GENETICAL STUDIES IN ACACIAS

II. LEAF CHARACTERS IN HYBRIDS BETWEEN BLACK AND GREEN WATTLES

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1. INTRODUCTION

THE investigations described in this paper follow directly on those of Philp and Sherry (1949) who, in 1943, made what was probably the first attempt to produce hybrids between black wattle (*Acacia mollissima*) and green wattle (*A. decurrens*) under controlled conditions. As a result of these cross-pollinations, many hybrid seedlings were obtained from two green wattle trees used as seed parents. They described in detail the methods of hybridisation and also the leaf characters of the parent trees of the F_1 hybrids, and of an open-pollinated family (presumed to be an F_2) from a naturally occurring hybrid.

By 1948, when wattle genetics was taken over by the Wattle Research Institute, the F_1 hybrids were flowering freely and in the following years, F_2 and back-crossed families were raised. The study of the characters, which appeared to be controlled by polygenes, was continued with a view to determining their behaviour in interspecific crosses. If information could be obtained on the segregation and recombination of leaf characters which are easily measurable, it could be argued that other characters, also controlled by polygenes, but more difficult to determine precisely, would behave in a similar manner and some indication of the possibilities of combining such characters in interspecific hybrids would be obtained.

2. MATERIAL AND METHODS

One of the two green wattle trees used by Philp and Sherry as seed parents, G33, was crossed with an unrecorded black wattle tree; the other, G35, with a tree numbered B18. There were a number of seedlings in the F_1 from G33, but only two survived and it was possible to self only one of these. Description has, therefore, been confined largely to five sister families from $G35 \times B18$. The two F_1 families from the above crosses were numbered H33/44 and H35/44 respectively. In H35/44, nine trees survived, but further work was restricted to five trees, namely H35/44/19, H35/44/21, H35/44/24, H35/44/25 and H35/44/30. For brevity these trees are referred to as H33/24 (from family H33/44) and H35/19, H35/24 etc. (from family H35/44).

The yield of seed from these trees was low, more especially following selfing and back-crossing to the green parent, and seed had to be saved from three seasons' bagging (1949-51) before sufficient could be accumulated to give reasonably-sized families.

Samples of leaves were taken when the F_2 and back-crossed families were $3\frac{1}{2}$ years old, at which age they had largely assumed their mature foliage. Six

leaves were taken at random from each tree with the limitation that, as far as possible, leaves from similar positions on the branch and of the same degree of maturity, were chosen. Leaves were pressed in the field and measurements made on the dried specimens in the laboratory.

The characters measured were : rachis length, rachilla length, pairs of pinnæ, and pinnule number, spacing, and length. Pinnule spacing was calculated by measuring the length of a pinna central on the leaf and dividing it by the number of pinnules on it. This measurement gives results which differ somewhat from those of Philp and Sherry, who used direct measurement of the spaces, and it has the disadvantage of introducing a ratio into some of the correlations. It has, however, proved to be an efficient way of scoring spacing and involves very much less labour than direct measurement. Measurements made on a central pinna were found to give a very good approximation to the average of all pinnæ on the leaf.

There were significant differences between the species for all the characters measured but, for simplicity, description has been confined to the last four, since these give a good picture of the salient differences in leaf form between the species.

3. FERTILITY OF THE F_1 HYBRIDS

Seed was collected from the F_1 hybrids following four different types of pollination, three of which, selfing and back-crossing to the two parents, were controlled by bagging. With the fourth type—open-pollination—there was a possibility of pollination by selfing, intercrossing between the F_1 trees, or natural back-crossing to the green and black parents. Because of the position of the trees, there was every opportunity for the F_1 hybrids to cross with green wattle, but much less possibility of pollination by black wattle.

Fertility was assessed first by the number of seeds set per bag and secondly by the mean number of seeds per pod. Fertility following different pollinations is summarised in table 1.

For the back-crosses, the F_1 trees were used as seed parents, and since emasculation is not practicable, selfed as well as back-crossed seeds may have been produced. It should be mentioned here that in both the F_2 families and in the back-crosses to green wattle, a considerable proportion of chlorotic seedlings or seedlings which were chimæras of chlorotic and normal tissues, appeared (Anon., 1952). Leaf measurements in the families from back-crosses to green showed subsequently that many of the seedlings were, in fact, due to self-pollination.

