Brassica napus (2N = 38), A TYPICAL SPECIMEN OF DWARF RAPE.

B. napocampestris (2N = 58), A SYNTHETIC AMPHIDIPLOID DERIVED FROM THE CROSS *B. napus* (DWARF RAPE) × *B. campestris* SSP. *nipposinica* (2N = 20).

SCOTTISH PLANT BREEDING STATION

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DIRECTOR'S REPORT

Foreword.—" To conduct investigations calculated to yield information of scientific interest, and especially information bearing upon the general problems of crop improvement, and to produce new and improved varieties of direct value to agriculture,"—these have always been the aims of the Scottish Plant Breeding Station. While a reasonable balance between these two objectives has constantly been kept in mind, the amount of effort devoted to each has understandably fluctuated from time to time. It is, however, safe to forecast that as the demands of agriculture become ever more exacting the need to gain new knowledge will become relatively more urgent. Indeed if the Plant Varieties and Seeds Act, 1964, which provides for the granting of proprietory rights to persons who breed or discover new plant varieties, is to fulfil its intended purpose then in order to avoid wasteful competition between commercial organisations and the grant-aided institutions the acquisition of " information of scientific interest " is likely to become the predominant Station activity. Within the applied field itself it is reasonable to predict that, because the value in terms of royalties from a *general* purpose cultivar can be expected considerably to exceed that from a *special* purpose cultivar of restricted use, the improvement of the less remunerative crops such as forage plants for " difficult " environments, will increasingly become the concern of the Station's Herbage Plants, Cereals and Brassica sections. The following grouping of the investigations now being conducted by these three units, under the single title of Forage Crops, is in the circumstances realistic for not only does it indicate the probable future trend of events but highlights a class of crops of peculiar interest to Scotland. Thus the Station's second aim can be stated currently in terms of two categories of crop : (*a*) Forage Crops, and (*b*) Potatoes. Though these two areas of research cater for different agricultural environments their respective programmes are by no means either agriculturally or genecologically speaking mutually exclusive, for, in the first place, as lowland arable farming becomes more intensive and specialised the more does it become dependent upon upland products, and, secondly, a common foundation in genecological research is a feature of both.

Forage Crops

Under this general heading are described the investigations concerned with brassica crops, cereals and herbage plants, investigations which not only reflect an appreciation of the above mentioned trend, but also of the growing importance to the Scottish economy of the relatively large acreage of arable land verging upon the "marginal", and of the very extensive areas of uncultivated natural grazings. Accordingly the forage crops programme takes into account the need to breed varieties adapted to marginal arable situations as well as to acquire genecological information regarding the detailed structure and potentialities of native vegetations.

Brassica Crops.—The emphasis here is on the breeding of new grazing types with greater productivity in terms of digestible dry matter than existing forms of rape or kale. Since rape is an essentially upland crop in Scotland a primary objective of the present work is to combine the hardiness of rape with the leafiness of selected oriental forms of *Brassica campestris*.

Attempts to synthesise rape (*B. napus*, $2n = 38$) directly by crossing tetraploid forms of *B. oleracea* ($2n = 36$) and *B. campestris* ($2n = 40$) have so far been unsuccessful. In contrast, however, *B. napus* and *B. campestris* are readily hybridized so that fairly large numbers of F_1 seedlings may be treated with colchicine in the production of the hexaploid *B. napocampestris* ($2n = 58$). Being an amphidiploid *B. napocampestris* populations show little segregation but this is obviously dependent on the degree of heterozygosity of the parental material. There may not, therefore, be much scope for selection for desirable agronomic characters once a particular synthesis has been achieved. As a consequence efforts are being made to produce a number of forms with the same genomic formula but of different genetical constitution from crossings involving different cultivars and subspecies of *B. napus* and *B. campestris*.

Synthetic *B. napocampestris* in which *B. campestris* ssp. *nipposinica* was one parent has possessed both hardiness and leafiness. In a preliminary yield trial the synthetic showed an increase in dry matter yield of 30% over the mean of 8 commercial rape cultivars in early January, an increase considered due to the numerous side-shoots which by then were well

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developed in the synthetic but were fewer and less well developed in rape (see frontispiece). The possibilities of better regeneration following grazing of the synthetic than of rape are suggested. The problem of lower seed fertility of *B. napocampestris* than commercial rape is being dealt with by a process involving the selection of high fertility plants from elite populations under polycross conditions.

B. napus × *B. oleracea* crosses made with regard to the synthesis of *B. napoleracea* ($2n = 56$) have proved more difficult (0.6 seeds per pollination) than *B. napus* × *B. campestris* (12.0 seeds per pollination).

Forms of fodder radish (*Raphanus sativus*, $2n = 18$) are being examined as potential parental material in view of the possibilities of synthesising *Raphano-brassica* inter-generic hybrids. Seedlings have been treated with colchicine in order to produce autotetraploids, the intention being to assess the potentiality of autotetraploid *Raphanus* itself and to use it in crosses with existing *Brassica* tetraploids in the hope of obtaining amphidiploids which might combine the vigour and resistance to disease of *Raphanus* with the hardiness of *B. oleracea*.

Within the " kale group " (*B. oleracea*) no selections or lines derived from inter-varietal hybridization have exceeded the commercial cultivar ' Canson ' in yield of leaf dry matter, or in the proportion of leaf to stem. Autotetraploids of ' Canson ' have been produced but are not yet at a stage when comparison can justifiably be made with their diploid progenitors. Considerable variation between C_1 families derived by selfing different C_0 plants was observed, which suggests that a period of breeding at the tetraploid level would seem to be essential before the true value of autotetraploids can be assessed. The indications at the moment are that unselected thousand-head kale autotetraploids do not differ significantly from diploids in total leaf dry matter.

