

THE NATURE OF THE INHERITANCE OF PERMANENTLY INDUCED
CHANGES IN *NICOTIANA RUSTICA*

III. F_5 GENERATION FOR FIVE CHARACTERS

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SUMMARY

Characters measured on the F_5 generation of two crosses, $p_3 \times nil_3$ and $nk_2 \times nil_1$ between conditioned lines of *Nicotiana rustica*, were analysed to study (1) the persistence of the segregation between F_1 individuals and (2) the conventional segregation in the later generations. Significant F_1 segregation was found in four characters in the cross $nk_2 \times nil_1$, height at flowering time, the length of the branch in the axil of the eighth leaf at flowering time, and the length and width of the eighth leaf, while it was nearly significant for the height of the eighth leaf at flowering time. This item was not significant for any character in the $p_3 \times nil_3$ cross. A standard biometrical genetical model was found to fit in the majority of cases confirming conventional segregation at the F_2 , F_3 and F_4 levels. Principle components analysis extracted three principle components from the seven characters measured in the F_5 generation. The three components were the same for each cross and this information together with estimates of the numbers of effective factors segregating in these crosses suggested that for both crosses the parental lines differed by about 13 effective factors.

1. INTRODUCTION

In an earlier paper Eglington and Moore (1973) have described the analysis of the effects of segregation in the F_1 and later generations, as seen in the F_4 and F_5 generations, of two selected crosses, $p_3 \times nil_3$ and $nk_2 \times nil_1$, between pairs of conditioned lines of *Nicotiana rustica*. These analyses were carried out on the characters final height and flowering time. Additional characters were also measured in the F_5 generation, two of which, height at flowering time and width of the eighth leaf, were referred to in the previous paper as exhibiting segregation between F_1 groups of plants. These two characters and three others measured on the F_5 generation will be examined here.

2. MATERIALS

The origin of the F_5 generation of the crosses $p_3 \times nil_3$ and $nk_2 \times nil_1$ and the experimental design have been described by Eglington and Moore (1973, Sections 1 and 2).

3. RESULTS

The F_5 's of the two crosses $p_3 \times nil_3$ and $nk_2 \times nil_1$ have been analysed separately because they differ significantly from each other both in the expression of several characters and in the presence or absence of F_1 segregation in intermediate generations.

(i) F_1 segregation

The analyses of variance of the individual crosses are presented in table 1 for the following five characters: (1) height at flowering time, (2) height of the eighth leaf at flowering time, (3) the length of the branch in the axil

TABLE 1

Analysis of variance of family means for the F_5 generation of the $p_3 \times nil_3$ and $nk_3 \times nil_1$ crosses grown in 1971