Following pollination with black wattle, on the other hand, there was a comparatively high seed-set in the F_1 hybrids and only a very small proportion of chlorotic seedlings occurred. It was concluded that the great majority of seedlings in these families were back-crosses and this conclusion was confirmed later by leaf measurements. It would seem, therefore, that the F_1 hybrids are much more fertile with the black than with the green wattle parent. The low fertility with the latter probably accounts for the comparatively low seed-set following open-pollination since, as has been mentioned, there was little likelihood of natural back-crossing to black wattle, but ample opportunity for crossing with green.

4. CYTOLOGY OF THE F_1 HYBRIDS

Since the hybrids showed considerably reduced fertility compared with the parents and produced abnormal types in the F_2 , it seemed possible that they might show chromosome irregularities at meiosis. Both parents and hybrids had the chromosome number $2n = 26$. At meiosis in the hybrids, 13 bivalents were formed with great regularity and in no instance was any chromosome abnormality observed. It was not possible to determine whether there was any reduction on chiasma frequency compared with the parents. In

TABLE 1
F₁ hybrids. Total seeds collected and mean per bag and per pod following different pollinations

	Selfed			× Green wattle			× Black wattle			Open-pollination	
	Total seeds	Mean per bag	Mean per pod	Total seeds	Mean per bag	Mean per pod	Total seeds	Mean per bag	Mean per pod	Total seeds	Mean per pod
H33/24	18 (3)	6.0	3.0	...	...	...	...	...	...	143	3.6
H35/19	119 (16)	7.4	1.0	35 (2)	17.5	2.3	130 (2)	65.0	3.8	40	1.7
H35/21	158 (15)	10.5	0.8	117 (8)	14.6	2.2	594 (5)	118.8	3.7	103	2.6
H35/24	91 (6)	15.2	0.6	...	...	...	...	...	...	139	3.5
H35/25	114 (16)	7.1	0.7	40 (2)	20.0	1.5	233 (2)	116.5	4.7	113	2.8
H35/30	15 (2)	7.5	0.9	...	...	...	...	...	...	...	...
Mean		8.9	1.2		16.0	2.0		106.3	4.0		2.8

Figures in brackets give the number of inflorescences on which the bags were undamaged.

view of the regular chromosome pairing and separation in the hybrids, it must be assumed that reduced fertility and abnormal seedlings in the F_2 are due to genic unbalance and not to cytological disturbances.

5. LEAF CHARACTERS IN THE PARENT SPECIES

Leaf characters on any one tree fluctuate with varying environmental conditions and with the age of the tree, so that comparisons between trees of different ages or on different sites are liable to considerable errors. Young trees tend to have comparatively large leaves with long, widely-spaced pinnules, whereas older trees have smaller, more compact leaves with shorter, closer-spaced pinnules and a lower pinnæ number. Philp and Sherry's measurements of the leaves of the original parent trees were made when the trees were ten years old and these measurements differed somewhat from the means of younger families from bulk seed and from those of open-pollinated progeny of single trees. For further comparisons during 1955, leaf measurements were made of 45 black wattle and 24 green

wattle trees (table 3) of approximately the same age and growing under similar conditions as the F_2 and back-crossed families. These groups gave somewhat different measurements from the parent trees, but the group means probably provide a better standard for comparison for the hybrid families than do the parent trees. Measurements on E5 and B5, the respective parents of the back-crosses, were also made when the trees were considerably older than the hybrid families and these also tend to give a somewhat distorted comparison. It should be noted, however, that while age and environment cause fluctuations in the characters, the differences between the species are

TABLE 2
*Mean leaf measurements and standard errors (single leaf)
of parent trees and F_1 hybrids*

Parent trees and F_1 hybrids	Pairs of pinnæ	Number of pinnules	Length of pinnules in mm.	Pinnule spacing in mm.
Green wattle G35 .	7.3 ± 1.13	...	9.6 ± 0.78	...
Black wattle B18 .	16.3 ± 1.62	...	3.3 ± 0.25	...
Green wattle E5 .	7.0 ± 0.42	27.0 ± 4.70	8.8 ± 1.25	1.76 ± 0.24
Black wattle B5 .	16.2 ± 2.07	49.5 ± 4.70	3.0 ± 0.15	0.85 ± 0.05
F_1 hybrid H35/19 .	12.4 ± 1.56	38.3 ± 4.06	4.6 ± 0.48	1.13 ± 0.10
F_1 hybrid H35/21 .	11.2 ± 0.99	34.2 ± 2.45	4.5 ± 0.39	1.27 ± 0.10
F_1 hybrid H35/24 .	13.8 ± 0.85	39.4 ± 2.26	4.8 ± 0.42	1.02 ± 0.10
F_1 hybrid H35/25 .	12.6 ± 1.56	39.2 ± 5.90	4.7 ± 0.46	1.10 ± 0.09
F_1 hybrid H35/30 .	11.8 ± 1.39	40.9 ± 2.60	4.7 ± 0.56	1.12 ± 0.12