Cereals, *Oats*.—One of the main objectives of the oat breeding programme is the production of improved varieties to meet the needs of farmers in upland and other marginal land areas. The appearance within recent years of high yielding barley varieties has resulted in the replacement of oats by barley over a large part of the more fertile low ground with the result that oats grown on marginal land now represents a much higher proportion of the Scottish oat acreage than formerly.

To cater more immediately for such areas selection has been carried on not only at Pentlandfield but at centres in Argyll and Inverness-shire. A differential response of varieties to environment noted at these centres provides two alternative approaches to the problem of crop improvement. The first involves the development of the special purpose type adapted to a particular environment but of limited application outwith that environment, the other the search for a versatile type whose relative performance is little affected by change of environment.

Further evidence has been obtained as to the complex nature of the inheritance of resistance to the oat stem eelworm, *Ditylenchus dipsaci*. In an attempt to confirm the results reported previously (*Record*, 1963, p. 12) a hybrid was produced between E.138, one of the most resistant oat lines bred at the Station, and the susceptible cultivar ‘ Ayr Commando ’. Six hundred and fifty-nine F_2 plants were grown to maturity, harvested individually, and each of the resulting lines was tested in the F_3. Relating the observed symptoms to the same nine classes in 1963 the results were as follows :—

E.138 (RESISTANT) × ‘ AYR COMMANDO ’ (SUSCEPTIBLE)

CLASSIFICATION OF F_2 IN NINE THEORETICAL CLASSES BASED ON THE ASSUMPTION OF TWO INDEPENDENT GENES FOR RESISTANCE.

Class	*Phenotype expression associated with*		*Observed*	*Predicted*	*Predicted Fraction of Total*
	Tolerant Factor	*Inhibitant Factor*			
1	Tall	Undilated	17	41	1/16
2	Height segregating	,,	37	82	2/16
3	Stunted	,,	24	41	1/16
4	Tall	Dilation segregating	39	82	2/16
5	Height segregating	,, ,,	242	166	4/16
6	Stunted	,, ,,	74	82	2/16
7	Tall	Dilated	21	41	1/16
8	Height segregating	,,	132	83	2/16
9	Stunted	,,	73	41	1/16
			659	659	

It was noted that while the general trend was similar to that reported in 1963 only 17 of the above lines were classed as homozygous for both tolerance and inhibition, i.e. resistant, against a predicted figure of 41 while at the other end of the scale there were 73 lines classed as susceptible. Again a total of 77 lines were classed as tall, i.e. tolerant, and 78 as undilated, i.e. inhibitant against a predicted 164 for each attribute, about half the expected number in each case, whilst 171 were stunted, i.e. intolerant, a figure which is very close to the expected number.

In the course of the assessment it was apparent that there was a range in the amount and nature of the dilation of the base of the plant, on which symptom the Inhibitant character is assessed, which was not consistent with the effect of a single gene but suggested rather the combined effect of two or more genes. There was present an aberrant type of plant with very slight dilation of the base.

It has also been noted that at the dosage level of 300 eelworm larvae per seedling the height of the plants, the attribute used for assessment of tolerance, is not independent of the extent to which the plant base is disturbed by the dilation effect, so that plants which are genetically alike in regard to tolerance may differ in height according to the amount of disturbance caused by the eelworm to the base of the plant. Because of this, and because the number of stunted plants observed, i.e. intolerant, is close to the expected number it is considered that tolerance is not inconsistent with the effect of a single gene, genetically independent of the Inhibitant factor but whose phenotype is subject to modification according to the genic background in which it occurs.

Further evidence of the complex nature of the inheritance of the Inhibitant character, as measured by degree of dilation, has been obtained from the examination of hybrid progenies arising from the crossing of differently derived resistant lines with common susceptible varieties. Homozygous resistant lines of hybrids derived from E.130, a bred strain, show no signs of dilation in the inoculation tests, while those derived from E.217, also a bred strain, show very slight dilation of the base similar to the type referred to above. When grown in heavily infested test plots in the field neither E.130 nor E.217 show any signs of eelworm attack, which, indeed, is true also for all homozygous lines classed as resistant as a result of the inoculation tests.

Since the winter of 1959 the "Burdiehouse" (Edinburgh) strain of eelworm, the most virulent strain so far encountered, has been used for the inoculation tests and test plots in the field. On the evidence available to date oat stem eelworm strains differ only in the severity of their attack but with the distribution in the current year of resistant oat selections to Advisory Officers in areas where attack by stem eelworm is prevalent, information as to resistance breaking strains, if such there be, should be forthcoming in the near future.

Barley.—Hybrid material bred, and selected for a number of generations, at the Plant Breeding Institute, Cambridge, was included in small-scale replicated trials at Pentlandfield. Following three years of such trials a number of promising lines have been noted for inclusion in field scale trials.

