SPBS Record 1964

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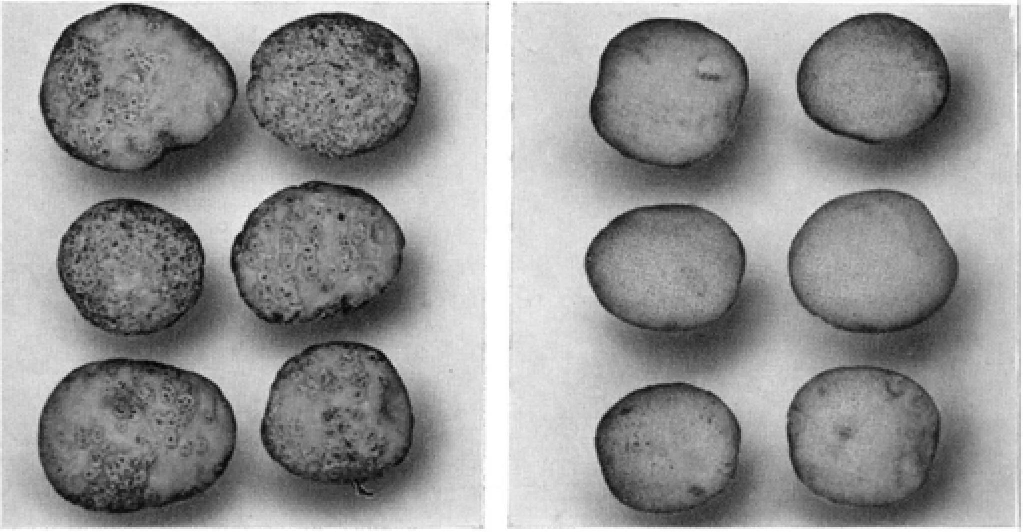

Common Scab Trial at Archerfield
Tubers of Susceptible 'Redskin' (*Left*) and Resistant Seedling 3070 d (3) (*Right*)

A Genecological Trial of Hill Grasses from 'Flushed' and Leached Soils

SCOTTISH PLANT BREEDING STATION
PENTLANDFIELD, ROSLIN, MIDLOTHIAN

RECORD

1964

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(1964)

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(1964)

DIRECTOR'S REPORT

Potatoes.—An early maturing seedling selection, Ref. No. 2558a(17), has completed the Merit Trials conducted by the Department of Agriculture and Fisheries for Scotland and has received commendation. This seedling was bred from 'Craigs Royal' and a selection derived from 'Aquila' (a German cultivar), 'Southesk' and the South American diploid species *Solanum phureja*. It has been named 'Pentland Glory.'

The Registration Authority's official description of 'Pentland Glory' is as follows :—

Maturity .	First Early.
Tuber . .	Kidney (long oval), thick, pointed at heel ; skin white, smooth ; flesh pale cream, fairly firm ; eyes on the point, shallow ; sprouts pink (very faint).
Foliage Type	'Arran Pilot'.
Foliage .	Haulm of low to medium height, flat-topped, spreading slightly ; stems of average frequency, medium thickness, green, occasionally branched ; wings narrow, mainly straight ; leaf of medium size, fairly long, open ; leaflets large, broad-oval, dark-green, glossy, lobes even ; secondary leaflets frequent, small, rounded.
Flower .	White, tinged green at tips, large, infrequent, anthers orange ; buds green.
Remarks .	Cropping : very good ; cooking quality : fairly good ; keeping quality : very good for an early variety ; field-immune from virus A, high degree of resistance to virus Y ; fair resistance to dry rot, susceptible to gangrene, moderate susceptibility to skin spot.

Three varieties raised at the Plant Breeding Station and grown commercially in East Africa have completed the Wart Disease and Identity Tests conducted by the Department of Agriculture and Fisheries for Scotland. They are 'Roslin Eburu,' 'Roslin Chania' and 'Roslin Mt. Kenya.' The fourth, 'Roslin Elmenteita,' proved to be susceptible to wart disease (*Synchytrium endobioticum* (Schilb.) Perc.).

As in previous years, samples of tubers were sent overseas for trial and experimental purposes. The blight epidemics that have occurred in several tropical and subtropical regions have created a greater need for resistant varieties adapted to short day-length conditions. For that purpose, 'Roslin Eburu' has been successful in East Africa and has also attracted attention in South Africa and neighbouring countries. A greater range of field resistant varieties is, however, required and attempts are being made to produce them.

Blight is also a problem in India, where resistant varieties covering a range of maturity groups are required. In cooperation with Dr Pushkarnath, Central Potato Research Institute, Simla, relatively unselected progenies raised at Pentlandfield have been forwarded for trial and selection under local conditions. During the past three years fully 7,000 such samples have been supplied and recent reports indicate that many promising types have been selected for further trial and multiplication.

The experiments designed to produce commercially acceptable seedlings with maximum resistance to blight were continued. For this purpose over 5,000 seedlings bred from blight resistant parents were raised and tested for reaction to race 1,2,3,4 of *Phytophthora infestans* (Mont.) de Bary. The majority of these progenies were bred for field resistance, the parent plants possessing no R genes effective against race 1,2,3,4. In the remaining progenies, new R genes were present and they segregated hypersensitives and susceptibles in Mendelian fashion. In the course of the tests the blight susceptible segregates were eliminated and both the hypersensitive and field resistant survivors were transplanted into pots and grown to maturity. At harvest they were selected on the basis of visible economic characters and 829 were retained for further trial and selection under field conditions.

Tests for reaction to race 1,2,3,4 were also carried out on 310 advanced selections raised in the general breeding programme. They were grown in pots and sprayed with a spore suspension when about 6 in. high. Some of them proved to be hypersensitive, due to the presence of a new R gene, while the remainder were evaluated for degree of field resistance.

The culture of race 1,2,3,4 used in the above screening tests has been employed for this purpose for several years and it has occasionally given rise to a blight lesion on plants which initially reacted as hypersensitive. This suggested that the culture was not uniform and contained an occasional spore capable of attacking plants possessing genes other than R_1, R_2, R_3 and R_4. Isolates from such lesions were tested for their reaction on a series of genotypes known to be hypersensitive to race 1,2,3,4 and five different races were distinguished. Among the genotypes were two from Canada and one from Germany which have been tentatively designated R_5 (Canada), R_6 (Germany) and R_7 (U.S.A. and Canada), by the Late Blight Investigations Committee of the Potato Association of America. Two further genotypes bred at Pentlandfield from *S. demissum* (C.P.C.2172), which was also the source of genes R_1, R_2, R_3 and R_4, showed by their reactions that they possess genes different from those tentatively labelled R_5, R_6 and R_7 in the U.S.A. Since more than one species is involved it is suggested that the numbering of R genes should be further considered in relation to the species from which they were derived.

Cultures capable of overcoming genes in addition to R_1, R_2, R_3 and R_4 were used in a study of " field resistance " on detached leaves of forty-eight seedlings and two named varieties. The varieties were placed in five groups according to the size of the lesions and the extent of sporulation in them. The most resistant seedlings, those with the smallest lesions and least sporulation, were placed in Group 1 while the most susceptible were placed in Group 5. An assessment of the " field resistance " of a number of the seedlings had been made previously under natural conditions in Mexico. The results from the tests using detached leaves showed a close correlation with those obtained in Mexico.

Twelve named cultivars and 252 advanced seedlings were tested for susceptibility to common scab under natural conditions at Archerfield, East Lothian. A number of the advanced seedlings were more resistant than 'Frühperle' and 'Ackersegen' which were the most resistant of the named varieties.

Six named cultivars and twenty-four seedling varieties which showed different degrees of susceptibility in the scab trial at Archerfield in 1962 were grown again at Archerfield and at two other centres where scab is reputed to be troublesome. At one centre, Parkconon, Arbroath, Angus, no common scab was observed, possibly due to the wet growing season being unfavourable to the development of the disease. At the other centre, Dunston Farm, Burton, Wirral, Cheshire, the tests were conducted by Mr B. C. Knight of the National Agricultural Advisory Service, Wolverhampton. The results obtained there were closely correlated with those obtained at Archerfield, suggesting that seedlings which appear to be resistant at Archerfield are likely to remain so elsewhere. These trials will be continued in 1964.

Extensive infection with black scurf (*Corticium* (*Rhizoctonia*) *solani* (Prill & Delacr.) Bourd & Galz.) occurred among tubers grown at Archerfield and the incidence of the disease was recorded. A number of the seedlings appeared to be resistant or only slightly affected by the disease and there was some evidence that their resistance was related to that of the parental material.

Thirty-two named and seedling varieties growing in the field at Pentlandfield were inoculated to investigate their susceptibility to blackleg (*Erwinia atrospectica* (van Hall) Jennison). In some varieties only small localised lesions appeared at the point of inoculations on the stems while in others complete collapse of the stems occurred. In many instances intermediate infection occurred but in any one variety expression of the disease was uniform. Among the apparently resistant varieties were some which have been found to be susceptible to blackleg in the field and it is probable that such varieties may carry the causal organism in the tubers. Whether tubers infected in this way give rise to infected plants in the following season has not been proved but further investigation is suggested.

In recent years gangrene (*Phoma solanicola* Prill. & Delacr. *sensu* Köhler) has occasionally proved troublesome ; therefore, tests were set up to evaluate methods of testing for susceptibility to the disease and to examine the susceptibility of thirty-three named and seedling varieties. Where the tubers were inoculated by wounding, the measurements of resulting lesions were recorded. One seedling proved to be the most resistant of all the material tested, and it was considerably less susceptible than ' Arran Consul,' the most resistant cultivar used as a control. Ten varieties were slightly more susceptible than ' Arran Consul,' showing a level of resistance similar to that of ' Royal Kidney.'

Tubers were also inoculated by dipping in a suspension of mycelium and spores of *P. solanicola*. In this case the conditions required to allow penetration of the fungus led to considerable development of dry rot and bacterial soft rot so that the results were not entirely satisfactory. However, this method gave an indication of the extent of infection through the " eyes " which was found to differ considerably in different varieties. In some, infection was mostly on the " eyes " while in others the " eyes " remained unaffected, even though numerous gangrene lesions were present on the tubers. On one variety infection was present only on the " eyes." The results obtained by the two methods of test were not correlated and it is evident that in tests for susceptibility to gangrene infection through wounds, lenticels and " eyes " must all be considered.

Tubers of 168 advanced seedlings were inoculated with a suspension of *Oospora pustulans* Owen and Wakef. in order to examine their susceptibility to skin spot. Resistance to the disease was evident in a number of seedlings.

The control of potato root eelworm by means of population-specific resistance still appears to be a practicable proposition. Therefore, the routine breeding to Merit Trials standard in the lines stemming from *S. tuberosum* subsp. *andigena* C.P.C. 1673, *S. multidissectum* and to a lesser extent *S. spegazzinii* (*S. famatinae*) was continued. The last named breeding line was originated by Professor Ross of the Max Planck Institute, Cologne. Its resistance gene F_a is indistinguishable at present from the gene H_1 ex C.P.C.1673. It is proposed to expand the *spegazzinii* line at the expense of the C.P.C.1673 line, partly in order to diversify the material, partly because C.P.C. 1673 itself was very susceptible to potato blight.

The inheritance of resistance in a less advanced breeding line ex *S. sanctae-rosae* is explained in an Occasional Paper, p. 41. The main factor responsible for this resistance proved to be a dominant gene which remains indistinguishable from the H_2 gene of *S. multidissectum* as far as the strains of potato root eelworm maintained at Pentlandfield are concerned. Experimental breeding is being done in connection with the F_b gene of *S. spegazzinii* and resistance in " *S. camarguense*," using material received originally from Professor Ross in both cases.

A collection of Central American potatoes, supplied by Professor Hawkes of Birmingham University, was screened for resistance to the Boghall and Duddingston strains of potato root eelworm with a view to maintaining the supply of selected, resistant material for genetic investigation. The material comprised up to five progenies each of *S. morelliforme*, *S. bulbocastanum*, *S. clarum*, *S. cardiophyllum* subsp. *ehrenbergii*, *S. pinnatisectum*, *S. sambucinum*, *S. agrimonifolium*, *S. oxycarpum*, *S. demissum*, *S. verrucosum*, *S. iopetalum*, *S. polytrichon*, *S. stoloniferum* and *S. polyadenium*. None of this material gave indication of worthwhile comprehensive resistance to the two strains, although there was a good deal of resistance to the Duddingston strain. This strain has been cultured selectively for longer than the Boghall strain and seems in consequence to be the more specialised and weaker strain. Since dominant genes for resistance to the Duddingston strain were already available in the breeding lines stemming from *S. multidissectum* and *S. sanctae-rosae*, none of the Central American material was selected for breeding purposes. South American potatoes thus remain the sources of all the resistance to potato root eelworm in use or under investigation at Pentlandfield.

Other investigations are concerned with the potato root eelworm itself, especially with the inheritance of " resistance-breaking " qualities, using breeders' strains of genetically fixed specificity as far as possible. Last year's *Record* reported a failure to detect biotypes of class 1,2 in F_1 and F_2 populations resulting from mixing strain 1 with strain 2. There was evidence of reduced viability in the F_1 and F_2 populations but no definite evidence of cross breeding. This prompted the development of a new technique which will be used this year to compare the percentages of resistance-breaking biotypes emerging from separate cysts which were produced last year by the same population in the same plant.

Breeding for combined resistance to X, Y and leaf-roll viruses was continued with the introduction of a further 8,700 seedlings into trials. Initial selections based on glasshouse tests for resistance to X and Y viruses and field assessment of economic characters reduced this number to approximately 1,200 seedlings for extended trial under exposure to infection with the leaf roll virus. Earlier selections which were exposed to infection at Elvingston, East Lothian, in 1962 were evaluated in field plots grown at Pentlandfield in 1963. Laboratory tests had indicated a low spread of leaf-roll in this material in 1962 (*Record*, 1963, p. 22) and this was confirmed in the evaluation plots which revealed an overall infection of 7·6 per cent as against

51 per cent in the corresponding trials of 1961. Indications obtained from current laboratory tests are that the spread of leaf-roll during 1963 was also very low both at Elvingston and at Cambridge. These low rates of infection considerably retard progress, and measures to overcome them are under active consideration at the experimental stage.

The utility of laboratory testing for the presence of leaf-roll in " carrier " material has been confirmed by graft tests from suspected carriers to indicator plants. In consequence the laboratory tests have been greatly extended to cover the whole of the material in advanced stages of trial.

From the trials carried out at Elvingston and Cambridge on seedlings entered for Merit Trials it was found that the new cultivar ' Pentland Glory ' is very resistant to virus Y with a score of no infections as compared with a mean of 42·4 per cent and a maximum of 95·4 per cent infection in control cultivars, and that it is also below average in its susceptibility to leaf-roll with an infection value of 4·7 per cent against a mean of 19·6 per cent and a maximum of 52·3 per cent.

Experimental work on the relationships between genes controlling reactions and resistance to X and Y viruses was continued in an examination of the relationships between genes controlling reaction to X viruses in cultivars of *S. tuberosum* forms of *S. tuberosum* subsp. *andigena* and *S. acaule.* It was established that whereas a gene controlling immunity from X viruses in *andigena* is independent of a gene with similar effect in *S. acaule,* a gene controlling necrotic responses to X viruses in *andigena* is allelic with the gene for immunity in *S. acaule.* Thus it would seem that there are two independent loci for genes controlling immunity from X viruses and that, on present evidence, only one of these, that in *S. acaule,* is also the locus of a gene controlling necrotic reaction to these viruses. The similarity in effect of the necrotic genes in *andigena* and in *S. acaule* together with their joint allelomorphy with the immune gene in the latter species suggest that the presence of the gene in *S. tuberosum* subsp. *andigena* is due to introgression of this species from *S. acaule.*

Further work with genes controlling reaction to Y and A viruses in *S. stoloniferum* has indicated identity of genes controlling immunity from these viruses in the lines C.P.C.28.4 and C.P.C.9 and allelomorphy between these genes and a gene controlling strong necrotic reactions to Y and A viruses in C.P.C.12. No relationship has yet been traced, however, between these genes and three other genes in the species which control differential effects to the Y and A viruses.

One hundred and forty-two seedlings raised from 'Saco' × 11-79 all proved to be susceptible to potato virus S. This result does not support our hypothesis for the mechanism of genetic control of immunity from virus S and further crosses will be made using other parents with 'Saco' which is the only known source of immunity from virus S in potato.

The group 4 strain of virus X (*Record*, 1963, p. 26) was inoculated to 34 potato cultivars of known reaction to potato virus X in order to obtain confirmation of its classification as a group 4 strain. The strain infected systemically 12 cultivars having no X-resistance genes; clear mottle symptoms were observed in most plants and the presence of the virus was demonstrated serologically both in these plants and in those with doubtful symptoms. Equivalent results were obtained with 2 cultivars having the Nx gene only, and the immunity of the cultivar 'Saco' was confirmed.

Nineteen cultivars containing the Nb gene (14 cultivars nxNb, 5 cultivars NxNb) reacted to the virus with a varying amount of necrosis. Many of these cultivars developed necrotic lesions on the inoculated leaves whilst others did not. The virus invaded systemically, usually giving rise to a necrotic mottle, the necrosis usually being more pronounced in those cultivars that had developed necrotic lesions on the inoculated leaves, and the virus was detected serologically in both necrotic and mottled plants.

'Pentland Falcon' reacted rather differently from all other cultivars; one or two necrotic lesions developed on the inoculated leaves and the plants later developed a systemic necrosis but the virus was not detected serologically in any of the several attempts made at different times. The significance of this reaction cannot be assessed until it is known whether the tubers produced by these plants contain virus or not.

The results of cross protection tests and serological cross-absorption tests indicate that the group 4 strain of virus X is very closely related to the C.P.C.2971 virus X isolate with which it was associated and that both are closely related to the group 2 strains of virus X and more distantly related to strains of groups 1 and 3.

Genecology and Herbage Plants.—Hill land species are not lacking in summer productivity and the best of them provide adequate nutrition for the grazing animal but the areas where they occur naturally are restricted and since it seems incontrovertible that sheep, for example, thrive best where they have access to different community types, the productivity of the hills could be increased by the extension of the better habitats. It is inevitable that ecology should be seen as a valuable aid to this end for its importance has been so frequently and rightly emphasised in the past that such an approach is now taken for granted. It is, indeed, essential that the relationship between organisms and their environment should be fully understood and in ecology this relationship is studied at the level of the taxon, usually the species. Genecology is no less concerned with plant-environment inter-relationships but here the emphasis is transferred from recognised taxa to such entities as the investigator is able to detect: these are the units of genecology and they are frequently not amenable to taxonomic treatment. In short the emphasis is on the patterns of variation coupled with a close study of the factors which occasion them. It is for this reason that the genecological studies of hill land species have been continued since it is becoming more and more apparent that such fundamental knowledge is basic to the control of vegetational change and could helpfully precede the evolution of new ideas in management.

The intensive examination of an individual flushed area on the Pentland Hills is the present central activity and many problems have arisen in the investigation of the edaphic environment. In particular a considerable amount of thought and experimentation was devoted to the analytical techniques of determining exchange capacity of soils with a view to improving the reliability and consistency of the results obtained. Most of the experimentation was carried out using dried, milled *Sphagnum* material provided by Dr Derek Ratcliffe of the Nature Conservancy, Edinburgh, because *Sphagnum* behaves as a fairly simple ion exchange medium and is, therefore, preferable to soil as experimental material. In addition it was hoped to be able to provide Dr Ratcliffe with reliable estimations of the cation exchange capacity of different *Sphagnum* species from differing habitats. It was, in fact, possible to give a list of fairly reliable values for twenty-seven species ranging from 65 to 124 milliequivalents/100 gm.. Material was available for six of the species from two different localities and the results were in good agreement. In general, those species which came from the most acid habitats had the lowest values. In addition to the satisfaction gained from being able to produce these results, the techniques which were modified in the light of these analyses have now been adopted for the routine analysis of soils. In addition to providing more reliable figures, a smaller quantity of material is now known to be adequate for a complete analysis and this latter finding has proved very important in several instances.

The genecological study of species which occur on flushed areas has been largely directed towards the detailed examination and evaluation of a field trial laid down in 1962 and consisting of spaced plants grown from the turves removed from the flush under investigation. The main object is to define the amount of variation within each species and to assess its relationship to the environmental conditions in different sites within the flush. It is conceivable that the relatively small area of flushed ground under study (approximately 200 square yards) could be covered by the extensive spread of only a few genotypes of each of the species concerned or alternatively there could be a large number of genotypes occurring very locally. In either case the distribution of the genotypes could be at random or allied to the gradients of edaphic conditions which have already been shown to exist. One of the primary problems was, therefore, that of assessing whether isolates from the sampled turves were from the same or different genotypes.

In the field trial it was quite obvious that some plants were so morphologically similar that they were likely to be ramets of a clone so a series of subjective assessments of the general appearance of all plants in the trial was made at intervals throughout the growing season. These assessments were always made without reference to previous scorings and on occasion with the help of additional observers. The mass of data was then sifted through very carefully and in the case of *Festuca rubra* it has been possible to apportion 247 isolates to 112 groups of similar phenotypes, each group consisting of between 1 and 10 isolates. It may be mentioned that according to the degree of importance attached to apparently trivial similarities and differences, the number of groups could be made to vary from 86 to 198 but the present grouping is thought to be soundly based allowing for a certain amount of natural phenotypic plasticity.

TABLE I

	Units employed	Group index number				
		33	2	14	26	20
Number of isolates		10	4	6	2	12
Position in flush*		30/4L	50, 55	60	75	80, 85
Leaf colour		Light green	Light green	Dark green	Light green	'Oily dark '†
Panicle colour		Khaki green	normal (dull purple)	normal	normal	normal
Infection with *Erysiphe graminis*		Moderate	slight	not infected	severe	moderate to severe
Culm length (excluding panicle)	cm.	54·6	52·9	50·2	45·5	48·0
Panicle length	cm.	7·7	7·9	6·9	8·3	7·3
Degree of compactness of panicle		1·9	2·1	2·5	3·5	2·6
Total panicles produced		211	299	125	5	335
Plant diameter	cm.	62	74	64	59	69
Plant height	cm.	31	31	29	25	31
Plant dry weight‡ (summer 1962)	gm.	16	36	37	29	55
Plant dry weight‡ (summer 1963)	gm.	73	120	110	93	114
Plant dry weight‡ (winter 1962-63)	gm.	2	8	6	2	5
Plant dry matter content (summer 1962)	%	29	27	26	34	27
K content	milliequivalents per 100 gms. dry leaf tissue	80	70	91	87	93
Ca		30	13	21	24	24
Mg		19	33	10	9	13
Na		1·9	1·7	2·0	1·6	2·2
Days to ear emergence §		7·6	6·5	9·3	—	7·0
Leaf length	cm.	16·1	18·8	22·4	28·7	25·6
Leaf width	mm.	2·0	2·9	2·1	2·3	2·7
Leaf index $\frac{\text{width}}{\text{length}}$	%	1·3	1·6	1·0	0·8	1·1

* Positions 30, 50, 60, &c., indicate the distance downhill in feet from the highest point of sampling, along a transect through the centre of the flush. 30/4L means 4 feet to the left of the central line at position 30.

† An imprecise term denoting a colour which seems distinct from " dark " or " light."

‡ Weight of aerial tissue removed when plant cut close to ground level, excluding culms.

§ Number of days from an arbitrary starting date (when ear emergence was imminent) during which a total of eleven or more panicles had emerged.