so great for most characters that variation within each species does not seriously affect the results. Leaf measurements for parents and hybrids are shown in table 2.

The species differ significantly in their means for each character and there is great variation within each species, trees differing significantly from each other for each of the characters (Philp and Sherry, *loc. cit.*). The shape of the frequency curves and the continuous variation within each species pointed to control by polygenes, while segregation gave trees having different combinations of these genes and hence different degrees of expression of the characters. For instance, both species show significant intraspecific variation for pinnæ number, but the ranges of the two species do not overlap. In both species, gametes differing in the number of genes for this character will be formed and, depending upon the assortment of these gametes, trees differing in pinnæ number may be expected in the F_1 hybrids. This expectation was fulfilled, for although the F_1 trees were approximately midway between the parents for all four characters, significant differences between sister F_1 hybrids occurred for all characters except pinnule length, and these differences persisted in later generations.

6. F_2 AND BACK-CROSSED FAMILIES

There was a wide range of variation in all four characters within the F_2 and, in some families, leaf types occurred which came close to black wattle at one end of the scale and to green wattle at the

TABLE 3

Mean leaf measurements and standard errors (single tree) of F_2 , back-crossed families, and bulk black and green samples

Family	No. of trees	Derived from	Pairs of pinnae	No. of pinnules	Length of pinnules mm.	Pinnule spacing mm.
H12/51	61	H35/19 s.	13.6 $\pm$ 1.8	40.1 $\pm$ 5.1	4.57 $\pm$ 0.85	1.14 $\pm$ 0.16
H13/51	100	H35/21 s.	11.9 $\pm$ 1.4	39.4 $\pm$ 5.1	4.87 $\pm$ 0.79	1.20 $\pm$ 0.16
H14/51	39	H35/24 s.	15.5 $\pm$ 2.3	43.9 $\pm$ 7.2	4.34 $\pm$ 0.60	1.03 $\pm$ 0.12
H15/51	41	H35/25 s.	15.2 $\pm$ 1.9	41.6 $\pm$ 5.5	4.83 $\pm$ 0.54	1.19 $\pm$ 0.13
H16/51	13	H35/30 s.	14.7 $\pm$ 1.7	40.4 $\pm$ 5.8	4.37 $\pm$ 0.41	1.08 $\pm$ 0.09
Diff. sig.			**	**	**	**
H17/51	43	H35/19 $\times$ B5	17.5 $\pm$ 1.7	50.7 $\pm$ 6.4	3.50 $\pm$ 0.34	0.96 $\pm$ 0.10
H18/51	34	H35/21 $\times$ B5	16.5 $\pm$ 1.8	46.2 $\pm$ 6.6	3.66 $\pm$ 0.49	0.97 $\pm$ 0.10
H19/51	32	H35/25 $\times$ B5	18.4 $\pm$ 3.0	48.6 $\pm$ 6.8	3.51 $\pm$ 0.38	0.93 $\pm$ 0.10
Diff. sig.			**	**		
H7/52	22	H35/21 $\times$ E5	10.3 $\pm$ 1.0	34.1 $\pm$ 4.6	7.36 $\pm$ 1.03	1.57 $\pm$ 0.19
H8/52	9	H35/25 $\times$ E5	11.3 $\pm$ 1.0	33.1 $\pm$ 3.4	7.52 $\pm$ 0.70	1.59 $\pm$ 0.10
H9/52	6	H35/19 $\times$ E5	10.8 $\pm$ 0.6	38.2 $\pm$ 3.4	6.91 $\pm$ 0.78	1.47 $\pm$ 0.17
Diff. sig.			*			
H11/51	36	H33/24 s.	11.9 $\pm$ 1.7	33.8 $\pm$ 6.3	4.29 $\pm$ 0.90	1.16 $\pm$ 0.18
Green	24	Bulk seed	9.3 $\pm$ 0.5	35.5 $\pm$ 3.3	7.95 $\pm$ 0.86	1.72 $\pm$ 0.13
Black	45	Bulk seed	17.6 $\pm$ 1.7	47.5 $\pm$ 5.3	3.01 $\pm$ 0.34	0.95 $\pm$ 0.09
Diff. sig.			**	**	**	**

s. = selfed.