Herbage Plants and Genecology.—While grasses bred for lowland arable conditions are extensively sown in " marginal " districts there would, nevertheless, seem to be a place in such districts for special purpose varieties, a possibility which is not being lost sight of in the breeding programme. Indeed at present the breeding programme is chiefly concerned with Italian Ryegrass, a grass which responds to liberal manuring and could well provide rich grazing complementary to that of low quality natural vegetation, particularly if it were to be sown in combination with a pasture type of brassica, e.g. a form of *B. napocampestris*. Perhaps the greater challenge is, however, presented by the hill land proper where the physical difficulties alone make any form of improvement applicable to arable land quite unrealistic. Here the naturally occurring mosaic of plant communities provides a variety of diets for the grazing animal, but it is the existence of small areas of vegetation above average quality which gives value to many a hill grazing. The aim is, therefore, to find ways of increasing the number, or expanding the territories, of the more nutritious types. To encourage change in this direction a much more detailed knowledge is required, embracing not only the components of the communities and those of the environment but the complex inter-relationship between them. To this end the investigations on flushed areas are continuing and increased attention has been given to the relationship between soil nutrient levels and the amounts taken up by the plants. Analysis of material from individual isolates of *Festuca rubra* (which may or may not be different genotypes) growing in a field trial showed rather wide variation in uptake of mineral nutrients, and it was obvious that better control of the environment was essential before any conclusions about the heritability of this kind of variation could be made. Attention was, therefore, transferred to greenhouse experiments where conditions could be more closely controlled. Analytical work has been extended to include Ca, Mg, Na, K, N and P in plant material, and croppings of five species grown from seed in pots were analysed at intervals over a period of one year. In all five species soil nitrogen level had a substantial effect on the uptake of phosphorus and potassium and little or no effect on calcium and magnesium: uptake of N, P and K fell as the experiment progressed and after nine months when there was little growth, addition of N alone (as NH_4NO_3) induced normal uptake of N, P and K and considerable growth, whereas addition of P or K alone had no effect. There was little difference between the species in their behaviour, but other more critical experiments are being carried out using seeds of seven species from plants obtained from the flushed site mentioned in previous reports and it is hoped by refined techniques to be able to demonstrate differences in their reaction to soil nutrient levels.

Analysis of croppings from quadrats on the above flushed site showed differences in N, P and K uptake in relation to soil pH; uptake was highest where pH was high and lowest where it was low. Estimates of the nitrogen supplying power of the soils on this site, obtained by the use of a new technique, suggest that nitrogen availability bears the same relationship to soil pH, but there is no evidence of variation in the availability of P and K.

Since it is known that there is a gradient of soil fertility in flushed areas, it is of importance to know whether there is a corresponding genetic gradient within the species which are present and so the genecological study of these species has been continued with particular emphasis on the pattern of variation in *Festuca rubra*. Genetic variation could bear a definite relation to soil conditions, indicating that adaptation is involved, but in order to define the variation it has been found necessary first to delimit individual genotypes. Self-incompatibility being the rule in this material cross-compatibility data have been used along with morphological and physiological criteria for purposes of genotype identification.

It had already been demonstrated that a single area of flushed ground contained a moderate number of genotypes which could be distinguished by a range of morphological and physiological characters but owing to the relatively small number of compatibility test results available at that time it was not possible to give more than an indication of whether different genotypes occupy particular parts of the soil gradient.

Much of the past season has, therefore, been devoted to a comprehensive programme of crosses, and plants which had been taken from the natural habitat were arranged in the greenhouse so that similar ones, particularly those from the same sampling point, occurred side by side. Crosses were carried out in such a way that the resulting pattern was a series of interconnecting rings having the effect of linking most of the plants together either directly or indirectly. By using this method in preference to diallel- and pair-crosses rather more information was derived from the same amount of work. Compared with the previous year seed setting was generally better, and very good compared with open-pollinated material. This was probably due to the use of wire frames to keep the pollination bags from collapsing.

Some 600 crosses, selfs and open-pollinations were performed, giving rise to over 1,500 seed samples after the panicles had been graded according to seed yield. The grading was found to be helpful in enabling conclusions to be drawn in borderline cases, but involved the technical difficulty of dealing with a large number of germination tests. This was overcome by performing the test *in situ* using the paper bag which had been employed to store the seed. For this purpose bags having one transparent cellophane surface and one ordinary paper surface were used, so that germination could be observed directly in the bag some days after it had been placed on a moist substratum at an appropriate temperature.

As a result of this crossing programme and obtaining further morphological information on plants growing in the field trial, it has been possible to gain a reasonably reliable picture of the pattern of genotype arrangement on the flush. This subject is treated at greater length in an Occasional Paper (p. 163).

As part of an investigation dealing with the nature of the factors which occasion changes in the composition of plant community mosaics work on localised ecotypic population differentiation has been extended to include *Potentilla erecta*, a species that occurs in a wide variety of communities and which a preliminary trial had shown to be susceptible to phytosocial selection.

In the first place information regarding the mode of reproduction in *P. erecta* was needed and for this purpose a series of controlled experiments was set up under greenhouse conditions. No seed was formed where unprotected plants were kept free from insects, but where honey bees were introduced the plants set seed abundantly. Individual plants were also kept under pollen-proof cages and a good seed set was obtained when pollen from one plant was transferred to the stigmas of another. Many attempts were also made to produce selfed seed but most of the selfed flowers remained completely barren. A few produced odd seeds which may have been the result of foreign pollen used to pollinate an adjacent flower on the plant. It is certain that *P. erecta* is self-incompatible but until the progeny from these crosses has been examined, the possibility of apomixis cannot be ignored since foreign pollen may be necessary only for seed setting. It is, however, well known that hybrids between *P. erecta* and *P. anglica* are common where the two species occur in proximity.

With the object of obtaining material for the comparison of habitat populations seed and plant samples were collected from four geographically separated localities where two obviously contrasting communities occurred in close proximity, one being grazed bent-fescue, the other *Molinia* dominated. That the respective *Potentilla erecta* constituents of the two communities differed markedly in plant size was demonstrated by measurements taken of the longest ungrazed stem on each plant at the time of collection. An analysis of variance of the figures obtained showed that there was a very high significant difference between stem lengths from contiguous habitats in each of the four areas. If the stem lengths from all four bent-fescue phenoecodemes are contrasted with those from the four *Molinia*-dominated, the difference is highly significant in spite of the fact that there are also differences of a high order between the geographically separated grazed phenoecodemes and between the equally separated *Molinia*-dominated ones. Thus in spite of spatial separation and significant differences which must reflect local conditions, the bent-fescue phenoecodemes are more similar to each other than those originating in the *Molinia*-dominated communities and the same is true in reverse.

to environmental selection and correlated to varying extents with many other readily measurable characters; and scape number, which varies independently of scape length. These colonies owe their origin to seed immigrants water-borne from a high altitude habitat. The variability carried by seeds fertilised in the wild and off individual plants is being compared with the variation exhibited by the colonial populations.

