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Genetical Analysis of Components of Overall Plant Shape

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Summary. The genetical control of six characters, which were taken as jointly reflecting the overall shape of the plant, was analysed using four true-breeding lines of *Nicotiana rustica*. F_1, F_2 and first backcross generations were raised from all of the possible pairwise combinations between the lines. The particular relationships between the lines provided a basis for the analysis which was an extension of the normal model fitting procedures described by Mather and Jinks (1971).

The first step in the analysis was to test whether the allelic differences present between the inbred lines P_1 and P_5 had been maintained in the two lines B_2 and B_{35}, derived from an earlier cross between the former. If the allelic differences between P_1 and P_5 were present between B_2 and B_{35}, it was possible to proceed straightforwardly by fitting a model consisting of m, two symmetrical [d]'s and the relevant non-additive parameters. If B_2 and B_{35} were homozygous for the same alleles at loci by which P_1 and P_5 differed, in other words if significant asymmetry in the gene distributions was present, the model had to be extended to cover the effects of such genes.

All six characters investigated were shown to be subject to genetical variation. From the composition of the genetical models that were necessary to account for the observations from each of the characters, it was inferred that they should be amenable to at least partially independent adjustment by selection.

Key words: Genetical analysis – Plant shape – *Nicotiana rustica*

Introduction

While different plants of *Nicotiana rustica* or of any other species may all have a general similarity of structure, simple observation of any character, such as leaf size, floral dimensions etc., reveals the presence of variation. Such variation is also clearly seen in the overall shape of the plant and must be taken here as indicative of differences in the basic pattern of development of the plants. Among inbred lines grown in Birmingham, however, there is only one major gene difference (normal v mophead) affecting overall plant shape which is readily discernible by its segregation in crosses (Mather and Vines 1952). Between plants homozygous for the normal gene there are no other sharp differences in overall shape, but they are clearly not all alike. The aim of the present experiment was to investigate the genetical control of such continuous variation between wild type lines for overall shape of the plant.

Although variation in plant shape can easily be assessed qualitatively, it is a complex character to quantify. It was necessary therefore, to examine various aspects pertaining to plant shape (Table 1). All the plants raised in the experiment were scored at the end of the growing season. Measurements were taken in millimetres of the overall height of the plant and of side branch lengths at successive

Table 1. The Six Characters taken as Reflecting Overall Shape of the Plant

Abbreviation	Character
T.N.N.	The total number of nodes produced by the plant
T.F.B.N.	The total number of branches bearing floral structures
F.F.B.N.	The node number of the first branch bearing floral structures
M.F.B.L.	The mean branch length of those branches bearing floral structures
F.H.	The overall height of the plant at the end of the growing season
Regression	The slope of the regression of flowering branch length on node number

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nodes, node 1 being the lowest. At the same time note was made of whether a branch carried, or had carried, any floral structures.

Characteristically the lowest nodes produce very small branches, as can be seen from the diagrammatic representation in Fig. 1, and their length progressively increases to a maximum, which occurs at the first flowering branch. Thereafter the branch length gradually diminishes, though all bear flowering structures. The shape of the plant could possibly be described by two regressions of branch length on node number. The first regression would relate to branches below the first flowering branch and the second would cover the branches above. In this study only the latter regression of flowering branch length on node number is reported since it covers a larger proportion of the plant. An example of fitting a linear regression to the first eighteen branches of the four true-breeding parent lines is given in Table 2.

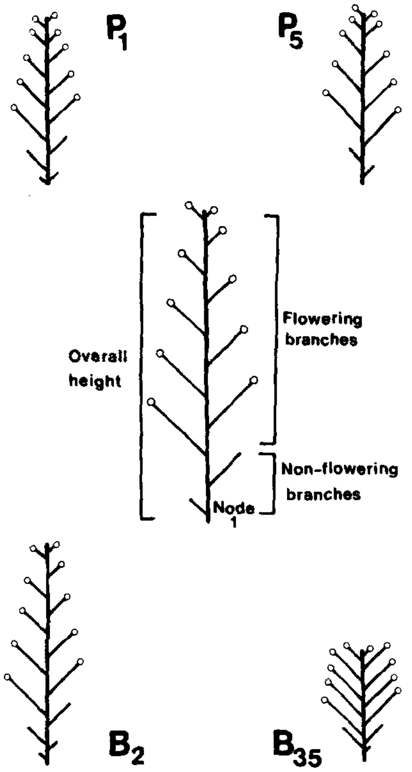

Fig. 1. The Centre is a Diagramatic Representation of a *Nicotiana rustica* showing the Principle Features of the Characters summarised in Table 1. The Corners show the Four True-breeding Lines used in the Investigation