* Significant at 5 per cent. level. ** Significant at 1 per cent. level.

other. The range of variation, however, did not extend over the same limits in each family and there were significant differences between the means for all four characters (table 3).

The scatter diagrams in figs. 1 and 2 show the range covered by each of the four characters in two F_2 families, H13/51 and 14/51, derived respectively from H35/21, the F_1 tree closest to green wattle, and H35/24, that nearest to black wattle. The means of the parent species and of the F_1 trees are shown by crosses on the diagrams, the

FIG. 1.—Segregation and correlation of pinnule number and pinnæ number in two F_2 families from $G35 \times B18$. Open circles, $H13/51$, the F_2 from the F_1 tree having the lowest value for the two characters ($H35/44/21 = H35/21$) and black circles, $H14/51$, the F_2 from the F_1 tree having the highest value for these characters ($H35/44/24 = H35/24$). In this and the following figures the characters in the parent tree or parent species are shown by vertical and horizontal arms of the crosses.

FIG. 2.—Segregation and correlation of pinnule length and pinnule spacing in same two families as fig. 1. Open circles $H13/51$; black circles $H14/51$.

vertical axis giving the mean for one character and the horizontal axis the mean for the other.

Except, possibly, for pinnule length, the mean expression of a character in the F_2 is clearly correlated with the degree of expression of that character in the F_1 parent. In back-crosses to the parent species, a similar correlation occurred. Three of the F_1 trees were crossed to a single tree of green wattle (E_5) and to a single tree of black wattle (B_5). The variation in families from two of these F_1 trees, $H_{35/21}$ having the lowest pinnule and pinnæ number and $H_{35/25}$ having higher numbers, is shown in figs. 3 and 4 respectively. A comparison of the two graphs shows that when the F_1 tree having the higher value for the two characters is used as parent, the means of the F_2 and both back-crosses derived from it are higher than when the F_1 parent with the lower pinnæ number is used. Apart from pinnule and pinnæ number, this parent-progeny correlation affects the overall appearance of the leaf as shown in pl. I. $H_{35/21}$ has a leaf-shape rather akin to that of green wattle while $H_{35/25}$ resembles black in general shape. The photographs show that the leaf-shape of particular F_1 parent trees persists to a considerable degree in both F_2 and back-crossed families.

In the back-crosses to green wattle, although the pinnule number approached or overlapped that of E_5 , from neither cross did the pinnæ number reach that of the green parent. In the back-crosses to B_5 , on the other hand, not only was there considerable overlapping of the black parent for both characters, but in the back-crossed progeny from $H_{35/25}$, individuals occurred which had a higher number of pairs of pinnæ than we have so far recorded in black wattle.

7. CORRELATION BETWEEN CHARACTERS

In the F_2 and back-crossed families, it was evident that recombination of leaf characters was not at random, but that there was a tendency for parental types to remain associated. Partial correlations were calculated for each pair of characters in the parents, the F_1 , F_2 and back-crossed families to determine the degree of this association (table 4, figs. 3 and 4).

In black wattle, pinnule spacing and pinnule length and pinnule spacing and number of pinnules, showed significant correlation ($P = 0.01$), while in green wattle, pinnule spacing and pinnule length were correlated ($P = 0.05$). The correlations in the parent species were surprising and may possibly be explained by the fact that pinnule spacing, pinnule length and number of pinnules on an individual tree are influenced by environmental conditions. For instance, shade leaves tend to have fewer, but longer and more widely spaced pinnules than leaves exposed to full sunlight. These differences within species are not great compared with differences between species, but any parallel variation in the three characters, however small, will show up as a correlation. In the hybrid families, the expression of these

FIG. 3.—Pinnule number and pinnæ number in the F_2 and back-crosses from H35/44/21 (= H35/21), the F_1 tree having the lowest value for these characters. Open circles H35/21 selfed (H13/51), triangles H35/21 crossed to green wattle tree E5 and black circles H35/21 crossed to black wattle tree B5.