Investigations into the heritability of yield components in Italian ryegrass were continued with emphasis on the rate of growth during the seedling stage. The examination of suitable field trial techniques for progeny testing was also continued. Since it had been found that in Italian ryegrass a sward planted at 6 in. × 6 in. gave a reasonable simulation of sward yielding ability whilst still permitting easy identification of individual plants, this density was adopted for two small uniformity trials. They were harvested in yard square units of 36 plants on three dates and preliminary results suggest that a rectangular plot of 2 × 1 yard is optimum for Italian ryegrass at this density.

A competition trial in box swards was harvested five times during the year. Two cultivars of ryegrass and two of cocksfoot were used in this trial and the results show that in general yields of mixtures of two varieties were rarely higher than the average of the components. Individual varieties in competition did, however, sometimes behave differently from the way expected on the basis of their behaviour in pure stand and it would seem that the latter does not always give a reliable guide to performance even in simple mixtures. A further report of this work appears as an Occasional Paper on p. 125 of this *Record*.

As in previous years, the cytology laboratory has acted as a service department to the Station as a whole. As part of this service experiments with grasses are in progress to investigate the extent to which mixoploidy is a consequence of colchicine treatment, and to what extent mixoploidy and aneuploidy persist after treatment. In addition, cytogenetic work continued with the examination of further samples of *Poa trivialis* from Scottish and French populations; one French sample was found to be 14 + 2, but all samples were otherwise normal, and tentative karyotypes of some of the material from each population have been prepared.

During last summer Miss Bennett spent five weeks in Greece at the Institute of Fodder Crops, Larissa, to assist in setting up a cytology laboratory to deal with breeding material in a fodder vetch programme, and to train staff in cytological techniques.

Potatoes

Breeding.—During 1964, trial and multiplication plots covering an area of 11 acres contained 10,613 single-tuber selections from the greenhouse, 3,738 selections in three-tuber plots, 518 in eight-tuber plots, 293 in forty-tuber plots together with multiplication plots of the Merit Trial seedlings and the named cultivars 'Pentland Falcon', 'Pentland Glory', 'Roslin Eburu', 'Roslin Riviera' and 'Roslin Sasumua'. A virus tested collection consisting of about 100 named varieties and seedlings were also grown in smaller plots.

Following the suggestions of Mr J. C. Hawkins of the National Institute of Agricultural Engineering, attempts are being made to produce varieties with strong stolons suitable for harvesting by a machine designed to pull the plants by the haulm and so procure the tubers free from clods and stones. Seven selections with relatively strong stolons were supplied in 1964 as trial material. The reports showed that 79.9% by weight of the crop of one seedling was harvested and bagged by the machine while three other seedlings showed over 60% so harvested. Attachment of 100% is not regarded as essential since tubers which break away from the stolons before reaching the conveyor are left on the surface of the soil and are readily gathered by hand.

With the increasing demand for processed potatoes consideration has been given to the selection of seedlings suitable for freezing and canning, i.e. varieties yielding numerous relatively small tubers. A number of selections of this type are being multiplied and tested for texture and flavour. It is hoped to obtain such varieties with strong stolons so that the crops could readily be harvested in an immature state by the pulling method referred to above.

In co-operation with Dr Pushkarnath, Central Potato Research Institute, Simla, a further consignment of over 5,000 tubers raised in the greenhouse in 1964 has been forwarded to India for trial and selection purposes. A report on material sent in the previous years indicates that many promising selections have been made and that 20 of the seedlings sent in 1961 have given "excellent performance" and are being multiplied for large scale trials.

Owing to the incidence of brown rot, *Pseudomonas solanacearium*, in East Africa, attempts are being made to locate sources of resistance to this disease. Samples of hybrid seed from a number of different sources were supplied to Mr R. A. Robinson, Kenya, for raising and testing under brown rot conditions. Preliminary reports show that although most of the seedlings raised proved to be susceptible, a small proportion was unaffected by the disease. Further trials, however, will be necessary to determine whether these seedlings were, in fact, resistant or have escaped infection.

Breeding specifically for field resistance to blight, *Phytophthora infestans*, has been continued as in previous years. Twenty-eight progenies bred for this purpose were raised and tested with a race of the fungus of wide host range. From these, 384 of the more resistant survivors were selected and grown to maturity in 6-in. pots. After further selection at harvest, 229 of them were retained for trial and multiplication in the field. Laboratory tests for field resistance were also carried out on about 400 advanced selections bred from blight resistant parents. The majority had no R genes effective against the race of blight employed and a measure of their field resistance was obtained. Samples of 82 of them were also forwarded to Mexico for test in the Toluca Valley, through the helpful cooperation of Dr J. S. Niederhauser of the Rockefeller Foundation. The report showed that some of them had field resistance in high degree since they were virtually unaffected in this severe test. The results obtained in Mexico and in the laboratory test corresponded reasonably well except in a few cases where new R genes induced a hypersensitive response to the race of blight employed in the laboratory test.

Samples of blight resistant selections adapted to short day-length conditions have been sent to many different countries overseas for experimental and trial purposes.

