GENETICAL STUDIES IN ACACIAS

IV. NATURAL HYBRIDS BETWEEN *ACACIA IRRORATA* AND *A. MEARNSII*

A. A. MOFFETT

Wattle Research Institute, University of Natal

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1. INTRODUCTION

AMONG trees grown from open-pollinated seed of *Acacia irrorata* collected in 1943 from Sevenoaks, Natal, a few appeared to be hybrids with *A. mearnsii* (formerly *A. mollissima*). The two species are closely related, but differ markedly in, among other characters, the number of glands on the leaves and in the scabrousness of the young stems and leaf veins. Subsequent segregation in selfed families from the suspect trees left no doubt that they were hybrids between the two species and the F_2 families were recorded in detail.

2. METHODS

The individual parent trees were not known, so to obtain estimates of the average characteristics of the parental species and their hybrids, 18 leaves from each of 3 trees of *A. irrorata*, 5 trees of *A. mearnsii* and 2 F_1 hybrids (H18 and H31) were examined. The number of juga (pairs of pinnæ) and the number of glands were recorded and the group mean was taken to be representative of the type concerned.

The glands occur on the upper surface of the rachis where they usually have a positional relationship to the juga, the exact arrangement depending upon the number of glands and juga on the leaf. For convenience in description the following terms will be used for glands in different positions on the leaf.

"Jugary glands." Those occurring contiguous to and immediately below the points of insertion of the juga.

"Interjugary glands." Those occurring between the consecutive juga, but apparently having no positional relationship to them.

"Apical and basal glands." The gland below apical and basal juga respectively.

F_1 families were raised from the two F_1 hybrids, H18 and H31. A sample of 6 leaves from each tree was scored for the number of juga and gland number and position. Back-crossing failed.

3. RESULTS

(i) Seedling characters

When the first seedling leaf in the F_2 family from H18 was scored a number of seedlings with yellow-green leaves, in contrast to the normal blue-green, were noted. This character was fairly clear cut and segregated—91 blue-green : 39 yellow-green, a ratio which fitted fairly closely to a 3 : 1 ($\chi^2_{(1)} = 1.733$).

The F_2 family from H31 also segregated for yellow-greens, but the position was more complex. When the first seedling leaf was scored there were 65 blue-green : 23 yellow-green, giving a very close fit to

a 3 : 1 ratio ($\chi^2_{(1)} = 0.004$). It was found, however, that at a second scoring, some 5 months later, a number of seedlings originally classified as blue-green had developed yellow-green foliage. These, together with some of the original yellow-greens, subsequently proved to be much-branched dwarfs. The ratio of normal to dwarf was 56 : 22, giving a close fit to a 3 : 1 ratio ($\chi^2_{(1)} = 0.427$). At this stage the overall ratio of blue-green normal : yellow-green normal : yellow-green dwarf was 43 : 13 : 22 which agrees with a 9 : 3 : 4 segregation ($\chi^2_{(2)} = 2.062$). It would seem that two genes are involved, one producing yellow-green seedlings at an early stage of growth and the other producing dwarf habit with yellow-green foliage as a concomitant.

(ii) *Scabrous and smooth*

The backs of the leaves, the young stems and, more particularly, the stem ridges of *irrorata* are rough to the touch, whereas those of *mearnsii* are smooth with no trace of roughness. The scabrousness of *irrorata* is due to a combination of two characters. First, the stems and the lower sides of the rachis and rachillæ of the leaves have numerous minute protuberances giving an uneven papillose surface. Second, on the papillæ groups of coarse hairs occur in a dense, but uneven, covering. In *mearnsii* the hairs, although more numerous, are much finer and are evenly distributed.

At first it appeared that the two F_1 hybrids, H18 and H31, were smooth like *mearnsii*, but a more detailed examination showed differences, not only from *mearnsii*, but between the two hybrids also. Under the microscope, the surface of both hybrids showed minute and, compared with *irrorata*, greatly reduced papillæ on their leaf and stem surfaces. The hairs, although almost as fine as those of *mearnsii*, had a slightly tufted distribution. These differences from *mearnsii* were more marked in H18 than in H31 and on the former a slight roughness could be felt on some of the older leaves.

The two hybrids were, however, very close to *mearnsii* in smoothness and it was surprising to find that in both F_2 families all the trees were distinctly scabrous to a greater or lesser degree. The majority were approximately intermediate between the two species, but a considerable range of variation occurred. No trees as smooth as *mearnsii*, or even the F_1 parent, were found, and, although some very scabrous trees were found, none was as scabrous as *irrorata*. Since neither parent character was fully recovered in the two F_2 families totalling 175 individuals, it seems likely that the inheritance of the scabrousness is polygenic. The F_2 families are expected to vary around a mean which lies between that of the F_1 and the mid-parent value, but in both F_2 families all the individuals were on the *irrorata* side of the F_1 parent. The most likely explanation lies in the difference in age and growing conditions of the F_1 and F_2 trees. The F_2 trees were younger than the F_1 and were subject to the restriction caused by

growing them in pots. It is possible that a combination of difference in age and restricted growth may have accentuated the scabrous character.

