with one's neighbours. If the overall advantage favours a territory sexual selection may now operate by the Fisher process to increase the territorial instincts beyond their advantage in natural selection. It would be interesting to compare the yearly death rates of parents and offspring from territories of different sizes and the yearly death rate of unmated individuals.

Fisher's concept of making the greatest contribution to future generations for a given amount of parental expenditure on reproduction provides a possible explanation of how territorial behaviour can be favoured in natural selection. Sexual selection may exaggerate this selective effect so that territory, display and social structure all evolve together. There is no need to postulate group selection which is of doubtful validity for any evolutionary mechanism. Perhaps many of the examples of the apparent adaptation of populations rather than individuals should be examined again with the help of Fisher's theory.

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CHLORIS GAYANA WITHOUT ANTHOCYANIN COLOURATION

A. V. BOGDAN

Grassland Research Station, Department of Agriculture, Kitale, Kenya

Rhodes grass (*Chloris gayana* Kunth), an important ley grass in the tropics, normally has a distinct purple colouration on the spikelets, the racemes of the panicle, the nodes of the stem, the lower leaf-sheaths and on the coleoptile in the seedlings. In northern Kenya (Baringo, Sigor, Marsabit) near the northern limits of *Chloris gayana* in East Africa, the purple colour is often less evident and there are forms with yellowish panicles only slightly tinged with purple. Plants without any anthocyanin colouration occur only very occasionally. In 1958 a few non-purple plants were found at the Kitale Grassland Research Station, in a seed field of the tetraploid (Bogdan, 1961) " Mbarara " variety (Kitale Introduction No. K53166) and four such plants were transplanted to an isolated plot. In the non-anthocyanin plants the young panicles are bright yellow in colour and these plants will further be referred to as Yellow (Y) as distinct from the normal Purple (P) plants. It was thought that the non-purple plants of *Chloris gayana* were recessive and homozygous for their colour genes and could, therefore, be used for studies of breeding behaviour and

of isolation requirements, in the same way that similar non-purple plants of *Lolium perenne* have been used at the Welsh Plant Breeding Station (Jenkin, 1931 ; Griffiths, 1950). The absence of purple colouration in seedlings made these plants particularly valuable for genetical studies.

In 1960 the yellow plants were crossed among themselves, and also with normal purple plants. This was first done in greenhouses with electric fans working during the flowering period, to increase the circulation of pollen. Two Y clones were placed together in one greenhouse for the time of flowering and a Y clone was placed together with a P clone in another house. Four hundred seeds of each mother plant were then planted in boxes. Seeds of $P \times Y$ produced 257 seedlings—all purple ; seeds of $Y \times P$ produced 103 seedlings—101 purple and 2 yellow ; seeds of $Y \times Y$ produced 94 seedlings—all yellow. All further crosses $Y \times P$ resulted in all purple seedlings and further $Y \times Y$ crosses in all yellow seedlings except one ascribed to imperfect isolation. These results confirmed the recessive character of the absence of anthocyanin in *Chloris gayana*. The presence of two yellow seedlings in the lot grown from seed of the yellow plant which flowered in the same house with a purple plant is explained by partial self-pollination, here to the extent of 2 per cent. The essentially cross-pollinating nature of *Chloris gayana* has thus been confirmed, at least for the Mbarara variety.

For a study of F_2 four purple plants were selected out of 101 purple seedlings grown from seed of the yellow mother plant crossed with a purple plant. They were apparently heterozygous in regard to their genes for anthocyanin colouration and are further referred to as H (Hybrid). In 1961 the heterozygous H plants were crossed among themselves and also backcrossed to Y clones. As before, the pollination was natural, without emasculation, but was done this time in the open because in 1960 the formation of seed in the greenhouses was rather poor. The crossing plants were reasonably well isolated from all other plants of Rhodes grass. Seeds from the crosses were planted in 1962 and the segregation of purple and yellow seedlings in F_2 suggests two pairs of complementary alleles. The numbers of purple and yellow seedlings is shown in table 1.