Table 2. An Example of Applying Linear Regressions to the First Eighteen Flowering Branches of the Four True-breeding Lines

Inbred	$\hat{b}$	Regression M.S.	Remainder M.S.
P_1	−26.463	678,599.5	2,214.4
P_5	−31.478	960,134.6	1,506.9
B_2	−23.756	546,842.6	1,988.5
B_{35}	−20.596	411,061.1	2,038.8

From the table it can be seen that the linear component accounts for a very large proportion of the variation in flowering branch length. Furthermore, when higher order polynomials were fitted, no significant reduction in the residual mean square was obtained, indicating that the remainder mean square measures random fluctuations about the regression lines and hence must contain a component that reflects developmental instability (Paxman 1956) as well as differences attributable to environmental variation. This aspect will not be discussed further here. For these crosses the linear regression coefficient can be taken as a sufficient parameter of plant shape and for simplicity has been termed 'Regression' in this paper.

'Regression' together with the other aspects investigated make up the six characters which have already been summarised in Table 1.

The Experiment

Design

Measurements were made on these characters in an experiment carried out in 1975 on families derived from four true-breeding lines, namely P_1, P_5, B_2 and B_{35}. The last two were inbred lines obtained from an earlier cross between P_1 and P_5 (Jayasekara and Jinks 1976). The four lines were crossed in all six possible pairwise combinations. From each F_1, an F_2 and first backcrosses (Bx) were raised, including all reciprocal families, as shown below for one of the pairwise combinations P_1 and P_5.

F_1	F_2	Bx_1	Bx_5
$P_1 \times P_5$	$(P_1 \times P_5) \times (P_1 \times P_5)$ $(P_1 \times P_5) \times (P_5 \times P_1)$	$P_1 \times (P_1 \times P_5)$ $(P_1 \times P_5) \times P_1$	$P_5 \times (P_1 \times P_5)$ $(P_1 \times P_5) \times P_5$
$P_5 \times P_1$	$(P_5 \times P_1) \times (P_1 \times P_5)$ $(P_5 \times P_1) \times (P_5 \times P_1)$	$P_1 \times (P_5 \times P_1)$ $(P_5 \times P_1) \times P_1$	$P_5 \times (P_5 \times P_1)$ $(P_5 \times P_1) \times P_5$

Each cross thus provides 14 families; 14 x 6 = 84 plus the four parental lines = 88 families when all 6 crosses are taken into account. Ten plants were raised from each family giving 880 plants in total.

Such an experiment yields data from which models can be fitted to the means of the generations from each cross. Thus the genetical variation of these characters, taken as reflecting plant shape, can be analysed using the familiar techniques of biometrical genetics. The analyses can be carried out for the six crosses separately using weighted least squares and the models tested for adequacy in the usual way as described by Mather and Jinks (1971). In this experiment the inbred lines are inter-related and each line is crossed to the other three, it is therefore more informative to fit a common model to all the families simultaneously using an approach similar to that of Snape, Law and Worland (1976).

Parameters

We can begin by considering the four true-breeding parent lines, two of which, B_2 and B_{35}, were derived from a cross between the other two lines, P_1 and P_5, as we have already noted. It follows that B_2 and B_{35} cannot differ at loci by which P_1 and P_5 were identical, apart from the trivial effects that mutation may have produced. Thus the four parents may display three types of distribution of alleles at a locus. The first is shown by loci at which P_1 and P_5, and hence B_2 and B_{35}, have identical alleles. The effects of such loci cannot provide genetical information in this experiment and they will merely contribute to the overall mean of the experiment: i.e., their effects will simply be reflected in the familiar biometrical parameter m.