(iii) *Numbers of juga and glands*

Over the 3 trees sampled, *irrorata* averaged 8.9 juga and 1.2 glands per leaf compared with 14.7 and 23.5 respectively for the 5 trees of *mearnsii* (table 1). There were significant differences between

TABLE 1
Mean number of juga and glands and standard errors (single leaf)
of A. irrorata, A. mearnsii and F₁ hybrids

Tree number		Number of juga	Number of glands
<i>A. irrorata</i>	8 . . .	8.2 ± 1.31	1.4 ± 0.51
<i>A. irrorata</i>	16 . . .	9.2 ± 0.88	1.1 ± 0.54
<i>A. irrorata</i>	29 . . .	9.4 ± 1.59	0.9 ± 0.42
Mean	. . . . .	8.9 ± 1.37	1.2 ± 0.31
Significant differences	. . . . .	*	**
<i>A. mearnsii</i>	18 . . .	14.3 ± 1.18	22.3 ± 4.29
<i>A. mearnsii</i>	41 . . .	15.9 ± 0.89	20.5 ± 4.60
<i>A. mearnsii</i>	51 . . .	13.2 ± 1.75	20.7 ± 4.34
<i>A. mearnsii</i>	80 . . .	15.1 ± 0.85	30.9 ± 4.30
<i>A. mearnsii</i>	85 . . .	14.9 ± 1.67	23.2 ± 4.88
Mean	. . . . .	14.7 ± 1.59	23.5 ± 5.86
Significant differences	. . . . .	**	**
Hybrid H18	. . . . .	12.4 ± 1.20	6.9 ± 2.66
Hybrid H31	. . . . .	11.2 ± 0.71	10.8 ± 0.81
Mean	. . . . .	11.8 ± 1.14	8.8 ± 2.76
Significant differences	. . . . .	**	**

* Differences significant ($P = 0.05$). ** Differences significant ($P = 0.01$).

trees within each species for both characters and the two F_1 hybrids, H18 and H31, differed significantly in both juga and gland number (table 1, figs. 1 and 2).

In both F_1 trees the number of juga was approximately midway between the parent species values, H18 being slightly lower and H31 slightly higher than the mid-parent value. In both families the range of variation in juga number extended from *irrorata* to *mearnsii*, and the parent means were scarcely exceeded at either end of the range. This behaviour was very similar to that found in crosses between *A. decurrens* and *A. mearnsii* (Moffett and Nixon, 1958).

The pattern of segregation for leaf glands was very different. The two F_1 trees differed significantly in gland number, but both

FIG. 1.—Number of jugas and number of glands in the F_2 from H18. Here, and in fig. 2, the values for the F_1 trees, and the means for the parent species and the F_2 are shown by crosses.

were much closer to *irrorata* than to *mearnsii*, showing some dominance of the *irrorata* parent for this character.

In both the F_2 families the range of variation did not extend between the two parental values, but was virtually confined between the mid-parent and *irrorata* values (figs. 1 and 2). In the F_2 from H31, the F_1 parent with the higher gland number, some trees had gland numbers which equalled, or came very close to, the number of juga on the leaf, but neither in these nor in any individual in either F_2 , were interjugary glands found. It was this absence of interjugary glands which curtailed distribution and pushed the means of the families towards the *irrorata* parent. If the *mearnsii* gland value had been assessed on jugary glands only, then the range of variation would have extended fully between the two parent values.

Since no interjugary glands occur in the F_2 families, if juga number and gland number were inherited independently, it would be expected that leaves with low juga numbers would tend, on the whole, to have the full complement of jugary glands more frequently than leaves with high juga numbers. This was not so and it was evident that within certain limits gland number is associated with or controlled by juga number.

To test whether this association was of the same order over all juga numbers, correlations were calculated for juga number and the ratio of glands to juga (gland number $\div$ juga number). In both F_2 families these correlations were significant ($P = 0.07$) being $r = 0.2752$ and $r = 0.4270$ for the families from H18 and H31 respectively. Evidently, leaves with high juga numbers tend, on the whole, to have a higher proportion of glands than leaves with low juga numbers.

In spite of the restricted range of F_2 gland numbers, the difference in value between the two F_1 trees was reflected in their respective F_2 families. The F_2 from H31, the hybrid with the higher gland number, had its mean and range of variation somewhat closer to *mearnsii* than that from H18. These differences between families were significant ($P = 0.01$) and are clearly shown by comparison of figs. 1 and 2.

(iv) *Gland position*

The majority of leaves examined from *A. irrorata* had a single apical gland, but leaves with two and, more rarely, three glands were found. The position of the second gland varied. In 13 of the leaves it was below the sub-apical jugum and in 8 below the basal jugum. When there were three glands per leaf the apical, sub-apical, and basal juga all had glands contiguous to them.

