NOTES AND COMMENTS

THE BREEDING SYSTEM OF *ARABIDOPSIS THALIANA*

J. W. SNAPE and M. J. LAWRENCE
Department of Genetics, University of Birmingham

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1. Introduction

Arabidopsis thaliana has been generally regarded as an automatically self-pollinating species and there is no doubt that individual plants raised in isolation in a glasshouse can set seed freely in this way. Several recent reports of variation within progenies obtained from natural populations of the species in Germany (Karbe and Röbbelen, 1968; Napp-Zinn, 1964), Czechoslovakia (Dobrovolná, 1967) and in the United Kingdom (Jones, 1968, 1971), however, have cast some doubt on this belief. Briefly, the results from these investigations, which concern metrical characters, show that (1) the variances of natural progenies are heterogeneous *inter se* and (2) that they frequently exceed those of laboratory inbred lines.

The simplest interpretation of these results is to assume that the greater variance of natural progenies is due to segregation of the genes, which determine the metrical characters in question, in the progeny of individuals heterozygous with respect to these loci; and that such individuals are heterozygotes because some outcrossing has occurred in their ancestry.

2. Materials and methods

The experiment reported here was designed to provide a direct test of this hypothesis. It concerns a pair of laboratory inbred lines, *Wilna-2* (Robbelen, 1965) and *Langridge* which breed true for glabrous leaves and for the customary sparsely distributed hairy leaves respectively, this difference being determined by a single gene.

Each of 10 plants of the *Wilna-2* line was closely (6 cm.) and completely surrounded by a ring of 6 plants of the *Langridge* line. Five of these groups of 7 plants were placed outdoors in an open situation (block 1) and the remaining five in a more sheltered position between a pair of glasshouses (block 2). Each group in both blocks was at least 2 m. from every other. The plants of both lines came into flower at approximately the same time during the normal flowering season of the species in 1970. Flowering was allowed to continue with a minimum of disturbance until the plants died naturally. At this time the plants had grown to approximately 30 cm. in height and their inflorescences had grown into one another. The *Langridge* line individuals were then removed carefully and ripe siliquae harvested from the *Wilna-2* plants on several occasions for three weeks.

The seed so obtained was sown individually in soil in the glasshouse the following autumn, 400 seeds being sown, where numbers permitted, from each harvest and each plant. Ninety-six per cent. of the seed sown germinated and a total of 10,395 seedlings were scored three weeks later when the first pair of true leaves were clearly visible.

3. Results and discussion

Now if each of the ten *Wilna-2* plants under test in this experiment had set seed by self-pollination alone, none of their progeny, mutation apart, would be expected to display the dominant wild-type trait, hairy leaves. In fact, 180 seedlings did so. There can be no further doubt, therefore, that the species is capable of some outcrossing even where, as in the present circumstances, inbred lines are concerned and the frequency of outcrossing is low ($1{\cdot}73 \pm 0{\cdot}12$ per cent.).