The two other types of distribution are concerned with loci at which P_1 and P_5 have different alleles. The first of these is applicable where the derived lines, B_2 and B_{35}, have become homozygous for different alleles at a locus and hence have maintained the difference between the original parents P_1 and P_5. With this type of distribution there are two obvious possibilities. One is where B_2 has become homozygous for the allele carried by P_1, and B_{35} for the allele from P_5. The additive effects of such loci will be designated $[d_1]$ (the square brackets indicating summation over all relevant loci). The other possibility is the reverse situation where B_2 carries the allele from P_5, and B_{35} that from P_1. The effects of which can be represented by $[d_2]$.

The remaining type of distribution is shown by loci at which both B_2 and B_{35} have become homozygous for the same allele, both lines thus resembling the same parent at such a locus. In this situation the alleles can be said to show an asymmetrical distribution. As with the previous distribution there are two possibilities: One being where B_2 and B_{35} have become homozygous for the allele present in P_1, whose summed effects can be shown as $[d_3]$; the other is when the allele from P_5 has been fixed, the combined effects of all such loci being represented by $[d_3]'$.

We have already noted that the first type of distribution, where all four lines carry the same allele, will not provide information of any analytical interest because of their constancy in this experiment. With the other two types of distribution it should be emphasized that although alleles displaying particular distributions will have their effects combined to give $[d_1]$, $[d_2]$, $[d_3]$ or $[d_3]'$, as is indicated by the square brackets, this does not imply a special physiological or mechanical relationship between such grouped loci but simply reflects the distribution between these four particular lines. This is clear when it is remembered that these distributions are the only ones possible between these four lines and however many genes are involved and whatever their effects, they must fall into one of these categories.

Analysis

Having considered the types of distributions of alleles, we must now turn to the estimation of their effects. With four parental lines there are three degrees of freedom for differences between them. Four parameters interest us and therefore it is clear that we cannot estimate all of them independently of one another. To see what can be obtained from partitioning the 3 df available, it is easiest to consider an example.

In the example given below, the biometrical expectations for the four lines are given together with three standard orthogonal comparisons for estimating the differences among them.

Inbred line	Biometrical Model		Comparison		
		Mean	A	B	C
P_1	$m + [d_1] - [d_2] + [d_3] - [d_3]'$	1	1	−1	−1
P_5	$m - [d_1] + [d_2] - [d_3] + [d_3]'$	1	−1	1	−1
B_2	$m + [d_1] + [d_2] + [d_3] + [d_3]'$	1	1	1	1
B_{35}	$m - [d_1] - [d_2] + [d_3] + [d_3]'$	1	−1	−1	1

In this example the estimates we obtain are:

$$\text{Mean} = m + \tfrac{1}{2}[d_3] + \tfrac{1}{2}[d_3]'$$

$$A = [d_1] + \tfrac{1}{2}[d_3] - \tfrac{1}{2}[d_3]'$$

$$B = [d_2] - \tfrac{1}{2}[d_3] + \tfrac{1}{2}[d_3]'$$

$$C = \tfrac{1}{2}[d_3] + \tfrac{1}{2}[d_3]'$$

It can be seen that comparisons A and B, although basically measuring $[d_1]$ and $[d_2]$ respectively, are confounded with effects due to the asymmetrically distributed genes. If we combine the estimates from A and B, we obtain $[d_1] + [d_2]$. In other words the effects are due solely to symmetrical genes. Comparison C measures effects due only to asymmetrical genes. We can therefore obtain the combined effects of, on the one hand, the symmetrical genes and, on the other, the asymmetrical genes but we cannot obtain any further separation of effects if all are present. If however, comparison C proves non-significant, thus showing no indication of asymmetrically distributed genes, then comparisons A and B will give direct estimates of $[d_1]$ and $[d_2]$ respectively and we will have separated the effects due to the two sorts of symmetrically distributed genes.