Measurements were also recorded for all plants for a considerable number of characters and whilst there was a fair range of variation within them, on the whole the members within each group formed by subjective assessments showed marked similarities and many groups were obviously morphologically differentiated in several characters. These character measurements can be seen in Table I, which gives a summary of character measurements in five groups within *F. rubra*. In as many cases as possible, crosses were carried out between plants within a group and plants of different groups and only in the latter crosses was any seed formed. Since *F. rubra* is self-incompatible the results are consistent with the theory that each of the five groups represents a separate genotype but since it is always possible that negative results have occurred by chance merely as a result of unfavourable conditions, it is proposed to repeat many of the crosses in order to obtain confirmation of the results. Where, however, there are many good morphological differences between groups, it must be presumed that these groups constitute genotypes. The same tests and analyses were repeated upon *Agrostis* and other species from the flush.

Presuming that the present grouping of isolates is at least approximately correct, the vegetation of a large part of the flush must be dominated by a moderate number of genotypes of *Agrostis stolonifera*, *A. tenuis* and *Festuca rubra* of which the latter two are most important. The method of sampling which was deliberately adopted has resulted in the isolation on average of 2·2 tillers of each genotype in *F. rubra* and 3·7 tillers of each *Agrostis* genotype. It would appear, therefore, that the vegetation is certainly not dominated by one or two genotypes and it is possible that this is because there is known to be a gradation of soil conditions. From the present results it would seem that though some genotypes are more abundant than others the variation in the proportions of *Agrostis* and *F. rubra* occurring in different areas of the flush could be a reflection of changes in genotype.

In the case of *F. rubra* there are indications from the figures for the dry weight of aerial tissue produced in summer 1963 that the sizes of plants growing in the field trial from tillers obtained from a given sampling point bear some relation to the proportion of this species at that point on the flush. A figure for the proportional presence was obtained by expressing the number of isolates of *F. rubra* as a percentage of the total number of tillers of all species obtained from each core and it was found that there is usually a greater mean plant weight from those sites which have a high percentage of this species. Since the sampling points have different soil characteristics, the transplantation to a relatively uniform environment must have involved changes for the plants of differing severity and so the general direction of changes of plant weight and percentage presence is probably more important than a good correlation of absolute values. This relationship holds fairly well for the main transect and the cross transect at the 60 ft. position. The cross transect at 30 ft. position does not show this relationship but the failure here might be due to rapid soil changes within a short distance or the low number of isolates. Certainly discrepancies in the other transects occur almost exclusively where the number of isolates is small, the corresponding plant weights always being higher than expected.

Several mineral analyses were carried out upon dried leaf material of *F. rubra* and the results for potassium content are the most consistent, the greater amounts occurring in leaves from plants obtained from the distal regions of the flush (65 to 85 feet from the origin). The reason for this is not yet known but it seems probable that there is a link between a physiological difference in the genotypes and soil differences obtaining in the flush.

While these studies are primarily concerned with obtaining information of a fundamental nature concerning the potentialities of *F. rubra* and other species and the relationship to existing soil conditions, it is hoped that they will eventually be of considerable value in connection with hill land improvement in general and with the use of artificial flushing in particular. Using a coarse filter of coiled nylon to prevent blockages in the half-inch polythene pipe, spring water is being applied in an artificial irrigation experiment on the Pentland Hills at up to 1,500 gallons per day. The vegetation of the area consists predominantly of *Nardus*, *Deschampsia flexuosa* and *Festuca ovina* and intermittent irrigation for rather more than a year has given rise to a conspicuously green, moist area which shows signs of being preferentially grazed. Earthworms are now obviously present. A similar system has been started at Arrivain, Dalmally, where a one-inch polythene pipe has been used to carry burn water from a small dam to an area of the hillside about 100 yards distant. In this case up to 8,000 gallons per day has been supplied since July 1963. At this site no effect on the vegetation is yet visible. Nevertheless, in both cases there has been a considerable improvement in the mineral status of the soil. This was investigated by taking soil samples at intervals along transects at right angles to the direction of flow of water and expressing the amounts of exchangeable cations as percentages of the soil cation exchange capacity. The figures for pH, Ca and Mg for the two artificially flushed sites and a comparable transect on a natural flush are given in Table II. K and Na are not shown as there has been little change.

TABLE II

CHANGES IN pH AND PER CENT SATURATION OF CATION EXCHANGE CAPACITY BY Ca AND Mg AS A RESULT OF ARTIFICIAL 'FLUSHING'

		Feet from point of maximum water flow									
		0	2	4	5	6	8	10	12	15	20
Pentlands Artificial Flush	pH	5·0			4·4			4·0		3·8	3·7
	Ca	40			23			16		9	9
	Mg	5·1			3·2			2·9		1·3	1·4
Arrivain Artificial Flush	pH	5·4	5·6	5·4		4·6	4·7	4·4			
	Ca	32	37	34		11	17	13			
	Mg	8	6	7		5	6	5			
Pentlands Natural Flush	pH	6·0	5·9	5·9		4·9	4·2	4·0			
	Ca	63	60	57		28	11	8			
	Mg	17	13	14		7	7	6			

The transect extended in all three cases into unflushed areas and it can be seen from Table II that at their lower extremities the levels of pH, Ca and Mg in the irrigated areas are very alike in all three cases. The approximate mean annual concentration of Ca in the water which has produced these changes is at Arrivain—2·0 mg/1 and on the Pentlands—20 mg/1. It is therefore apparent that despite widely differing Ca concentration and length of time and rate of application of the water approximately the same result has been achieved in terms of the Ca status and pH of the soil. At Arrivain there has been an increase in soil Ca by a factor of approximately three and on the Pentlands of approximately four. It remains to be seen to what extent and how quickly the change will be reflected in the vegetation.

TABLE III

VARIATION IN SWARD PRODUCTIVITY AND CATION CONTENT IN RELATION TO SOIL CATION LEVEL

			Cation content milliequivalents/ 100 gm. dry weight			Soil cation level % saturation of cation exchange capacity		
Position (Ft.)	Fresh wt. (gm.)	Dry wt. (gm.)	Ca	Mg	K.	Ca	Mg	K.
50	79	20	32	20	61	56	24	0·8
60	127	28	30	20	69	61	14	1·6
70	91	26	29	16	60	56	13	1·5
((*60/6L)	72	24	25	15	47	36	11	3·0)
80	56	19	27	13	49	51	11	1·4
90	48	20	17	16	34	29	7	1·8

Investigation of the naturally "flushed" area mentioned in the *Records* for 1962 and 1963 has continued along the lines outlined in the *Record* for 1963. Owing to difficulties with the instrument for measuring o_2 diffusion rate and to the abnormally wet summer of 1963, little progress has been made with investigation of this factor. The season was so wet that the differences between the wettest and dryest parts of the flush were minimal throughout the period from the spring of 1963 to the spring of 1964. These difficulties applied to a

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* The bracketed line is for a sampling point 6 ft. to the left of the main series, inserted in the appropriate position in the vegetation series.

"Position" refers to the distance from the top of the transect. There is no running water below 50 ft.

lesser extent to investigations of soil moisture by means of buried gypsum resistance blocks; it was possible to demonstrate a gradient of soil moisture but the season was so unrepresentative of normal conditions that it has not been possible to obtain an estimate of the range of variation in various parts of the flushed area. A preliminary investigation has been made of the productivity of various parts of this flush and of the mineral levels in the vegetation. Wire letter-trays approximately 10 in. × 15 in. were inverted and pegged down in six positions, covering a range of sward types along a transect running down the centre as mentioned in the *Record* for 1963. The vegetation was plucked by hand at regular intervals to simulate grazing. Table III gives the mean results for two samples covering the period June to August with the appropriate soil analysis figures for comparison.

At this stage it is difficult to know to what extent the variation is due to soil differences or to changes in the species composition of the sward or to other unknown factors. However, these results are sufficient to warrant an extension of this approach, and using similar methods it is hoped to build up a picture of the movements of mineral nutrients in this "micro ecosystem" and of the relation to grazing and uptake by the sward. Analyses are available of the cation content of *Festuca rubra* from the previously mentioned field trial, and *Festuca ovina* and *Agrostis stolonifera* from greenhouse grown material: these are shown in Table IV. These species, along with *Agrostis tenuis*, are the most prominent species on the sites sampled; it therefore does not appear likely that change in species composition is having a great effect.

TABLE IV

CATION CONTENT OF SWARD SPECIES

	Milliequivalents/100 gm. dry weight		
	Ca	Mg	K.
Festuca rubra	c.25	c.15	c.85
Festuca ovina	21	15	98
Agrostis stolonifera	24	22	98

In view of the possible genetic variation in *Festuca rubra* of ability to take up potassium which has been mentioned above, the apparent relationship between soil calcium level and sward potassium content is of considerable interest, particularly as there is no relationship with soil potassium. It suggests that there may well be a selection pressure for ability to take up potassium where both calcium and potassium are relatively low.

It is intended to extend these studies to include nitrogen and phosphorus, with a particular view to finding out to what degree they influence the productivity and/or species composition of natural swards. Analysis of soils from flushes in other parts of the Pentland Hills has, in general, confirmed the value of expressing exchangeable cations as a percentage of the cation exchange capacity. In all cases there was good correlation between vegetation, soil pH and Ca level expressed in these terms when there was usually no meaningful relationship between absolute levels of exchangeable Ca and either vegetation or pH. Work on these flushes continues.

The accumulation of information concerning the physiological relationship between the genotype and its edaphic environment makes a further contribution to the common knowledge that the expression of the phenotypes can vary considerably in contrasting environments. It is obvious that transplants to an experimental garden at a relatively low elevation cannot exhibit the precise morphological or physiological attributes which characterise them in their natural hill habitat. The problem of differences between the original habitat and the garden environment becomes acute, however, when the desirability of providing seed of natural hill grasses arises. The varying response to environment is almost certainly less marked in the case of transplants of a genotype from a natural population than in the case of the progeny of a cross between genotypes from different populations. In the latter case, the delicate gene balance may well have been disturbed resulting perhaps in the loss at lower elevations of genotypes which would have proved useful in hill conditions. Responses to the environment of the lowland garden are not necessarily a good indication of the responses which can be expected on the hill and it therefore seems inevitable that selections must be made from progeny growing in a hill garden. Since it is conceivable that as the edaphic conditions are ameliorated by irrigation and *Nardus*, for example, is removed by grazing, it would be necessary to introduce good types of the naturally occurring better grasses. In order that parents may be selected under hill conditions an area has been fenced off on an exposed ridge of the Pentland Hills and Dalapon applied to remove the existing vegetation. This area will be available for testing the reaction of progenies of *Agrostis tenuis* and other species of hill grasses in the search for suitable parent material.

Some time was spent in the past year on the production of seed of *Trifolium repens* in connection with work which is in progress at the East of Scotland College of Agriculture on root nodule formation in upland clovers. It was necessary to obtain seed from hill plants in isolation in order to avoid any risk of contamination from lowland varieties so plants obtained from the flush under examination were multiplied vegetatively and kept in a small insect-proof greenhouse. A small hive of bees, which had not been in contact with clover plants, was placed in the house and over 45 gms. of good seed was successfully harvested at the end of the season.

Cytological investigations in connection with the genecological work involved some 500 root tip and leaf examinations on the hill grass species. The routine analyses provided no unexpected results save that in *Poa subcaerulea* there was evidence of a degree of aneusomaty with chromosome counts ranging from 60 to more than 100 in the same plant.

A number of techniques were developed to assist in batching routine serial work in the laboratory, and to improve technical efficiency. Of these the most important are the use of solubilised pretreatment agents to reduce pretreatment times, and the development of a grass leaf-tissue technique which has ensured the availability of suitable material for examination throughout the year, and resulted in a considerable saving in greenhouse space. An investigation into the general question of solubilised pretreatment agents is being carried out, since the use of solubilised alphabromonaphthalene has proved so useful. A study of hill populations of *Poa trivialis* has been started, and samples of this species will be examined for chromosomal polymorphism with a view to utilising this phenomenon in further studies of population dynamics in this species.

Two greenhouse trials were conducted during the year analysing the growth over a three-week period of four Italian ryegrass cultivars. The trials were identical except that one was sown in January and the other in July. The main object of the experiments was to study the inheritance of various components of seedling yield and progeny from selected plants is at present under examination. Several additional interesting points, however, emerged from the 1963 trials. The cultivars concerned were 'Hinderupgaard,' 'S22,' 'Melle' and a commercial tetraploid. The rate of increase of top weight was highest in the tetraploid and lowest in 'S22' and 'Hinderupgaard,' 'Melle' being the best of the diploids for this character. 'Melle' also showed a high value for net assimilation rate in the 1963 trials.

Although the relative order of performance of the varieties was similar for both sowing dates, differences were more marked in the January sowing. Taking 'S22' as 100, increases in top weight in the January sowing as measured over the three weeks 7th March to 29th March were 'Hinderupgaard' 110, 'Melle' 131 and the tetraploid 145; while for the July sowing over the period 25th August to 15th September the corresponding values were 99, 110 and 114.

In both field and box sward experiments carried out in previous years at the Station the variety 'Melle' has performed well, consistently outyielding 'S22' by about 10 per cent over the season and this superiority has been more marked in early cuts than in those taken later in the season. It is suggested that growth analysis based on greenhouse experiments is giving results consistent with those obtained from sward trials and that the diploid variety 'Melle' and some tetraploid cultivars appear to be relatively more efficient under shorter days and lower light intensities than 'S22.'

Cereals—*Oats.*—A selection which has been in trial over the past ten years as Aa 732 has now been named 'Shearer.'

The new cultivar has been found suitable for a wide range of Scottish conditions. It is early maturing, and by reason of its plump grain has been described as a good bruising oat. In trials it has consistently outyielded 'Early Miller' and 'Yielder' and may be recommended for upland and late districts where these two cultivars are known to succeed, except on land infested with Oat Stem Eelworm, to which pest 'Shearer' is less tolerant than 'Early Miller.' 'Shearer' has also been found to give a reasonable crop on soils of above average pH (around 7) although it would not be advised for the more extremely alkaline soils.

The Registration Authority's official description of 'Shearer' is as follows :—

PEDIGREE 'ABUNDANCE' × 'EARLY MILLER'

Young Plant	Habit		Semi-erect
Leaves	Colour		Medium green
	Shape		Medium length. Medium width to broad
	Poise		Semi-erect to erect Slight droop at tip
	Hairs. Lamina.	Upper surface	Present, usually few.
		Lower surface	Absent
		Margin	Present, few
		Junction	
	Sheath		Present or absent, few
	Under-hairs		
Flag leaf	Poise		Semi-erect
	Width		Thick
	Hairs at node	Above	Absent
		Below	Absent
Panicle	Type		Equilateral
	Colour		Light green
	Size		Large, open. 5 to 6 nodes
	Poise of branches		Mainly horizontal, tips drooping
	Base of branches	Swelling	Present
		Hairs	Absent
	Spikelets	No. of grains	Ususally 2, occasionally 3
		Poise	Pendulous
	Glumes		Medium to large. Open
	False nodes		Absent
Primary Grains	Shape		Medium length and width
	Tip shape		Medium length. Intermediate
	Glaucocosity		Present
	Hairs	Base	Absent
		Outer Pale	
		Rachilla	Absent
	Awns		Occasional
Primary Grains	Colour		White
	Fracture		Straight
	Base		Bevelled
Secondary Grains	Base		Bevelled
Straw	Length		Long
	Standing power		Poor Breakage frequently occurs half-way up stem
Maturity			Early
Thousand-seed weight			Average (36·4)
Kernel Content			Average (74·3%)

(1964)

The main objectives of the oat breeding programme are, as in previous years, the selection of types suited to particular Scottish environments, and the selection for resistance to Oat Stem Eelworm.

In the course of time it became quite evident that selection at a central station to suit some of the more difficult environments could only be made on the basis of a few clearly defined characters, while types perhaps better adapted to those environments were liable to be rejected. By 1952 the growing of unfixed hybrid material at centres within appropriate environments was considered, but the immediate problem was one of choosing sites reasonably typical of particular sub-optimal environments. Following meetings with Regional officers of the North of Scotland and West of Scotland Agricultural Colleges, two problem areas for oat cultivation were broadly defined. One was in the general area of the Spey valley and Strathnairn, in Inverness-shire, which is in the rain shadow of the Monadhliath mountains, and where much of the oat cultivation is on light gravelly soils with summer droughts a persistent problem, and the other in North Argyll, where high rainfall producing a vigorous weed growth is associated with a low level of soil fertility.

Selection Centre sites in those areas were sown with hybrid material for the first time in 1953 and in subsequent years small-scale trials of fixed selections have also been conducted at the centres and from a comparison of these trials with similar trials at Pentlandfield it soon became apparent that there was a differential response of varieties to environments in terms of grain and straw yield as well as in other respects, and that those which were most successful at Pentlandfield were not necessarily the most successful in the other environments. In the years during which this work at the Selection Centres has been carried on there has been a considerable change in cereal cultivation in Scotland with barley displacing oats in many areas, but this effect has been most noticeable in the more fertile districts and it is perhaps significant that in the environments originally defined as problem areas oats is still the important cereal crop.

In 1963 the Selection Centres were near Boat of Garten in Inverness-shire and North Connel in Argyll, at both of which centres excellent growing conditions were experienced. In addition to the Selection Centre at Boat of Garten, facilities were retained at Daviot for the testing of the many selections which originated there, and again growing conditions were excellent. It was, however, a wetter season than usual; no drought was experienced at Daviot and a group of five selections outyielded the control varieties both at Boat of Garten and Daviot. Whether they will be equally successful in a dry year remains to be seen. Selection and testing for the more fertile environments of Southern Scotland is carried on at Pentlandfield and on an area of highly alkaline soil in the East Lothian, put at the Station's disposal by the Forestry Commission, where types tolerant to manganese deficiency are selected and tested.

The technique of selection for resistance to the Oat Stem Eelworm has been further improved by the construction of a new holder for a hypodermic syringe designed to give uniform small doses of inoculum with accuracy. This holder, described in the 1963 issue of the *Record*, was completed in time for the series of inoculation experiments which commenced in October, and over 55,000 seedlings have been tested for resistance during the winter months.

Arising from these inoculation experiments some 200 new resistant selections are introduced into trials for yield and other agronomic characters each year and some of the most promising selections from earlier work are now in trials at the Selection Centres as well as at Pentlandfield.

An experiment which commenced in 1962 to determine the effect of successive cropping with a resistant variety on the Stem Eelworm population in the soil has given indications that after only one resistant crop plots of a susceptible variety are less severely affected than those on which no resistant variety has been grown. The plots on which this experiment is being conducted have been cropped continuously with oats since 1959, in which year they were artificially contaminated with plant material collected from infested fields.

Barley.—As a result of an agreement reached in 1962 between the Scottish Plant Breeding Station and the Plant Breeding Institute, Cambridge, Pentlandfield is now functioning as a barley selection centre for Cambridge material in the same way as the Inverness and Argyll centres function as regional Selection Centres for oats of Pentlandfield origin. Hybrid material received from Cambridge was again sown at Pentlandfield in 1963. Despite unfavourable weather conditions it was possible to make some assessment of field characters during the growing season, and after harvest to eliminate those selections which exhibited undesirable grain characters. The most promising hybrid selections are being grown again in 1964.

Brassica Crops.—Further forms of *Brassica campestris* obtained mostly from Japan were planted in small plots for observation. The majority flowered early, and did not suggest that they had any future in a breeding programme directed towards producing new hardy, leafy brassicas. The oriental sub-species *nipposinica* contained a larger number of early flowering plants than in previous seasons, whilst tetraploid forms of ssp. *pekinensis* and *nipposinica* also showed a tendency to flower early. The only material to show any definite promise in this group were hybrids between 4x turnip-rape and 4x *nipposinica*. Growth of these plants was fairly rapid, and the abundant leafage produced gave good ground cover at 2 ft. × 2 ft. spacing after about ten weeks. Virtually no stems were formed and dry matter content of leaves in mid-October was just under 10 per cent. Outer leaves died back in mid-winter but there was regeneration from the base, and it might well be that the very low growing point of this type of plant would facilitate regeneration after grazing.

Hybrids between the entire-leaved turnip 'Gelria' and ssp. *nipposinica* were vigorous and leafy, but this material has already been shown to be frost susceptible. Club-root tests on F_3's have shown that at least in respect of the one strain of *Plasmodiophora* used it is possible to combine the leafiness and rosette habit of ssp. *nipposinica* and the resistance of 'Gelria.'

A visual comparison was made between adjacent plots of a synthetic hexaploid *B. napo-campestris* and three well-known commercial *B. napus* (rape) cultivars. The synthetic produced a greater number of leaves than rape and appeared generally leafier but showed more tendency to lose its outer leaves in winter. Plants of similar constitution survived the very severe winter 1962-63 and regenerated well in the spring. Seed fertility of C_2 generation of *B. napo-campestris* was approximately 50 per cent that of commercial *B. napus* seeded under similar conditions. There was considerable variability in the yield of seed per plant so that fertility could no doubt be further improved by selection.

(1964)

Selection to improve general growth characters and fertility of auto-tetraploids continues. Crosses between tetraploid forms of *B. oleracea* and *B. campestris* have proved very difficult to effect, although reputed to be easier than between diploids. Experiments are being carried out to find the best method of growing excised embryos *in vitro* and so overcome incompatibility between embryo and endosperm. Less than 10 per cent of embryos excised showed signs of growth and of these a number were considerably distorted. Contamination of cultures by fungi and bacteria was reduced to below 5 per cent.

Of numerous hybridisations within the *B. oleracea* group, progenies of kohl-rabi × thousand-headed kale although segregating for the desired low-growing, rosette habit, were lacking in vigour and showed a tendency to run to seed in the first year. F_2 hybrids of the cabbage 'Muirheads Flatpol' × thousand-headed kale were examined with a view to selecting high-yielding forms with a high leaf : stem ratio and good side-shoot development. Hybrids of the cross 'January King' cabbage × thousand-headed kale although hardy were not highly productive. F_2's of the backcross triple hybrid thousand-head : kohl-rabi : broccoli × thousand-headed kale were compact and short-stemmed, leaves were numerous but small.

Curly kale (*B. oleracea* v. *fimbriata*) has been used in crosses at the tetraploid level with other varieties of *B. oleracea* such as thousand-headed kale (v. *fruticosa*), kohl-rabi (v. *gongylodes*) and hardy cabbage (v. *capitata*) cultivars. Curly kale has been shown in one trial to outyield the best commercial cultivars of thousand-headed kale in respect of total leaf lamina, mainly due to its very high lamina : petiole ratio. In this respect curled-leaved and furled-leaved segregates from crosses between cabbage cultivars and thousand-headed kale are of particular interest.

The short-stemmed, leafy, commercial thousand-headed kale 'Canson' was used as a yardstick by which to assess the merit of various selections and hybrids within the *B. oleracea* group. Trials involved both spaced and unthinned plants. Progenies of plants selected from 'Canson' did not differ significantly from the commercial cultivar in total dry matter of leaves or fresh weight leaf : stem ratio. All selections showed significantly greater stem length. In a trial of spaced plants derived from selfed and polycross commercial thousand-headed kale, the total fresh weight of self progenies was up to 40 per cent lower than that of corresponding polycross progenies. In four out of five comparisons the differences were highly significant. The deleterious effect of inbreeding for only one generation was thus illustrated.

The swede 'Pentland Harvester' was included in machinery trials by the East of Scotland College of Agriculture at Lintlaw, Berwickshire, and by the National Institute of Agricultural Engineering at Bush Estate, Midlothian. In both trials 'Pentland Harvester' proved superior to other cultivars in uniformity, habit of growth and general suitability for mechanical harvesting.

Publication

BENNETT, ERNA (1964). A rapid modification of De Lautour's technique for grass leaf chromosomes. *Euphytica*, **13**: 44-48.

A modification of De Lautour's technique for grass leaf chromosomes is described, a modification which makes possible rapid sampling and bulk processing of grass shoot tissues for cytological examination. These tissues have a number of advantages over the root-tip tissues normally used for this purpose, the most important of which is that the supply of suitable cells in division is independent of season.