Derivatives of *Solanum demissum* at Pentlandfield were found to possess three R genes different from the six already recognised in that species and they were designated R_7, R_8 and R_9. The gene provisionally designated R_7 (U.S.A. and Canada) by the Late Blight Investigations Committee of the Potato Association of America is now regarded at Pentlandfield as R_6 in the *S. demissum* series of R genes, the R_6 (Germany) being transferred to the series for *S. stoloniferum*. Nine new races of *P. infestans*, all derived from race 1,2,3,4 were recognised by means of the new R genes.

The seedlings undergoing test in the Merit Trials of the Department of Agriculture and Fisheries for Scotland and several named cultivars were assessed for "field resistance" using detached leaves and race 1,2,3,4,5,7 of *P. infestans*. By the same method thirteen seedlings which had proved hypersensitive or very resistant in 1963 were retested using race 1,2,3,4,5,7, race 1,2,3,4,6,7, race 1,2,3,4,7 and race 1,2,3,4,7,8. Of the four seedlings which were hypersensitive in 1963, three remained so in these tests while one was susceptible to race 1,2,3,4,7,8. The high degree of "field resistance" shown by the remaining seedlings in 1963 was maintained.

A collection of advanced selections and eight seedling progenies were tested for susceptibility to common scab, *Streptomyces scabies*, under natural conditions at Archerfield, East Lothian. As in previous tests, the results with some of the seedlings were promising, their resistance being as good as or better than that of the resistant control varieties. In order to confirm the resistance of selected seedlings further trials were conducted in Cheshire in collaboration with Mr B. C. Knight of the National Agricultural Advisory Service, Wolverhampton. As previously, the results obtained at the two centres were closely correlated.

Tubers of seedlings entered for the Merit Trials of the Department of Agriculture and Fisheries for Scotland, and named cultivars as controls, were inoculated with *Oospora pustulans* Owen & Wakef. to examine their susceptibility to skin spot. A few showed considerable resistance in both the skin and the "eyes". Some of the seedlings were inoculated on lifting both in mid-September and mid-October. Little difference was noted in the susceptibility of the skin at either date of lifting but the sprouts of those lifted in October tended to be more severely affected.

Breeding for resistance to potato root eelworm, *Heterodera rostochiensis*, continues and three first early seedlings now under official test have the population-specific kind of resistance conferred by the gene H_1 of *Solanum tuberosum* subsp. *andigena*. As an alternative to H_1, the gene H_2 of *S. multidissectum* is not expected to be very useful as too many field populations of potato root eelworm already break the resistance conferred by it. Its genetic combination with H_1, however, appears to produce a considerable level of resistance to a very wide range of naturally occurring populations. This information comes from correspondents in England, the Netherlands and Germany, who tested H_1H_2 material sent out from Pentlandfield. It also appears that clones of genotype class H_1H_2 can vary in their level of resistance to the same population, which is almost certainly due to the fact that *S. multidissectum* originally had some genetically obscure resistance in addition to H_2. Fourteen clones incorporating H_1 and H_2 were chosen for multiplication at the forty-tuber stage in 1965. Eight of them derive their H_2 gene from *S. sanctae-rosae*. This is an instance of indistinguishable resistance genes from different sources being given the same general label for the time being.

Five clones incorporating the gene Fa of *S. spegazzinii* were also selected for multiplication at the forty-tuber stage in 1965. The gene Fa is nearest in effect to the gene H_1 of subsp. *andigena*.

Thirty-six clones resulting from intercrosses between *S. vernei* × *S. tuberosum* hybrids, which were expected to show a range of polygenic resistance to potato root eelworm, were tested against the Duddingston strain (class 1), and the Boghall strain (class 2), three plants of each being tested against each strain in 1964. Other plants of the same clones were grown outside for observation of agronomic characters. This enabled clones with better tuber conformation and more resistance than the hybrids to be selected and crossed with clones of *S. tuberosum* incorporating H_1. The eventual objective is to bring together H_1 and H_2 in a background of polygenic, comprehensive resistance from *S. vernei* and so to obtain material with the highest possible level of initial resistance to all populations.

Six progenies resulting from the first backcross of Ross' *S. camarguense* × *S. tuberosum* hybrids to *S. tuberosum* were grown on from tubers so that a range of identical material could be tested against each of the Boghall and Duddingston populations. None of the plants remained cyst-free and there was no evidence of segregating resistance. This meant that there had been general decline in resistance in the first backcross generation as compared with the hybrid generation. *S. camarguense*, the original stock of which was received from Professor H. Ross of the Max Planck Institute, is, therefore, another possible source of polygenic comprehensive resistance to potato root eelworm.

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In a long term experiment, begun in 1955, sixteen plots each nine feet square were deliberately infested with the Boghall population of potato root eelworm ; since then they have grown annually a range of resistant potatoes bred from subsp. *andigena* C.P.C.1673 or C.P.C.1692, always the same clone per plot. The material bred from C.P.C.1673 was the more resistant initially. In 1964, the plots were sampled to provide soil for a pot experiment. This showed that the infestations in plots which had supported resistant clones bred from C.P.C.1673 had died out to such an extent that they produced only one or two cysts in susceptible clones and none in the resistant varieties bred from C.P.C.1673. In contrast the level of infestation in the plots which had supported resistant clones bred from C.P.C.1692 remained sufficient to produce large numbers of cysts on susceptible control clones, but the material bred from C.P.C.1692 was still relatively resistant.

Virus Investigations.—Studies on the relationships between genes controlling reactions and resistance to X and Y viruses in several tuber-bearing *Solanum* species were continued. In *S. tuberosum* subsp. *andigena* the irregular but occasional appearance of susceptible plants in material derived from parents triplex for a gene controlling necrotic reaction to virus X has provided evidence of double reduction in gamete formation. In *S. chacoense* linkage has been established between genes controlling necrotic reactions to virus X and virus Y, respectively. The Y locus of *S. chacoense* has also been found to be linked with a locus controlling necrotic reaction to virus X in *S. sparsipilum*. The two X loci, however, although each the site of genes controlling similar reactions, are not identical and in hybrid material show linkage relationships which suggest that they are situated on opposite sides of the Y locus of *S. chacoense*.