Two points should be noted. First, in this example, P_1 and P_5 show dispersion between the genes with different types of distribution from which we obtain $[d_1] + [d_2]$ and $\frac{1}{2}[d_3] + \frac{1}{2}[d_3]'$. By choosing another example, P_1 and P_5 could show complete association, in which case we would get $[d_1] - [d_2]$ and $\frac{1}{2}[d_3] - \frac{1}{2}[d_3]'$: In other words we would estimate the two differences instead of the two sums. Since P_1 and P_5 can display varying degrees of association and dispersion, different combinations of sums and differences can arise. Thus, in general the summation of comparisons A and B does not necessarily give rise to the sum of $[d_1]$ and $[d_2]$ but merely some combination of them. Similarly comparison C will consist of effects due to $[d_3]$ and $[d_3]'$ but the exact combination of them will be unknown. Nevertheless if comparison C is non-significant we will only be misled in assuming the absence of asymmetrically distributed genes in the rare event of $[d_3]$ and $[d_3]'$ cancelling one another's effects. If such an unusual event occurs, $[d_3]$ and $[d_3]'$ will cancel out in C but will reinforce one another in A and B and lead to erroneous estimates of $[d_1]$ and $[d_2]$.

The second point is that although we can reasonably assume the absence of asymmetrically distributed genes if comparison C turns out to be non-significant, we cannot automatically infer their presence from a significant estimate associated with C. This is so because we have ignored the possibility of non-allelic interactions being present. If $[d_3]$ and $[d_3]'$ are absent but interactions are present between $[d_1]$ and $[d_2]$, comparison C may prove significant, but in this case due solely to the interactions. A significant effect stemming from comparison C could therefore be due to asymmetrically distributed genes, non-allelic interaction or a combination of both.

Utilising only the four parental lines we have no method of separating the additive effects of asymmetrical genes and non-allelic interaction. We cannot tell, therefore, whether comparisons A and B, which could provide estimates of $[d_1]$ and $[d_2]$, are being influenced by the effects of asymmetrically distributed genes. If we raise the F_1's and F_2's from crosses between P_1 and P_5 on the one hand and B_2 and B_{35} on the other, then the means of the equivalent generations have identical expectations in the two crosses unless asymmetrical gene distributions are present (Jayasekara and Jinks 1976). This relationship will hold whether or not non-allelic interactions (which with F_1's and F_2's will be of the [l] type) are present, as can be seen from inspection of the relevant generations given in Table 3. The test of the difference between $(\bar{F}_1 + \bar{F}_2)$ from P_1 by P_5 and $(\bar{F}_1 + \bar{F}_2)$ from B_2 by B_{35} against the appropriate standard error will provide an unambiguous indication of asymmetry in the gene distributions.

The analysis using orthogonal functions becomes impossible to apply when we wish to utilize all the data concerning a character obtained in this experiment. Also, as we have already seen, when asymmetrical gene distributions are present, the estimates of the [d]'s are correlated with each other and with any interactions that are present. A much more satisfactory approach is provided by the use of weighted least squares described by Mather and Jinks (1971) which permits the analysis of all the data simultaneously as well as allowing for the correlations between estimates.

The genetical expectations for the means of the different sorts of families raised in this experiment are set out in Table 3 which includes parameters to describe the non-additive components of variation. These latter parameters are set out fully for the components related to $[d_1]$ and $[d_2]$ on the left of the table. The right side of the table is confined to $[d_3]$ and $[d_3]'$ and their relevant [h]'s, but the other non-additive components could easily be written down.

Before actually applying the analysis to the data obtained in the experiment, two points should be made. First, when considering a pair of lines it is customary to assign to the larger parent + [d], and to the smaller – [d]. With four lines, although it is possible to achieve this for all the [d]'s, it is much simpler to fit the parameters as they stand in Table 3 and then, from the signs of the estimates obtained, ascribe to each [d] any necessary alteration of sign. Secondly, even applying weighted least squares to the data from all types of family, it is not possible to estimate all four [d]'s simultaneously. We have already seen, however, that $[d_3]$ and $[d_3]'$ tend to combine in their estimation and therefore it seems sensible to treat them as one in the analysis. We can achieve this by specifying either $[d_3]$ or $[d_3]'$ in which case, however, none of the estimates of additive genetic effects will be simple reflections of $[d_1]$, $[d_2]$, $[d_3]$ or $[d_3]'$ as defined. They will in fact all contain effects due to the asymmetrically distributed genes left undefined. It is better therefore to test for the presence of asymmetry using the appropriate F_1's and F_2's as has already been described, and on the outcome of this, include $[d_3]$ or $[d_3]'$ only if its presence proves necessary. If asymmetry is in fact indicated, the decision between $[d_3]$ and $[d_3]'$ can be made on which of the two parental line means, P_1 or P_5, is closer to the overall mean of the derived lines, B_2 and B_{35}.