OFFICIAL IMMUNITY TESTS AND MERIT TRIALS FOR POTATOES

T. M. W. Davidson

The Merit Trials exist for the benefit of the potato trade in the United Kingdom and are under the aegis of the Department of Agriculture and Fisheries for Scotland. The aims of the trials are to screen seedlings, selected and submitted by breeders, in order to give authoritative views on those seedling varieties worthy of commendation and to discourage the introduction of inferior seedlings as new cultivars (Anon., 1962). The trials function as a final selection of seedlings based upon a wide range of tests of relevant qualities and properties and include a Wart Disease and Identity Test which is, to a certain extent, obligatory. The Potato Section of the Scottish Plant Breeding Station take full advantage, not only of these facilities, but of certain other tests of an advisory nature also available to breeders. As the Merit Trials play such a decisive role in the introduction of new "Pentland" varieties an outline of the organisation, scope and methods of test is given here.

The trials are centred at the Agricultural Scientific Services Station at East Craigs and extend over a period of from one to three (occasionally four) years. The routine tests are carried out by the scientific staff of East Craigs with certain confirmatory assessments by other organisations but all decisions as to the relative merits of the seedlings under trial are confined to an independent body of farmers and scientists who serve on the Potato Trials Advisory Committee at the invitation of the Department of Agriculture and Fisheries of Scotland. They meet three times during the year to inspect the seedlings under trial in the field and in storage. The collated results for every seedling are considered by the Committee at the end of each growing season. Seedlings from each year of trial are rejected by the Committee when they fall below a standard requirement set by the performance of commercial varieties used as controls. Any seedling considered to be "of a grade of excellence at least equal to that of standard varieties," at the completion of the trial period, receives "commendation" from the Department of Agriculture and Fisheries for Scotland, subject to certain minor requirements.

(1964)

Prior Selection and Propagation

An arterial system of selection and propagation is carried out by the Potato Section of the Scottish Plant Breeding Station. After an initial selection in the greenhouse, where up to two-thirds of the seedlings may be discarded, one tuber from each of the remainder is planted at the propagation centre, Blythbank, in the following year. The seedlings are reselected each year. After four years at Blythbank, a final selection is made and the remaining seedlings are entered for the Official Merit Trials (Table I). In the 5th, 6th and 7th years at Blythbank only those seedlings undergoing concurrent trials are propagated. All the seedlings are maintained throughout at a standard of health equivalent to that of stocks being grown for a V.T. (virus-tested) certificate of health.

TABLE I

THE MAIN PROPAGATION STREAM AT BLYTHBANK SHOWING THE CONCURRENT YEAR OF MERIT TRIAL

Year at Blythbank	No. of seedling units (1963)	No. of plants per unit	Tuber requirement, per unit, for Merit Trial in the following year	Year of Merit Trial
1st	10,000	1		
2nd	3,000	3		
3rd	500	8		
4th	300	40	70	
5th	18	1/25th acre	450 (550)*	1st
6th	7	1/8th acre	1,006	2nd
7th	5†	1/2 acre		3rd

* 1st Early varieties.

† One of the five final-year seedlings was commended in 1963 and named ' Pentland Glory '.

(1964)

Tests in use in the Merit Trial

The tests are designed to discover faults and weaknesses in a seedling which could cause it to be a commercial failure. Over the three years of trials the tests are increased in size and diversity and take into account all the factors which are known to limit the utility of commercial varieties. Many official bodies throughout the United Kingdom co-operate in the trials and report their findings to East Craigs (Table II). The tests fall into three general categories, namely, cultural, disease resistance and quality.

Cultural Tests

(*a*) *Field observations.* The following field observations are made on all plots of seedlings under trial.

(i) Habit. The seedlings are examined for abnormality, for freedom from " wild " characteristics such as coarseness and excess stolon growth, also for the amount of cover over the drill, which should be adequate for weed control.

(ii) Virus content and purity. The plots are examined visually to ascertain the level of health and purity. In most cases, the seed tubers for the plots have come directly from the breeders and the standard of health and purity apparent in each is indicative of the standard prevailing within the parent stock.

(iii) Maturity. Maturity is judged by the yellowing of the senescent haulm. In comparison with control varieties the seedlings are designated 1st Early, 2nd Early, Early maincrop and Late maincrop.

(iv) Description. A detailed morphological description of the haulm is made initially and checked in each successive trial year.

(v) Blight. In a normal year when late blight is prevalent, plots of seedlings, known to have some blight resistance, are examined for blight lesions at the end of the growing season.

(*b*) *Yield.* As good yielding capability is essential, seedlings are rigorously tested for this with current commercial varieties

TABLE II

THE DISTRIBUTION AND SCHEME OF TESTING IN THE MERIT TRIAL FOR EACH SEEDLING AND CONTROL VARIETY

Year of Trial	Official Body.	Test Centre	Section or Outstation	Site of Test	Size of test in tubers utilised		Test
					From Breeder	Once Grown	
1st	D.A.F.S.	East Craigs	—	Field	36		Field observations : Yield
							Tuber „ : Quality
		„	—	„	6		Identity
		„	Pathology	Laboratory	10		Wart Disease (1st)
	N.I.A.B.	Cambridge	—	Field	6		Field observations
2nd	D.A.F.S.	East Craigs	Pathology	Laboratory		40	Dry Rot (Stab) (1st)
		„	„	„		100	„ „ (Riddle) (1st)
		„	„	„		50	Gangrene (1st)
		„	„	„		10	Blight (1st)
		„	—	Greenhouse		16	Viruses X, A, B and C (1st)
		„	—	Field		42	Frost recovery (1st)
	M.A.N.I.	Kilkeel	„	„		5	Wart Disease
	Min. of Ag.	Harpenden	„	Laboratory		5	„ „
	D.A.F.S	East Craigs	„	„	10	6	„ „ (2nd)
		„	—	Field	6	6	Identity (2nd)
		„	—	„	216		Field observations : Yield
							Tuber „ : Quality
		„	Ayrshire	„	120		Early yield
		„	East Lothian	„	40		Virus " Y " and leaf-roll (1st)
	N.I.A.B.	Cambridge		„	50		Field observations : Yield
		Terrington	N. England	„	100		Propagation for 3rd year field trials in England
3rd (or 4th)	D.A.F.S.	East Craigs	Pathology	Laboratory		40	Dry Rot (Stab) (2nd)
		„	„	„		100	„ „ (Riddle) (2nd)
		„	„	„		50	Gangrene (2nd)
		„	„	„		10	Blight (2nd)
		„	„	„		40	Skin Spot
		„	—	Greenhouse		16	Viruses X, A, B and C (2nd)
		„	—	Field		42	Frost recovery (2nd)
		„	—	„	6	6	Identity (3rd)
		„	—	„	216		Field observations : Yield
							Tuber „ : Quality
		„	Ayrshire	„		120	Early yield (2nd)
		„	East Lothian	„	40		Virus " Y " (2nd)
		„	„	„		40	Virus leaf-roll Index
	N.O.S.C.A.	Craibstone	—	„	216		Field observations : Yield
	W.S.A.C.	Auchincruive	—	„	216		„ „ : „
	N.I.A.B.	Cambridge	—	„	50		„ „ : „
		Terrington	—	„		290 (ex. N. England)	„ „ : „
		„	England	„		(„ „)	Yield

D.A.F.S.	Department of Agriculture and Fisheries for Scotland.
N.I.A.B.	National Institute of Agricultural Botany.
M.A.N.I.	Ministry of Agriculture, Northern Ireland.
Min. of Ag.	Ministry of Agriculture Fisheries and Food.
N.O.S.C.A.	The North of Scotland College of Agriculture.
W.S.A.C.	The West of Scotland Agricultural College.

as controls. After adequate yield trials in the first and second years, seedlings in the final year are grown in replicated trials at each of three centres in Scotland as well as undergoing extensive yield trials in England. The crop is passed over riddles to find the proportion of ware tubers to seed-sized tubers and " chats."

As an extra trial, First Early seedlings in the second and final year of trial are grown in the early potato district of Ayrshire to test their capacity for early bulking as compared with ' Epicure,' the long-established variety of the district.

(*c*) *Tuber observations.* The following observations are made on the crop from all yield trial plots.

(i) Shape. Good, well-filled even tubers are essential for promising seedlings. Acceptable shapes are rounds, ovals and kidneys with medium to shallow eyes and free from surface irregularities and indentations.

(ii) Colour. The colour of the skin is noted. Dark reds and purples are not usually acceptable. The permanence of the colour in parti-coloured seedling tubers is examined.

(iii) Internal blemishes. A sample of tubers is cut from each unit to assess the amount, if any, of hollow heart, internal rust spot, spraing, net necrosis and blight infection.

(iv) External blemishes. The presence of lesions of common or corky scab is noted as well as other weaknesses such as a tendency for second-growth cracking, hair cracking or being easily bruised when handled.

(v) Uniformity. The ware tubers are examined for uniformity in size and should not be " small in the run." (This term indicates that the sample is relatively numerous but small in size.)

(*d*) *Identity.* The second and third year intakes of tubers from breeders are checked as being identical to that of the previous year by growing adjacent plants from new and once-grown tubers. The seedlings are also inspected to ensure that they are, in fact, distinct and not synonymous with other varieties.

(*e*) *Frost recovery.* The aim of this trial is to assess the rate of recovery from frost damage of early-maturing seedlings. Plots of these seedlings and the control variety ' Epicure ' are planted early in the hope that there might be foliar damage from frost. In the event of no frost damage the leaflets of the plants are " burned " evenly by a freezing agent. The recovery made thereafter is, for each, compared with that of ' Epicure.' ' Epicure ' is exceptional in its ability to recover from frost damage.

Disease Resistance Tests

(*a*) *Wart Disease* (*Synchytrium endobioticum*). A seedling must be judged to be immune (field-immune) from Wart Disease before it is considered for " commendation." The bulk of the testing is done in the laboratory using a modified Glynne-Lemmerzahl technique (Glynne, 1926; Lemmerzahl, 1930, 1931). On exposure to infection, if the tuber responds with sufficient defence necrosis to the development of the pathogen, it is deemed to be " immune " from Wart Disease. A small field test is carried out in Northern Ireland. There, the seedlings are exposed to natural infection in a contaminated field and are examined for the presence of Warts in the late summer.

(*b*) *Blight* (*Phytophthora infestans*). Tests for blight resistance involve the reaction of both the leaflet and the tuber to infection. In the summer, leaflets are detached from seedlings, placed in moist containers and sprayed with a suspension of blight spores. Two races of the fungus are used. After harvest, halved tubers are inoculated in the same manner. The development of blight lesions, in every case, is reported.

(*c*) *Dry rot* (*Fusarium caeruleum*). Surface-sterilized tuber samples are stab-inoculated with a spore-suspension of the Dry Rot organism in November and in February and are thereafter incubated in high humidity at room temperature. This gives a measure of the susceptibility of the flesh of the tuber to Dry Rot. At the same times as above tests are carried out which simulate normal grading and storage in the presence of infection. Tuber samples are smeared with spore-infected soil shaken on a hand riddle and then the treated tubers are incubated in cool conditions. At the time of scoring tubers are counted either as healthy or infected.

(*d*) *Gangrene* (*Phoma solanicola*). This test is also carried out in November and in February. Inoculation is by dipping sterilized tubers into a spore suspension of the gangrene organism. Incubation is at low temperature and at a high humidity. Two isolates of the fungus are used independently to add diversity to the test. The degree of susceptibility to gangrene is found by a calculation which is based on the number and diameters of the lesions of each test sample.

(*e*) *Skin Spot* (*Oospora pustulans*). This test is carried out on freshly dug tubers in September and October. Tuber samples after being sterilised, are inoculated by dipping them in a spore-suspension. The infected tubers are then stored at room temperature and at high humidity for a month followed by cool conditions and the extent and severity of the Skin Spot lesions are ascertained in March.

(*f*) *Viruses X, A, B and C*. The susceptibility or hypersensitivity of seedlings to the viruses X, A, B and C is ascertained by grafting infected scions on to representative clones, growing in pots, in a greenhouse. Plants which respond to this treatment with a lethal top necrosis show hypersensitivity to the virus and in consequence are "field immune." A recovery and identification of the virus is attempted from the remaining plants which may be showing no symptoms or systemic mottles. Recovering and identification of the virus is proof of susceptibility. Seedlings with immunity from these viruses have not yet been encountered in the trials.

(*g*) *Virus Y and leaf-roll*. To test for presence of resistance to virus Y or leaf-roll, samples of the seedlings and of control varieties are planted in a trial in an area in East Lothian where the natural spread of these viruses is normally ensured. Infected plants are incorporated systematically throughout the trial plot. Current year infections with virus Y are detected by leaf sampling and inoculation on to tobacco plants on which virus Y symptoms are a systemic mottle. To find the amount of leaf-roll infection which had occurred within the seedling sample the progeny from the tested plants is grown in the following year and scanned for symptoms of leaf-roll.

(*h*) *Eelworm*. Although seedlings which have been bred for eelworm resistance undergo the same tests as others, additional tests, aimed at identifying the specificity of this resistance with regard to eelworm strains, are being operated at East Craigs.

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Quality

Quality is a most elusive attribute for which to test. At East Craigs certain objective tests are used, however, to give an indication of quality, namely Specific Gravity and Dry Matter. In conjunction with cooking tests, the specific gravities and dry matters of seedling tuber samples are obtained by using a potato hydrometer. In general, the higher the dry matter content the better is the quality.

With the expansion of the crisping industry there is a greater need for varieties having a relatively low reducing-sugar content and for those which respond to "conditioning." This is the process used by manufacturers to lower the reducing-sugar content of tubers which have been stored in cool conditions of storage. Prolonged storage in cool conditions induces a build up of reducing-sugar within the tubers and such tubers produce dark-coloured crisps on cooking. Tubers with a high reducing-sugar content may be "conditioned" to a greater or lesser degree, depending on the variety, by holding them for two weeks or more at 75°F.

Routine tests for sugar content are made at present at East Craigs and steps are being taken to ensure that the "conditioning" potential of seedlings may be assessed in the future. The method of testing for cooking quality is as described by Lugt *et al* (1962) and is now the official testing method used in many countries on the continent as it gives uniformity of treatment.

An even sample of tubers is peeled by hand and steamed, without the addition of salt, in a glass pan containing a metal tripod which prevents the tubers from coming into contact with the water. The assessment of the quality and type of the cooked potatoes is made by a trained panel who follow an agreed system of scoring various qualities which lead to classification for utility. Cooking quality is assayed in all the years of trial at East Craigs and at other centres. The tests are duplicated in each of the 2nd and 3rd years, one series being carried out by the School of Domestic Science, Edinburgh.

Other Features of the Trials

Mention has been made of the obligatory nature of an official Wart Disease and Identity Test for new varieties. This is true as only those seedlings which have been tested for their reaction to Wart Disease, and found distinct from other varieties, are acceptable in the Department's scheme for the inspection of growing crops. There is no other official restriction on the certification of a new variety except that its name must be approved by the Department.

The breeder's stock of a seedling in the Merit Trials must have been found, by inspection, to be of Foundation Seed standard before it is considered for " commendation."

With the breeder's consent the National Institute of Agricultural Botany make use of remaining seed stocks after a seedling has achieved " commendation " for further trials of the new cultivar.

I wish to thank Dr J. L. Hardie and other members of the Scientific Services of the Department of Agriculture and Fisheries for Scotland for their help.

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INHERITANCE OF RESISTANCE TO POTATO ROOT EELWORM (*HETERODERA ROSTOCHIENSIS* WOLL.) IN A BREEDING LINE STEMMING FROM *SOLANUM SANCTAE-ROSAE* HAWKES

J. M. DUNNETT

Tests at the Scottish Plant Breeding Station in 1956 resulted in the selection of *Solanum sanctae-rosae*, a diploid species of wild potato, as a source of resistance to the Duddingston strain of potato root eelworm (Dunnett, 1959). This strain had previously broken down the resistance conferred by the gene H (Toxopeus and Huijsman, 1953) of *S. tuberosum* sub sp. *andigena* C.P.C. 1673. Another strain, the Boghall strain, was taken to exemplify many naturally occurring populations which do not break down the resistance of C.P.C. 1673. The original selections of *S. sanctae-rosae*, which were raised from a seed sample P.H. 328 supplied by Professor Hawkes of Birmingham University, resisted this strain also. Such possibly comprehensive resistance could be genetically indivisible and therefore especially valuable, or could be due to a combination of two complementary, strain-specific, types of resistance, which would be less valuable.

It was decided to study the inheritance of resistance to the Duddingston strain in backcrosses to commercial *S. tuberosum* and to investigate the correlation between resistance to the Duddingston and Boghall strains in one of the later generations.

Parental material.—Breeding began with three clones of *S. sanctae-rosae*. All were self-incompatible in common with most diploid potatoes (Hawkes, 1963) and only one pair appeared to be fully interfertile (average number of seeds per berry = 379). Their progeny 3552 was germinated on colchicine agar and two tetraploid seedlings resulted from this treatment. Both were self-fertile and were crossed with commercial *S. tuberosum*. Nearly all the " seeds " shrivelled up on drying when *S. sanctae-rosae* 4n was the female parent, suggesting a high degree of female sterility. The reciprocal crosses yielded small seeds, the majority of which could be germinated on moist filter paper. The first backcrosses to

S. tuberosum (B_1) were made with emasculated hybrids as the female parents and seed-set was low, averaging 16 seeds per berry. This partial female sterility disappeared in the B_2 generation.

Attempts to utilise unreduced gametes produced by *S. sanctae-rosae* in crosses with *S. tuberosum* as the female parent, the direct method of obtaining tetraploid hybrids, were not successful, yielding two triploids only. These triploids differed markedly in resistance to the Duddingston strain. This was the first indication that the resistance would prove to be of a discontinuous or segregating type.

Inheritance of resistance to the Duddingston strain.—The tests of resistance were done in a heated sand plunge by growing transplanted seedlings in 3-inch pots containing a sandy culture medium of 40 eggs/gm. infectivity. Root-balls were tipped out of the pots after about eight weeks and any cysts seen on the exposed but otherwise undisturbed roots were recorded.

Table I is the complete record of the breeding ex *S. sanctae-rosae* and the segregations obtained with the Duddingston strain. About 8 per cent of the seedlings in the B_2 resistant class were not completely free from cysts but showed not more than three cysts. In contrast to this, cysts were crowded on at least some of the roots of all the susceptible segregates. The B_2 cross of a susceptible B_1 segregate resulted in a progeny (4716) which was scored 0 resistant : 99 susceptible, hence it was unlikely that any susceptible segregates in the other B_2 progenies escaped detection.

All the eight B_2 segregations approximated to a 1 : 1 ratio consistent with the inheritance of a dominant resistance gene in *simplex* × *nulliplex* crosses. The most obvious discrepancy was 14 : 31 recorded in the smallest progeny (4714) but even this was not a significant deviation from 1 : 1 ($P = 0{\cdot}07$). The overall ratio of 370 : 367 was close to unity.

In retrospect, the inheritance of resistance as breeding progressed in accordance with Table I was probably as follows, using S*r* to denote the new dominant resistance gene. The two diploid seedlings of *S. sanctae-rosae* were either both S*rsr* or one was S*rsr* and the other S*r*S*r*. They were crossed to produce the progeny 3254, in which no susceptible seedlings were recorded because the level of additional or " background "

TABLE I

SEGREGATIONS OF SEEDLINGS RESISTANT AND SUSCEPTIBLE TO THE DUDDINGSTON STRAIN

Generation	*Year*	*Progeny reference*	*Resistant parent(s)*	*Segregation resistant : susceptible*	*Hypothetical ratio*
P_1 *S. sanctae-rosae*	1959	3254	PH328/2† × PH328/3†	45 : 0	
F_1	1960	3550	3254/1†† . ♂	47 : 15	5 : 1
S. sanctae-rosae		3551	3254/1†† . ♀	1 : 0	
×		3552	3254/2†† . ♂	2 : 48	0 : ∞
S. tuberosum		3554	3254/2†† . ♀	1 : 0	
B_1	1961	4149	3550/8	10 : 8	1 : 1
		4150	3550/9	3 : 5	? 1 : 1
		4151	3550/10	2 : 6	? 0 : ∞
		4152	3550/15	2 : 0	?
S. sanctae-rosae		4153	3550/19	4 : 4	1 : 1
×		4154	3550/21	1 : 0	?
2 *S. tuberosum*		4155	3550/24	1 : 0	?
		4156	3550/25	7 : 10	1 : 1
		4157	3550/27	5 : 1	? 5 : 1
		4158	3550/32	2 : 4	? 1 : 1
		4160	3550/52	1 : 0	?
		4161	3550/57	3 : 1	? 1 : 1
		4162	3551/1	11 : 7	1 : 1
B_2	1962	4711	4150/2	49 : 49	1 : 1
		4712	4153/6	56 : 43	1 : 1
		4713	4156/6	46 : 53	1 : 1
S. sanctae-rosae		4714	4156/14	14 : 31	1 : 1
×		4715	4156/16	50 : 49	1 : 1
3 *S. tuberosum*		4716	4156/20	0 : 99	0 : ∞
		4717	4162/6	57 : 42	1 : 1
		4718	4162/15	46 : 53	1 : 1
		4719	4162/19	52 : 47	1 : 1
		Total B_2 segregations excluding 4716		370 : 367	1 : 1

† *sanctae-rosae* diploid. †† tetraploid.

resistance was still sufficient to compensate for the absence of S*r* in the recessive part of the progeny. The seedling 3254/2 belonged to the recessive part of the progeny, whereas 3254/1 was S*r*s*r* because after chromosome doubling and crossing with *S. tuberosum* they gave F_1 segregation approximating to 0 : ∞ and 5 : 1 respectively, provided that all seedlings showing even a single cyst were classed as susceptible. This proviso was justified on the grounds that the background resistance had weakened to the extent that cysts were beginning to appear on the recessive seedlings, whereas the same level of background resistance combined with S*r* always ensured freedom from cysts.

With autosyndesis the expectation in the B_1 generation should have been 5 : 1 ratios together with four times as many 1 : 1 ratios. Such a trend was certainly suggested by the B_1 segregations but numbers were too small to be helpful, due to the partial female sterility already mentioned. Seedlings showing one to three cysts in the B_1 and B_2 generations were classed as resistant because the estimated counts of cysts on true susceptible segregates varied from 150 upwards. This meant that the loss of background resistance in these generations was such that the now more or less isolated gene S*r* could not completely suppress cyst formation by the Duddingston population.

Scope of resistance in relation to strains.—Selected B_2 clones were tested again a year later by growing them from tubers in two series of 4-inch pots containing standardised Boghall and Duddingston culture medium, when the perforated can method (Dunnett, 1957) was used to record cysts. This gave two cyst indices in the form of cysts per 100 windows-with-roots for each clone, one index with each strain, enabling a scatter diagram (Fig. 1) to be produced. It includes a control point arrived at by plotting the average cyst index of six plants of a fully susceptible control clone infected by the Duddingston population against a comparable figure obtained with the Boghall strain.