FIG. 4.—Pinnule number and pinnæ number in the F_2 and back-crosses from H35/44/25 (= H35/25), an F_1 tree having a high value for the two characters. Open circles, H35/25 selfed (H15/51), triangles H35/25 crossed to green wattle tree E5 and black circles H35/25 crossed to black wattle tree B5.

characters was of a different order and there is little doubt that the significant correlations shown in table 4 are due, in part at least, to the association of genes which determine the characters.

The number of individuals in the F_1 was too low to determine with any degree of certainty whether there was any significant correlation between the characters. There was, however, some indication that pairs of characters tend to be associated. Taking again two of the most divergent F_1 trees, H35/21 and H35/25, the former having the lower number of pairs of pinnæ also had a lower number of pinnules, and wider spacing between the pinnules than the latter (table 2, plate I). Correlation of characters in the F_1 , if it really occurs, would point to a pleiotropic effect of the genes concerned.

In the F_2 families, all combinations of pairs of characters showed correlation to a greater or lesser extent, that between pinnule spacing and pairs of pinnæ being weak and showing significance only when the five F_2 families were grouped.

Tests were made for each pair of characters to determine whether there were significant differences in the correlation coefficients within each group of families derived from the H35 hybrids. For the most part the differences were well within the limits of sampling errors, but in the F_2 group, for two pairs of characters the correlations differed significantly between the families, those between pinnule spacing and pinnule length at the 5 per cent. level and between pinnule number and pairs of pinnæ at the 1 per cent. level (table 4). Since correlations between parental characters in segregating generations may be due to pleiotropy, gametic and zygotic elimination, or linkage, it must be assumed that the five F_1 trees, from which these F_2 families were derived, differ amongst themselves for one or more of these factors. The correlations can hardly be due to pleiotropy since, if they were, they would be expected to be consistent and not to show abrupt changes such as occur in the F_2 . Gametic and zygotic elimination may account for some of the overall correlation of characters, but it seems unlikely that they are responsible for the heterogeneity in the F_2 families. If they were the cause, it is improbable that only one out of the six pairs of characters would be affected, as is clearly the case in H14/51, and it is likely that differences in the fertility of the F_1 trees on selfing would occur. As shown in table 1, there is no indication of any such differences. It seems probable, therefore, that the heterogeneity of the correlations is due to changes in the linkage relations of the characters concerned.

There was no evidence of heterogeneity in the back-crossed families, except possibly in the back-cross to black wattle, where the coefficient between pinnule number and pairs of pinnæ approached the level of significance. When the families were grouped within each back-cross, the correlation coefficients were very much of the same order as the F_2 , taking into account the smaller number of individuals involved.

TABLE 4
Partial correlations between pairs of characters in parent species, F_1 , F_2 , and back-crossed families
 A = pinnae spacing; B = pinnae length; C = number of pinnae; D = pairs of pinnae

Family	Number of trees	D.F.	r AB CD	r AC BD	r AD BC	r BC AD	r BD AC	r CD AB
Black	45	41	+0.615**	-0.430**	-0.154	+0.083	+0.044	+0.091
Green	24	20	+0.408**	-0.329	-0.221	+0.201	+0.068	+0.115
F_1	5	1	+0.484	-0.165	-0.052	+0.645	-0.688	+0.916
$H_{12/51}$	61	57	+0.821**	-0.640**	-0.043	+0.402**	-0.275*	+0.422**
$H_{13/51}$	100	96	+0.791**	-0.487**	+0.222*	+0.346**	-0.376**	+0.643**
$H_{14/51}$	39	35	+0.723**	-0.681**	+0.210	+0.467**	-0.481**	+0.157
$H_{15/51}$	41	37	+0.465**	-0.418**	+0.270	+0.295	-0.484**	+0.685**
$H_{16/51}$	13	9	+0.640**	-0.062	-0.074	+0.191	-0.325	+0.250
χ^2 Heterogeneity	...	4	11.282	6.835	3.748	3.940	1.896	13.393
P	...	...	0.05-0.02	0.20-0.10	0.50-0.30	0.50-0.30	0.80-0.70	<0.01
Average r	254	229	...	-0.538**	+0.154*	+0.365**	-0.387**	...
$H_{17/51}$	43	39	+0.613**	-0.474**	+0.011	+0.239	-0.260	+0.322*
$H_{18/51}$	34	30	+0.726**	-0.201	+0.004	+0.266	-0.296	+0.721**
$H_{19/51}$	32	28	+0.631**	-0.554	+0.283	+0.593**	-0.557**	+0.607**
χ^2 Heterogeneity	...	2	0.752	2.750	1.553	3.514	2.234	5.703
P	...	...	0.70-0.50	0.30-0.20	0.50-0.30	0.20-0.10	0.50-0.30	0.10-0.05
Average r	109	94	+0.656**	-0.423**	+0.088	+0.363**	-0.364**	+0.549**
$H_{7/52}$	22	18	+0.835**	-0.788**	-0.105	+0.773**	-0.268	+0.297
$H_{8/52}$	9	5	+0.381	-0.259	-0.495	+0.506	-0.182	+0.421
$H_{9/52}$	6	2	+0.513	-0.879	+0.351	+0.191	+0.117	+0.586
χ^2 Heterogeneity	...	2	2.288	2.265	0.913	1.256	0.164	0.182
P	...	...	0.20-0.10	0.20-0.10	0.70-0.50	0.70-0.50	0.95-0.90	0.95-0.90
Average r	37	22	+0.773**	-0.733**	-0.162	+0.718**	-0.236	+0.336