| Item | $p_3 \times nil_3$ | | | | $nk_3 \times nil_1$ | | | | |
|------------------------------------|--------------------|--------|---------------|------|---------------------|--------|---------------|------|--|
| | d.f. | M.S. | Test | P | d.f. | M.S. | Test | P | |
| Character 1 | | | | | | | | | |
| 1. F_1 groups (F_1) | 4 | 27.21 | V.R. (2) | n.s. | 4 | 248.91 | V.R. (3) | * | |
| 2. F_2 groups in F_1 (F_2) | 4 | 163.42 | V.R. (4) | ** | 5 | 48.14 | V.R. (3) | n.s. | |
| 3. F_3 groups in F_2 (F_3) | 9 | 22.76 | † | — | 10 | 42.15 | V.R. (4) | ** | |
| 4. F_4 groups in F_3 (F_4) | 18 | 13.75 | χ^2 (10) | *** | 20 | 11.49 | χ^2 (10) | *** | |
| 5. Blocks (B) | 1 | 177.46 | V.R. (8) | *** | 1 | 360.66 | χ^2 (10) | *** | |
| 6. $B \times F_1$ | 4 | 0.96 | V.R. (8) | n.s. | 4 | 7.58 | χ^2 (10) | n.s. | |
| 7. $B \times F_2$ | 4 | 3.99 | V.R. (8) | n.s. | 5 | 2.19 | χ^2 (10) | n.s. | |
| 8. $B \times F_3$ | 9 | 6.87 | χ^2 (10) | ** | 10 | 8.51 | χ^2 (10) | n.s. | |
| 9. $B \times F_4$ | 18 | 4.33 | χ^2 (10) | n.s. | 20 | 4.20 | χ^2 (10) | n.s. | |
| 10. Replicates | 602 | 3.03 | | | 707 | 4.72 | | | |
| Character 2 | | | | | | | | | |
| 1. F_1 groups (F_1) | 4 | 13.16 | V.R. (3) | n.s. | 4 | 52.39 | V.R. (3) | n.s. | |
| 2. F_2 groups in F_1 (F_2) | 4 | 9.26 | V.R. (3) | n.s. | 5 | 29.81 | V.R. (3) | n.s. | |
| 3. F_3 groups in F_2 (F_3) | 9 | 11.63 | χ^2 (10) | *** | 10 | 15.86 | V.R. (4) | ** | |
| 4. F_4 groups in F_3 (F_4) | 18 | 1.71 | χ^2 (10) | n.s. | 20 | 3.40 | χ^2 (10) | *** | |
| 5. Blocks (B) | 1 | 9.06 | χ^2 (10) | ** | 1 | 2.48 | χ^2 (10) | n.s. | |
| 6. $B \times F_1$ | 4 | 0.93 | χ^2 (10) | n.s. | 4 | 3.03 | χ^2 (10) | n.s. | |
| 7. $B \times F_2$ | 4 | 1.61 | χ^2 (10) | n.s. | 5 | 1.00 | χ^2 (10) | n.s. | |
| 8. $B \times F_3$ | 9 | 0.95 | χ^2 (10) | n.s. | 10 | 1.09 | χ^2 (10) | n.s. | |
| 9. $B \times F_4$ | 18 | 0.59 | χ^2 (10) | n.s. | 20 | 1.97 | χ^2 (10) | n.s. | |
| 10. Replicates | 602 | 1.02 | | | 707 | 1.32 | | | |
| Character 3 | | | | | | | | | |
| 1. F_1 groups (F_1) | 4 | 82.03 | V.R. (3) | n.s. | 4 | 253.57 | † | — | |
| 2. F_2 groups in F_1 (F_2) | 4 | 42.89 | V.R. (3) | n.s. | 5 | 47.16 | V.R. (3) | n.s. | |
| 3. F_3 groups in F_2 (F_3) | 9 | 45.41 | V.R. (4) | * | 10 | 15.01 | χ^2 (10) | *** | |
| 4. F_4 groups in F_3 (F_4) | 18 | 15.70 | χ^2 (10) | *** | 20 | 4.79 | χ^2 (10) | n.s. | |
| 5. Blocks (B) | 1 | 63.04 | χ^2 (10) | n.s. | 1 | 118.90 | V.R. (6) | n.s. | |
| 6. $B \times F_1$ | 4 | 1.60 | χ^2 (10) | n.s. | 4 | 16.03 | χ^2 (10) | ** | |
| 7. $B \times F_2$ | 4 | 3.16 | χ^2 (10) | n.s. | 5 | 3.40 | χ^2 (10) | n.s. | |
| 8. $B \times F_3$ | 9 | 2.92 | χ^2 (10) | n.s. | 10 | 1.82 | χ^2 (10) | n.s. | |
| 9. $B \times F_4$ | 18 | 3.32 | χ^2 (10) | n.s. | 20 | 1.90 | χ^2 (10) | n.s. | |
| 10. Replicates | 602 | 2.82 | | | 707 | 3.86 | | | |
| Character 4 | | | | | | | | | |
| 1. F_1 groups (F_1) | 4 | 15.83 | V.R. (3) | n.s. | 4 | 20.34 | † | — | |
| 2. F_2 groups in F_1 (F_2) | 4 | 16.69 | V.R. (3) | n.s. | 5 | 6.74 | V.R. (3) | n.s. | |
| 3. F_3 groups in F_2 (F_3) | 9 | 7.64 | V.R. (4) | * | 10 | 4.04 | χ^2 (10) | ** | |
| 4. F_4 groups in F_3 (F_4) | 18 | 2.34 | χ^2 (10) | *** | 20 | 0.49 | χ^2 (10) | n.s. | |
| 5. Blocks (B) | 1 | 28.36 | χ^2 (10) | n.s. | 1 | 47.06 | V.R. (6) | ** | |
| 6. $B \times F_1$ | 4 | 0.61 | χ^2 (10) | n.s. | 4 | 1.85 | χ^2 (10) | * | |
| 7. $B \times F_2$ | 4 | 0.82 | χ^2 (10) | n.s. | 5 | 1.06 | χ^2 (10) | n.s. | |
| 8. $B \times F_3$ | 9 | 0.13 | χ^2 (10) | n.s. | 10 | 0.64 | χ^2 (10) | n.s. | |
| 9. $B \times F_4$ | 18 | 0.65 | χ^2 (10) | n.s. | 20 | 0.51 | χ^2 (10) | n.s. | |
| 10. Replicates | 602 | 0.65 | | | 707 | 0.63 | | | |
| Character 5 | | | | | | | | | |
| 1. F_1 groups (F_1) | 4 | 14.12 | V.R. (3) | n.s. | 4 | 21.94 | V.R. (3) | * | |
| 2. F_2 groups in F_1 (F_2) | 4 | 5.87 | V.R. (3) | n.s. | 5 | 8.56 | V.R. (3) | n.s. | |
| 3. F_3 groups in F_2 (F_3) | 9 | 6.95 | V.R. (9) | *** | 10 | 3.12 | V.R. (4) | ** | |
| 4. F_4 groups in F_3 (F_4) | 18 | 0.94 | V.R. (9) | n.s. | 20 | 0.71 | χ^2 (10) | ** | |
| 5. Blocks (B) | 1 | 12.61 | V.R. (9) | *** | 1 | 29.06 | χ^2 (10) | *** | |
| 6. $B \times F_1$ | 4 | 0.52 | V.R. (9) | n.s. | 4 | 0.75 | χ^2 (10) | n.s. | |
| 7. $B \times F_2$ | 4 | 0.41 | V.R. (9) | n.s. | 5 | 0.22 | χ^2 (10) | n.s. | |
| 8. $B \times F_3$ | 9 | 0.22 | V.R. (9) | n.s. | 10 | 0.30 | χ^2 (10) | n.s. | |
| 9. $B \times F_4$ | 18 | 0.80 | χ^2 (10) | ** | 20 | 0.41 | χ^2 (10) | n.s. | |
| 10. Replicates | 602 | 0.40 | | | 707 | 0.37 | | | |