In the normal F_2 the recorded figures are remarkably close to the 15 : 1 ratio expected for two pairs of alleles. In the progenies of $Y \times H$ backcrosses the observed figures are again very near to the expected ratio of 3 : 1. However, in the progenies of $H \times Y$ backcrosses the observed figures deviate very considerably from the expected ratio, with $P < 0.01$. This deviation can be explained by the poor qualities of the yellow plants as male parents (this has been noticed on other occasions). Moreover, the growth of non-purple seedlings resulting from backcrosses with yellow plants as male parents, was often arrested very early, before it was possible to decide about the colour of the coleoptile. The non-purple seedlings were generally weaker and grew more slowly than the normal purple seedlings. In 1960 the mean air dry weight of 100 18-day-old purple seedlings was found to be 16 gr. as compared with 10 gr. for the yellow seedlings.

The segregation figures indicate that two complementary genes govern the anthocyanin colouration in *Chloris gayana*, as in *Lolium perenne*. Following Jenkin (1930), and some earlier authors, these genes can be denoted as R and C. There is, however, some difference in the inheritance of purple or red colouration in the two grasses. Jenkin has found that in *Lolium*

perenne the red colour appears only when both dominant factors, R and C, are present ; if either of them is absent then the plants show no red pigment. In *Chloris gayana* the position seems to be reversed and the purple colour appears when either both or one of the dominant genes are present. Only when they are both absent, or, in other words, when they are both in their recessive form of c and r, do the plants show no traces of purple colouration.

The non-anthocyanin yellow Rhodes grass described in this paper is not vigorous and not leafy enough to warrant its introduction into cultivation. It has, however, an interesting and perhaps valuable feature which

TABLE 1

Segregation of purple (P) and non-purple (Y) seedlings in F_2

Crosses	No. of seedlings				χ^2	P
	recorded		expected at 15 : 1 or 3 : 1 respectively			
	P	Y	P	Y		
	$F_1 \times F_1$ progenies					
H×H	1002	69	1004·00	67·00	0·064	0·80
	Backcrosses to Y					
Y×H	347	117	348·00	116·00	0·011	0·90
H×Y	591	138	546·75	182·25	14·324	<0·01

seems to be connected with the absence of anthocyanin. In normal purple varieties of Rhodes grass certain physiological disorders are often accompanied by intensification of purple colouring, a fact well known for many plants (Onslow, 1925). The first sign of the effect of drought on Rhodes grass is often shown in the purple colour of the leaves. The infection by a *Helminthosporium* fungus is also accompanied by more pronounced purple colour around the infected points and in a considerable portion of the leaf seemingly not otherwise affected. The leaves of the non-anthocyanin variety develop little if any purple colouration even when diseased, they seem to suffer from drought much less than the leaves of the ordinary types, and with the onset of the dry season the herbage remains green for a longer time. The non-purple variety seems also to be highly resistant to *Helminthosporium*. It is not clear how these phenomena are connected with the absence of anthocyanin.

The non-anthocyanin variety has been used in an exploratory trial to study the contamination of Rhodes grass when two or more varieties are grown in close proximity. In 1960 a plot of the yellow variety, 100 feet by 46 feet, was planted with mixed roots of several clones, and this was surrounded by a 6 feet strip of the normal purple Mbarara variety. Samples

PURPLE RHODES GRASS

4' ● 67(36)

7' ● 63(17)

10' ● 42(17)

16' ● 29(11)

YELLOW RHODES GRASS

PREVAILING WIND

26' ● 22(11)

38' ● 33(10)

2'	5'	11'	17'	17'	11'	8'	5'
●	●	●	●	●	●	●	●
75	68	73	52	16	23	21	24
(41)	(36)	(36)	(30)	(8)	(10)	(12)	(12)

38' ● 20(8)

YELLOW RHODES GRASS

26' ● 25(6)

14' ● 37(21)

8' ● 33(11)

5' ● 41(27)

2' ● 39(27)