* Significant at 5 per cent. level.

** Significant at 1 per cent. level.

8. DISCUSSION

Although green and black wattles may be crossed without much difficulty, the hybrids show considerable sterility compared with the parents. Since meiosis is regular, this sterility cannot be due to gross cytological abnormalities, but must be attributed rather to gene differentiation between the species, leading to genetic or zygotic elimination or to weakly offspring. Gametic elimination almost certainly occurs, but was not easy to assess since pollen is shed in the form of pollinia, each consisting of sixteen grains. There was, however, considerable evidence of zygotic elimination, since failure occurred at all stages from tiny embryos to full-sized, but shrivelled and inviable seeds. Such elimination must necessarily restrict recombination of parental characters and it is not unreasonable to suppose that zygotes having potentially the greatest genetic diversity are the most likely to be eliminated. The F_1 hybrids from G35 were, on the whole, well below the average vigour of the parents and they showed chlorosis in the early stages of growth (Philp and Sherry, *loc. cit.*). These symptoms of unbalance were accentuated in the F_2 , where many abnormal and semi-lethal types occurred (Anon., 1952). The individuals on which the leaf characters were measured must, therefore, be considered to be the more balanced residue remaining after the more extreme types had been eliminated.

Most of the differences between the species showed blending inheritance and may be assumed to be controlled by polygenes, but at least one major gene difference occurred also. The difference in the period taken to ripen seed, four months in green wattle and fourteen months in black wattle, appears to be governed by two major genes, either or both of which, when dominant, causes the seed to ripen in the shorter time (Anon., 1955). Leaf characters, however, were all polygenic in inheritance and their behaviour is of considerable interest, since characters of economic importance are likely to behave in a similar manner.

Anderson (1939) has studied in detail recombination in species crosses in *Nicotiana*, and the behaviour of the wattle hybrids would seem to be very similar, taking into account the greater heterogeneity of the wattle parents. He showed that recombinations in the F_2 of species hybrids are only an insignificant fraction of the possible recombinations on free assortment and that there is a strong tendency for parental characters to stay together. This tendency is obvious in the leaf characters studied in wattle hybrids, but it is not confined to the leaf characters only, for although our records are not completed, it is evident that F_2 trees having a foliage type close to one or other of the parents also have flower colour and stem ridges close to that parent. This is in line with Anderson's conclusion that "all quantitative characters of an organism are closely linked with one another". Such linkage of characters is of considerable practical importance.

It must be assumed that, in wattle hybrids, characters of economic importance such as general hardiness and the percentage, colour, and quality of tannin will follow the pattern of the leaf characters and will, in general, tend to be associated with other, possibly undesirable, characters of the parent from which they were derived and that it may be difficult or impossible to separate them. The fact that pinnule number and pinnæ number are fairly closely correlated in three F_2 families and not in the fourth ($H_{14/51}$) shows, however, that for some characters at least, the association may be broken at an early stage in the breeding programme.