Results

The data for all six characters summarised in Table 1, are set out in Table 4. It will be seen that reciprocal crosses

Table 3. Genetical Expectations for the Means of the Generations Raised from Crossing the Four Inbred Lines in all Possible Pairwise Combinations

Cross	Family	m	$[d_1]$	$[d_2]$	$[h_1]$	$[h_2]$	$[i_{11}]$	$[i_{12}]$	$[i_{22}]$	$[j_{11}]$	$[j_{12}]$	$[j_{21}]$	$[j_{22}]$	$[l_{11}]$	$[l_{12}]$	$[l_{22}]$	$[d_3]$	$[h_3]$	$[d_3]'$	$[h_3]'$
Parents	P_1	1	1	−1	.	.	1	−1	1	.	.	.	.	.	.	.	1	.	−1	.
	P_5	1	−1	1	.	.	1	−1	1	.	.	.	.	.	.	.	−1	.	1	.
	B_2	1	1	1	.	.	1	1	1	.	.	.	.	.	.	.	1	.	1	.
	B_{35}	1	−1	−1	.	.	1	1	1	.	.	.	.	.	.	.	1	.	1	.
P_1 and P_5	F_1	1	.	.	1	1	.	.	.	.	.	.	.	1	1	1	.	1	.	1
	F_2	1	.	.	½	½	.	.	.	.	.	.	.	¼	¼	¼	.	½	.	½
	Bx_1	1	½	−½	½	½	¼	−¼	¼	¼	¼	−¼	−¼	¼	¼	¼	½	½	−½	½
	Bx_5	1	−½	½	½	½	¼	−¼	¼	−¼	−¼	¼	¼	¼	¼	¼	−½	½	½	½
P_1 and B_2	F_1	1	1	.	.	1	1	.	.	.	1	.	.	.	.	1	1	.	.	1
	F_2	1	1	.	.	½	1	.	.	.	½	.	.	.	.	¼	1	.	.	½
	Bx_1	1	1	−½	.	½	1	−½	¼	.	½	.	−¼	.	.	¼	1	.	−½	½
	Bx_2	1	1	½	.	½	1	½	¼	.	½	.	¼	.	.	¼	1	.	½	½
P_1 and B_{35}	F_1	1	.	−1	1	.	.	.	1	.	.	−1	.	1	.	.	1	.	.	1
	F_2	1	.	−1	½	.	.	.	1	.	.	−½	.	¼	.	.	1	.	.	½
	Bx_1	1	½	−1	½	.	¼	−½	1	¼	.	−½	.	¼	.	.	1	.	−½	½
	Bx_{35}	1	−½	−1	½	.	¼	½	1	−¼	.	−½	.	¼	.	.	1	.	½	½
P_5 and B_2	F_1	1	.	1	1	.	.	.	1	.	.	1	.	1	.	.	.	1	1	.
	F_2	1	.	1	½	.	.	.	1	.	.	½	.	¼	.	.	.	½	1	.
	Bx_5	1	−½	1	½	.	¼	−½	1	−¼	.	½	.	¼	.	.	−½	½	1	.
	Bx_2	1	½	1	½	.	¼	½	1	¼	.	½	.	¼	.	.	½	½	1	.
P_5 and B_{35}	F_1	1	−1	.	.	1	1	.	.	.	−1	.	.	.	.	1	.	1	1	.
	F_2	1	−1	.	.	½	1	.	.	.	−½	.	.	.	.	¼	.	½	1	.
	Bx_5	1	−1	½	.	½	1	−½	¼	.	−½	.	¼	.	.	¼	−½	½	1	.
	Bx_{35}	1	−1	−½	.	½	1	½	¼	.	−½	.	−¼	.	.	¼	½	½	1	.
B_2 and B_{35}	F_1	1	.	.	1	1	.	.	.	.	.	.	.	1	1	1	1	.	1	.
	F_2	1	.	.	½	½	.	.	.	.	.	.	.	¼	¼	¼	1	.	1	.
	Bx_2	1	½	½	½	½	¼	¼	¼	¼	¼	¼	¼	¼	¼	¼	1	.	1	.
	Bx_{35}	1	−½	−½	½	½	¼	¼	¼	−¼	−¼	−¼	−¼	¼	¼	¼	1	.	1	.