† No real test of significance is available as both the block interaction and a lower main effect are significant.

n.s. Probability is non-significant. * Probability = 0.01-0.05; ** Probability = 0.001-0.01; *** Probability < 0.001.

of the eighth leaf at flowering time, (4) the length of the eighth leaf and (5) the width of the eighth leaf, these will be referred to as characters 1 to 5 from here on. The analyses have the same structure as those presented in Perkins, Eglington and Jinks (1971, p. 450) as extended by Eglington and Moore (1973) to include the F_4 and F_5 generations.

The differences between F_1 groups (Item 1) are those which were generated by segregation in the F_1 generation, the size of the effects depending on the original F_1 segregation and on the persistence of the effects through to the F_5 generation. Reference cannot be made to previous generations for comparison as no characters other than final height and flowering time were measured before the F_5 generation.

The $p_3 \times nil_3$ cross has no character for which the difference between F_1 groups is significant, in the cross $nk_2 \times nil_1$, however, characters 1 and 5 show a significant difference between F_1 groups. Two other characters, 3 and 4, have no direct test for differences between F_1 groups because of their significant interaction with blocks (Item 6). However, if the estimated variance component due to the block interaction is subtracted from the mean square for differences between F_1 groups and the derived mean square is tested against the largest significant hierarchical main effect by variance ratio, the significance of the differences may be estimated. Such adjustment shows the differences between F_1 groups to be significant for both characters ($P = < 0.001$ for character 3 and $P = 0.001 - 0.005$ for character 4).

(ii) F_2 , F_3 and F_4 segregation

From table 1 it can be seen that the effects of segregation in the F_2 , F_3 and F_4 generations can be detected among the F_5 progenies although it is significant infrequently at the F_2 level and never significant at all three levels for any one cross/character combination. The nature of this variation can be investigated by fitting by least squares procedures (Mather and Jinks, 1971) a model with an additive (D), dominance (H), and additive environmental (E_1) component of variation which assumes Mendelian autosomal inheritance, independence of genes in action and in distribution and no genotype-environmental interactions, to the four rank variances $V2F_c5$, $V3F_c5$, $V4F_c5$ and $V5F_c5$ (tables 2 and 3) derivable from the analyses of variance in table 1.

This model was satisfactory, having a significant joint regression and no significant residual or heterogeneity between blocks for characters 3 and 4 in the cross $p_3 \times nil_3$. H was significant in block 1 and 1+2 but not in block 2 for character 3 (table 5). Further analysis showed that the part of the joint regression over blocks due to H was significant at the 1.5 per cent. level. H was not significant for character 4 and a model with D and E_1 only was adequate. Both D and E_1 were found to be significant for character 4 but not for 3.