Since segregation occurs in the F_1 , it may be possible by choice of parent trees and by selection amongst the hybrids to start off with a relatively advantageous combination of characters, and since there is a parent-progeny correlation between the F_1 parent and its offspring, this advantage will tend to be passed on to later generations. For instance, the F_1 parent of family $H_{14/51}$ was closer to black wattle in leaf characters than the other F_1 hybrids and the mean of $H_{14/51}$ was also closer to black than the other F_2 families. Since all quantitative characters in an organism tend to be linked, it is probable that the tannin characteristics of this family will, on the whole, be closer to black wattle than those of a family having leaf characters more akin to the green parent. Even among the small number of F_1 hybrids derived from $G_{35} \times B_{18}$, there was a range of genotypes and it must be expected that if the numbers in the F_1 were greater, or different trees from the species used to make crosses, this range would be greatly increased. Thus, the F_1 hybrids from the green wattle tree G_{33} were, on the whole, as vigorous as open-pollinated seedlings from that tree, whereas the hybrids from G_{35} were considerably lower in vigour than its open-pollinated progeny (Philp and Sherry, *loc. cit.*). It is evident that only by making a large number of crosses between different trees from the two species, and by growing a considerable number of F_2 families from the resulting hybrids, could any assessment of the range of variation in the hybrids be reached.

Although great diversity may be expected, it is worth while considering from a practical point of view, the economic value of green and black wattle hybrids. Commercially, black wattle is almost the only species grown, but green has certain attributes on the credit side. It is generally considered to be hardier under dry conditions, it produces straighter (but possibly more brittle) poles, it appears to be less susceptible, but not resistant to damage by bagworm (*Kotochalia junodi*), and probably by froghopper (*Bythoscopus cedaranus* and *Lygidolon lævigatum*), and to recover more quickly when attacked. On the debit side, green wattle has thinner bark, sharp stem ridges which render stripping more difficult, and tannin with higher colour values and poorer quality than black wattle. The credit characters of green wattle are rather vague and of a type hard to assess; they are of the kind it is difficult or impossible to follow

Photographs of typical leaves of green and black wattles, two diverse hybrids from the same parents and the selfed and back-crossed families from these hybrids.

through the welter of hybrid segregation without making elaborate tests. Possibly the most important and most favourable of these characters to pursue would be the partial tolerance to bagworm attack. But because of the preponderance of black wattle grown, the bionomy of the bagworm is largely adjusted to this species and it seems highly probable that, with its high biotic potential, the bagworm would quickly swing over and attack green wattle just as severely as black if the relative amounts of the two species were reversed. Force is lent to this argument by the fact that although bagworm is an insect primarily attacking species of *Acacia*, in recent years it has attacked and defoliated oaks, pines, eucalypts, and other species (Ossowski, 1956), and has established a breeding cycle on oaks (Ossowski, personal communication).

In practice, it will seldom or never be possible to incorporate one or more quantitative characters of one species with those of the other species without affecting other characters also (Anderson, *loc. cit.*). If, for instance, we wish to combine the high quality tannin of the black wattle with the partial bagworm resistance of the green wattle, then we shall probably have to sacrifice some of the quality on one side and some of the resistance on the other. Where the resistance is of doubtful value this is clearly a bad bargain.

It would seem, therefore, that unless some more clear-cut, or at least easily assessed, advantages are discovered in green wattle, it would be unwise to embark on an elaborate programme attempting to combine its somewhat vague advantages with those of black wattle. There is, however, one exception. The shorter time taken to ripen seed in green wattle appears to be controlled by two major dominant genes. As far as we know, this character has no economic value *per se*, but from a breeding point of view it would be of great value to have seed ripening in four months instead of fourteen. The indications are that by a back-crossing technique transfer of this character from green to black wattle will be a relatively easy matter.

9. SUMMARY

1. Hybrids between green and black wattles can be produced relatively easily, but show a considerable reduction in fertility compared with the parents.

2. Four leaf characters selected for detailed study appeared to be polygenic in inheritance, but significant differences between F_1 trees from the same parents occurred for all four characters. These differences tended to persist in the F_2 and back-crossed families, showing a parent-progeny correlation.

3. Recombination of the characters of the two parents does not take place at random, but there is a marked tendency for characters coming in from one species to remain associated. For some characters there are, however, abrupt changes in the correlation value between F_2 families derived from the same original parents.

4. Because of the blending nature of polygenic characters and the tendency for parental characters to remain associated, it is concluded that, unless some desirable character controlled by major genes is detected in green wattle, a large-scale breeding experiment to attempt to combine the qualities of the two species is not justified.

10. REFERENCES

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