The points lying along the horizontal axis represent segregates incorporating the gene S*r* for resistance to the Duddingston strain. They are completely distinct from the segregates lacking S*r*, which had a minimum cyst index in the region of 40. Since a cyst index of even 5 would have indicated that

DISTRIBUTION OF RESISTANCE TO STRAINS IN PROGENIES EX *S. SANCTAE-ROSAE*

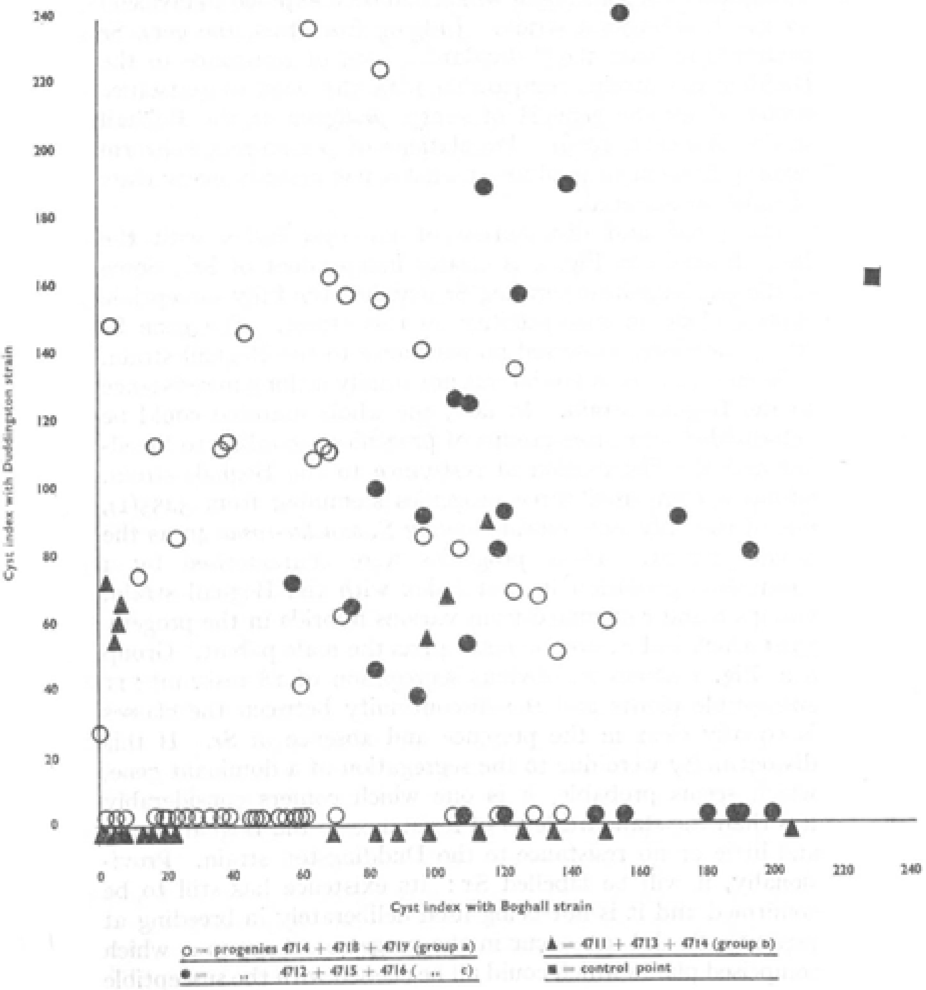

FIG. 1.

the production of new cysts was more than sufficient to maintain population density (Dunnett, 1957), the B_2 material clearly retained no useful resistance to the Duddingston strain in the absence of S*r*.

No cysts could be seen on the root-balls of 92 per cent of the segregates incorporating S*r* which had been exposed to invasion by the Duddingston strain. Judging from this, the gene S*r* conferred at least the "standard" level of resistance to the Duddingston strain, comparable with the level of resistance conferred by the gene H of subsp. *andigena* to the Boghall strain (Dunnett, 1960). Populations of potato-root eelworm invariably seem to produce at least a few cysts in every class of resistant material.

The range and distribution of the cyst index with the Boghall strain in Fig. 1 is clearly independent of S*r*. Some of the seedlings incorporating S*r* matched the fully susceptible control clone in susceptibility to this strain. The gene S*r* itself, therefore, conferred no resistance to the Boghall strain.

Even so, the B_2 material was not totally lacking in resistance to the Boghall strain. In fact, the whole material could be sub-divided into three groups of progenies according to breeding and the distribution of resistance to the Boghall strain. Group *a* comprised three progenies stemming from 3255(1), one of the only two hybrids having *S. sanctae-rosae* 4n as the female parent. These progenies were characterised by a continuous gradation in cyst index with the Boghall strain. Groups *b* and *c* stemmed from various hybrids in the progeny 3550 which had *S. sanctae-rosae* 4n as the male parent. Group *b* in Fig. 1 shows an obvious segregation of 18 resistant : 11 susceptible plants and the discontinuity between the classes is equally clear in the presence and absence of S*r*. If this discontinuity were due to the segregation of a dominant gene, which seems probable, it is one which confers considerably less than the standard level of resistance to the Boghall strain and little or no resistance to the Duddingston strain. Provisionally, it will be labelled S*x*: its existence has still to be confirmed and it is not being used deliberately in breeding at present. S*x* did not occur in the progenies of group *c*, which comprised plants which could all be classed with the susceptible segregates in group *b*.

Conclusions

In conferring the standard level of resistance to the Duddingston strain and no resistance to the Boghall strain, the gene *Sr* ex *Solanum sanctae-rosae* was indistinguishable from the resistance gene ex *S. multidissectum* P.H. 1366 (Dunnett, 1961) as far as these strains were concerned. Both genes are being used in breeding at Pentlandfield, either separately or each in combination with the gene H of subsp. *andigena*. This diversifies the material because *S. sanctae-rosae* and *S. multidissectum* are taxonomically very distinct species, being placed in different series of Hawke's classification of potatoes (1963). There are indications already from the work of Jones and Pawelska (1963) that it may eventually be possible to distinguish between the gene *Sr* of *S. sanctae-rosae* and the resistance gene ex *S. multidissectum*.

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HISTORICAL PERSPECTIVES IN GENECOLOGY

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III. THE "CONFLICT OF CATEGORIES"

IV. PROSPECTIVE

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I. Introduction

The progress of human thought depends upon the interaction of a large number of factors, and rarely occurs at an even pace. In the case of the development of evolutionary and genecological ideas this has been particularly so. Ideas have changed when new techniques have opened the way to new data. In the course of these changes there was—and is—inevitably controversy to be found.

Controversy is at the heart of change. It would be hard to find examples of change which have taken place without it. Stemming from the clash of new data with old ideas, controversy is vigorous and creative—only in the climate of ossified data and the paralysis of thinking which is a consequence does controversy become something sterile. Science always welcomes the question which asks, " Are we sure that we are not wrong ? " and invites controversy. Speaking of systematics, in the throes of its present controversy, Constance (1957) said that " it is healthy but in a profound state of change." It would be even more appropriate to the situation to say, " it is healthy, *and* in a profound state of change."

In this light the present paper is written. It has two aims—to establish a concept of genecology as a major discipline, and to make clear the applied nature of this discipline. It will be necessary to discuss the controversy around the impact of experimental data upon taxonomy, and to consider how, in the mass of current and recent controversy on the problems of species and races, taxonomy and genecology have become too entangled, to the detriment of each. It will be necessary to discuss " species problems," and the point made by Hogben (1940) that there is not one species problem but many is not forgotten. For the purpose of the relevant parts of the present discussion consideration will be confined to what will be referred to for convenience as the taxonomic species problem and the biological species problem, and the interaction between them will be considered. The statement of Gregor (1963) that there is " a need to appreciate the distinction between using the results of experimentation to facilitate reaching taxonomic decisions, and using them to define taxa " is considered as being particularly pertinent in this connection.

Since a view of genecology is expressed in this paper which may at first appear broader than most, genecology is defined here as the study of the genetic mechanisms which operate within organisms, and between organisms and their environment, at the level both of the individual and of the population, viewed as a process, which at the population level produce those changes known collectively as micro-evolution.

Many problems are discussed here, and answers are suggested to some. It is hoped, even if most of the answers themselves pose new problems, that this will not detract from their usefulness. This, after all, is the way that science works.

II. Retrospective

When the evolutionary ideas of Darwin, lacking as they did an understanding of the particular nature of inheritance, came into contact at the beginning of the present century with the newly-rediscovered laws of Mendel, a sharp division developed. Despite the contributions of Hardy and Weinberg in 1908 which, using Mendelian data, demonstrated the maintenance of heterozygote equilibrium in populations, the rift between the " blending evolution "-ists and the " mutationists " and other ultra-Mendelianist protagonists of various single-factor hypotheses of evolution (Mayr, 1963 : ch. 1) was deep and intense. Among the latter an extreme position was maintained by Lotsy (1916) whose theory of evolution by hybridisation argued that evolution depended completely upon the assortment and re-assortment of a pre-existing collection of genes and their alleles, which were considered unalterable in much the same sense as the chemical elements were considered unalterable.

Then in three years, at the end of the 1920s, three mathematical treatments of evolution were published by Haldane (1924, 1932), Fisher (1930) and Wright (1931). These exercised a powerful synthetic influence on evolutionary thought. Although Waddington (1953, 1957 : 60) expresses the view that these works contributed little that was fundamentally new to biological thought—an opinion to which Haldane (1953) felt called upon to express a reply in defence of the mathematicians —they at least had an immediate effect in stimulating new experimental work supported by a wider understanding of the balance between natural selection and mutation, and of its operation at the level of the population rather than of the individual. On the genetical side, the development of the theories of dominance by Fisher (1928, 1931, 1939), Haldane (1930, 1939) and Wright (1934), the work of Nilsson-Ehle (1909) and East (1910) on multiple factor inheritance followed by that of Harland (1936), Silow (1939) and others on modifiers and the interaction of genes, laid the foundations for the development of the concept of balanced polygene complexes begun by Mather (1942, 1943), and further developed in the balance hypothesis of Dobzhansky (1955), Lerner's (1954) genetic homeostasis, and the concept of the epigenotype (Waddington, 1957).

Pioneer studies in the synthesis of evolution and genetics were carried out by Turesson in a long series of experiments begun in 1916 (1922a, 1922b, 1923, 1926, 1929). That Turesson's work escaped the attention of most of the geneticist stream of the synthetic movement initiated by the papers of Haldane, Fisher and Wright may be attributed to the fact that the Mendelianists were for the most part too concerned with " pure " genetic problems. Another reason is certainly the fact that Turesson himself gave to his ecotype concept an ecological-taxonomic connotation, partially derived from his experimental demonstration of the existence of parallel habitat-types (or ecotypes) in different species. Though on the one hand Turesson's papers might reasonably be regarded as experimental starting points for the synthesis of the evolutionist and mutationist viewpoints at least equal in importance to the theoretical works already mentioned, it might also—equally reasonably—be held that as a consequence of his comparisons of the ecospecies with the Linnaean species, they were probably the origin of the future taxonomic-biological species controversy which is still with us to-day, and which forms a part of the subject of this review. Certainly they carried within themselves the seeds of much future controversy.

Nevertheless Turesson clearly showed as a result of his transplantation experiments that the genetic constitution of local populations within a species is the resultant of the action upon " the heterogeneous species-population " of " habitat factors " (1925) and that " as a result of (such) genotypical responses of the species-population to different habitats, isolated units are formed within the species " (1922 : 341). Thus Turesson showed the manner in which natural selection operated upon the range of genetic variability presented to it by the species to produce physiologically and morphologically differentiated "habitat-types" or "ecotypes" which could become isolated from each other, but he also pointed to data which demonstrated that habitat-types isolated from similar habitat-types displayed certain morphological features derived from different habitat-types from which they were not isolated (1922 : 339). These data already carry in embryo the principles of the "Founder Effect" described by Mayr (1942 : 237).

The genetic nature of the differences characterising local races of animals was shown by Sumner (1924) in a similar series of transplantation experiments begun about the same time as those of Turesson. Under very marked artificially maintained environmental changes, the comparative stability of the various colour races of the animal was maintained in a striking manner. In this and in subsequent animal work the term "race" has been used to refer to forms which correspond to the "ecotypes" of plants, and in this paper the terms are used synonymously.

Turesson did not specifically investigate isolation as a race-forming factor, but in demonstrating that natural selection acts upon the genetic variability continually presented to it by the species population, it is clear that the extent of this variability and the nature of the final result are dependent upon the supply of genetic material. In this respect Turesson's rôle was to place the many interacting factors of evolution in their respective relations to each other. Isolation as such has been investigated from quite early times upon island populations, and Darwin's conclusions, following his study of the Galapagos fauna, need no mention—" it was such cases as that of the Galapagos Archipelago which chiefly led me to study the origin of species" (Darwin, 1888). The effect of isolation on populations of mice in the Western Islands of Scotland was examined by Jameson (1898). An important paper of D. S. Jordan (1905) was entitled "The Origin of Species by Isolation." Work of Hagedoorn and Hagedoorn (1921) on isolated populations of rats on ships is referred to by Turesson.

Isolation, by limiting the supply of genetic material to a population, has been shown by many workers to have a clear influence upon the final characteristics of the population. In a remarkable paper, overlooked for many years but recently published in English, Chetverikov (1926) examines the evolutionary process from the standpoint of modern genetics and, drawing from the theoretical works of Hardy and Pearson and from experimental work on *Drosophila*, he reaches a number of general conclusions relating to mutation, selection and isolation. Referring to the " enormous rôle which the factor of isolation plays in the origin of species variability " he goes on to show that isolation, which he divides into geographical isolation, isolation in time, and ecological isolation, " under the conditions of a process of continued accumulation of mutations becomes, by itself, a cause of intraspecific (and consequently eventually also of interspecific) differentiation." Written at a time when many still held mutations to be a laboratory artefact, induced by culturing under artificial conditions—a view answered by Chetverikov by the simple expedient of inbreeding collections of wild *Drosophila*—it is refreshing to read this paper and to reflect upon its contemporary pertinence.

The effect of isolation is to produce discontinuities between populations or, as stated by Crosby (1954), " where isolation between populations of the same species arises, then evolution may take the special course of speciation." Turesson chose his experimental material from strongly contrasting habitats, though it is fair to say that at this stage in the development of genecological ideas it was probably essential to do so, and his quantitative and population studies were minimal, so that discontinuities were very evident. By applying detailed quantitative and statistical methods to populations of *Plantago maritima*, Gregor and his colleagues (1936, 1938, 1939; and Davey and Lang, 1939) were able to show convincingly that variation was continuous in the populations which they studied, and indeed that population differentiation could occur unaccompanied by spatial isolation (Gregor, 1930 : 23). Gregor (1938 : 44) found " that local population differences were not necessarily associated with the presence of peculiar growth forms but were due to changes in the numerical relations between types," bringing to the fore the important fact that the characteristics of the individual may have less genecological —or indeed taxonomic—relevance than the characteristics of the population, a view supported also by Mayr (1942 : 7) in his affirmation that " the population, or rather an adequate sample of it, has become the basic taxonomic unit." The continuous variation demonstrated by Gregor and his coworkers in populations of *Plantago maritima* is only a special case of a phenomenon of very general occurrence. Langlet (1934) showed for certain physiological characters in *Pinus* *silvestris* a " continuous range in variability " of a type confirmed by a great deal of later work on trees by Pauley and Perry (1954), Irgens-Möller (1957), Callaham (1959), Vaartaja (1960), Langlet (1963) and Mergen (1963). Certain criticisms were directed at Langlet's early work by Turesson (1936), but there seems little doubt that the continuous variation which was described by Langlet is a general phenomenon. Rensch (1936) also discusses the widespread occurrence of continuous variation, and much data have also accumulated from considerable research on intra-specific variation by a number of workers (Sumner, Dobzhansky, Timofeeff-Resovsky, *inter alia*).

Huxley (1938) discussed the phenomenon of continuous variation, and proposed the term " cline " to cover this type of variation, since " it would seem certain that, once attention is concentrated on this subject, regularities of intra-group variation will be found to be common—the rule rather than the exception." As far as intra-specific variation is concerned, this view has been confirmed by subsequent general experience, and the term " cline " quickly received general adoption. It is interesting to note that Huxley proposed the cline as a further step in the direction of synthesis in taxonomy, which, " after a phase of splitting, adopted the integrating principle of geographic replacement, thus uniting numerous forms previously styled species as geographical races or sub-species of a polytypic species " but which should " go still further in the direction of synthesis " (*loc. cit.*).

It was in the study of the continuous variation characteristic of clinal situations that a clearer understanding became possible of discontinuous variation. Regarding a cline as arising out of a set of conditions permitting the free and unrestricted flow of genes between the populations comprising it, Huxley (1938) described how the continuous gradation of characters will become broken up by various forms of isolation which, " by impeding the flow of genes will accentuate the mean adaptive differences between adjacent groups, as well as in some cases introducing non-adaptive differences." A picture emerges of clinal gradients the slopes of which are not constant, but " tend to be considerably steeper along certain zones " (Mayr, 1942 : 98). Huxley (1940) refers to work by Sumner with *Peromyscus* which shows a " stepped cline for increased pigmentation from the coast inland, eventually flattening out altogether," and he interprets this in terms of a selection for cryptic coloration which is not very intense, and a gene-flow between adaptively different groups which is locally restricted to produce a narrow zone of intergradation for the character in question. " The steep clines across the intergrading zones will have a purely genetic cause, while the general inter-group cline and internal clines will be adaptive " (p. 33). Van Steenis (1957), in a consideration of similar clinal situations affecting plants, went rather farther and argued that " clines are the primordial stages from which can be derived discontinuous populations by the continued force of isolation." Essentially the same view is expressed by Mayr (1942 : 97) when he considers that " the more clines are found in a region the less active is species formation."

These advances in the understanding of the relations between continuity and discontinuity, between populations and the forces of natural selection, reached a productive peak at the end of the 1930s with the publication of a number of well-known works (Dobzhansky, 1937, 1941, 1951 ; De Beer, 1938 ; Darlington, 1939 ; Clausen, Keck and Hiesey, 1940 ; Goldschmidt, 1940 ; Huxley, 1940 ; Huxley, 1942 ; Mayr, 1942 ; Sinskaya, 1942). In fact and in tone—as well as in titles—these works were synthetic. By their detailed study of the genetic nature of natural discontinuity they also inaugurated the " biological " species problem. They brought together the mass of results from the experimental work of the 1930s—and to this a very large contribution was made by what Waddington (1953) calls the Russian school, and to whom many of us not always irreverently apply the name of " Drosophilists "—and considered this in the light of its impact on existing concepts of the species and its sub-divisions. When one reflects upon the protracted efforts to amalgamate the taxonomic view of the species as a discontinuous, discrete, reference point, and the often continuous relationships between biological units as disclosed by experiment which have resulted from their efforts at a synthesis, one wonders sometimes whether this process has not gone too far, and perhaps farther than was intended by the synthesists themselves.

There is no doubt that the concept of the biological species which emerged from the experimental and theoretical work of the 1930s was a dynamic one of an entity which responded genetically at the level of the local population to the influence of natural selection in a largely quantitative way—in as many ways, in fact, as there are environmental situations to accommodate it, of which one of the most striking examples is perhaps still that demonstrated in the work of Sinskaya and Beztuzheva (1931) on climatic, phytosocial and human selection in *Camelina sativa.* But while the genetic nature of specific and intra-specific groups was shown to be derived from the extent to which gene-exchange occurred between groups, incomplete and gradual reproductive isolation between species and even genera led to a blurring of the margins between them. When attempts were made to use the " results of experimentation . . . to define taxa " this created difficulties and disagreements in the erection of the discrete categories necessary to taxonomic treatment.

In a discussion of this problem, the terms " alpha " and " omega " taxonomy were coined by Turrill (1938), and one still hears reference to them. The former is traditional, herbarium-based, depending primarily and almost exclusively upon morphological criteria, and Turrill saw this changing under the influence of new evidence provided by the sciences of cytology, genetics, physiology, chemistry and so on, acquiring depth, as it were, to become the omega taxonomy of the future. As a statement of taxonomic principles Turrill's paper is outstanding, but one feels that it voices the cause of a simplicity long dead. The problem is not merely one of absorbing new data, from however sophisticated a source, into a classification which to be useful requires that organisms be distinguished by discontinuities however small or artificial, and which if not useful cannot be justified at all. To incorporate the new data of the experimentalists into taxonomy requires more than a mere process of the accumulation and incorporation of new data. What is required is a technique sufficiently discriminating as to enable continuity, for example, to be categorised and placed accurately within a reference system. One has only to look at the many attempts to define and re-define the taxonomic species in the light of the new experimental data to realise that this is an impossible, and purposeless, task. Turrill (1938), when speaking of omega taxonomy, expresses the view that we are probably now but a little way towards beta taxonomy. Yet the difficulties increase with every advance, rather than become less, a fact that is in itself a just cause for suspecting that our current concepts, unable to give birth to practices capable of dealing with accumulating information, have a defect somewhere. "One cannot help feeling," remarks Cain (1959), "that a taxonomic practice that worked only where too little was known about its subject was hardly the best possible, scientifically." What might the problem look like in fifty years' time? We are keenly aware, with Mayr (1942), that "what we consider as new systematics in 1941 may indeed be very old systematics in fifty years' time." The "new systematics" of 1941 are already very old systematics.

Quite apart from attempts to define categories in biological terms, and the problems this raises, another problem is encountered when these categories are incorporated into the taxonomic hierarchy, and it is assumed that positions within the hierarchy reflect "biological" relationships, rather than taxonomic affinity. The problem of the classification, too, of apomicts and persistent inbreeders would still remain to be answered, as would the equally complex one of what might be termed "obligate out-breeders." Mayr (1942 : 103) states that "no system of nomenclature and no hierarchy of systematic categories is able to represent adequately the complicated set of inter-relationships and divergences found in nature." To those who would regard this as a cry of despair it might be salutary to reflect upon the alternatives to a complete schism between taxonomy and experimental data. Such alternatives there have been. They can be grouped into two distinct schools. There is what can be called the school of amalgamation, and there is the school which, recognising essential differences in purpose and approach, argue the case for a *lingua franca*.

Attempts at amalgamation began with the development of new systems of categories such as the ecotype-ecospecies-coenospecies series of the genecologist Turesson, or the convivium-commiscuum-comparium series of the taxonomist Danser (1929), and continued by the expedient of coining a new term to meet each new difficult situation. In a recent memorandum (Sylvester-Bradley, 1952) to the Systematics Association some hundred or so infra-specific terms and categories are listed, all of which represent efforts to re-define in taxonomically useful terms new experimental evidence, and seldom used except by their authors. Lam (1959), in a recent review, commented that it was this seemingly endless generation of new terms which was "an expression of despair." It is a pity that he rather spoils the effect by coining a few himself in the same paper. As if Taxogenesis and Neotaxonomy—replacements for terms already existing and blessed already with synonyms—were not enough, he throws in, among others, terms such as nomtaxa and nattaxa.

Early genecological workers attempted to give their data the respectability of traditional taxonomic treatment by the re-definition of taxonomic categories in terms which embraced their new findings, just as taxonomists sought to reconcile taxonomy with the new data by re-definitions of terms. If it had been a simple matter of merely adding more facts, albeit of finer levels of discrimination, this would have been the solution to the problem, and the path to the omega taxonomy would have been smooth. Before the accumulation of data began to make it clear that such a direct assimilation was impossible, and that much of the new data contradicted rather than supported existing taxonomic categories, most genecologists did in fact regard their work as supplementing taxonomy. The work of Gregor and his colleagues (1936 and later papers) was described as " Experimental Taxonomy " (Clements and Hall, 1922), and concerned itself with the " recognition of the small taxonomic units." In a similar way Camp and Gilly (1943) coined the term " Biosystematy " to describe their work, which sought " to delimit natural biotic units " and to apply to these a system of nomenclature.