In the cross $nk_2 \times nil_1$ the D, H, E_1 model was satisfactory for all characters except 1, a model omitting H , however, was still adequate for characters 2, 3, 4 and 5 and D was significant for characters 2, 3 and 5 but not for 4. E_1 was significant throughout. Where the model was not satisfactory (Characters 1, 2 and 5 in the cross $p_3 \times nil_3$ and character 1 in the cross $nk_2 \times nil_1$) this was due to a significant residual. When the joint regression was tested against this significant item it was non-significant. Presumably a more complex model is required which allows for the failure of some of the

TABLE 2
Rank variances for the F_5 generation of cross $p_2 \times nil_3$

| | $V2F_{c5}$ | $V3F_{c5}$ | $V4F_{c5}$ | $V5F_{c5}$ |
|--------------------|------------|------------|------------|------------|
| <i>Character 1</i> | | | | |
| Block 1 | 17.5836 | 6.2801 | 10.2351 | 29.2042 |
| Block 2 | 24.2684 | 8.5324 | 7.8426 | 31.4876 |
| Blocks 1+2 | 41.4520 | 14.8125 | 18.0777 | 60.6918 |
| <i>Character 2</i> | | | | |
| Block 1 | 0.7428 | 3.1557 | 1.2673 | 10.0052 |
| Block 2 | 1.9742 | 3.1330 | 1.0270 | 10.4707 |
| Blocks 1+2 | 2.7170 | 6.2887 | 2.2943 | 20.4759 |
| <i>Character 3</i> | | | | |
| Block 1 | 5.8943 | 8.9670 | 11.6226 | 26.1557 |
| Block 2 | 5.6178 | 15.1990 | 7.4019 | 33.0388 |
| Blocks 1+2 | 11.5121 | 24.1660 | 19.0245 | 59.1945 |
| <i>Character 4</i> | | | | |
| Block 1 | 1.8623 | 1.7790 | 1.8434 | 6.6886 |
| Block 2 | 2.5148 | 2.1073 | 1.1497 | 6.2477 |
| Blocks 1+2 | 4.3771 | 3.8863 | 2.9931 | 12.9363 |
| <i>Character 5</i> | | | | |
| Block 1 | 0.6131 | 1.6474 | 1.1651 | 4.1874 |
| Block 2 | 0.9577 | 1.9364 | 0.5662 | 3.7297 |
| Blocks 1+2 | 1.5708 | 3.5838 | 1.7313 | 7.9171 |

TABLE 3
Rank variances for the F_5 generation of cross $nk_2 \times nil_1$.

| | $V2F_{c5}$ | $V3F_{c5}$ | $V4F_{c5}$ | $V5F_{c5}$ |
|--------------------|------------|------------|------------|------------|
| <i>Character 1</i> | | | | |
| Block 1 | 7.1380 | 13.5931 | 7.3386 | 49.0106 |
| Block 2 | 5.4433 | 11.7370 | 8.3585 | 45.3390 |
| Block 1+2 | 12.5813 | 25.3301 | 15.6971 | 94.3396 |
| <i>Character 2</i> | | | | |
| Block 1 | 3.9501 | 5.2495 | 2.0174 | 14.7355 |
| Block 2 | 3.7522 | 3.2268 | 3.3539 | 11.6367 |
| Blocks 1+2 | 7.7023 | 8.4763 | 5.3713 | 26.3722 |
| <i>Character 3</i> | | | | |
| Block 1 | 5.5564 | 4.4841 | 2.1938 | 35.4960 |
| Block 2 | 7.0833 | 3.9314 | 4.4974 | 41.6875 |
| Blocks 1+2 | 12.6397 | 8.4155 | 6.6912 | 77.1835 |
| <i>Character 4</i> | | | | |
| Block 1 | 1.5540 | 1.2217 | 0.4250 | 0.6966 |
| Block 2 | 0.3969 | 1.1169 | 0.5460 | 5.9133 |
| Blocks 1+2 | 1.9509 | 2.3386 | 0.9890 | 12.6099 |
| <i>Character 5</i> | | | | |
| Block 1 | 1.1042 | 0.9639 | 0.4713 | 3.8848 |
| Block 2 | 1.0923 | 0.7498 | 0.6465 | 3.5988 |
| Blocks 1+2 | 2.1965 | 1.7137 | 1.1178 | 7.4836 |