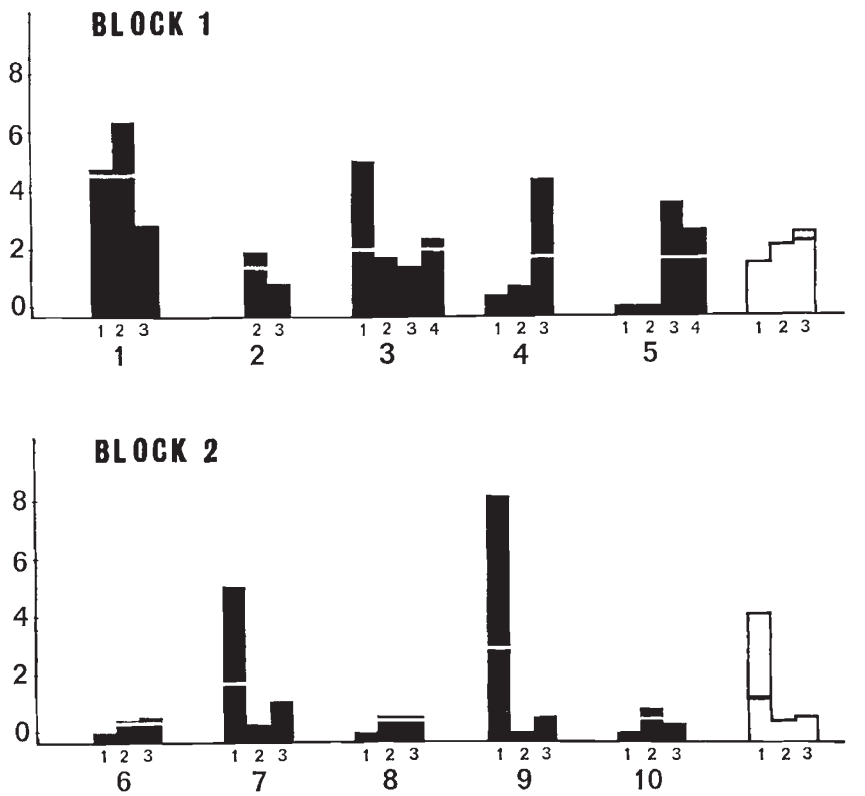

Fig. 1.—Variation of outcrossing frequency (%) between harvests, plants and blocks. The height of each bar shows the frequency of outcrossing among the progeny of the indicated harvest (small number) and plant (large number). Plant averages are shown by the white line which interrupts the tall bars. Block averages for each harvest are shown in the right-most groups (white bars) and the overall average for each block is shown by the black line interrupting the tall bars.

Further analysis of these data reveals, however, that the frequency of outcrossing varies significantly over blocks, harvests and plants in a manner which suggests a possible cause of cross-pollination in this material. Thus the frequency in the first block is 2·15 per cent., while inthe more sheltered second block it is only 1·19 per cent.—a difference which, at first sight, might be taken to suggest that cross-pollination takes place when the inflorescences of adjacent plants come into contact because of wind movement. But on this argument we should also expect that the frequency of cross-pollination

would increase as the inflorescence became more developed in older plants. The progeny raised from siliquae which were taken in the last harvest should, therefore, contain a higher proportion of wild-type seedlings than those of earlier harvests. It turns out, however, that in block 2, it is the progeny of the first harvest which contains the highest proportion of wild-type seedlings, there being no difference other than that which can be ascribed to sampling

TABLE 1

The analysis of variation of the proportion of wild-type seedlings in the progeny of different blocks, harvests and plants. The method used is an extension of the three-dimensional $2 \times 2 \times 2$ *contingency* χ^2 *table (Kendall and Stuart, 1961; Crawford-Sidebotham, 1970). In the present case the data may be considered to comprise a four-dimensional* $2 \times 2 \times 3 \times 5$ *contingency table. All the items shown are significant at less than the* 0·1 *per cent. level.*

Source	d.f.	χ^2
Blocks (B)	1	12·816
Harvests (H)	2	18·562
B × H	2	49·007
Plants (P)	8	79·892
P × H	16	235·168

in either the remaining harvests of this block or any of the first. Nor, for that matter, are the plants in either block consistent in this respect. Physical contact between plants must, therefore, in this material at least, be ruled out as the chief cause of cross-pollination.

Now although visits by insects of any species to open flowers of *Arabidopsis* are uncommon in the urban environment in which this experiment was performed, hover-flies (*Syrphidae*) have been observed occasionally to visit plants in the glasshouse. Though none were seen to visit the plants of this experiment, such casual, infrequent visits as we might expect from them could generate the heterogeneous frequencies of outcrossing obtained. The slightly higher frequency detected among the progenies of the plants of first block would, on this argument, be a consequence of their greater availability to the foraging activities of such insects. Furthermore, in a more rural environment, the frequency of cross-pollination between plants might well be higher both because of the greater number of visitors as well as the greater number and density of plants in a natural population.

4. SUMMARY

1. The frequency of natural outcrossing among plants of two inbred lines of *Arabidopsis thaliana* has been found to be $1{\cdot}73 \pm 0{\cdot}12$ per cent.

2. There was considerable plant to plant variation around this value which suggested that the cause of cross-pollination was due chiefly to occasional visits by hover-flies, rather than by physical contact between closely adjacent plants.

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