have been pooled within generations since no evidence of any reciprocal differences was found for any of the characters studied. In Table 4 the inbred line means are based on 10 plants, the F_1 means on 20 plants while each F_2 and Bx mean depends on 40 observations.

The analysis employing weighted least squares was applied separately to all six characters. The simplest genetical model to describe adequately each of the characters is set out in Table 5 in terms of the significant [d] parameters. In this table, the significant estimates of the parameters are also given together with the χ^2's testing the adequacy of the models.

The analyses proceeded straightforwardly and only two of the characters warrant further comment. The first of these is F.H. where our analysis shows that between P_1 and P_5 the genes are predominantly dispersed but that during the inbreeding to produce B_2 and B_{35} they have tended to become associated. This is of interest since it agrees with the expectations for this character in that B_2 and B_{35} were selected as the tallest and shortest of 82 inbred lines described by Perkins and Jinks (1973) and agrees with the later analysis of these four lines by Jayasekara and Jinks (1976). The present analysis is also concordant with earlier investigations of this character in showing significant [i] type interaction to be operative (Jinks, Perkins and Pooni, 1973).

The other character which requires comment is Regression, where the basic data consist of linear regression coefficients. First, it should be noted that when tested against the remainder mean square, significant heterogeneity was detected between the regressions of plants belonging to a single family. Such heterogeneity was used to provide the standard errors, as given in Table 4, and therefore the weights used in the model fitting procedure. Secondly it should be noted that the basic observations on this character are all negative, making m negative. To be

Table 4. The Means and Standard Deviations of the Families Raised in the Experiment for all Six Characters Studied