In *A. mearnsii* each jugum almost invariably had a contiguous gland and, since the great majority of leaves had more glands than juga, a variable number of interjugary glands occurred also. These were frequently smaller and not so well developed as the jugary glands. When the number of interjugary glands is less than the number of

FIG. 2.—Number of jugas and number of glands in the F_2 from H_{31} .

juga they are usually situated in the more distal interjuga spaces and, as gland number increases, they occupy these spaces in a sequence extending towards the base of the leaf. With very high gland numbers

FIG. 3.—Diagram showing numbers and positions of the glands in *A. irrorata*, *A. mearnsii*, the F₁ hybrid and F₂ family from H31.

interjuga glands are found between all the juga, frequently more than one to an interval, and, sometimes, rudimentary glands may occur on the rachillæ also. In this investigation glands on the rachillæ were not considered, counts being confined to those on the rachis.

The F₁ tree, G31, had, on the average, only a slightly lower number of glands than juga. There was always a basal gland on the leaves

and, when there were fewer glands than juga, it was almost invariably the juga immediately above the basal which lacked glands.

The F_1 tree, G18, had on the average leaf slightly more than half as many glands as juga. Of the 37 leaves examined, all but 3 had basal glands, while the remaining glands, irrespective of number, were arranged in sequence from the apical gland downwards (fig. 3). Interjugary glands were not found on either of the F_1 trees.

The orderly arrangement of the glands on the leaf was more obvious in the F_2 families with their wide range of gland and juga numbers. All the F_2 trees, including those which averaged only two glands per leaf, almost invariably had apical and basal glands. When there were more than two glands they again formed a sequence from the apical gland towards the base. In no instance were interjugary glands found, even when the quota of jugary glands was complete, or almost complete.

In F_2 trees from H18 with very low gland numbers, 14 leaves were found which had only one gland each, and in all these, in contrast to *A. irrorata*, this gland was invariably in the basal position. A further 7 leaves were noted in which the apical gland was missing. It would seem, therefore, that in the hybrids the dominant position of the apical gland in *irrorata* has been lost and that the basal gland has assumed greater importance.

4. DISCUSSION

The overall pattern of inheritance points to gland number being controlled by a polygenic system, but with limitations due to other factors. In the first place, the low gland number is dominant to some extent in the hybrids, tending to bias the F_1 and the F_2 segregation towards the *irrorata* parent. Secondly, gland number and juga number are interdependent to some extent and, finally, there is a hierarchy in gland position which may effect gland numbers. The apical and basal glands have precedence, their occurrence and position being established first. In these there may be some dominance of the basal position, presumably coming into the hybrid from *mearnsii*, over the apical position which is usual for *irrorata*. When these two gland positions have been filled glands are allocated, depending on the total number, to each jugum in turn and in sequence down the rachis until the jugary positions are all filled. The results suggest that until the quota of jugary glands is complete interjugary glands do not occur. When they do occur, as in *A. mearnsii*, the sequence of occurrence again tends to be from the top of the rachis down, although this alignment is not so clear cut as for jugary glands. This situation suggests that gland positions are filled in order of precedence with increasing gene "dosage" for glands. Thus with the lowest dosages, only apical and basal glands occur, while increasing dosage gradually adds to the sequence of jugary glands until all positions are filled.

If this is correct it is not until there is a fairly high gene dosage for glands that interjugary glands occur. The two species differ widely from each other in gland number and it is likely that a considerable number of genes control the inheritance. The wide divergence between the two parents, coupled with a degree of dominance of low gland number, may determine that in the comparatively small F_2 families effective gene dosage for glands does no more than reach the level at which jugary positions are filled. No F_2 trees were found in which jugary positions on all leaves were completely filled, although some came very close to having full complements.

The position may, however, be much more complex, since the suggestions made above do not take into account the relationship between juga number and gland number, or the mechanism which must exist to determine the orderly allocation of glands on the leaf. It is possible that hybrids between species which do not differ quite so widely in gland number (e.g. *A. decurrens* and *A. mearnsii*) would throw more light on the inheritance of interjugary glands.

5. SUMMARY

Three characters, scabrousness, juga number and gland number have been studied in naturally occurring hybrids between *A. irrorata* and *A. mearnsii*.

The scabrousness of *irrorata* appeared to be almost completely recessive in the F_1 hybrid, but in the F_2 there was a wide range in the degree of scabrousness. Neither of the parental types was fully recovered.

The number of juga per leaf was intermediate between the two species in the F_1 . In the F_2 the range in juga number extended from one species to the other.

Gland number in the F_1 was closer to *irrorata* than to *mearnsii*. In the F_2 the range of variation was curtailed and extended only between the mid-parent and *irrorata*. No interjugary glands were found in the hybrid seedlings.

Glands are allocated to the juga in a definite order, the basal and apical glands being predominant. With increasing gland number the glands occur on the leaf in sequence from the distal juga to the base.

6. REFERENCE

- MOFFETT, A. A., AND NIXON, KATHLEEN M. 1958. Genetical studies in Acacias. II. Leaf characters in hybrids between green and black wattles. *Heredity*, 12, 199-212.