.9	24.1	148.0	15.2
I	129.1	23.3	151.0	82.7	135.5	39.2	86.5	78.7	139.5	35.2	23.4	24.5
Ae	1.9	9.8	36.4	34.4	30.3	21.2	51.1	29.8	34.2	18.2	35.2	11.5
De	89.7	14.9	65.1	35.9	21.3	26.8	115.9	50.7	21.2	24.1	7.3	11.5
Ie	104.8	23.3	273.5	82.7	80.3	39.2	232.9	78.7	83.2	35.2	88.0	24.5
D/A	1.79		1.58		1.23		1.22		1.48		1.42	
I/A	1.22		1.83		1.90		0.44		2.06		0.22	
Ae/A	0.02		0.44		0.43		0.26		0.51		0.34	
De/A	0.85		0.79		0.30		0.59		0.31		0.07	
Ie/A	0.99		3.32		1.13		1.19		1.23		0.84	

genetic variance of a segregating generation, measured as deviations from the population mean, is partitioned into various orthogonal components representing main effects and interactions. Based on the principle of maximizing the additive effects of genes, these least squares estimates of the components of genotypic variance fail to provide a correct evaluation of the relative importance of dominance and epistasis (Jana, 1971). By the use of the linear combination model described by Seyffert (1966) a straightforward evaluation of the relative importance of additive, dominance and epistatic effects of two gene loci controlling anthocyanin content in *M. incana* R. Br. was possible. The six populations used in the present investigation were ideally suited for the application of the simple additive model. Two equally frequent alleles at each locus have biochemically definable functions. Using the anthocyanin molecule as a clearly definable unit, the genes are involved in the same action chain, changing the quality of the pigment pattern and influencing the total pigment content in the cells. The quantitative phenotypes associated with the nine genotypes in these two-locus systems could be assessed from the complete 4 × 4 diallel cross in each group.

Table 6. *The combined estimates of parameters in two genetic backgrounds. The subscripts i and j refer respectively to the first and second loci under investigation*

Genetic background	1: $l^+l^+uud^+d^+$ 2: $l^+l^+u^+u^+dd$				1: $b^+b^+uud^+d^+$ 2: bbu^+u^+dd			
Loci under investigation:	b^+/b, v^+/v				l^+/l, v^+/v			
Year:	1965		1966		1965		1966	
Parameter	Extimate	S.E.	Estimate	S.E.	Estimate	S.E.	Estimate	S.E.
y	595.4	22.7	725.2	11.2	566.0	22.1	630.5	11.0
a_i	83.4	22.7	77.0	11.2	31.0	22.1	103.6	11.0
a_j	− 0.03	22.7	28.1	11.2	57.8	22.1	70.6	11.0
d_i	147.2	34.0	90.2	18.9	83.4	40.5	150.5	16.9
d_j	36.8	35.9	45.6	18.3	38.7	31.6	66.4	16.3
aa_{ij}	−20.2	22.7	8.4	11.2	−21.9	22.1	−19.5	11.0
ad_{ij}	16.4	35.0	18.3	18.3	44.9	31.6	− 6.9	16.3
da_{ij}	113.7	34.0	−34.6	18.9	111.6	40.5	−51.1	16.9
dd_{ij}	2.5	51.1	−36.6	31.5	28.6	53.8	−55.9	26.7
yb	265.8	22.7	324.1	11.2	134.4	22.1	172.1	11.0
a_ib	− 1.7	22.7	− 8.9	11.2	47.9	22.1	74.9	11.0
a_jb	−22.0	22.7	9.1	11.2	7.5	22.1	− 2.6	11.0
d_ib	−29.9	34.0	3.6	18.9	31.0	40.5	117.7	16.9
d_jb	−65.7	35.9	32.1	18.3	−30.0	31.6	20.5	16.3
$aa_{ij}b$	−35.9	22.7	−23.0	11.2	− 9.3	22.1	3.3	11.0
$ad_{ij}b$	−46.9	35.9	−13.8	18.3	−52.1	31.6	− 6.6	16.3
$da_{ij}b$	101.4	34.0	−13.6	18.9	57.6	40.5	−49.8	16.9
$dd_{ij}b$	120.5	51.1	−47.8	31.5	78.0	53.8	−14.5	26.7