When it became clear that the emerging picture of organic nature did not fit well into existing or indeed possible patterns of orthodox taxonomy, and that amalgamation did not offer hope for the resolution of the contradiction, a second line of thought emerged. Recognising the irreconcilable nature of the contradictions between concepts of biological units on the one hand (distinguished at the intra-specific level by mostly quantitative characters of adaptive significance, and at all other levels by a more or less complete inter-sterility) and concepts of taxonomic units on the other (distinguished at all levels by mostly qualitative characters of little apparent adaptive significance), and at the same time recognising the urgent need that the disciplines should freely inter-communicate, Gilmour and Gregor (1939) published proposals for a terminology which was " neutral." This was the -deme terminology, which enabled the entities under consideration to be described without commitment to any taxonomic hierarchy or nomenclature. As Gregor (1948) has pointed out, genecology concerns itself with natural populations, and with problems of their origin, structure and properties, and not with their arrangement into systems of classification or nomenclature. An extended treatment of the -deme terminology was published by Gilmour and Heslop-Harrison (1955), who intimated at the same time that a number of taxonomists and genecologists had given their support to the proposed terms. Nevertheless, the -deme terminology was not brought into the widespread use its origins would suggest it deserved. A discussion of the reasons for this will be postponed until some of the problems arising out of the entanglement of taxonomy and genecology have been considered.

III. The "Conflict of Categories"

It has already been suggested that the species problem which has consumed the energies of so many workers over the past three decades had its origins in part with Turesson himself, and this opinion has been expressed also by Heslop-Harrison (1955), who remarks that the simple fact that Turesson gave his experimental categories names which bore the suffix "-species" may have sown so "great a measure of confusion about the concepts involved in this type of classification" as we have seen. The real roots of the species problem are to be found in the fact that the term "species" has been employed for, in this context, two entirely different entities—the one a unit of evolutionary change, the other a unit of identity. The genecologist studies the process, the taxonomist the end product. When, in what is admittedly a simplification, Hogben (1940) describes taxonomy as a convenient card index of distinguishable types, he goes on to remark, "The procedure we adopt in making it has little to do with experimental enquiry into the nature of heritable variations. . . . So it has always seemed to me a misfortune that Darwin called his best-known work 'The Origin of Species.'" With these feelings we must wholeheartedly agree.

Just as genecology seemed obsessively directed to a rethinking of taxonomic relationships, and assumed such names as Experimental Taxonomy, New Morphology (Thomas, 1931), New Systematics (Hubbs, 1934; Huxley, 1940), Genonomy (Epling, 1943), Biosystematics (Clausen, Keck and Hiesey, 1945; Lawrence, 1951), and Neotaxonomy (Lam, 1959) and

(1964)

others, and produced the crop of terms already referred to (Sylvester-Bradley, 1952), the first impact of its data struck taxonomy just at a time when taxonomy seemed to be obsessively involved in phylogenetic re-thinking (Bessey, 1915; Hutchinson, 1926, 1934; Wettstein, 1935, to mention only a few, but see also Turrill, 1942; Davis and Heywood, 1963), an inheritance from Darwin and the post-Darwinian naturalists of the late nineteenth century. The conjunction of these circumstances made it almost inevitable that genecology should be called upon to subserve phylogeny. There were those who opposed a phylogenetic tendency in taxonomy, even before the advent of genetics, and among them was T. H. Huxley, who regarded phylogeny as a hypothesis and objected to its introduction into such a precise science as taxonomy on the grounds that it would sow serious confusion. It should be borne in mind, however, when considering the nineteenth century, that the use of the term " common descent " with reference to groups of organisms does not necessarily carry phylogenetic implications, as Mayr (1957) has pointed out, showing that this term stems from the definition of the species which was given prominence by Ray " that like is descended from like, and itself produces its like." Nevertheless, phylogeny took a firm hold on taxonomic thinking, and this was strengthened rather than otherwise with the advent of genetics. On page two of his compilation of genecology, 'The New Systematics,' Huxley (1940) states, " Fundamentally, the problem of systematics, regarded as a branch of general biology, is that of detecting evolution at work." The phylogenic view was expressed at the same period by the systematists Lam (1939) and Sprague (1940), the latter saying that " taxonomy may be defined as scientific classification of the different kinds of living organisms according to their proven or inferred phylogenetic relationships." Geneticists have also given expression to phylogenetic views of taxonomy, among them Lamprecht and Mayr, for example. Mayr (1942 : 280) observes that, " summarising this evidence (on taxonomic groups), we may say that the 'natural system' of the modern taxonomist is based on phylogeny, and that the higher categories are monophyletic units." The case of Simpson (1961) is a rather special one, for although (p. 221) he states that " taxa reflect evolutionary factors involved in their origin and development, and this highly meaningful relationship is prominent among the several reasons for insisting, as far as practicable, on the evolutionary approach to classification," he is a palæontologist dealing with the special problem which the species (and perhaps even more the genus) presents to workers with certain groups in this field. This becomes clear in his chapter five, where we may read how " species in time, as segments of phylogeny, raise special problems of the sub-division of unbroken successions of species and the treatment of branching lineages." Elsewhere in the same work (p. 11) Simpson defines taxonomy as " the theoretical study of classification, including its bases, principles, procedures and rules " and distinguishes this from what he calls Darwinian taxonomy, the essential principles of which are that " taxonomic groups are the result of descent with modification, or of phylogeny in the term now more usual " (p. 53). Such a distinction, had it been more widely applied, might at least have avoided the degree of confusion which we have seen.

The relationship between taxonomy and phylogeny is discussed at length in Huxley (1942). We read (p. 394) that " a classification based on the idea of phylogenetic descent must at best remain highly speculative, for, save in a few fossil lineages, we do not and cannot know the actual course of events in the evolution of a group." Later, however (p. 401), Huxley concludes, " Thus, while taxonomic practice inevitably rests upon the evaluation of characters, and while phylogenetic relationships must always (in the absence of full palæontological data) remain a deduction, the phylogenetic idea, whether directly, or symbolically in the form of a modifiable archetype, may and often does aid the taxonomist in evaluating his characters and in framing his categories." It is clear from this discussion that the " apron-string " of phylogeny is carefully held. How much so uncertain a set of deductive premisses as phylogeny offers can contribute to the inductive framework of taxonomy is a matter of question. The point made by Calman (1940) that " many zoologists nowadays would find it difficult to divest themselves entirely of evolutionary preconceptions " in taxonomy seems more pertinent than most, and portrays a sadly unscientific frame of mind.

Meanwhile the views of most geneticists remained essentially phylogenetic as far as taxonomy was concerned. Dobzhansky (1941) states " since the time of Darwin and his immediate followers the term ' natural classification ' has meant in biology one based on the hypothetical common descent of organisms." In the later edition (1951) of the same work this passage has become, " since the time of Darwin the term ' natural classification ' has meant one based on the common descent of organisms " (p. 257). In Stebbins (1951) we read " The need for an amplified taxonomy for dealing with the problems of evolution has been recognised by the better (sic) taxonomists since the acceptance of Darwin's theory." In the same work there is what seems to be a mild rebuke for the taxonomist who does not adopt the phylogenetic approach—" nevertheless many systematists, even in modern times, have not adopted the point of view or a method of attack on their problems which is acceptable to the scientist who is interested primarily in evolution." It must have seemed very obstinate of Turrill (1936) to say that " the first function of the taxonomist is the theory and practice of classification " because " exact identification is a first consideration in biological experiments." The same might be said of Cain (1959) when he says that " what is required is a system of reference that is not tendentious, but allows us to refer unambiguously to the things we are talking about."

Cain's comments to-day are as pertinent as Turrill's twenty-five years ago, for the phylogenetic approach to taxonomy has persisted. Huxley (1959) quotes Mayr, Linsley and Usinger (1953), who say that " the aim of modern taxonomy as usually formulated is expressly to produce a classification which reflects phylogeny." Lam (1959), in his review of taxonomy, presents a defence of the phylogenetic point of view, and contrasts " static taxonomy " and " dynamic taxonomy." Bradshaw (1962) states " that taxonomy is not just blind pigeon-holing of all the different forms of living creatures according to some arbitrary scheme in the mind of the taxonomists, but that it is recording the divergences that have occurred during the process of evolution." Wardlaw (1963) proposes a new taxonomy, the aims of which " will be to specify, classify, and, if necessary, to codify not the morphological or other characters, but the major processes that are, and have been, involved in the evolutionary trends and morphogenetic parallelisms in representative taxa." " Taxonomy," says Löve (1964), " is the science of affinities and its object is to invent a scheme of classification which mirrors not only the phylogenetic relations that unite different groups of organisms, but also the phylo-

(1964)

genetic similarities at each taxonomical level." But—as Harris (1964) remarks—" we should be diffident about building a fairy palace when the ordinary man wants a simple room where he can work."

That taxonomy should assume a phylogenetic bias in response to the Darwinian inheritance on the one hand, and the evidence of genecology on the other, can be traced to certain background misconceptions concerning the nature of taxonomic laws and relationships. Gilmour (1937, 1951, 1958, 1964), Heslop-Harrison (1955), Cain (1956, 1958, 1959a, 1959b), Cain and Harrison (1958) and, more recently Davis and Heywood (1963) and Lubishev (1963), have drawn attention to philosophical and historical aspects of taxonomic theory. Among other things, the logical significance of the term " natural affinity " is pointed out, and in this connection it is worth noting that the phylogenetic interpretation of this term which is part of the current confusion of thinking in taxonomy cannot be attributed to Darwin, who used it—correctly—to imply classification by not one, but many, characters (Lubishev, p. 416). Gilmour (1951), in a paper the importance of which deserves particular emphasis, has shown how " as regards history, we can see how a failure to appreciate the general principles of classification, and to apply them to living things, has led biologists to seek other aims for taxonomy (than classification) in order to fill the vacuum created." These aims led them, in one direction, towards the phylogenetic taxonomy which would express " the proven or inferred " relationships of descent. In another direction it led to the taxonomy of the " biological species concept."

The population studies of the genecologists and geneticists which acquired momentum in the 1930s led to the conclusion that " species are reproductively isolated Mendelian populations " (Dobzhansky, 1935). The examination of continuous clinal variation produced data which showed how local steepening of clinal gradients can lead to " raciation " (Blair, 1943) by restrictions of gene-flow through the operation of extrinsic or intrinsic factors. The term " speciation " applied to the same phenomenon seems more hopeful than accurate. Data on much work of this kind functioned in a cumulative manner to refashion thinking on the nature of what will be called here the natural units of discontinuity, which are called species. As observed by Muller (1940 : 254), at the level of the species the quantitative restriction in gene-flow which leads to the differentiation of intra-specific groups yields thereby to a qualitative change—" there is no other stage of divergence which, like speciation, involves the entrance of a qualitatively different factor, having a direct influence upon the process of divergence itself." But it should be pointed out, perhaps, that this stage is merely that at which the term " species " happens to have been applied.

Genecological studies cast a brilliant light upon the origins of the discontinuities which have impressed man for so long—the same discontinuities which, according to Mayr (1949), are recognised as clearly by the savage as by the taxonomist. One might even say with some justification that it was a blinding light, since in so dramatically highlighting the origin of those characteristics of populations which were the concern of the taxonomist, genecologists were diverted, in the guise of " experimental taxonomists " and " biosystematists," into the field of taxonomy and the " biological species " concept. The further clarification of the interaction of selection and population variability, and its quantitative analysis, was left to a very small number of workers. With these exceptions, the " proper study " of genecology was neglected. Thus, while Darlington (1933, 1939), for example, used new genetical data to present a brilliant analysis of genetic systems and their rôle in gene-exchange and isolation, others sought to " define taxa " on the basis of experimental evidence.

Mayr (1940) defined species as " groups of actually or potentially interbreeding populations which are reproductively isolated from other such groups." Timofeeff-Resovsky (1940) in more detailed terms describes the species as " a group of individuals that are morphologically and physiologically similar (although comprising a number of groups of the lowest taxonomic category), which has reached an almost complete biological isolation from similar neighbouring groups of individuals inhabiting the same or adjacent territories." The species, according to Thorpe (1940), is " a population of individuals prevented from interbreeding with all other populations by physiological differences (in the widest sense) whether or not structural differences are also present. A species is thus regarded as that stage in evolution at which physiological isolating mechanisms become virtually complete." This may be compared with Dobzhansky's observation that " the species is a state in an evolutionary process." The species definition of Huxley (1942) adds to the common criterion of interfertility the criteria of geographical distribution and morphological distinctness, a point of difference from the definition of Thorpe —" In most cases a species can thus be regarded as a geographically definable group, whose members actually interbreed or are potentially capable of interbreeding in nature, which normally in nature does not interbreed freely or with full fertility with related groups, and is distinguishable from them by constant morphological differences."

Numerous examples of similar biological species definitions can be found in the literature, and some of these have been discussed recently by Beaudry (1960) and Davis and Heywood (1963). In certain features these definitions resemble one another, particularly on the criterion of interfertility and a degree of reproductive isolation. As Grant (1957) observes, " the reproductively isolated population, whether it is called a species or some other name, represents a major biological unit," but he does add the point that the word " species " might be qualified to " biological species." Apart from these common features, however, any reduction to a common definition would be impossible. One recalls the remark of Mayr (1942) that " it seems as if all the conclusions and generalised laws derived from a study of taxonomic material were dependent to a high degree on the nature of this material and the background of the student." " The species concept," says Huxley (1940), " however loosely framed, will not apply to all groups."

The frequent reference to the potential ability to interbreed is an important feature of biological species definitions. It is worth noting, therefore, particularly in the discussions below on the attempts to assimilate experimental data into taxonomy, the point made by Turrill (1938 : 357) that " it is what actually occurs rather than with what can or might occur under artificial or hypothetical conditions that the taxonomist has to deal." Mason (1950) similarly emphasises that " the taxonomist cannot operate in the field of potential situations."

The genecological studies on the species which led to these " biological species " definitions had two consequences. One was a great increase in the number of references to the " objective reality " of the species. Mayr (1948), reviewing the nature of the species, states that " species are products of nature and not specially made for the convenience of the museum man." Beckner (1959) includes among the theses of the "New Systematics" the view of the species as "the taxon with the highest degree of objectivity" which "differs in kind from all other taxa." Beaudry (1960) says, "There is no doubt that the species is something objective, material, that is constituted by a substance incorporated in a mass." Gilmour (1940) discusses the undesirable consequences of the use of such phrases and states that they have "tended to give such groups a false appearance of 'metaphysical objectivity.'" One even finds reference to the "reality" of "systematic groups," which have been described as "groups of individuals characterised by one or several common heritable characters and having a common area of distribution" (Timofeeff-Resovsky, 1940). This passage is quoted from a discussion entitled "Mutations and the Formation of Taxonomic Groups"!

Clearly one cannot argue with the realities of the discontinuities which these workers have sought to define. Nor can one be unaware of the necessity of investigating natural groups genetically. But—despite views such as that of Beaudry (loc. cit.) that "the sophisticated arguments of various kinds of philosophers cannot hold when confronted with the impressive bodies of data about the reality of the species"—the confusion of Shadow for Substance, and the establishment of a logical identity between the units of natural discontinuity and the units of taxonomic discontinuity must be opposed as creating considerable confusion, and indeed some degree of mysticism. When the proponents of the biological species concept state that the species is objectively real, they mean that the observed discontinuity has an objective reality. As long as the term "species" is employed in this context, that is, the genetic context of reproductively isolated populations—though it would be better qualified, either as suggested by Grant, or as biospecies, or some such designation—its use may be legitimate. But phrases such as the "objective reality of taxa" are not. The case can be illustrated by reference to Stebbins (1951 : 30), where we read that "all taxonomic entities including varieties or sub-species and species as well as genera and higher categories, are not simple units, but complex systems of populations." What we are told, in effect, is that (1) species, &c., are taxonomic entities ; (2) species, &c., are complex systems of populations ; (3) taxonomic entities are complex systems of populations. This may or may not be what we are intended to take from this statement, but the fact that we are able to do so is an indication of the laxity of language and thought which have been applied to the species problem. In the same work, two pages later, we read, " Taxonomic categories *are based upon** these discontinuities between series of populations." This statement is clear. Juzepchuk (1958) refers to Korzhinskii (1892), who " distinguished between real units existing in nature . . . and taxonomic units that represent something conditional, the circumscription of which is subjective ; these were species, sub-species, varieties, &c." As stated by Dobzhansky (1951 : 256) " It should be made explicit that what a systematist is operating with are categories of classification."

The second consequence of the intensive genecological species studies, and the development of the " biological species " concept, was the attempt to introduce micro-evolutionary and biological evaluations into orthodox taxonomic arrangements by the formulation of " natural " hierarchies based upon the experimental evidence of breeding relationships. The first such attempt was that represented by the ecotype-ecospecies-coenospecies series of Turesson (1922a, 1922b, 1923, 1926, 1929), though it was not until the last of these papers that fertility-sterility criteria of relationships were introduced, and then only on the basis of such inter-breeding as occurred " in nature." Turrill (1946), reviewing the ecotype concept, emphasises that its aim was primarily ecological, seeking " an understanding of the Linnaean species from the ecological point of view." Nevertheless, from the convivium-commiscuum-comparium series of Danser (1929) until the memorandum of Sylvester-Bradley (1952) to the Systematics Association, the hundred or so terms of which attest to the extent of subsequent efforts at the biological definition of infra-specific groups, the sole criterion of relationship has been that based upon breeding relationships. Despite the view of Clausen, Keck and Hiesey (1940 : 243) that " experiments . . . have shown that taxonomic relationship between forms is roughly proportional to their ability to exchange genes "—and this concept has been behind several decades of effort to amalgamate genecology and taxonomy—this is by no means more than approximately true. Apart from the fact, as pointed out by Heslop-Harrison on a number of occasions and again recently (1962b), classifications

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* Italics mine.—E. B.

based upon tests of inter-fertility must be regarded as artificial, or special purpose, classifications, there is the further point made by Gregor (1948), and echoed by Heywood (1959), who remarks upon the impracticability of fitting any system of discontinuous and discrete categories to the continuous nature of the variation with which genecology is largely concerned, and has been well established by Gregor and his co-workers, and by Langlet, Sumner, Huxley and others since the 1930s. It is true that one major school of genecology, that of Clausen, Keck and Hiesey (1940, 1945), has maintained the existence of discontinuity between ecotypes which is amenable to taxonomic treatment at the sub-specific level, but in a later examination of the same range of material they considerably modify their conclusions, and admit the occurrence of both continuous and discontinuous variation (Clausen and Hiesey, 1958a). Even in such cases where ecotypes are discontinuous, whether due to discontinuous sampling or to environmental or genetical discontinuity, Lawrence (1945) and Heywood (1959) have shown that they need not, and do not, correspond with taxonomic divisions such as sub-species.

The conflict of categories, as it has been called by Heslop-Harrison, which has developed as a consequence of genecological studies, owes its origins therefore, in the first place, to certain premisses on the validity of biological criteria, and on the possibility of fitting the continuously varying results of micro-evolutionary processes to discrete taxonomic reference points, which are increasingly regarded as unsound. In the second place, the absence of any coherent theory of taxonomy, as pointed out by Gilmour, and a failure to appreciate the nature of taxonomic affinity, as pointed out by Cain (1958) and Cain and Harrison (1958), permitted not only the penetration of taxonomy by "biological" and "objective" concepts of the species and an inflation of the significance of experimental and breeding data as taxonomic criteria, but also large-scale taxonomic revision based upon experimental evidence. Valentine (1949) cites several examples of such revisions, and proposes a number of species definitions based upon biological criteria, from which it is necessary by definition to exclude apomictic groups. Heywood (1963a) comments that such attempts at the biological delimitation of species simply cause "a semantic problem by necessitating another term for the majority of species about which this is not true," the illogical ends of which can be seen when Dobzhansky (1958) asks, "Are there species in asexual organisms ?" and in observing that the naming of the clusters of biotypes which occur in such groups is an arbitrary process, remarks that "with these forms, the systematist loses the guiding light which pilots him towards recognition of the biological species in sexual outbred organisms." For example, Camp (1951) refers to three treatments of the genus *Rubus* which appeared within months of each other, produced by three outstanding American botanists, who ascribe to the genus 381, 205 and 24 species respectively, using approximately comparable areas of geographic distribution and limits of generic delimitation. Differences in opinion on the assignment of taxonomic rank and the delimitation of species thus produce three quite different taxonomic pictures.

Yet, is the position so very much better in the case of the sexually reproducing organisms ? It is hard to agree that it is. What appears to be the main difference is that disagreement on the taxonomic treatment of apomictic and asexual organisms occurs arbitrarily at a level which is defined in practice as the species level, in order to avoid excessive "splitting," but takes place mostly at the intra-specific level in the case of the sexually reproducing ones, or wherever some degree of natural discontinuity might be (but so often is not !) provided by restrictions to gene-flow. By far the greater part of genecological investigation is centred around the question of intra-specific variation, and as much—or more—attention has been directed by proponents of the "biological species" concept to establishing some degree of correspondence between the units of natural discontinuity and the units of taxonomic discontinuity at the intra-specific as at the specific level. Not only did the now classical papers of the 1930s devote themselves almost exclusively to such variation, but a greater part of the discussions of 1938 to 1942 already referred to was concerned specifically with that degree of population differentiation which is normally treated by the taxonomist as sub-specific. The merely quantitative nature of the differences between specific and sub-specific distinction is illustrated by the remarks of Weatherby, summing up a discussion on the sub-species by Fernald (1940), Clausen (1941), Fosberg (1942) and Weatherby (1942)—"I think it is safe to say that, because of inadequate knowledge for generalisation, not one, from Linnaeus to Du Rietz, has been able to produce (a definition) which either he or anyone else could apply over any wide field with consistency or satisfactory results. This condition (it was) hoped to see corrected by the use of data provided by that immensely promising line of research, experimental taxonomy; but almost in the same breath (one) is forced to admit that it cannot now be done"—the comment of Mayr (1942) that " no system of nomenclature . . . is able adequately to represent the complicated set of inter-relationships and divergences found in nature," already quoted in an earlier part of the present paper, comes again to mind to give support to the view that problems of species and sub-species, in both apomictic and amphimictic organisms, are not different problems in anything other than a quantitative sense.

Further support for such a view is to be found in several recent papers. Valentine and Löve (1958), examining the process of gradual speciation, list a number of taxon pairs, including the well-known case of the silenes, where decisions as to taxonomic status are inconclusive, and remark that " there are in fact a number of cases in which it is impossible to reach a definite decision; when this is true, so long as the taxa are clearly described and recognised, arguments about status are not very important." Van Steenis (1957) feels that such groups at present regarded as species could be regarded as sub-species, but Hawkes (1963) states with reference to this view that " it is more convenient to consider such vicariads as species pairs." Schmalhausen (1949) speaks of the ill-defined lower limits to the sub-species, referring to adaptive differences in local races " which constitute, within the limits of the species, a continuous series of forms between the two extreme sub-species." In Meikle (1957), Cain observes that both the lower and the upper limits of the sub-species are ill-defined, and says that " taxonomists have so far failed to establish satisfactory standards for the determination of specific and sub-specific differences."

Indeed, these comments do more than merely support the case that species problems and sub-species problems are identical in biological terms, even in the case of taxonomic sub-species defined on the basis of geographical replacement as proposed by Du Rietz (1930) and Rothmaler (1954). They show that in spite of the " biological species " concept, and the belief that this concept has brought to taxonomy a new objectivity, decisions on the delimitation of critical taxa are based on subjective criteria and criteria of convenience, contrary to the opinion expressed by Löve (1964) that " the biological species concept is the only definition that is universal." Heywood (1963b), who says—questionably—that " so far, the intrinsic value of a biological species concept has not been challenged," nevertheless reaches the conclusion that " the factual, non-arbitrary and so-called objective biological species is, on analysis, shown to be based on criteria which are difficult to apply in practice."