An earlier report that the genes controlling necrotic reactions to virus Y in *S. microdontum* (*S. simplicifolium*) and *S. chacoense* are allelic and probably identical (*Record*, 1962, p. 23), suggested that the character of necrotic reaction to virus Y might be useful in introgression studies between these two species. With this purpose in view 27 lines of *S. microdontum*, *S. chacoense* and their natural hybrids were examined for their reactions to virus Y. The results were promising and further work in this direction is in progress.

The relationships of genes controlling reactions to virus Y and virus A in *S. stoloniferum* are gradually becoming clearer and there is now evidence of six different genes of which only two are proved alleles. Breeding appropriate to examining the relationships of these genes, both among themselves and also with those already reported and symbolised in the literature, has been carried out.

To supplement the information already given on the reactions to viruses of the Birmingham University collection of wild species (*Record*, 1963, p. 30-34), 47 seed lines were tested for their reactions to viruses X and Y. The following lines were fully susceptible to both viruses: *S. morelliforme* lines 1507, 1510, 1613, 1644, 1781, 1805 and 1809; *S. clarum* lines 1827, 1833, 1839 and 1894; *S. pinnatisectum* lines 1426, 1435, 1456 and 1457; *S. agrimonifolium* lines 1851, 1853, 1854, 1891, 1892; *S. oxycarpum* lines 1643, 1645 and 1649; *S. demissum* lines 1295, 1296, 1601 and 1657; *S. verrucosum* lines 1527, 1528, 1532, 1546 and 1658; *S. polytrichon* line 1467; *S. stoloniferum* lines 1520 and 1703; and *S. polyadenium* lines 1568 and 1569. The *S. pinnatisectum* line 1455 was susceptible to virus X but segregated for reaction to virus Y, approximately half the progeny being susceptible to the virus and half being resistant. *S. ehrenbergii* lines 1427 and 1492, *S. sambucinum* lines 1439 and 1442, *S. polytrichon* line 1669, and *S. stoloniferum* lines 1388, 1392, 1554 and 1720 were all susceptible to virus X but resistant to virus Y on sap inoculation. The resistance of these lines was, in each case, apparently based on hypersensitivity to virus Y since graft inoculation almost invariably induced necrotic reactions in varying degrees of severity.

An improved method for use in the serological detection of potato virus Y has been developed. Using an electrically-driven roller press, one volume of sap from the plant to be tested was expressed directly into two volumes of 0.5M borate buffer and the diluted sap was then centrifuged for 30 min. at 7,500 r.p.m. Sap clarified in this way gave strong precipitation reactions with specific antiserum but did not flocculate non-specifically even after prolonged incubation at 45°C. All other methods of clarification that were tested resulted in less satisfactory products.

In further studies of the reactions of potato cultivars to the group 4 strain of virus X, symptoms in the second year of infection were examined. These agreed with the first year symptoms in both type and severity, cultivars known to carry the Nb gene exhibiting necrosis varying in severity between cultivars. One of four plants of 'Pentland Falcon' (in which virus was not detected serologically in the first year of infection) was shown to be infected. The plant was highly necrotic and a possible interpretation of the results is that 'Pentland Falcon' is duplex for the Nb gene. Only one inoculation of the four attempted was successful in infecting 'Monika', a German cultivar. The cultivar may have a degree of field resistance to virus X in addition to the Nb gene it carries, but this possibility needs to be tested by inoculations with other strains of virus X.

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PLANT INTRODUCTION AND GENETIC CONSERVATION : GENECOLOGICAL ASPECTS OF AN URGENT WORLD PROBLEM

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CONTENTS

Summary. The first domestication of wild plants by mankind nine thousand years ago is a definitive feature of the Great Neolithic Revolution which, by increasing the productivity of human labour, permitted not only the first great population expansion of the human species, but also the first steps of man towards civilisation. Mangelsdorf (1965) observes that man's rise from a state of savagery to one of civilisation began when he accidentally set in motion, and himself became involved in, the genetic forces of evolution acting upon animals and plants under domestication.

The first plant domestications were limited in their geographical range by tribal and ethnic boundaries, and in their variety by the fact that once specific needs were satisfied by the introduction of a cultigen the further stimulus to domesticate others necessarily diminished. Kupcov (1965) shows that with the development of world wide trading relations by humanity the distribution of cultigens on a world scale became possible, and at this point the immense variety of innumerable locally cultivated species became apparent for the first time. Vavilov first showed the extent of the genetic variation which mankind had created in this way.

Plant introduction is of increasing rather than decreasing importance today. On the one hand, Bernal (1962) states that the task of getting enough food still remains the major task of humanity even in this scientific age. On the other hand, even in advanced technological communities where the problem of undernourishment has been solved, scientists must continue to search for new resources in order to enrich our social environment.

The immense genetic diversity of the varieties of cultivated plants is the consequence of thousands of years of directed evolution by man. But in every case the results of plant breeding and artificial selection by man must face the final arbitration of natural selection. This does not limit man's ability to direct evolution, however, for he is able to cause natural selection to operate under conditions of his own design upon genetic material of his own choice. It is the central concern of genecology to understand and control the interaction between adaptive genetic variability and the forces of natural selection. Therefore genecology is of special and practical importance in the continued control by man of the forces of evolution.

Since plant introduction involves the transfer of genetic entities from environments of which they are the adaptive consequences and to which they are attuned to environments in which they are untried, the study of the genetic structure of organisms and of their populations is necessary if the genetic responses to such changes are to be understood and predicted.