Considering the extinction of 1% HCl-methanol extract of flower tissues at wave-lengths between 400 and 600 mμ as a measure of anthocyanin concentration, average phenotypic value of each genotype was estimated. With the exception of the b^+/b and v^+/v loci in the $l^+l^+uud^+d^+$ background in 1966, either single or double heterozygotes showed higher extinction peaks than any of the homozygous genotypes. The double heterozygote showed higher peak than double homozygotes in nine out of the twelve cases. When homozygous for the positive allele at the other locus, single heterozygotes usually had higher extinction values. In all cases where heterozygotes had higher extinction values than the corresponding

Table 7. *The pooled estimates of parameters classified into six major types, summarized from the results presented in Table 6.* $Ab = |a_ib| + |a_jb|$, $Db = |d_ib| + |d_jb|$ and $Ib = |aa_ib| + |ad_ib| + |da_ib| + |dd_ib|$

Genetic background	1: $l^+l^+uud^+d^+$ 2: $l^+l^+u^+u^+dd$				1: $b^+b^+uud^+d^+$ 2: bbu^+u^+dd			
Loci investigated:	b^+/b, v^+/v				l^+/l, v^+/v			
Year	1965		1966		1965		1966	
Parameter	Pooled estimate	S.E.	Pooled estimate	S.E.	Pooled estimate	S.E.	Pooled estimate	S.E.
A	83.4	32.1	105.1	15.9	88.8	31.2	174.2	15.6
D	184.0	49.4	135.8	26.3	122.1	51.4	216.9	22.6
I	152.8	74.7	97.9	42.5	207.0	77.6	133.4	37.4
Ab	23.7	32.1	18.0	15.9	55.4	31.2	77.5	15.6
Db	95.6	49.4	35.7	26.3	61.0	51.4	138.2	22.6
Ib	304.7	74.7	98.2	42.5	197.0	77.6	74.2	37.4
D/A	2.21		1.29		1.37		1.25	
I/A	1.83		0.93		2.33		0.77	
Ab/A	0.28		0.17		0.62		0.44	
Db/A	1.15		0.34		0.69		0.79	
Ib/A	3.65		0.93		2.22		0.43	

homozygotes, the estimates of dominance were relatively large, and in half of such cases, additive × dominance and dominance × dominance epistasis were considerable. Thus dominance and epistasis seem to be responsible for heterosis with regard to anthocyanin content in *M. incana* flower tissues. Whenever heterosis was the result of epistasis, it was mainly due to additive × dominance type of interaction. Heterosis at a locus was evidently not a property of the locus alone. It was the manifestation of a coordinated genetic process. The ultimate phenotype is an integrated and delicately balanced function of the entire genotype of an individual. The complexity of the genetic situation in the presence of epistasis can be suitably described in the words of Hayman (1958) as, one may be erroneous by saying that an allele *A* is dominant to *a* without a qualification such as only in the presence of the dominant allele *B*.

In all the six cases, the F_2 segregation ratio of visually recognizable flower colours shows dominance of alleles having positive contributions towards the phenotype. Quantitative genetic analysis of pigment content in the flower tissues reveals that dominance is the most important type of gene action in the production of anthocyanins in these six populations. By the aid of the paper chromatographic technique Seyffert (1960) investigated the roles of the four flower colour loci, b^+/b, l^+/l, u^+/u and v^+/v, and found that the glucosidation of the 5-position of the molecule depends on positive alleles u^+ and l^+, respectively. The subsequent glycosidations and acylations with carbocylic acids (p-coumaric, caffeic and ferulic acids) are controlled pleiotropically by u^+ and v^+, and biochemically explainable epistatic actions exist between the gene pairs, $l^+ - u^+$ and $u^+ - v^+$. On the basis of the so far available information on the biochemical functions of these genes, the importance of nonallelic gene interactions, ranging from 25% to 65% is not unexpected. The alleles at the b^+/b locus influence the oxidation in the 3′-position of the side phenyl ring of the anthocyanins. The b^+-genotypes contain cyanidin derivatives, whereas the *bb* genotype has pelargonidin derivatives. Although no interaction between b^+/b and the remaining three loci was evident from the biochemical analyses, estimates of epistasis varied from 20% to 63% in the genetic systems consisting of b^+/b and v^+/v, or b^+/b and l^+/l loci, depending on the year and the genetic background. Seyffert (1962) concluded that the nature of interaction between any two of the flower colour loci depends on the genetic background. The results presented in Tables 6 and 7 indicate considerable variation in the relative magnitude of epistasis in slightly different genetic backgrounds, whereas additive effects of the loci remained most stable.