Is this confusion, then, the only achievement of the period of the biological species concept in taxonomy ? If not, what then of positive value has been achieved ? Attention has been confined so far mainly to negative aspects of the period, to the birth of the inseparable twins, " Systematics " and " Speciation," which indeed were seen so seldom apart that genecologists and taxonomists alike might be equally forgiven for frequently mistaking the one for the other. The words of a song by Danny Kaye come vividly to mind :—

. . . we walk alike, we talk alike.
And what is more
we hate each other very much ;

Even to-day it is possible to observe a certain finely developed territorial sense—" the species, however, is a taxonomist's unit and he has prior claim on it. . . ." Frequent impassioned attacks and defences of taxonomy on the one hand and of " biological " concepts on the other are still a not uncommon feature of discussions which have consumed several decades. Simpson (1945) notes that " taxonomy, a generation ago, was a term of reproach." Camp (1951) speaks with great vigour of " the mouldy shroud of taxonomy." Valentine and Löve (1958) complain that " the morphological concept of the species has fallen into some disrepute." Rogers (1958) defends taxonomy saying " description *per se* must not be undervalued as a scientific act." Heywood (1959) speaks of the taxonomy which " the geneticists would thrust upon us." Turrill has frequently defended taxonomy from the " more or less confusing comprises " which have sought to improve it. In doing so they have had the potential effect of destroying it and replacing it with something quite different, either an essay in interpretive " pseudophylogeny," or a composite theory of evolutionary pathways. Feelings have often been high. Apprehensively, the solution to Danny Kaye's problem comes, again vividly, to mind :—

> . . . how I wish I had a gun
> and shoot the other one
> and only be one.

So much for the negative aspects of what has made its mark on history as " The Species Problem."

But already in the late 1930s certain positive developments became evident. Following the warning of Gregor (1939) that " a too precipitate amalgamation of experimental and traditional taxonomy would almost inevitably have repercussions detrimental to the present usefulness of the established morphological system," Gilmour and Gregor (1939) published proposals for a " neutral terminology " the " -deme terminology "—which, non-hierarchical and detached from any taxonomic connotation whatever, was designed to offer an extremely flexible series of terms capable of describing any chosen aspects of the micro-evolutionary relationships among groups of organisms of any specified taxon. This was done by using a suffix " -deme," to which could be added any of a virtually unlimited number of descriptive prefixes, such as " topo-," " gamo-," " eco-," " geno-," and so on, and the authors of the proposals then, and now, have consistently drawn attention to the " neutral " character of the suffix. As Gilmour (1960) states, " it carries no implication that the individuals exhibit any other relationship than that they belong to a specified taxon. In particular, it carries no implication that they form a population, in either the topographical or an inter-breeding sense ; these, and other implications, are indicated in the terminology by prefixes."

It is unfortunate that zoologists who, according to Cain (1959), are accustomed to regarding the units of evolution " only in terms of geographically definable populations in bisexual species, have wrongly used the word ' deme ' for these, thereby greatly impairing its generalisation and usefulness." The word " -deme " was never intended to be used alone. Its use in this way detracts from its immense value as the " neutral " suffix of the initial proposals, and of the later development of these by Gilmour and Heslop-Harrison (1955). Deme was first misused in the sense of a " local breeding population within a species "—*i.e.*, as a substitute for the term "gamodeme," or "topodeme," by Huxley (1942 : 203). Its misuse continued, in the same sense, by Carter (1951 : 121), Mayr, Linsley and Usinger (1953), Simpson (1953), Dobzhansky (1955), Wright (1955), Wright (1956), Grant (1957), Lam (1959), Simpson (1961) and Mayr (1963). Wright (1955) speaks of the "sub-division (of the species) into many partially isolated local populations, now known as demes," and later in the same paper this misused term acquires a new sophistication in the phrase "inter-deme" selection. As Heslop-Harrison (1962a) observes, "it is scarcely necessary to point out that this makes nonsense of the whole intention of the system."

Whether it is to such misuse that we must look, as Cain (1959) suggests cogently, for the limited application made of the -deme terminology, or not, it remains the only existing set of proposals which are of universal applicability and are completely unattached to orthodox taxonomy. The point has been made succinctly by Cain (p. 316) that "Gilmour and Gregor have proposed that the units of evolution should not be confused nomenclaturally with the units of reference, and have produced a very well-designed terminology based on the root '-deme' for the units of evolution." There is increasing evidence that this is becoming widely recognised, as the need for the separation of "Systematics" from "Speciation" is increasingly appreciated. It is not incautious to expect that the correct use of the "-deme terminology," and a clear appreciation of its purpose, may do more than any other single step to dispel the muddled thinking which has clouded both genecological and taxonomic thought for such a long time.

The -deme terminology solves no taxonomic problems nor genecological problems. It seeks to solve a problem of communication between disciplines. Understood, and correctly applied, it can bring an end, as far as taxonomy is concerned, to the "tyranny of the biological species concept." Taxonomy may then set about the task, stated so ably by Gilmour, Cain, and Cain and Harrison, of constructing a fabric of maximum utility based upon philosophical and logical foundations sufficiently healthy to resist such diversions or extraneous intrusions as has happened in the case of phylogeny and the biological species concept.

It is not necessary to agree with Camp (1951) that it is a function of taxonomy to deal with the problems of biosystematics to agree with his readiness radically to alter taxonomic nomenclatural structure (in a consideration of the three stages in taxonomic knowledge described by Camp and Gilly (1943)—the stages of exploratory study, then of systematic study and finally of biosystematic study) whenever it is realised that classical taxonomy is inadequate to the tasks demanded of it. Not only do such conclusions lend strength to the general statement by Gregor (1963) that "attempts to redefine orthodox categories are virtually an admission that much genecological information is not amenable to taxonomic treatment along traditional lines"; they also lend added point to the statement of Gilmour (1951) that when taxonomic categories "are seen as human contrivances constructed for human purposes, there is, of course, nothing shocking in abandoning them if they do not serve the particular purpose we have in mind at the moment." As has been remarked by Huxley (1942) in the same connection, "the Sabbath was made for man, not man for the Sabbath."

Turrill (1942) ends his review with a definition of the task of the systematist, which "is twofold: to prepare as many special classifications as are needed for special biological investigations, or to make available material for others to construct such special classifications, and to make a general classification which shall express as far as possible in rational order all that is known concerning plants and animals. This last is an ideal which, even if never attained, is one which may well make the systematist proud of the magnitude of his task . . . which in the process of attempted attainment must make taxonomy what it should be, the focal point of biology." "Taxonomy," says Heywood, "is a progressive series of states of knowledge. It is information processing for biology." There is no doubt that, in framing classifications consonant with these views, discussions must—to use Turrill's words—"touch some of the deeper issues of philosophy." To avoid such issues will be to leave the taxonomy of tomorrow open to the same "sweeping indictment" as Sokal (1963) levels at it to-day when he says, "The forward thrust of biological sciences in this century has largely by-passed the philosophy and practices of taxonomy." The crisis in physics which threatened its conceptual foundations a generation ago (Caudwell, 1939) could only be resolved by deep philosophical re-appraisals. Without these its fate would be stagnation. It would be a pity, when so much is on the move in taxonomy, that this should waste for a failure to come to grips with similar re-appraisals.

" Classification," states Gilmour (1951), " is a fundamental pre-requisite for all conceptual thought, whatever the subject material of that thought. The primary function of classification is to construct classes about which we can make inductive generalisations . . . there will be one, as it were, general purpose classification, more natural than others in the sense that more inductive generalisations can be made about its classes. This classification should not, however, be regarded as an approximation towards a single, ideal, scheme, but as a permanently flexible arrangement, changing as new knowledge is acquired and incorporated into it." He concludes, therefore, that " clearly the primary aim of taxonomy, on this basis, must be the construction of classes about which scientifically useful inductive generalisations can be made." The introduction by Turrill (1954) of the concept of " synthetic taxonomy " represents a closer approach to such a classification than the same author's earlier " omega " taxonomy. The idea of an attainable " absolute " has been discarded. Recognition of the necessity of such a step has resulted in an approach to taxonomy, for all that it is more modest, which is for this reason philosophically more sound and far-reaching and seems set fair, in the freedom of this recognition, for a more fertile development.

Upon what kind of basis can we expect to see this flexible and synthetic taxonomy erected ? Will it be, for example, constructed within the framework of Linnaean nomenclature, or not ? Hall (1929) questioned the utility of the existing nomenclature in dealing with units smaller than species, and suggested the preparation of provisional numbered lists of such units, where they could be retained until exact designation was possible. More recently Cain (1959b) has spoken of how, in order to obtain the benefit of an agreed nomenclature and protection from homonymy for " what we are talking about " we must " commit ourselves to an opinion on the generic relations of every form before we can name it at all." He quotes Lack (1946) who argues for the omission altogether of " the tyranny of sub-specific names." Camp (1951) is not alone, therefore, in considering that existing nomenclatural procedures may have to go. When this may be, or what the form will be which replaces it are questions that it will be

(1964)

possible to answer only with the acquisition of new experience. Certain currents, however, are already perceptible.

Already indeed, in the late 1930s, when the uneasy amalgamation of experimental data and the orthodox categories of traditional taxonomy had as yet produced only vague forewarnings of the conflict which was to come, Ginsburg (1937, 1938) referred to the hazy nature of category delimitations, and the intuitive process by which they were applied. He proposed (1938, 1939) numerical techniques for the determination of population divergence, by the use of an index which he called the " divergence index." These ideas were not developed, however. It is intriguing to reflect on the " hybrid index " (Anderson 1936) of the same period, and on the relative fates of the two techniques. Ginsburg (1939) observes, in considering the number of characters which may be employed in population comparisons, that " the number of such characters may be almost indefinitely increased," calling to mind the later statement of Mayr (1942) that " the number of characters available for comparison is limited only by the patience of the observer." This idea is inherent in the recent techniques of numerical taxonomy, now made a practical possibility with the advent of electronic data processing. Numerical taxonomy, developed within the past decade by Michener and Sokal (1957) Sneath (1957, 1958), Sokal and Michener (1958), Lubishev (1959), Morishima and Oka (1960), Rogers and Tanimoto (1960), Sneath and Sokal (1962), Sokal and Sneath (1963) and Sokal (1963) must be seen as the logical development of the work of Ginsburg, as well as that of Fisher (1936), Anderson and Owenby (1936) and others. Hedberg (1958) also proposed the use of numerical criteria for species delimitation. For some years sub-species separation has been effected in practice, in cases where overlap of characteristics occurs, on the basis of the " seventy-five per cent rule " (Amadon, 1949). It may well be that the developments over the past few years which have led to numerical taxonomy indicate, despite present shortcomings which may limit its usefulness and applicability for a time, that this is one of the directions in which we must look if we are to foretell the future of taxonomy, since there is no doubt that certain of its essential pre-requisites are also necessary conditions to the attainment of taxonomic objectivity.

In the first place, taxonomic affinity is based upon observable, or "phenetic," similarities. There is, therefore, an implicit need for the "segregation of taxonomic and phylogenetic concepts" (Sokal, 1963), and morphology must replace homology as the source of taxonomic raw materials. The argument of necessity thus supports the arguments of logic. Valentine (1962) expresses the view that there are good reasons that taxonomic judgments should be made on the basis of morphological characters, and adds that this is a general view. Heywood (1963b) states that "no matter what the theoretical definition of the biological unit, the initial evidence or recognition of membership must be primarily morphological." It is not necessary to assume, as does Löve (1964), that the use of morphological characters is associated in any way with "quasi-typological" concepts.

A second condition of Adansonian numerical taxonomy is that all characters are considered as equivalent. There is no weighting of any characters. This, says Sokal (1963), "can be defended on numerous genetic and logical grounds. The simplest demonstration of the illegitimacy of weighting characters is shown in the futility of any effort to define a consistent system for weighting these." Cain and Harrison (1958) examine logical principles involved in the idea of a single character and reach comparable conclusions with regard to weighting. But in distinguishing between functionally correlated and mathematically or logically correlated characters they warn that "it would be wrong to take as separate characters what are mathematically or logically necessary consequences of each other." The elimination of character weighting is a major step towards the elimination of the subjective element in taxonomy.

It is a practical need which has called forth the methods and principles associated with numerical taxonomy, coupled with the extremely rapid data processing made possible by technological advance. Microbiology and entomology have adequate practical reasons for seeking a system of classification which can unequivocally assign to one taxon or another the organisms with which they deal. It seems to have been forgotten in the confusion wrought by the diversions into the fields of phylogeny and the biological species concept that it was a similar need which led to the system of Linnaeus, which sought not to define an absolute, but to identify the plants so important to the medicine of his day. As Cain (1959) says,

" what is required is a system of reference that . . . allows us to refer unambiguously to the things we are talking about." Bremekamp's (1939) view that " the aim of classification is to be serviceable " seems at last to have become a practical and immediate possibility.

The present author is not a taxonomist. It would be foolhardy for this reason alone to carry a discussion of practical taxonomy beyond this point of departure. The need to disentangle genecology from taxonomy demands a certain amount of untangling of the separate elements themselves. For taxonomy it is sufficient to say that there is a rapidly growing wealth of new techniques for the accumulation and practical treatment of taxonomic data. A brief glance at the immediate past is sufficient, in the experience of any biologist, to confirm the view that it is always only a matter of time and technical development before apparently " identical " races may be taxonomically differentiated. " If it were found to be vitally important to recognise very small groupings," says Heywood (1959), " this could be achieved given time and labour." The taxonometric use of large numbers of phenetic characters may, by virtue of the large numbers alone, be sufficient for such differentiation. The peculiarly discrete nature of the phenetic differences at the chromosome level which was first fully discussed by Levitsky (1931), and which has been used for species, sub-species and even population differentiation (*e.g.*, Heneen and Runemark, 1962), has still to be fully exploited. Failing evidence from such sources, there are still the virtually untapped resources of the recent techniques of chemical, chromatographic and serological methods to be drawn upon " to facilitate reaching taxonomic decisions."

The march of taxonomy without recourse to anything more sophisticated than morphology can well be illustrated by reference to the plant parasitic cyst-forming nematodes of the genus *Heterodera*. The genus originally had one species, but it became clear, as experience accumulated, that there were a number of races which affected different host plants. The races were given varietal and sub-specific names, but distinctness of host, life-history, and distribution indicated in time that specific status was more appropriate. It was only after such status had been given to the majority of the " races " within the single species of the genus that further studies showed that there were sufficient differences of form—some so striking as to cause one to wonder that they had ever been considered similar—to enable their recognition on this basis alone. This was the result of the work of a very small number of investigators—particularly of Hijner, Oostenbrink and Den Ouden (1953), Oostenbrink and Den Ouden (1954) and Cooper (1955)—over a very small number of years. In the same way " identical " races of the genus *Meloidogyne* have now been separated by Taylor, Dropkin and Martin (1955). These advances resulted from the examination of characters which had not been examined before, and support the view that an increase in the number of characters alone may lead to the resolution of many critical taxa. The physiological races which are particularly common in parasites and have been described in plant parasitic nematodes by, for example, Christie and Albin (1944) and Du Charme and Birchfield (1956), and resistance-breaking strains such as those described by Dunnett (1957), remain. How long will it be, if these are not found to yield to the Mendelian analysis of major-gene effects, before they do yield, either to techniques which merely demand an increase in the number of characters examined, or to such new techniques as that employed, for example, by Micks (1954) for the separation of the *Culex pipiens* complex using chromatography, or such as depart from recognised methods as strikingly as that employed by Thorpe and Lade (1961) for the differentiation of birdsong using " sound spectrographs " ?

There seems to be a great deal more truth in the slogan—" The difficult we do at once ; the impossible may take a little time "—than one might at first think. In science, the impossible is, by definition, that which will take a little time.

IV. Prospective.

Before attempting to define the future tasks of genecology, or to trace its possible future lines of development, it is first necessary to clarify our views on its present function. What is genecology ? With what does it concern itself ? A definition might be sought, for example, among the many synonyms which have been proposed from time to time. But as we have seen, these have been influenced by taxonomic thinking, and a glance at them is sufficient to show that they lack, with one exception, any reference to the essential feature of that which they seek to define—that it is a process. Experimental

Taxonomy, Experimental Morphology, New Morphology, New Systematics, Genonomy, Biosystematics, Neotaxonomy—not one of these indicates that the essential characteristic of the relationships with which genecology concerns itself is that they are dynamic. The exception, Experimental Evolution, and particularly the term micro-evolution (Timofeeff-Resovsky, 1940), have come into fairly general use to describe certain aspects of genecology, but genecology is broader in its scope than either. If a definition is needed, then it must be sought apart from such terms as have already been coined. Such a definition has been offered in the introduction to this paper. It may be expressed also in terms of gene action. Mather (1955) states that genes " take part in three basic types of interaction (using this term in its statistical sense of departure from simple additivity of effect): (1) that between alleles which we call dominance, (2) that between non-allelic genes which is often termed epistasis (though this term was used earlier in a more restricted way), and (3) that between the effects of genes and environment." Genecology concerns itself directly with this last type of interaction, and with the others indirectly through their effects on the genotype-environment interaction.

It should not be necessary, therefore, to emphasise the practical and immediate importance of genecology. But it has suffered a long pre-occupation with taxonomy and the delimitation of taxonomic categories, under the influence of the biological species concept. No less than taxonomy, and under one or other of its " biosystematic " guises, it has been diverted from its " proper study." Frequently sterile discussions on the degree of taxonomic divergence attained by natural groups, and on their taxonomic status, have resulted. Constance (1953) speaks of the " aliases and somewhat various disguises " that have served to keep genecology well hidden, and remarks that genecology has " slipped away from the realm of plant ecology to that of plant taxonomy, to the great gain of the latter and the great, if still largely unrecognised, loss of the former." One must add to this pertinent observation that, irrespective of the direction of the loss, it has been to the great loss also of genecology. With the segregation of " Systematics " from " Speciation," which will free taxonomy from the tyranny of the biological species concept so that it may develop according to its own laws, the " experimental taxonomic" or "biosystematic" concept of genecology will also give way to one which will permit the development of genecology as a genetic study broader in its scope, even, than genetics itself. It will not then be possible to read, as one may to-day, that genecology—in contrast with applied sciences—seeks "to answer botanical problems primarily for their scientific interest and as a demonstration of basic biological principles." Although among ecologists Daubenmire (1959) states that the ecotype, not the species, is the fundamental ecological unit, this is a rare attitude in ecological works, and one may still read textbooks of quantitative ecology in which no mention is made of genes, of ecotypes, or of adaptation (*e.g.*, Williams, 1964), despite the facts to which Watson and Gregor (1956) draw attention, that genecological findings "demonstrate differences between plant communities which the orthodox ecological classifications do not reflect," and that these may have a practical significance for improvement techniques.

Convincing evidence of the practical importance of genecology can be seen by examining the agricultural problems of those parts of the earth which rely completely upon plant introduction. Tikhomirov (1960) illustrates the striking northward advance of the limit of agricultural cultivation in the U.S.S.R. in the period 1916-1960, which has been made possible by genecological studies on the natural flora of the tundra, and on plant-permafrost relationships. Likewise, Australia a century ago, as Frankel (1957) observes, "was devoid of an economic flora which could satisfy the needs and aspirations of civilised man. Every plant used in any of the more intensive types of land utilisation has come from beyond the sea." Frankel emphasises that introduction itself is only a first step, to be followed by "genetic adjustment to the new environment. All too often this phase is neglected, and a new crop is judged by its performance at the original—*i.e.*, unadjusted level of adaptation." From this last remark it may be concluded that in Australia also the significance of genecology can fail to be understood, despite its widely accepted importance there. This serves to illustrate how reluctantly outdated attitudes yield to new knowledge.

Plant introduction is now a matter of world interest, and plant collections for material suitable for incorporation into breeding programmes are now concentrated upon ecotypes of known characteristics, an outlook which is owed directly to genecological studies. For example, McWilliam and Cooper (1963) and McWilliam and Hoen (1963) report on the investigation of physiological mechanisms underlying the adaptation of contrasting ecotypes, and on the incorporation of ecotypic characteristics into breeding lines. The examination of indigenous species, also, has increasingly been concentrated at the level of ecotypic intra-specific variation, a field which is specifically and peculiarly the province of genecology. "Benefits to be derived from research of this nature," states Tisdale (1962), "include increased predictability of the reaction of species and communities on particular sites to management or improvement practices."

Under the stimulus of practical necessity a science flourishes. This is as true to-day as it has been in the past since the origin of mathematics, astronomy, or chemistry—or even of language; if anything is to be learned from the lessons of history, it is that the search for knowledge has always been directly related to the practical need of man to exploit his environment to his greater advantage. Indeed, Huxley (1942 : 387) has defined evolution itself in strictly comparable terms—"Evolution may be regarded as the process by which utilisation of the earth's resources by living matter is rendered progressively more efficient." The same view is expressed by Mayr (1949). The drive to understand micro-evolution is no different in this respect than the driving force of any other science, and aims at the better utilisation of the earth's resources to man's own purpose. Man seeks to understand evolution in order to direct it, and it may reasonably be expected that a rapid development of genecology as an applied science will result from man's present increasing need fully to utilise the earth's resources. This is to be seen already in the vigour with which genecological research is being pursued in those countries which have been mentioned above.

In this discussion it is the intention, primarily, to examine the practical aspects of genecology, and to consider no more than a few of the probable paths to be taken by applied genecology in the immediate future. This is by no means to say that important advances are not being, or are not yet to be, made in the field of theoretical research, for such in fact is far from being the case. The practical importance of applied genecology, however, requires to be emphasised, and it is the aim of the present review to meet this need. It is necessary to consider past and current theoretical work only in order to draw together those features which are relevant to an understanding of applied genecology.

The variation with which genecology is concerned is adaptive and continuous—*i.e.*, polygenic. " Most if not all of the characters that ordinarily are considered to be components of fitness in a population are quantitative characters," states Sokal (1962)—" natural selection should affect these more than any other characters, and they are expected to and have been shown to respond rapidly and vigorously even to minor changes in environmental conditions." " Almost all economic characters with which the plant breeder has to deal," observes Panse (1958), " are polygenic in inheritance." Falconer (1960) says that " the variation of each metric character reflects to a greater or lesser degree the variation of fitness ; and the variation of fitness can theoretically be broken down into variation of metric characters." Mather (1953) states that we may feel confident that " continuous variation mediated by polygenic systems " is " a regular feature of wild populations. Our confidence must be strengthened when we recall that this is indeed the commonest kind of variation in those populations of domestic plants and animals which we term varieties, breeds and herds." Like all variation, this is the product of the reaction between the forces of mutation and recombination on the one hand and those of selection on the other, but it possesses a number of distinctive characteristics. To use Sumner's (1930) phrase, it is due to the action " of a large number of synergistic genes of individually small effect," and it responds to selection in such a way that its class frequencies present a more or less normal distribution. The reaction between variability and selection—which at the population level is the definitive reaction of evolution—is amenable to study in a number of different ways. Mather, for example, defines selection according to its type of action in initiating or maintaining trends in the distribution pattern of the variation in a population, distinguishing stabilising selection, which is the type mainly encountered under natural conditions, from disruptive selection and from directional selection which is the type associated with the artificial selection of domesticated plants and animals. Waddington (1957) discusses these in considerable and stimulating detail. Thoday (1959) distinguishes eight such types of selection, and Edwards (1963) discusses another.

It is evident from selection experiments, and from centuries of breeding and selection experience, that the amount of variability which is latent in organisms is very great. Many workers have commented upon this. Mather and Harrison (1949) conclude their examination of the effects of selection by stressing " the large capacity of the reserves of hidden variability within a species." Stebbins (1958) remarks upon the " enormous store of hidden variability " carried by certain natural populations, and Mayr (1963) speaks of polygenic inheritance as a storage system of enormous capacity which " can readily respond to the slightest shift in selection pressure." Mather (1953) states that " the greater part of the stored variation is not expressed in the phenotype but is hidden in the genotype at any given moment so that the possibilities of selective response are much greater than the range of phenotypes would suggest. Linkage will serve to increase the fraction of the variability that is hidden." The practical consequences of the release of such variability is shown, for example, by Clausen (1952),who reports that the desirable characteristics of different ecotypes which are crossed may be surpassed by their progeny. Heterosis may be considered as a special case of the release of concealed variability in which its expression is all in the direction of increased vigour. Cooper (1954) demonstrates the release of considerable variability when some species of *Lolium* are grown in conditions which differ from those to which they have become adapted, as do Clausen and Hiesey (1958b) for various other species.