Adaptive responses within populations to changing selective forces depend upon the maintenance of a reserve of polygenic variability. Polygenic variability may be held in concealed form, and it permits populations not only to be genetically heterogeneous while expressing phenotypic uniformity, but also to respond adaptively to changes in environment with great speed and sensitivity. This has important implications in plant breeding, as has been shown by Gregor and Sinskaya among others.

Among the important environmental components acting upon plant populations and leading to genetic adaptation are climatic factors. Nuttonson (1957) states that climate decides what can be cultivated, whereas soils and other factors indicate mainly to what extent climatic opportunities can be realised. Therefore studies in comparative climatology are important in plant introduction. Such studies, stressed by Vavilov, have been extensively developed in recent years in order to define the crop environment in a quantitative way. Knowledge of the macro-climate and of the micro-climate of crops must form a basis of any future comprehensive understanding of the nature of the changes involved in transferring crops from one environment to another, of the forces leading to crop adaptation, and will be important in determining the distribution of crop plant genetic variability in the world.

Vavilov's studies of the world distribution of genetic variability in cultivated plants laid the foundations for a new phase of plant introduction, the principles of which will be scientifically based on a wide knowledge of applied crop genecology. But Vavilov also presents a new concept of plant breeding.

Factorial concepts in plant breeding have led to a serious loss of genetic variability. Even in the world centres of genetic variability, Vavilov's gene-centres, crop varieties of extreme uniformity are replacing the diverse local varieties, and invaluable genetic diversity is being lost. Such a loss is disastrous. Genetic diversity in the form of locally adapted land-races and related wild species within the gene-centres is a world resource of inestimable value, and must be consciously conserved and utilised. This can only be done by the cataloguing of world

genetic resources, by the creation of research institutes within the genecentres with the task of maintaining genetic resources *in situ* or in living collections on the basis of detailed local knowledge of the genetic potential of the region, by the establishment of protected areas for genetic conservation, and by the development of new breeding techniques in which the population-environment complex is seen as a dynamic system, and genetic variability as a quality to be preserved.

Введение растений и генетическая консервация : генетически-экологические аспекты важнейшей мировой проблемы.

Эрна Беннетт.

Шотландская селекционная станция.

Резюме :

Первое одомашнивание диких растений человеком девять тысячелетий тому назад является решающим фактором великой неолитической революции, которая, увеличивая производительность труда человека, привела не только к первому значительному увеличению человеческого рода, но и к первым шагам человека к цивилизации. Мангельсдорф (1965) отмечает, что развитии человека от состояния дикости к цивилизации начался, когда он случайно привел в движение, оказавшийся вовлеченным в него, генетические силы эволюции, дейсвующие на животных и растения в условиях одомашнивания.

Первые одомашнивания растений были ограничены как с точки зрения их распространения географически, так и в отношении племенных и зтнических границ, а также в разообразии их форм, из-за того, что дальнейший стимул к одомашниванию других видов растений уменьшился тогда, когда введение культигена удовлетворило видовые потребности. Купцов (1965) показывает, что по мере развития всемирных торговых отношений распространение культигенов стало возможным в мировом масштабе, и, в зто время впервые обнаружилось колоссальное разнообразие местных культурных видов. вавилов впервые показал количество и распространение генетического разнообразия, созданного человеком.

В наше время интродукция растений становится все более важной проблемой. С одной стороны как сказал Бернал (1962), задача обеспечения человечествах достаточным количеством пиши остается еще самой главной задачей, даже в этом веке, отличающимся такими блестящими научными достижениями. С другой стороны, даже в наиболее технически-развитых обществах, где пробпема питания решена, ученым приходится постоянно искать новые ресурсы, чтобы обогатить нашу общественную среду.

Огромное генетическое разнообразие культурных растений представпяет собой результат тысячелетней эволюции под руководством человека. Но в каждом случае результаты селекции растений и искусственного отбора человеком должны считаться с условиями естественного отбора. При этом человеческая способность к руководству все еще не ограничена, потому что он способен причинять естественный отбор определенным условиям по своему усмотрению и на основе генетического материала, который он сам выбираст. Главная цель генетической экологии (genecology) состоит в том, чтобы понимать и контролировать взаимодействие между адаптивной генетической изменчивостью и силами естественного отбора. Поэтому генетическая экология имеет особую практическую важность для осуществления непрерывного руководства человека эволюционными силами.

Так как введение растений влечет за собой передачу генетических существ среды, адаптивными следствиями которой они являются и к условиям которой они привыкли—к той среде, к условиям которой они еще не привыкли—изучение генетического строения организмов и их популяций необходимо, если мы хотим понимать и предсказывать генетическую реакцию.

Адаптивные реакции внутри популяций к изменяющимся селективным силам зависят от сохранения резерва полигенетической изменчивости. Полигенетическая изменчивость может существовать в скрытом виде, и позволять популяциям быть не только генетически гетерогенными, будучи в то же время фенотипически единообразными, но также позволяет реагировать к изменениям среды с большой скоростью и чувствительностью. Уже в упомянутой работе Грегора и Синской отмечается, что этот фактор имеет большое значение для селекции растений.

Самые важные из окружающих факторов, которые действуют на популяции растений и приводят к генетической адаптации — являются климатические факторы. Нэттонсон (1957) сказал, что климат решает, что именно можно культивировать ; тогда как почвы и другие факторы указывают, до какой степени можно осуществить климатические возможности. Итак, изучение сравнительной климатологии важно для введение растений. Такие исследования, благодаря Вавилову, недавно получили значительное развитие для того, чтобы орпеделить среду культурных растений количественно.