TABLE 4

Analysis of variance to test the fit of the D, H, E, model to data of the F₆ generation, or of the D, E, model if this was fitted

| Item | $p_3 \times nil_3$ | | | | $nk_2 \times nil_1$ | | | |
|--------------------------------|--------------------|--------|-------------|------|---------------------|---------|-------------|------|
| | d.f. | M.S. | Test | P | d.f. | M.S. | Test | P |
| <i>Character 1</i> | | | | | | | | |
| 1. Joint regression | 3 | 743.26 | V.R. (2) | n.s. | 3 | 1643.36 | V.R. (2) | n.s. |
| 2. Residual | 1 | 60.99 | V.R. (AMS1) | * | 1 | 43.05 | V.R. (AMS1) | * |
| 3. Heterogeneity of regression | 3 | 9.99 | V.R. (4) | n.s. | 3 | 3.12 | V.R. (4) | n.s. |
| 4. Remainder | 1 | 0.27 | | | 1 | 1.08 | | |
| <i>Character 2</i> | | | | | | | | |
| 1. Joint regression | 3 | 76.85 | V.R. (2) | n.s. | 2 | 211.72 | V.R. (AMS2) | *** |
| 2. Residual | 1 | 5.16 | V.R. (AMS1) | ** | 2 | 2.16 | V.R. (AMS1) | n.s. |
| 3. Heterogeneity of regression | 3 | 0.26 | V.R. (4) | n.s. | 2 | 2.47 | V.R. (4) | n.s. |
| 4. Remainder | 1 | 0.05 | | | 2 | 1.41 | | |
| <i>Character 3</i> | | | | | | | | |
| 1. Joint regression | 3 | 790.56 | V.R. (AMS2) | *** | 2 | 1555.62 | V.R. (AMS2) | *** |
| 2. Residual | 1 | 19.53 | V.R. (AMS1) | n.s. | 2 | 2.54 | V.R. (AMS1) | n.s. |
| 3. Heterogeneity of regression | 3 | 8.46 | V.R. (4) | n.s. | 2 | 10.47 | V.R. (4) | n.s. |
| 4. Remainder | 1 | 26.67 | | | 2 | 1.10 | | |
| <i>Character 4</i> | | | | | | | | |
| 1. Joint regression | 2 | 52.31 | V.R. (AMS2) | *** | 2 | 42.10 | V.R. (AMS2) | *** |
| 2. Residual | 2 | 0.33 | V.R. (AMS1) | n.s. | 2 | 0.21 | V.R. (AMS1) | n.s. |
| 3. Heterogeneity of regression | 2 | 0.16 | V.R. (4) | n.s. | 2 | 0.40 | V.R. (4) | n.s. |
| 4. Remainder | 2 | 0.14 | | | 2 | 0.10 | | |
| <i>Character 5</i> | | | | | | | | |
| 1. Joint regression | 3 | 13.11 | V.R. (2) | n.s. | 2 | 16.25 | V.R. (AMS2) | *** |
| 2. Residual | 1 | 1.17 | V.R. (AMS1) | * | 2 | 0.01 | V.R. (AMS1) | n.s. |
| 3. Heterogeneity of regression | 3 | 0.10 | V.R. (4) | n.s. | 2 | 0.02 | V.R. (4) | n.s. |
| 4. Remainder | 1 | 0.08 | | | 2 | 0.02 | | |

AMS1 = Average mean square of Items 3 and 4.

AMS2 = Average mean square of Items 2, 3 and 4.

Other symbols as in table 1.

assumptions listed earlier but further parameters could not be fitted to these data as only four statistics were available.

(iii) *Effective factors*

Estimates for the numbers of effective factors segregating in this model were obtained using the formula.

$$k = \frac{(\frac{1}{2} \text{ range})^2}{D}$$

as described in the previous paper (Eglington and Moore, 1973). The estimates obtained were eight for character 4 in the $p_3 \times nil_3$ cross and five for both characters 2 and 5 in the $nk_2 \times nil_1$ cross.