Concealed adaptive variability has a number of components, the analysis of which is still the subject of research and much discussion. First, the work of Dubinin and his co-workers (1934), which showed a marked reduction in the fitness of experimental populations of *Drosophila* when made homozygous —to the extent that only 80 per cent remained viable—and of Fisher (1939), who measured marked increases in fitness in heterozygotes of *Paratettix*, led Dobzhansky and others (Dobzhansky, 1950 ; Pavan *et al* 1951 ; Cordeiro and Dobzhansky, 1954 ; Ives, 1954) with the aid of statistical techniques devised by Wallace and Madden (1953), to investigate the relationship between fitness and heterozygosity sufficiently for Dobzhansky (1955) to state his " balance hypothesis " of the adaptive norm

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of a population, according to which " the adaptive norm is an array of genotypes heterozygous for more or less numerous alleles, gene complexes and chromosomal structures. Homozygotes . . . occur . . . only in a minority of individuals, and make these individuals more or less inferior to the norm in fitness." Such heterozygosity, for which " recent work indicates near-universality " (Sokal, 1962), is the first component of concealed variability.

The second component has a longer history, and dates from the work of Nilsson-Ehle (1909) and East (1910) on multiple factors, which demonstrated gene interaction. In the work of Harland (1932) on variation in the expression of dominance, this was attributed to the action of large numbers of modifier genes, acting upon " major " genes, of such importance that Harland expressed the view that " the modifiers really constitute the species." Anderson (1939) speaks of the " chromosomal ground substance " as the basis of the modifier effect. " Evolution," states Wright (1955), " depends on the fitting together of favourable complexes from genes that cannot be described in themselves as either favourable or unfavourable." Caspari (1963) says that " the adaptive value of a gene is dependent not only on its structure but also on its environment, which may be internal or external. The adaptive value of a gene depends on other genes with which it is associated." It is sobering to recall the views of Chetverikov in 1926 on the subject of gene interaction—" Each gene does not act isolatedly from the whole genotype, is not independent of it, but acts *within it*, in relation to it. *The very same gene will manifest itself differently, depending on the complex of the other genes in which it finds itself.* For it, this complex, this genotype, will be the *genotypic milieu*." Any gene change, such as might occur in response to selection, according to Mather (1955), " will be conditional on, and must therefore wait on, adjustment of the rest by further genetic change " within this genotypic milieu.

Finally, there is that component of the variability which is concealed by linkage. Mather and Harrison (1949) draw attention to " the power of correlated response due to linkage, to change characters even against the trend of natural advantage." " Large reserves of potential variability are maintained and can be freed by recombination, as experiment has shown us time and time again," says Mather (1955), and " short-term responses to selection will be conditioned by the store of variation and will reflect its organisation." Manning (1955) discusses the persistence of genetic variation in the highly selected seventh generation of inbred lines of cotton, and quotes Harland's (1934) experience with similar, but thirteenth generation, material which still responded to selection, and considers possible explanations, among them " that fortuitous crossovers in chromosome segments, held in heterozygous condition, had released variability favourable to selection." The release of variability in highly selected lines which have been maintained at a selection plateau for a number of generations is a well-known effect, made possible, according to Lerner (1954) by the " utilisation of whatever new free genetic variability becomes available through mutation or crossing over." Thoday and Boam (1961) examine accelerated responses to selection in experimental lines, and argue " that the event making possible the accelerated response is probably a recombinational event." Linkage groups may themselves be regarded as composite units of polygenic effect, subject to modification by recombination. Mayr (1954) refers to the population genotype as an " adapted system so contrived by natural selection that its component genes yield highly fit combinations with most other genes present in the same gene pool," but recombination, by the re-assortment of such combinations, may be assumed to yield variations in fitness on either side of the adaptive norm.

The earlier view that there may be qualitative differences between major genes and polygenes no longer appears likely. Brenner (Waddington, 1959 : 28) discusses the molecular changes which have been shown (*e.g.*, Ingram, 1956, 1957) to be the basis of some mutations, and observes that the resultant genetic effect may range from complete mutational inactivation of the gene to changes " which might be phenotypically unrecognisable." He refers to molecules which, though differing in certain amino acids, may replace each other physiologically and which might only be distinguished by chemical analysis. " The distinction between genes concerned with Mendelian characters and those concerned with metric characters lies in the magnitude of their effects relative to other sources of variation," states Falconer (1960) ; it " marks the difference between those which we can study individually, and whose properties are therefore fairly easily discovered, and those which we cannot study individually and whose properties can only be deduced by indirect means."

At all times in studies concerned with the genetic responses of populations or the constitutional responses of individuals to environmental factors, the theoretical background should be kept firmly in mind. This is increasingly so at the present time as techniques for the analysis of polygenic situations, both experimental—such as that reported recently by Chai (1961)—and theoretical, as for example in the papers of Milkman (1960) and Gilbert (1961), become available. When, however, Mayr (1959) considers the complexity of present-day mathematical models and theoretical techniques, and remarks that mathematical analyses are getting so that no more than a handful of biologists can understand them, he asks if we are right in applying so generalising a technique as mathematics to a system of unique events such as evolution. Do we tend to agree so readily with this because we happen not to be in that particular handful of biologists ?

The reaction between quantitative, adaptive, variability on the one hand and selection on the other is dynamic, even when in equilibrium. There is in addition a greater or lesser degree of fluctuation. The fluctuating nature of environmental forces and its effects is discussed by Mather (1953), and by Bradshaw (1964), who graphically illustrates a number of cases of interaction between genotype and fluctuating environmental conditions, and considers some of the problems they pose to applied genecology. At the level of the individual, response to such conditions may take the form either of phenotypic plasticity or of developmental homeorhesis (canalisation), both of which are considered under the term phenotypic flexibility by Thoday (1953), and little is yet known of the mechanisms involved in either response. " Our knowledge of such responses is limited," according to Clausen and Hiesey (1958b), " because only few investigations have been undertaken to study organisms in highly diverse environments." Whatever the response of an individual to environmental pressures, however, such responses are those of genotypes which are the result of an earlier response at the population level to the same or similar environmental conditions, as a consequence of selection acting on the normal mechanisms of gene recombination and exchange. Both types of individual response are of interest to the plant breeder, who often selects in favour of plasticity of phenotypic expression, so that increases in soil fertility may be reflected in correspondingly increased crop yields. But the genotype in which developmental reactions are more strongly canalised, which is capable of attaining a more or less fixed degree of phenotypic expression in a range of environments, is also of great economic importance. Such genotypes can form the basis of selection and breeding programmes which aim at the attainment of economic yields under adverse conditions, such as drought or cold. The possibilities of such objectives are to be seen in the striking case quoted by Gregor (1956) of a genotype of *Poa pratensis* which out-performed even locally adapted races at each one of a number of climatically diverse and widely separated centres.

Under cultivation, as pointed out by Frankel (1959), farming " methods reduce not only the number of effective components of the environment ; they tend to reduce the environmental variation within comparable areas." In such conditions outbreeding plants particularly may respond adaptively as a result of normal micro-evolutionary mechanisms in the direction of genotypic stability and phenotypic uniformity, but selection carried out under these conditions may, as in other situations, be very rapid. Morley (1959) quotes a number of cases of the rapidity with which ecotypic differentiation may occur. Snaydon (1963 and unpublished) seeks to apply quantitative criteria to the problem of adaptation in an attempt to estimate its precision, and presents data which show very rapid adaptive responses indeed in grass swards. There is also evidence that the operation of natural selection in long-established grassland may, possibly by the co-adaptation of polygenic complexes, lead to extremely stable genotypes, such as have been shown by the Scotia cultivars of perennial ryegrass and cocksfoot. These are not products of artificial selection, but of natural selection, and have been multiplied from collections made in the course of extensive genecological surveys.

The sustained operation of adaptive micro-evolution over long periods of time, under the local environmental conditions of specified areas, has given impetus to ecotypic studies in many economic crops. In forestry breeding programmes, provenance investigations assume considerable importance. On page 56 of the present paper a number of works on tree ecotypes is referred to. These and other recent contributions

—*e.g.*, Vincent (1958) and Vincent and Polak (1962) on European larch and Wright Bingham and Dorman (1958), Callaham and Metcalf (1959), Wright and Bull (1962) and Bourdeau (1963) on species of pine—highlight the rôle of applied genecology in forestry. Vasil'chenko (1963) stresses the necessity of utilising fully adapted local races as stocks for a large number of berry and tree fruit crops in the far north of the Soviet Union. The necessity of genecological investigations for the improvement of subterranean clover (Morley and Frankel, 1959), forage grasses (Tarkovski 1959) and legumes (Sinskaya, 1960), sugar maple (Kriebel and Wang, 1962), ladino clover (Stanford, Laude and Booysen, 1962), maize (Tavchar, 1962), cotton (Christidhis, 1963), lucerne (Crescini, 1963), and many other crops can be recognised from even a fragmentary examination of the literature.

Land races of cultivated plants, which are the products of generations of conscious and unconscious selection by man and are highly adapted to the environmental conditions of often quite restricted localities, represent enormous and untapped genetic reserves. Janossy (1962), for example, refers to more than 200 races of maize in Hungary alone, which have been used to contribute much improved yields and enhanced fitness and disease resistance to more than 800 lines. Christidhis (1963) stresses the need to conserve such genetic resources in cotton. The increasing attention being afforded by international agencies such as the Food and Agriculture Organisation of the United Nations (1955; Whyte, 1961; see also F.A.O. Plant Introduction Newsletter) to projects for plant exploration and introduction, for collections of habitat-populations and the preparation of reference collections, is an indication of the wide recognition of this need. Proposals of this nature demonstrate a concern which is to be welcomed, and supported as an indication of a trend towards a more effective and world-wide direction and control of micro-evolution. But as they stand, and appear to be accepted by the majority of the participant members of international bodies, they are fraught with danger. Should projects of this sort be carried out in disregard of the genecological principle of the adaptive but dynamic unity of the organism and its environment, the consequences at best might be the waste of an invaluable fund of scientific effort and considerable financial resources, and at worst might be disastrous to at least the rarer gene pools which contribute to the world's total gene reserves. Two aspects of the dangers arising from inconsiderate "genetic prospecting" deserve particular emphasis.

Not only is the balance of the equilibrium attained between the components of variability and the forces of natural selection exceedingly fine, but the adaptive responses to changes in selection pressure have been shown to be unexpectedly rapid, as work which has already been quoted has strikingly shown (Morley, 1959; Sokal, 1962; Mayr, 1963; Snaydon, 1963; see also Gregor, quoted by Huxley, 1942 : 223), and these responses will begin to operate with the first generation following any change in environmental conditions. Stocks of material can therefore be maintained only in the vegetative condition, an immense complication to a large collection, which will require frequent replacement of the majority of the races comprising it, quite apart from such genotypes as are not sufficiently flexible as individuals to survive at all.

The second danger is greater. The concealed adaptive variability of a genotype has a number of components which have been discussed above (p. 86). A greater part of this is contributed by what has been called the "balance" of the genotypic milieu, or the co-adaptation of favourable complexes of "genes that cannot be described in themselves as either favourable or unfavourable." *That is to say that the genecological unit of function is not the gene, or cistron, which is the genetic unit of function, but the balanced gene-complex.* The breakdown of such complexes has been described by a number of workers, including Clausen (1952), Cooper (1954), Clausen and Hiesey (1958b) and Sinskaya (1958), with the release of considerable variation, and though Heslop-Harrison (1959) shows that part of this effect is probably due to the collapse of homeostatic mechanisms, the effect of the genetic component is not in dispute. To the extent that developmental homeorhesis is itself an adaptive response, breakdown of this process may be expected also to be the result of a breakdown of co-adaptation in the genotypic milieu. The rôle of co-adapted gene-complexes also suggests that attention to genetic reserves in land races is at least as important as to the reserves of wild ecotypes—a suggestion which has been made by Gregor (unpublished)—since the former will be more fully adapted to the monocultural conditions of most cultivated populations.

Crop genecologists can view only with deep misgivings the many proposals which are made from time to time for the establishment of international collections of ecotypic material, because the basic error in such proposals is one which has arisen in disregard of essential genecological principles. The genecologist would rather see a World Reference Index of gene resources, particularly of land races and cultivars, as well as of wild ecotypes. This would be contributed to by research stations, field stations and sub-stations in every country, where biologists with detailed local knowledge would preserve ecotypic races *in situ* under conditions in which they have evolved and to which they have become adapted, or in culture in the immediate vicinity in comparable environmental conditions and with the same climate. A valuable effect of such a policy would also be to encourage a rapid and vigorous development of biological research in the ex-colonial and developing nations.

Librarians have a saying that the clever librarian is not the one who knows, but the one who knows where to find out. The same might be said of the plant breeder ; the clever one is not he who has, but he who knows where to get, the genetic material necessary to his programme. To provide the necessary crop genelogical services at every regional and local centre with the task of contributing to the World Reference Index of genetic stocks is a more realistic means to this end than the vast, centralised, and improvident international collections which appear to be the aims of present-day administrators.

The survey of the earth's gene resources is probably as concerned with the search for disease resistance as with the discovery of sources of increased yields and improved qualities. It is intended finally to discuss, therefore, certain genecological aspects of host parasite relations—that rather special, if thorny, case of population environment interaction—which surprisingly has yet received little genecological attention. It is a field particularly well suited to such studies, as is pointed out by Harberd (1964). The genotypic adaptation of a population, a necessary consequence of any population environment interaction, a result of the action of selection pressures on population variability, is maintained by a complex of co-adapted gene combinations which may attain a degree of stability and are polygenic in expression. When a parasite is part of the total environment of a population, the host population may be expected to show adaptation to this as to any other environmental factor, and this will show the normal features of polygenic

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inheritance—*i.e.*, it will be expressed variably by different genotypes within the population, with a peak frequency at the adaptive norm. The range of deviations from the norm will be a measure of the intensity of selection pressure, of its degree of transient fluctuation, and of the host capacity to respond flexibly either by phenotypic plasticity or by developmental homeorhesis (Mather, 1953; Thoday, 1953). Simultaneously with the course of adaptation in the host there will be, also necessarily, pathogen adaptation, so that host adaptation will be taking place under the action of a selection pressure which is itself altering. This is merely a special case of a very general event of which, for example, several instances are described by Bradshaw (1964). Susceptibility in the host will be at a selective disadvantage. For the same reason the selective trend in the pathogen will be in the direction of diminished virulence. In such a host parasite system the host population may be expected to be resistant to the parasite in such a way that resistance will show a normal distribution in the host population. Since virulence itself shows a trend, and is the operative selective factor leading to adaptive resistance in the host population, the nature of the selection effected by it will be directional rather than stabilising. The equilibrium position may be expected to correspond to a higher, rather than a lower, level of resistance, though it will not necessarily be complete in the sense of immunity from infection. Van der Plank (1949) calls resistance of this type general resistance, and says that it " does not necessarily amount to complete and absolute immunity. All that is needed is that it should be adequate. Adequacy, but not necessarily unbreakable immunity, is the point about general resistance." To the plant breeder the term adequacy might most satisfactorily be considered as the ability to accept infection without being harmed.

This is, of course, the " field resistance " of the plant breeder. Black (1960) describes field resistance to *Phytophthora infestans* in potatoes, and shows that fewer lesions are formed in resistant plants, which spread slowly, and sporulation is sparse. Field resistance, says Driver (1962) is " based on the capacity of the plant cell to reduce infectivity and to slow growth and development of the fungus," but there is general agreement that field resistance is a compound of factors, of which as many are related to population characteristics as to the characteristics of any individual, and this is evident from the data quoted by

Umaerus (1963). To the breeder who has become accustomed to thinking in terms of major gene resistance and Mendelian segregations the quantitative variation associated with field resistance, and its inseparability from considerations of the population, are seen as disadvantageous, so that breeding has tended to confine itself to major gene resistance, and field resistance has been only reluctantly accepted.

Major gene resistance itself is not without practical disadvantages, of which the most generally admitted is the regular occurrence of resistance breaking pathogen strains. As a result breeding resolves into a step by step evasion of the pathogen. Harberd (*loc. cit.*) considers some of the consequences of resistance breeding in terms of the action of major genes. There is no ultimate vision of permanent or stabilised resistance, as with field resistance, which " is evolutionarily stable and not likely to be upset by changes in the pathogen " (Driver, 1962), but only a perspective of perpetually limited scope. Genecological considerations, however, point to other disadvantages which, though of a conceptual nature, carry serious long-term implications.

In spite of the fact that the balance concept of the genotype as a co-adapted system of gene complexes is a decade old (Lerner, 1954 ; Dobzhansky, 1955 ; Waddington, 1957)—and the " genotypic milieu " of Chetverikov is four decades old—the concepts and practices of major gene resistance-breeding have been confined to the consideration of isolated mutational events in which the gene is the unit. This has led to a tendency to study the gene in isolation from its " genotypic milieu," and separate from the total population environment interaction of which the " genotypic milieu " is the adaptive consequence. The gene is seen as a stable entity, which will not be destroyed by extensive breeding but merely redistributed, while the balanced gene-complex which is so much more fragile is ignored, tossed about, and destroyed, despite the fact that, in the words of B. P. Pal, it represents " all the plant breeding work carried out by Nature over thousands of years."

Breeding work based upon the disease resistance conferred by major genes has been regarded by those who are aware of the limited period of its effectiveness—which will be greater or less according to the manner of propagation of both host and pathogen—as a short-term policy of rapid effect, and field resistance as a long-term project, with little promise of any striking short-term improvements. It would seem that too long a pre-occupation with genes of major effect may obscure from view the rapidity of adaptive responses under polygenic control, which has been referred to already (pp. 90 and 92). There is every reason to believe that applied genecology might demonstrate even more rapid responses to selection for field resistance by devising techniques, for example, which will aim to maintain, rather than destroy, such adapted gene-complexes as already exist. This might be particularly the case if land races are used as source material, since they are fully adapted to the conditions of monocultural cultivation, which further emphasises the especial value of the gene resources of this type of material.

Pal has warned of the serious danger of " gene erosion." A World Reference Index has been referred to above, and is one measure which can prevent this. The fullest application of genecological methods and concepts in all fields of selection, breeding and husbandry is an indispensable measure to the same end.

It has been the aim of this paper to attempt a synthesis, as well as an untangling, of several disciplines. Genecology is itself a synthetic science drawing together evolution, ecology, physiology, and genetics. It has sought to bring quantitative expression to relations which have a history of intractibility, the relations between and within genotypes, and between genotypes and their environment. It is, above all, an applied science with immediate and urgent applications to human needs. The author hopes that this, at least, emerges from the discussions here.

It is painfully clear that scientific problems pose a vast task to the extraordinarily inadequate numbers of biologists whose task it is to answer them, and it is impossible to mount any serious attack on them without a significant increase in scientific staffs and facilities (see *e.g.*, Huxley, 1940; Thorpe, 1940). Proposals which have been made recently for an International Biological Project (Bernal, 1962 : 73; Sharp, 1962), similar in scope and design to the very successful International Geophysical Year, carry great promise for the maximum development of world scientific resources around such problems as have been reviewed here.

Just as the interdependence of different disciplines is essential to the attainment of a balanced synthesis of scientific effort, so is the inter-relationship between theory and practice, and the reference by Kapitsa (1962) to Kelvin's image of this relationship is worth recalling—" Kelvin likened theory to millstones and experimental data to the grain which is poured in between these millstones. The product—flour—is used for the benefit of all people. It is quite clear that the millstones themselves, however long they turn, cannot produce anything useful—this theory is working on itself. But the quality of the grain is important, and bad grain cannot give nutritious flour. Therefore, a high quality of experiment is, like a high quality of theory, a necessary condition for the healthy development of science." In genecology, as in any other science, a high quality of practice and a high quality of theory are equally essential to its healthy development.

As was remarked in the introduction the answers to present problems pose new problems. The analysis and quantitative expression of the many population-environment and genotype-environment interactions which have been referred to is such a problem. Old problems may be stated in terms of new problems, more clearly seen, themselves pointing to further problems, and this is a continuous process to which any concept of an absolute or final truth is foreign. " Truth," according to Levy (1938), " is the summation of man's experience at any given moment, it is a lantern that illumines his next few steps, past truth becomes incomplete as a greater truth replaces it ; it is an instrument for the creation and working out of a human purpose, becoming sharper and more effective as that purpose itself becomes clearer, and as man's reading of natural process becomes more and more accurate."

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INTER-RELATIONSHIP OF GENOTYPE AND PHENOTYPE IN A VARYING ENVIRONMENT

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The genecologist is interested in the inter-relationship of genotype and environment. By tradition he is interested in the occurrence of such interactions within species, particularly at the level of the plant population, since it is at this level that evolutionary novelties are tested in the hard reality of existence. It is at the level of the population that we are likely to be able best to understand the origin and adaptive significance of the characters which ultimately become included in fully developed species.

As a result of such investigations we now have a picture of the plant species as in a very fine balance with its environment. No matter what environmental factor is involved evolution takes place within the species in relation to it. Turesson first emphasised the role of the environment in causing evolutionary differentiation within species. Subsequent work has served to show that this is true whether the factor is climatic, edaphic or biotic, and that such evolution can occur, not only on a grand scale in relation to major environmental changes, but also on a very minute scale in relation to very local variations in environment. Natural selection has a powerful and all pervading effect on plant species.

Our theoretical understanding of the processes involved has also increased enormously, as a result of the work of Wright Fisher and others, paralleling the empirical approach of the genecologist. The highly desirable complete fusion of the two has however not yet taken place. It is for instance surprising that in theoretical studies the coefficients of selection that have been used most widely have been ·01 and ·001. Unwittingly, the use of these figures has done a disservice to the study of evolution in suggesting that natural selection usually

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does not give more than 1 per cent selective differential; this is clearly nonsense and is only now being corrected. A great deal more work is certainly necessary to quantify the effects of natural selection that have so far been demonstrated only empirically.

But whether we take an empirical or an analytical view, one important aspect of the inter-relationship of genotype and environment remains, to which little attention has been paid. For reasons of simplicity we tend to assume that environments are relatively uniform, or if they do vary, they do so in some simple, systematic manner. Yet it is clear that the environment experienced by any population of plants is neither constant nor varying in a simple manner. As well as systematic seasonal changes, individual seasons differ in their severity from year to year. Biotic factors change markedly in their intensity from one period to another. Soils may change only little from season to season, but commonly vary markedly from one area to another: since a plant has little control over where its seeds fall, one generation may grow in highly fertile conditions and the next in very poor. Wide fluctuations are an essential characteristic of the environment of almost every plant.

What are the consequences of these changes? In what way are the processes of evolutionary adaptation to short-term, fluctuating, environmental conditions likely to differ from adaptation to long-term environmental changes?

Since the environment has a direct influence on the growth of plants, any change in the environment will affect the growth of a plant. The general growth of a plant determines its fitness,—*i.e.*, its ability to survive and reproduce. So a change in environment potentially leads to a change in fitness. If the environmental change is long-term the processes of evolution in populations normally lead to the selection of individuals adapted to the new environment and the elimination of the individuals which were adapted to the old environment. If, however, the environmental change is short-term such directly adaptive changes in gene frequency are not very effective. Every time the environment changes there is a loss of unadapted individuals. If the changes are repetitive there will be a continuous loss of individuals as selection first acts in one direction and then in the other. At the same time what adaptive changes in the population do occur will always be too late, the population being always adapted to the environment of the past rather than that of the present. This can be demonstrated theoretically (Crow, 1955). It will be particularly true when the duration of the environmental fluctuation approaches that of the life cycle of the species in question. If the duration of the environmental fluctuation is shorter than the life cycle of the species then no adaptation of this sort, whatever its advantages or disadvantages, will be possible.