In general, the components of genetic effect can be arranged in order of their importance as dominance > epistasis > additive. This overall order of importance was unchanged when combined analyses over two years were performed. Epistasis was found to be more important than additive effect in 1965, but its relative role was substantially reduced in the next year. The combined analyses of two years, as well as of two genetic backgrounds revealed that the order of stability of the genetic effects was additive > dominance > epistasis.

An interesting feature of the present investigation is that although we are concerned with the genetic analysis of a metrical character, we are actually dealing with the effects of a few genes in terms of some biometrically definable parameters. The genes have conspicuous major effects and their functions are not completely interchangeable. The quantitative differfences in anthocyanin content are alternative manifestations of the genetic differences. Only when these differences are taken into account, we are able to observe the variations in gene actions due to environment. It is generally believed that the continuous variation in quantitatively inherited characters is the result of the cumulative effects of a large number of genes, each with a small effect. The influence of environment on such characters is considered to be large. The character we have studied here is controlled by the so-called major genes, but shows

continuous variation. The pigment content in the flower tissues of *M. incana* is a quantitative measure of the biochemical effects of these genes involved in the biosynthesis of anthocyanins. The influence of environment on the effects of the genes is indeed considerable. Thus it seems reasonable to conclude that an appreciable environmental influence is not limited to those characters which are controlled by the polygenes. No recognizable effect of environment on the qualitatively inherited traits may be merely our inability to detect intangible differences in the intensity or quality of the phenotypes in different environments. Considering the flower colour differences in *M. incana*, we cannot rule out the possibility that environment has appreciable but yet undiscovered influence on the biochemical functions of the genes conditioning pigment formation in the plant cells. Investigations on this important aspect of gene-environment relationship at biochemical level should go a long way in formulating a more comprehensive view of the quantitative genetic systems than hitherto existing.

Zusammenfassung

In der selbstbefruchtenden Gartenpflanze *Matthiola incana* wurde eine Reihe weitgehend isogener Linien entwickelt, die sich in idealer Weise zur Untersuchung der Beiträge einzelner definierter Gene und Genkombinationen zu einem quantitativen Merkmal eignen. Das Material wurde in 6 Gruppen eingeteilt. Jede Gruppe besteht aus 4 homozygoten Eltern, die sich aus der Variation zweier Loci mit je zwei Allelen vor einem gemeinsamen genetischen Hintergrund ableiten und nach dialleler Kreuzung alle kombinatorisch möglichen Genotypen ergeben. Jeder diallele Satz stellt somit ein genetisches System mit zwei Loci dar, dessen qualitative Beiträge zur Modifikation der Anthocyanmoleküle bekannt sind und dessen quantitative Beiträge zur Gesamtkonzentration der Anthocyane gemessen werden. In diesen vereinfachten genetischen Systemen können die Phänotypenwerte der 9 Genotypen durch 9 biometrische Quantitäten beschrieben werden, von denen 8 den genetischen Effekten der variierten Loci und einer dem Beitrag des genetischen Hintergrundes zugeschrieben werden können. Anhand eines einfachen linearen Modells werden Parameter für die additiven, Dominanz- und Epistasieeffekte der einzelnen Gene aus einem Satz von 9 Gleichungen mit 9 Unbekannten direkt geschätzt. Eine Erweiterung des Modells erlaubt die Schätzung der Parameter in verschiedenen Jahren und mit wechselndem genetischem Hintergrund. Für die Ausbildung des quantitativen Merkmals „Anthocyangehalt der Blüten von *Matthiola incana*" erwiesen sich die Dominanzkomponenten als der entscheidende Typ der Genwirkung. Ferner wurde ein erheblicher Epistasieanteil geschätzt, jedoch waren diese Beiträge nicht konstant, da sie über die Jahre variierten und eine starke Abhängigkeit von der Art des genetischen Hintergrundes zeigten. Der relative Anteil der additiven Komponenten erwies sich dagegen zwar als gering, jedoch sehr stabil. Beobachtete Heterosiseffekte müssen zum Teil den Dominanzkomponenten, zum Teil der Interaktion zwischen additiven und Dominanzkomponenten zugeschrieben werden.

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Dr. S. Jana
Crop Science Department
University of Saskatchewan
Saskatoon, Saskatchewan (Canada)

Prof. Dr. W. Seyffert
Institut für Biologie der Universität Tübingen
Lehrstuhl für Genetik
Auf der Morgenstelle 1
D-74 Tübingen (Germany/BRD)