TABLE 5

Estimates of parameters and their significance for those cases in which the model fitted was satisfactory, estimates are for the two parameter model except for the one case where H was significant

| Cross | Character | Parameter | Block | | |
|---------------------|-----------|-----------|------------|-------------|------------------|
| | | | 1 | 2 | 1 and 2 combined |
| $P_3 \times nil_3$ | 3 | D | -2.65 n.s. | 2.52 n.s. | -0.07 n.s. |
| | | H | 580.07* | 468.64 n.s. | 524.36* |
| | | E_1 | 8.21 n.s. | 18.09* | 13.15 n.s. |
| | 4 | D | 3.06** | 3.89** | 3.48** |
| | | E_1 | 6.58*** | 6.02*** | 6.30*** |
| | | | | | |
| $nk_2 \times nil_1$ | 2 | D | 7.00** | 6.01* | 6.51* |
| | | E_1 | 14.33*** | 11.41*** | 12.87*** |
| | 3 | D | 6.68 n.s. | 8.01* | 7.35* |
| | | E_1 | 34.88*** | 41.08*** | 37.88*** |
| | 4 | D | 2.07* | 0.80 n.s. | 1.43 n.s. |
| | | E_1 | 6.52*** | 5.87*** | 6.19*** |
| | 5 | D | 1.64* | 1.55* | 1.59* |
| | | E_1 | 3.78*** | 3.51*** | 3.65*** |

Symbols as in table 1.

4. CONCLUSIONS

The analysis of the F_5 generation of the crosses $p_3 \times nil_3$ and $nk_2 \times nil_1$ shows F_1 segregation, expressed as differences between groups of plants in the F_5 descended from different F_1 individuals, to be present in the F_5 generation of the $nk_2 \times nil_1$ cross for four out of the five characters and possibly for the fifth character also ($P = 0.10 - 0.05$). This confirms the analysis of earlier generations (Perkins, Eglington and Jinks, 1971) and of the characters final height and flowering time in the F_5 generation (Eglington and Moore, 1973) which indicated the persistence of the effects of an F_1 segregation to later generations at least in the $nk_2 \times nil_1$ cross. Significant effects of an F_1 segregation have now also been found in the F_3 generation of two crosses, $nk_2 \times p_3$ and $np_1 \times k_3$, of a 4×4 diallel set of crosses between nk , p , np , and k lines for both the characters final height and flowering time (Moore, unpublished).

In the majority of cases the variation from the F_2 generation onwards can be explained by a biometrical model consisting of an additive genetical, an additive environmental and in one case a dominance component of variation. This supports our earlier conclusions (Eglington and Moore, 1973) that this segregation is of the conventional kind.

That more than one, and possibly many effective factors are involved in the differences between lines which have received different conditioning treatments, previously indicated by estimates of three, three and five for $p_3 \times nil_3$ final height and flowering time and $nk_2 \times nil_1$ flowering time, respectively, is confirmed by the new estimates of eight for the length of the eighth leaf in $p_3 \times nil_3$ and five for the height of the eighth leaf at flowering time and for the width of the eighth leaf in the cross $nk_2 \times nil_1$.

Not all these characters, however, can be considered independently as

were final height and flowering time in the previous paper. Three principle components were extracted from the correlation matrix between the seven characters measured in the F_3 by principle components analysis. These components were the same for each cross and were (1) the length of the branch in the axil of the eighth leaf and the two leaf measurements, (2) flowering time and the height of the eighth leaf at flowering time and (3) height at flowering time and final height.

These three principle components are consistent with the first three factors extracted by factor analysis, to which the principle components analysis approximates, from an analysis of fifteen characters of 82 inbred lines derived from a cross between varieties 1 and 5 of *N. rustica* (Eaves and Brumpton, 1972).

Conditioning would thus appear to have caused lines to differ by a number of effective factors for three independent groups of characters suggesting an overall difference ascribable to at least 14 effective factors between p_3 and nil_3 . The minimal number of effective factors common to flowering time (i) and the height of the eighth leaf (j) in $nk_2 \times nil_1$ can be calculated in the following way

$$\hat{k}_{ij} = r_{ij}(k_{ii}k_{jj})$$

where r_{ij} is the genotypic correlation between the i th and j th character and k_{ii} and k_{jj} are the numbers of effective factors calculated for i and j (Eaves and Brumpton, 1972). \hat{k}_{ij} , to the nearest whole number, equals 1, giving an overall difference between nk_2 and nil_1 of about 13 effective factors.

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HOMOLOGOUS POLYMORPHISM AND NICHE EQUIVALENCE IN THE BUTTERFLY GENUS *CHLOSYNE*

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SUMMARY

The inheritance of a colour polymorphism exhibited by the larvae of *Chlosyne gorgone* is reported to involve two loci with dominance at each locus in addition to the presence of a dominant epistatic relationship. The identity of the