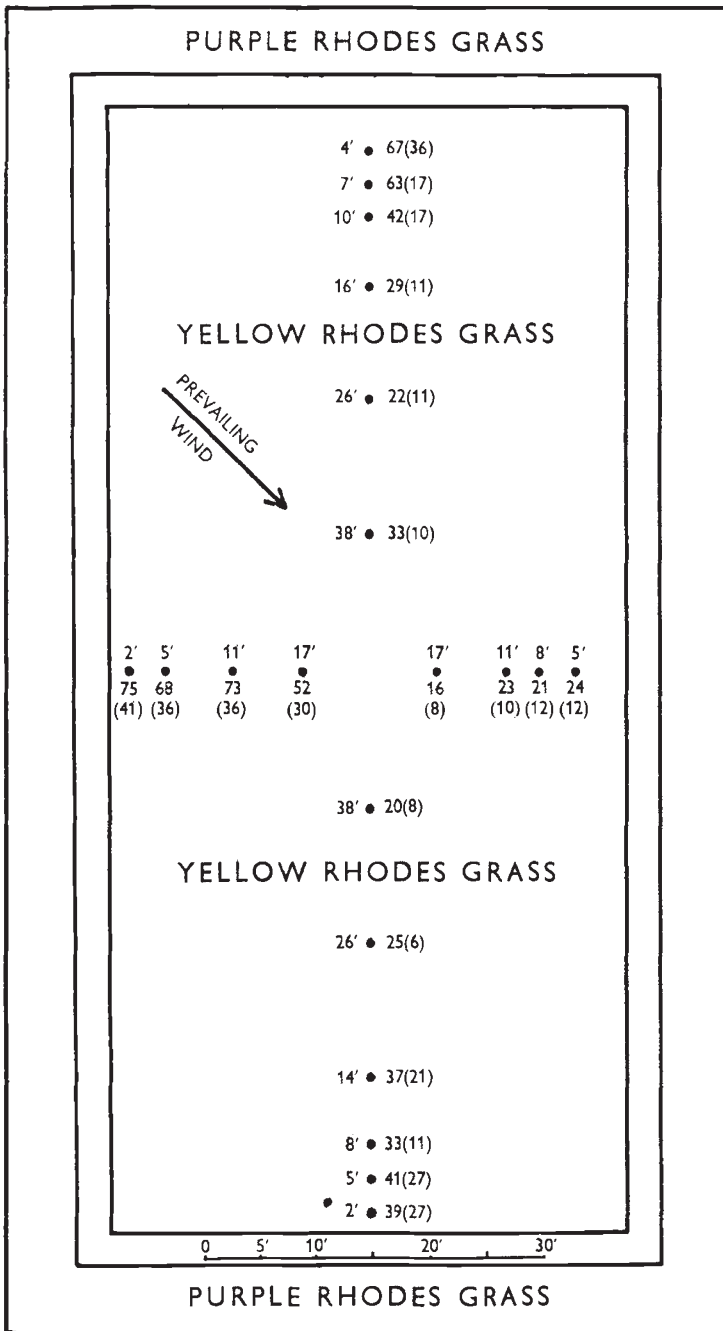0   5'   10'   20'   30'

PURPLE RHODES GRASS

FIG. 1.—Contamination of recessive yellow Rhodes grass at various distances from the surrounding dominant purple Rhodes. The figures show the numbers of purple seedlings as a percentage of all germinated seeds ; figures in brackets denote the percentage of purple seedlings in relation to the total number of seeds placed for germination.

of seed were taken from several points at various distances from the purple plants and the seedlings were examined for colour. The arrangement of the trial and the percentage of purple seedlings germinated from seed samples taken at various distances from the purple plants is shown in fig. 1. This trial was planted before the best seeding yellow clones were selected, the seed formation was therefore generally poor with a large proportion of small under-developed seeds. These poor seeds either did not germinate or the seedlings died before they could be classified for colour. Of the weak and abnormal seedlings which could be classified for colour, nearly all were non-purple, so I believe that most, if not all, poor seeds would have produced non-purple seedlings. The figures for the percentage of purple seedlings based on the *total number of seeds* placed for germination, and not on the number of classified seedlings would, perhaps, be closer to the percentage contamination if both varieties had good seed formation. Even these figures (given in brackets in fig. 1) show considerable pollen contamination which is mostly higher than that obtained by Bateman (1947), except in the zone close to contaminant. It is intended to repeat the trial on a larger scale using only clones with fairly good seed formation, and also to do one on the lines of Griffiths' study at Aberystwyth (Griffiths, 1950). Nevertheless, even this imperfect trial has shown that contamination can be high and that a good distance may be required to isolate varieties, at least those with the same chromosome numbers.

1. SUMMARY

A non-purple variety of *Chloris gayana* has been studied at the Kitale Grassland Station in Kenya for the inheritance of anthocyanin colouration. The non-purple plants have been found to be recessive and homozygous for colour and the segregation ratio in F_2 suggests that two complementary genes are involved. The non-anthocyanin plants have been used to confirm the xenogamous nature of *Chloris gayana* and to investigate the degree of pollen contamination which has been proved to be quite considerable.

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