Cross	Family	TNN	TFBN	FFBN	MFBL	FH	Regression
Parents	P_1	25.5 ± 0.7	15.2 ± 0.7	11.1 ± 0.7	244.6 ± 17.1	1002.0 ± 38.0	−29.8 ± 2.9
	P_5	24.3 ± 0.6	17.9 ± 0.7	7.4 ± 0.9	283.2 ± 12.8	1041.1 ± 65.7	−31.2 ± 2.0
	B_2	28.6 ± 1.1	17.6 ± 0.8	11.9 ± 0.5	254.4 ± 17.4	1421.0 ± 56.3	−24.0 ± 2.6
	B_{35}	24.3 ± 1.3	16.7 ± 1.0	8.6 ± 1.0	255.4 ± 16.3	771.0 ± 30.8	−21.42 ± 1.7
P_1 and P_5	F_1	27.2 ± 0.5	19.3 ± 0.5	8.9 ± 0.5	307.8 ± 12.8	1218.7 ± 36.7	−30.3 ± 2.3
	F_2	26.8 ± 0.5	18.4 ± 0.4	9.4 ± 0.4	284.4 ± 10.4	1079.5 ± 30.8	−29.1 ± 1.2
	Bx_1	26.9 ± 0.5	16.9 ± 0.4	10.9 ± 0.5	254.6 ± 7.1	1078.6 ± 25.0	−27.2 ± 1.7
	Bx_5	26.0 ± 0.4	19.1 ± 0.3	7.9 ± 0.3	289.6 ± 6.8	1054.5 ± 26.3	−28.5 ± 0.9
P_1 and B_2	F_1	27.6 ± 0.9	15.8 ± 0.7	12.6 ± 0.8	268.4 ± 13.6	1320.0 ± 26.3	−34.7 ± 3.5
	F_2	27.9 ± 0.5	17.6 ± 0.4	11.3 ± 0.4	269.5 ± 6.5	1264.0 ± 24.9	−28.6 ± 1.2
	Bx_1	27.5 ± 0.4	16.6 ± 0.4	11.9 ± 0.4	262.4 ± 6.3	1157.8 ± 22.8	−30.0 ± 1.4
	Bx_2	28.6 ± 0.6	17.2 ± 0.5	12.5 ± 0.4	268.4 ± 8.6	1361.8 ± 23.2	−29.0 ± 1.4
P_1 and B_{35}	F_1	27.2 ± 0.5	18.7 ± 0.5	9.5 ± 0.4	277.3 ± 8.3	1037.5 ± 20.5	−26.1 ± 1.2
	F_2	25.8 ± 0.3	17.9 ± 0.4	8.9 ± 0.3	275.9 ± 6.5	940.2 ± 20.2	−26.1 ± 1.0
	Bx_1	27.4 ± 0.4	16.9 ± 0.4	11.5 ± 0.4	253.9 ± 7.6	1030.9 ± 20.4	−24.9 ± 1.1
	Bx_{35}	25.4 ± 0.4	17.9 ± 0.4	8.5 ± 0.4	256.4 ± 6.9	861.4 ± 17.5	−21.6 ± 1.0
P_5 and B_2	F_1	28.6 ± 0.7	19.4 ± 0.5	10.1 ± 0.9	284.0 ± 12.4	1325.5 ± 29.0	−29.7 ± 1.2
	F_2	28.6 ± 0.7	19.7 ± 0.5	9.9 ± 0.4	266.5 ± 10.3	1222.2 ± 36.2	−27.1 ± 1.3
	Bx_5	27.2 ± 0.5	19.4 ± 0.5	8.7 ± 0.3	273.5 ± 7.8	1139.9 ± 32.3	−28.5 ± 1.0
	Bx_2	28.3 ± 0.7	17.6 ± 0.5	11.6 ± 0.5	275.7 ± 9.5	1347.1 ± 25.0	−30.8 ± 1.7
P_5 and B_{35}	F_1	25.3 ± 0.7	18.4 ± 0.6	8.0 ± 0.5	270.2 ± 10.1	943.8 ± 34.0	−27.9 ± 1.5
	F_2	24.6 ± 0.4	18.9 ± 0.4	6.7 ± 0.3	269.8 ± 9.5	851.8 ± 17.4	−28.3 ± 1.2
	Bx_5	25.7 ± 0.5	19.4 ± 0.5	7.3 ± 0.4	275.2 ± 8.3	944.5 ± 23.7	−28.1 ± 0.8
	Bx_{35}	24.9 ± 0.5	18.0 ± 0.4	7.8 ± 0.4	240.7 ± 8.4	805.6 ± 17.8	−21.4 ± 0.9
B_2 and B_{35}	F_1	27.8 ± 0.8	19.4 ± 0.6	9.4 ± 0.5	299.8 ± 9.5	1139.0 ± 36.4	−27.4 ± 0.9
	F_2	26.9 ± 0.4	18.2 ± 0.4	9.5 ± 0.5	279.2 ± 8.8	1081.5 ± 26.5	−25.5 ± 1.2
	Bx_2	28.8 ± 0.4	18.5 ± 0.4	11.2 ± 0.4	295.3 ± 8.5	1355.9 ± 22.3	−30.1 ± 1.0
	Bx_{35}	26.8 ± 0.4	18.2 ± 0.4	9.1 ± 0.5	272.1 ± 7.8	973.9 ± 23.9	−23.6 ± 1.0

TNN – Total node number. TFBN – Total flowering branch number. FFBN – First flowering branch number. MFBL – Mean flowering branch length. FH – Final height. Regression – The linear regression coefficient of flowering branch length on node number.