However a species can adapt to short-term fluctuations by processes other than directly adaptive changes in gene frequency. It was argued above that such changes in gene frequency were the outcome of changes in fitness of the individuals composing the population in relation to the new environment. If however the individuals present were able to maintain their fitness no matter how the environment changed maximal adaptation would be maintained without the occurrence of any changes in gene frequency. In other words, in a fluctuating environment those genotypes which will have the highest average fitness will not be those with high fitness in only one condition but those which can maintain or maximise fitness under all conditions. It is these genotypes which will be favoured by natural selection.

Maintenance or maximisation of fitness in a fluctuating environment cannot be a passive process. It must depend on the ability of the individual plant to react in a positive manner to environment by the adjustment of the morphological and physiological characteristics of its phenotype. A plant growing in grassland may be taken as an example. At one time it may be subjected to heavy grazing: this will affect not only the plant itself but also the surrounding plants. At another time grazing may not occur. The plant can now grow undisturbed. However so also can the surrounding plants causing severe competition. A plant that retains a dwarf growth form adapted to grazing would be rapidly eliminated on cessation of grazing: a plant that could adjust its growth form in adaptation to lack of grazing would not. The same arguments apply in reverse to a species with a growth habit fixedly adapted to lack of grazing. Thus under conditions of fluctuating grazing a plant which can adjust its life processes in relation to environmental fluctuations will have a higher adaptive value than those which cannot. Such plants will be those that show high *plasticity* in particular characters—*i.e.*, that have particular characters (morphological or physiological) whose phenotypic expression is able to be altered by the environment.

Since the control of every process resides in the genotype, plasticity must be, *a priori*, genetically determined. If it is genetically determined, then it must be subject to natural selection. Plants occupy a wide variety of habitats, in which the occurrence of fluctuations of environment varies greatly: the mediterranean climate is an example of an environment with not only a marked seasonal fluctuation but also marked variation in seasons from one year to the next: by contrast the tropical rain forest varies much less. In some habitats conditions may be relatively uniform in time but not uniform in space, and a single plant may be confronted with the need to adapt to several environments at once. This is particularly conspicuous in aquatic habitats where there are three distinct environments, (*a*) under water (*b*) water surface (*c*) air above water, occurring adjacent to one another. We might therefore expect to find that evolutionary divergence in plasticity will have taken place in adaptation to the differing occurrence of fluctuations in different habitats.

A few examples will show that this is true. The mediterranean and other more arid habitats have already been mentioned. In the central valley of California all the rain falls during the winter months. The flora is therefore predominantly annual. In 1962-63 the rainfall was 25", much of it falling in March and April. In 1963-64 the rainfall was 11", nearly all falling by the end of January. The effect of this on the vegetation is considerable. But a large number of species—*e.g.*, *Bromus mollis* and *Avena barbata* possess a considerable plasticity of behaviour in adaptation to this. Thus in one site in 1963 *Bromus mollis* was 2 ft. high, well able to compete with the surrounding vegetation, with a correspondingly high number of seeds. In 1964 the same species was only 6" high: under the arid conditions it developed quickly and early and thereby matured good seeds although these were few in number. High plasticity of this sort is common in many such annual species. It is for instance also common in annual weeds which find themselves in entirely different habitats (different crops, different densities, different fertility levels) from one year to the next. Such marked plasticity is not found in related species occupying more stable habitats.

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In aquatic habitats there has been evolution of a very precise and spectacular type of plasticity which can be related to the distinctive nature of the environments available. Thus many species of *Ranunculus*—*e.g.*, *R. peltatus* possess marked heterophylly permitting the species to exploit under water and water surface habitats. However, species which live in shallow water or mud—*e.g.*, *R. hederaceus* have only expanded leaves, and those growing in deep water—*e.g.*, *R. trichophyllus* only dissected leaves.

The evidence of the evolution of different levels of plasticity in response to different levels of environmental fluctuation is considerable. It is more extensively reviewed elsewhere (Bradshaw, 1964). It seems difficult to believe that it is not an essential aspect of the processes of evolution and adaptation in plants. Recent theoretical analyses of the effect of developmental flexibility on fitness of population by Levins (1963) confirm this view. But both sorts of evidence are inductive. What is lacking is direct experimental evidence. Up to the present the genecologist has been most concerned with describing and investigating adaptation in relation to specific standard environmental conditions, and seems to have paid little attention to adaptation in relation to fluctuating conditions.

The agricultural scientist and farmer are perhaps more aware of the problem. Fluctuations in environment leading to alterations in output of agricultural products are highly undesirable, and a body of evidence has accumulated showing that crops and varieties differ in their stability of fitness and their ability to respond to optimal conditions. But again little critical work has been done to investigate such responses, and the possibility of breeding for them. The need for such work has been already emphasized by the Director of the Scottish Plant Breeding Station (Gregor, 1956).

What investigations are likely to yield profitable results particularly in a somewhat agricultural context? There seem to be two proper approaches.

(*a*) *Ecological.* Some factors are liable to fluctuate more markedly than others. These include temperature and incidence of rain, soil fertility, grazing, and crop density. We need to discover the extent of the ability of plants to develop both morphological and physiological plasticity in adaptation to such variation. We also need to understand and demonstrate

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its adaptive value. To do this we may take the traditional approach to the genecologist, and examine species to see whether populations occurring in different environments differ in their plasticity. But to discover this plasticity and analyse its adaptive value, experiments involving examination of material under specific, contrasting conditions will be necessary. Each particular type of plasticity will require its own technique of examination.

There is a considerable amount of evidence which shows that agricultural varieties differ in their response to variation in density—*e.g.*, sorghum, flax, etc. But it would be valuable to see how common is the occurrence of such differences in plasticity in wild as well as cultivated plants. Since crop-density is not always precisely controlled, response to unavoidable fluctuations in density is of economic importance.

Soil fertility can be controlled. However, we are now subjecting our crops to higher and higher levels of fertilisers. There is need here to know whether we are employing the varieties which show the greatest response to the high levels occurring. While the cereal grower is aware of this, the pastoralist has paid little attention, although evidence is now accumulating of considerable differences in response to nutrient level variation within species—*e.g.*, in *Lolium perenne* and *Dactylis glomerata* (Crossley, 1963).

In areas where seasons vary markedly from year to year we have already seen that some species—*e.g.*, *Bromus, mollis* can adjust their growth to such variations so as to maintain maximum fitness. But critical analyses of such adaptations are few, and we have little clear idea of the degree of development of such plasticity that is possible. This is particularly important to the agriculture of semi-arid areas.

The grazing animal can cause wide variations in the environment of pasture plants. We have always tacitly assumed this, but only recently have we come to realise the need for examining critically the response of pasture material to grazing conditions. It has led to the discovery that the ability of particular material to maintain fitness under grazing conditions is not necessarily indicated by its performance under other conditions (Lazenby and Rogers, 1960). Recently Black (1960) has shown the significance of the ability of *Trifolium* species to elongate their petioles when surrounded by other vegetation.

Here is an elegant example of a character whose plasticity is of considerable adaptive significance.

While variation in morphological characters is most readily apparent, plasticity of physiological characters must not be forgotten. In some habitats wide fluctuations in temperature and light intensity are found. It is now becoming clear that plants can adjust their basic physiological process of photosynthesis and growth in response to such fluctuations. Populations of a single species from different environments differ markedly in their powers of adjustment as has been shown for *Lolium perenne* (Cooper, 1963) and *Solidago virgaurea* (Bjorkman and Holmgven, 1963). In all cases the differences can be correlated with the conditions existing in the original habitats of the populations. Though the evidence is so far rather meagre, it suggests that physiological adjustment is as important as morphological adjustment in adaptive plasticity.

For some characters, however, maximum fitnesss occurs when that character is held constant. Such a character appears to be that of seed size. It is a conspicuous characteristic of all wild plant species that while numbers of seeds may vary widely, seed size is held extremely constant. But this is not necessarily true in cultivated species. There is an interesting comparison in the cultivated sunflower: this shows considerable variation in seed size with change of density (Harper, 1961). Yet the wild sunflower does not (C. B. Hieser, personal communication). There is indirect evidence that the same may be true of other crops—*e.g.*, barley. Here then breeding for higher yield seems to have caused loss of stability in this character.

As has been already mentioned the agriculturalist is clearly interested in stability of final yield in whatever form this yield may be. Everyone must be well aware of varieties differing in their stability of yield (examples are given in Simmonds 1962). But despite the obvious economic implications, the basic causes and the best way of achieving such stability still need further investigation. Stability of yield must at least in part be due to considerable adjustments in the processes contributing to final yield, whether morphological or physiological. The problem has recently been reviewed by Allard and Bradshaw (1964).

(*b*) *Genetical*. The second direction of attack is on the genetic control of such plasticity. While it is easy to argue that plasticity must be under genetic control, this is no substitute for actual analysis of this control and the determination of the ease by which it can be changed by selection. In animals recently a body of evidence has accumulated to show that the ability to respond to environmental stimuli is genetically controlled and can be readily selected (Waddington, 1961). No equivalent evidence exists for plants. The lack of knowledge of genetic mechanisms leading to stability of final yield in crop plants is a case in point. Stability seems to be determined by both additive and non-additive gene action. At present specific types of heterozygosity seem to be likely to be the most effective method of obtaining stability (Allard and Bradshaw, 1964).

We even know very little of occurrence of variation in plasticity between genotypes and populations within species. We therefore need careful genetical analyses made of both simple type of plasticity, such as response to density, and more complex types, such as heterophylly in water plants It seems likely that the situation will be remedied over the next decade A study of density response in flax and other species has been started at Bangor, and Dr C. D. Cook at Liverpool has an analysis in progress of the genetics of heterophylly in *Ranunculus*. A series of studies on stability in barley and other crops is being carried out at Davis, California, by Dr R. W. Allard. Studies on physiological adjustment in various Californian species is being carried out by Dr H. A. Mooney at Los Angeles and by Drs Wm. Hiesey and M. Nobs at Stanford, and in various herbage species by Dr J. R. Cooper at Aberystwyth. It is to be hoped that there are and will be many others.

In conclusion it can be said that current interest in the mechanism of gene action tends to let us believe that the organism is just the result of the inexorable operation of the genetic determinants in the original zygote. But no organism can escape from its environment : this is a fact only too well appreciated by the agriculturalist. However, the amount that an organism is influenced by the environment is not just determined by the environment ; it is determined also by the gene systems of its own genotype that control and canalise development. The concept that the effect of the environment on the expression of a genotype is limited by that genotype has many ramifications. In relation to fluctuating environments we know so little about its importance that there is great need for further investigations from both evolutionary and agricultural points of view.

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GENECOLOGY AND BREEDING FOR DISEASE RESISTANCE

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For the most part genecologists have been interested in the genetical reactions of species individually to environmental circumstances. It is true that some workers have studied several species, but they have tended to examine those species independently. In their discussions they have sometimes mentioned that all or many of the species in a community would possibly react genetically to changes of environment and theorised on the possible repercussions of this. It is only recently, however, that a start has been made with the experimental investigation, concurrently, of the several species in a community. (McMillan, 1959, 1960.)

One such trial on a large scale of the species in the local grassland communities was recently completed at the Scottish Plant Breeding Station, and there is considerable evidence in this work that the genetic reactions of the different species are correlated. It seems likely that genecological investigation will tend more and more towards a study of the complementary genetics of the several species in an association. We can expect this to be a profitable field for study since species in association are likely to have complementary genetic systems for either or both of two reasons. Firstly, the several species will all react to their common environmental selection, and secondly, in so far as each species is itself a factor in the environment of the others, any favourable change in one would need to be matched by changes in the others if they are to succeed in competition.

Species associations are of many different kinds (McDougall, 1918) varying from the relatively loose association between two species with similar ecological tolerances to the much more specific relationship between host and parasite. This latter relationship, because of its immense economic importance, has been the subject of a considerable amount of genetic research and the results make fascinating reading for the genecologist. In fact, it might be fairly stated that situations encountered in breeding for disease resistance sometimes come very much closer to ideal systems in population genetics than do many of those that genecologists have chosen to study.

Interest in the inheritance of disease resistance followed very soon after the rediscovery of Mendel's work in 1900. In 1905 Sir Rowland Biffen published a paper in which he showed that resistance to yellow rust in wheat was inherited as a simple Mendelian dominant. As is now well known, resistance conferred on a crop variety by the addition of a resistance allele is not necessarily permanent. In only a relatively few instances have resistant selections remained free of a disease over a prolonged period. An example is potato wart disease, where resistant cultivars which have been grown for fifty years or more afforded, until very recently, completely satisfactory control of the disease. The usual story is that after a few years new, or hitherto unrecognised, races of the pathogen capable of infecting the resistant selections have become prevalent. As an example, an historical review of varieties of oats grown in the corn belt of the United States (Stevens and Scott, 1950) shows that the average usefulness of varieties resistant to stem and crown rust was only five years. The difference between these two patterns of case history is essentially related to the biological characteristics of the two species concerned, but more especially with the biology of the pathogen. Diseases which become prevalent again soon after the release of new resistant crop varieties are characterised by such features as: very efficient, rapid and wide dispersal of pathogen spores; the principal source of infection an asexual spore; a sexual stage in the life history of the pathogen; and the crop highly homogeneous—either a self-pollinating species or reproduced vegetatively (Griffiths, 1958). These are, in fact, the characteristics which we might expect would lead to the rapid evolution of a new race of the pathogen. All characteristics are not necessarily present, of course, in every disease situation in which breeding for resistance has been dogged by the emergence of previously unknown races of the pathogen—thus the sexual stage is very rare in the potato blight organism, though the other three characteristics are present. It is perhaps noteworthy that a high proportion of the diseases which have been to date permanently controlled by plant breeding are soil borne, where the pathogen is denied the advantage of an efficient spore dispersal mechanism.

The breakdown of resistance following the origin of new physiological races of the pathogen is in genecological terms a direct response of the pathogen to a changing environment. For the most part a resistant crop selection differs from its predecessors (so far as disease control is concerned) in the possession of an extra factor for disease resistance. Any race of the pathogen having the necessary genetical constitution for virulence on the superseded variety only needs to mutate at one locus overcoming the new resistance to evolve a new successful race. If conditions are such that the new resistant material is showered with spores that are only prevented from establishing a parasitic relationship by a single locus it can only be a matter of time before such a new virulent mutant arises. In this way each virulence mutant in the pathogen would be paired with one resistance locus in the host—host plants carrying a number of resistance factors would only be susceptible to races of the pathogen that carried at least as many virulence factors, and those at the right, complementary, loci. We might expect such a genetical relationship of host and parasite from genecological considerations, but to do so in fact would be a case of being wise after the event. The credit for unravelling this gene for gene hypothesis belongs to Flor (1955, 1956), who has so elegantly demonstrated its existence in the rust disease of flax. The theory has been amplified by Person (1959), who argues that the hypothesis ought to hold in other host-parasite relationships and claims that the available evidence suggests that it does.

A particularly interesting feature of Flor's work is his demonstration that the most prevalent physiological races of the pathogen at any one time are those which contain the least number of virulence alleles compatible with survival on the currently commonest flax varieties (Flor, 1953). Thus at each virulence locus which is not required to overcome a specific resistance locus the avirulent allele is competitively superior to the virulent one. This underlines his findings that the loci of the two species are complementary to one another —virulence at a particular locus is a disadvantage except when it is necessary to overcome a particular form of resistance.

The recognition that each resistance locus confers a different and independent type of resistance, and that each needs to be overcome independently by the pathogen to establish a disease relationship is of great practical importance. It has long been recognised that wild species used as donors of resistance in breeding work carry resistance at many loci. Clearly this is why such species remain resistant. A pathogen will mutate at one locus to overcome one form of resistance with relative ease, but a barrage of resistance factors, each of which has to be overcome independently, and all at the same time, effectively maintains the resistance. This then is perhaps what is required to produce varieties which are permanently resistant. As Flor and others have suggested, a resistant selection which confronts the pathogen simultaneously with two or preferably more new forms of resistance is much more likely to remain resistant than one having only a single new allele. Indeed the position is perhaps even more serious: by offering the pathogen resistance factors one at a time we are not only inviting it to produce a new virulent race but we are teaching it step by step to overcome all of our potential genetical defences. If we use the various resistance factors of a donor species and add them into crops one at a time we will in the course of things guide the pathogen until it is able to parasitise a hitherto resistant species. If we then turn to further donor species it can only be a matter of time before we exhaust the world's supply of resistance and crops become uniformly susceptible. The inevitable consequence for any crop so afflicted would be its virtual loss to world economy. To think of just a single possibility, the prospect of a world without wheat is not a happy one.

The appreciation of the advantages of being two steps ahead of the pathogen instead of only one has already had its effect on plant breeding, but not without some opposition. For instance, Johnson (1961) in his aptly titled article "Man Guided Evolution in Plant Rusts" views the "pryamiding" of resistance genes into varieties as potentially dangerous because of the possibility of producing super races of the pathogen. Clearly if the useful life of a variety with two new resistance factors is less than twice that of the single step ahead variety, Johnson's criticism is valid. The problem is then to assess—or to observe—the risk, and this will vary according to the situation in hand. One of the foremost points to consider is the effectiveness of the sexual cycle in the pathogen, since a sexually reproducing species has the advantage of both mutation and recombination. Thus where the pathogen is asexual, and has overcome several or many resistance factors singly it may yet be possible to build up from those same resistance factors varieties that are several steps ahead of the fungus with a reasonable chance of their remaining resistant. Such a programme where the pathogen has an efficient sexual stage would have little hope of success. This is most graphically illustrated by a comparison of the case histories of breeding for rust resistance in wheat between North America and Australia (Waterhouse, 1952). In the absence of the alternate host, barberry, the pathogen in Australia is essentially asexual so that new physiological races are simply mutants of the old, whereas in North America new physiological races originate from a combination of mutation and recombination. Another point which will be especially important where the pathogen has an efficient sexual stage is whether "new" resistance factors introduced from other species are literally new to the crop, for if the pathogen has already had the opportunity of overcoming that form of resistance the virulence allele may yet exist, perhaps in very low frequency and yet sufficient to negate our efforts. Thirdly, we must make an allowance for the possibility that two independently inherited resistance loci might be duplicate factors, that is each leading to the same type of resistance so that a single mutant in the pathogen might overcome both. Theoretically it seems unlikely that such a situation will occur often but we would be wise not to forget the possibility. Both of these last points, whether the resistance loci are literally "new" to the crop and the possibility of duplicate factors, lead to the same conclusion. In any particular case experimental evidence might indicate that a new resistant material was a certain number of steps ahead of the pathogen, but we should recognise that the estimate is a maximum and that in fact the progress might be represented by a lesser number of steps. The moral is obvious—safety lies in numbers, and the aim should be to prepare materials carrying as many new resistance factors as possible.

Following this analysis we must consider whether such a theoretical ideal—materials carrying several new resistance factors—is attainable in practice. The standard techniques for the recognition of physiological races of pathogens depend on their reactions with a series of known host genotypes. In like manner the determination of the resistance genotype of a host depends on observing its reaction with a series of known races of the pathogen—and indeed even this is not always possible since it can only be practised when the pathogen concerned is easily maintained in a pure culture. Using these techniques we can only recognise those resistance loci of the host that are already partnered by virulence loci in the pathogen. These resistance loci are, therefore, not new to the crop, and although we might proceed from here to achieve permanent resistance when the pathogen was asexual, we could not hope for success with a sexual pathogen. More generally, what we need is a technique for recognising, or at any rate, differentiating between, new resistance factors which have not yet been partnered by virulence mutants in the pathogen. This is not beyond our technical ability.

Our basic techniques for producing resistant materials—whether we use the long established backcross procedure or come to rely more and more on radiation techniques—all lead essentially to modifications at single loci. If the materials are crossed with their susceptible progenitors they give rise to typical monohybrid segregations: either one to one in the immediate progeny or three to one in the succeeding progeny depending on whether the locus is heterozygous or homozygous. A whole series of separate backcross derivatives crossed with the susceptible might give this result but they might do so as a consequence of resistance at different loci. Whether or not this were so could be determined by crossing the different resistant lines one with another. Assuming this were done before the end of the backcross programme, when the resistance loci were in the heterozygous state, the immediate progeny would segregate 3 : 1. Two-thirds of the resistant plants in these progenies would themselves be heterozygous at one locus and yield a 3 : 1 ratio in the succeeding generation, but the remaining third would either be homozygous at one locus (when the non-segregating resistant progeny would indicate that the parent lines carried resistance at a common locus) or heterozygous at two loci. This latter case would be recognised in that the progeny segregate 15 resistant to one susceptible. Furthermore, one-fifteenth of these resistant plants would be homozygous resistant at both loci—

that is, pure breeding for two steps ahead of the pathogen—and these plants could be recognised from the fact that they yield the double heterozygote on crossing to susceptibles and thus 15 : 1 in the F_2. If all possible crosses had been made between the original new resistant lines we should be able to enumerate the resistance loci and give them some sort of symbolic recognition. Thus we should know which of the two step ahead lines could be crossed to give plants heterozygous at four resistance loci, and to this extent the task of building up the higher numbers would be eased. On the other hand, we should expect only one in 256 of the progeny of such a tetrahybrid to be homozygous at all four loci so that many plants would have to be tested in order to find it. Clearly the effort involved in building up the higher numbers increases rapidly as we raise our standards.

A programme of this type for producing varieties carrying several new resistance loci could only succeed if the supply of the initial single locus lines was adequate. The rate at which these can be produced depends largely on the number of people engaged in the work, and it seems certain that more breeders would be needed than are at present employed. Furthermore, assembling the different resistance loci into single lines would add four or five years to the normal breeding programme if the aim was to produce a variety four steps ahead, with greater delay if the aim was more advanced. Both considerations suggest that the work would be expensive, and by present standards the cost might be very great indeed. Even so the cost is not likely to be large in relation to that, for instance, for putting a man on the moon, and the rewards might be incomparably greater.

Since the object of so much genetical juggling is to produce a material which is permanently resistant to a particular pathogen we should need to take any further precautions that seem desirable to this end. Though theoretical considerations suggest that a four step ahead variety should remain free of infection we can only find out if this is so by producing such a variety and releasing it through the normal seed channels. Unfortunately, the organisation of the seed trade does not give our new variety much of a chance. This comes about from the fact that our hopes for the new variety lie not only in its being four steps ahead of the pathogen, but also in its being four steps ahead of other varieties. If varieties were produced which bridged the gap between it and the susceptibles we should once again be offering the pathogen the easy way to undermining our efforts. As soon as our new variety became freely available it would be crossed with other varieties. This would happen to some extent naturally but also as a result of breeders' efforts for yet further improvements, possibly in other directions. The inevitable consequence is that the collection of resistance loci would be diluted, and in time a bridging series could arise. This calamity could only be prevented by stricter control of the seed trade. In order to give the new selections a fair chance to succeed it is essential that the gap between them and their predecessors is maintained and so censoring machinery would be required to ensure that all seed offered for sale was either comparable with the earlier varieties or equal to (or in advance of) the new. The same machinery might be responsible for maintaining standards in the new varieties since it is possible that there would be a natural tendency to revert, and this in itself could lead to a bridging series. Machinery of this type might be established in the trade on a voluntary basis once the need for it were widely appreciated, and this would be preferable to legislation, but however organised the cost of running it would be another heavy item to debit against the breeding programme when considering its worth.

This brief account necessarily reduces plant breeding problems to their simplest terms, and it would not be proper to conclude without emphasising that the success of a programme of the type described would depend very much on breeders' skills that have not been mentioned. Plant breeders are concerned with a very much wider range of plant characters than just resistance to a specified disease. A permanently resistant variety could have no economic value if it failed to produce the high yield and high quality demanded of modern crops, so that, supposing it works, the scheme outlined is only a partial solution to the problem of breeding for disease resistance.

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