Table 5. The Specification of the Models for each of the Six Characters: Top part of the table is in terms of the significant [d] parameters; Lower portion of the table gives the estimates of the significant parameters obtained and the χ^2 testing the goodness of fit of observed with expected

	T.N.N.			T.F.B.N.			F.F.B.N.		M.F.B.L.		F.H.			Regression		
	m	$[d_1]$	$[d_2]$	m	$[d_1]$	$[d_2]$	m	$[d_1]$	m	$[d_2]$	m	$[d_1]$	$[d_2]$	m	$[d_1]$	$[d_3]$
P_1	1	1	−1	1	−1	−1	1	1	1	−1	1	1	−1	1	1	−1
P_5	1	−1	1	1	1	1	1	−1	1	1	1	−1	1	1	−1	1
B_2	1	1	1	1	−1	1	1	1	1	1	1	1	1	1	1	−1
B_{35}	1	−1	−1	1	1	−1	1	−1	1	−1	1	−1	−1	1	−1	−1
m	26.301 ± 0.152			17.662 ± 0.134			9.619 ± 0.081		256.766 ± 3.479		984.019 ± 27.845			−28.513 ± 0.423		
$[d_1]$	1.490 ± 0.148			0.862 ± 0.130			2.349 ± 0.19		–		196.626 ± 6.971			−4.081 ± 0.436		
$[d_2]$	0.787 ± 0.140			0.735 ± 0.134			–		9.475 ± 2.472		152.779 ± 7.386			–		
$[d_3]$	–			–			–		–		–			−3.949 ± 0.443		
$[h_1]$	1.395 ± 0.312			1.308 ± 0.275			–		26.446 ± 5.341		189.570 ± 38.044			–		
$[h_2]$	–			–			–		16.189 ± 5.488		35.710 ± 17.355			−2.280 ± 0.737		
$[i_{11}]$	–			–			–		–		67.433 ± 30.003			–		
$[i_{12}]$	–			–			–		–		48.048 ± 12.376			–		
χ^2	32.07 df. 24			28.05 df. 24			38.61 df. 26		30.02 df. 24		29.56 df. 21			35.14 df. 24		
P	10-20%			20-30%			5-10%		10-20%		10-20%			5-10%		

consistent we have made the significant [d]'s negative also. The last point concerning this character, which makes it unique among the six investigated, is that significant asymmetry in the gene distribution was detected which required $[d_3]$ to be included in its genetical specification, as can be seen from inspection of Table 5.

Discussion

It is clear from the analyses that, perhaps not surprisingly, all six characters display significant genetical variation. What can now be asked is whether the six characters are controlled by the same genes or whether they are subject to at least partially separate adjustment by selection. It will be remembered that the different [d]'s imply different distributions of the alleles. Therefore, effects associated with the different [d]'s cannot spring from the same genes. Thus if we observe variation in the pattern of any of the [d]'s between the characters it must imply at least partially separate genetic control. This will in fact hold true even in the presence of asymmetrically distributed genes which as we have seen affect the interpretation that can be placed on estimates of the [d]'s.

Considering the genetical descriptions as given in Table 5 it is clear that the majority of the characters require different specifications to fit the observed results. The exceptions are perhaps F.H. and T.N.N., which at least require the same [d]'s, but even here F.H. has certain significant features (e.g. non-allelic interactions) which T.N.N. does not. This in itself implies a difference in action of the genes for the two characters even if exactly the same genes were involved. The need to specify different patterns of parameters for the various characters indicates that the inheritance of the six characters is at least to some degree different and therefore the characters should be capable of being adjusted independently, at least in part, by selection.

One further feature of the results should also be noted, namely that only one of the six characters shows evidence of asymmetry in the distribution of its genes. However, one of the characters, F.H., is not expected to show asymmetry since B_2 and B_{35} were the two extremes for this character from the 82 inbred lines produced. They also were the two extremes for flowering time. Being opposite extremes, it is likely that allelic differences between P_1 and P_5 affecting this character, have been retained between B_2 and B_{35}, but with their distributions altered to give complete association. Nevertheless, leaving aside F.H., only one of the five remaining characters showed detectable asymmetry whereas it might be expected that the same allele would be fixed in both lines by chance at half the loci affecting these characters. Various reasons could be suggested to explain the apparent paucity of asymmetrically distributed genes. The most likely explanation may lie with the analytical procedure in that asymmetrical gene effects are only included in the model if our initial tests indicate their necessity. Each test is based on only 120 plants from the experiment and therefore relatively large effects will be required for significant differences to be detected. In this way the analysis is tending to be biased away from showing the presence of asymmetrical gene distributions; this could possibly explain the apparently low frequency of such gene distributions.

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