Знание макроклимата и микроклимата культурных растений должо быть основой будущего обширного понимания природы существенных изменений при перенесении культурных растений из одной среды в другую, так и для понимания сил, вызывающих адаптацию растений, а это, в свою очередь, служит важным фактором при определении распространения генетической изменчивости культурных растений на земном шаре.

Работы Вавилова по изучению всемирного распространения генетической изменчивости культурных растений положили начало новому этапу в введении растений, научные принципы которого основаны на широком понимании прикладной генетической] экологии культурных растений. А также Вавилов ыъдвинул новую теорию селекции растений.

Теории, которые сосредоточились на моногенических факторах в селекции растений (factorial concepts), исключая адаптивную полигеническую наследственность, привели к катастрофической потере генетической изменчивост, в так называемых Вавиловских центрах происхождения, разные виды культурных растений предельного единообразие заменяют разнообразные местные виды, и, при этом теряется ценное генетическое разнообразие. Такая потеря—катастрофична. Генетическое разнообразие в виде местно адаптивированных популярных форм растений (land-races) и родственных диких видов внутри центров происхождения растений является мировым ресурсом, не поддающимся оценке, и этот ресурс следует сознательно сохранять и использовать. Этого можно достать лишь путем генетических ресурсов, путем создания исследовательских институтов внутри центров происходения растений с целью сохранить на месте генетические ресурсы или сосредоточить сортаменты живущих культурных растений на основании подробного генетического потенциала района, путем установления защищенных районов для генетической консервации, путем развития новых селекционных приемов, где комплекс популяции и среды будут рассматриваться как динамическая система, а генетическая изменчивость как качество, которое належит сохранять.

Foreword

The interaction between quantitative genetic variability and natural selection is the central concern of studies in genecology (Bennett, 1964 : 52, 82). This interaction lies also at the core of all applied plant science. The practice and the advancement of agriculture are intimately interrelated with problems of genotype-environment and population-environment interaction. The results of plant breeding and artificial selection must in every case face the final arbitration of natural selection. " The question of environment and the interaction of the organism and the environment," says Vavilov (1951), " is one of the most important branches of breeding." Artificial selection cannot and may not ever completely imitate on a practicable scale the continuous action and minute discrimination of natural selection. This does not limit the extent of man's intervention in, nor his control over natural selection, however, for he may direct it by introducing to it genetic material of his own choice and cause it to act under conditions of his own design. This, indeed, has been implicit in the empirical patterns of human agricultural activity since the beginnings of plant cultivation.

In the course of the present century man's former empiricism has yielded to and been given expression and lucidity by an almost explosive development of scientific activity which,

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though unprecedented, seems to be but a modest portent of the future's possibilities. Research in applied plant science since the renaissance of the early decades of this century has expanded beyond the boundaries of any single comprehensive view. One of the most pressing of current world scientific problems is the organisation and classification of this knowledge so that it may be utilised. In many fields of scientific enquiry the time has come for a drawing together of data from scattered sources, and its integration, so that present advances may be assessed and future advances more effectively projected. The aim of this review is to play a very small part in this task. It seeks to bring together, in the light of an earlier discussion (Bennett, *loc. cit.* 81 *et seq.*), a scattered literature in genecology which has a bearing on problems of plant introduction and genetic conservation. Already Whyte (1946, 1960) has extensively reviewed the genotype-environment interaction at the level of the individual, and has drawn attention to many as yet unsolved problems of environmental response. Plant introduction and genetic conservation are pre-eminently concerned, however, with the genotype-environment interaction at the population level. This is the province of genecology. That genecology up until now has contributed so little to the urgent problems associated with the need for extended plant introduction, and particularly for genetic conservation, must be considered to be a consequence of the misdirection of much genecological effort into channels of academic and frequently sterile discussion.

The history and scope of plant introduction

For nine thousand years mankind has practised plant introduction unconsciously and without awareness of the consequences of his actions. Childe (1942, 1956) describes how the first introductions probably took place, and how the transition from food-gathering to food-producing, a transition which he has called the neolithic revolution, first set man upon the road from savagery to civilisation. There is evidence that among humble groups of peoples, " while men hunted, women—we must suppose—had collected among other edibles the seeds of wild grasses, ancestral to our wheat and barley." In a charming postscript to a recent account of the evolution and domestication of cultivated plants Whyte (1963) makes a " graceful acknowledgment " of the same fact. The ruderal character of the species of cultivated plants has been remarked upon by a number of writers, including Anderson (1949) and Müntzing (1959). Anderson has spoken of man's first crops as ' dung-heap super-weeds ' and describes how early man created suitable ecological niches in the disturbed habitats of his trash and dung heaps for the quick-growing plants he would later utilise as crops. He made these heaps " everywhere he halted and, as he unconsciously bred the quick-growing weeds capable of utilising soils high in nitrogen, he also unconsciously carried them about from place to place and gave them previously unparalleled opportunities to cross with others of their kind and thus build up into superweeds. From these weeds some of his crops were bred." Such midden plants would later be selected and eventually be deliberately sown in land prepared for the purpose. Cowgill (1960) presents evidence to support the view also proposed by Childe that the neolithic revolution realised such an increase in the carrying capacity of land and the productive capacity of human labour that it permitted the first great population expansion of the human species. As Mangelsdorf (1965) observes, " Man's rise from a state of savagery to one of civilisation began when he accidentally set in motion and himself became involved in the genetic forces of evolution acting upon animals and plants under domestication."

Despite their lack of conscious direction, mankind's early domestications were remarkably successful, at least as seen in retrospect. Harlan (1956) remarks that " neolithic man . . . succeeded in surveying the plant kingdom so thoroughly that nothing really significant has been added to the human diet since." Against this statement, however, certain facts must be balanced. From studies such as those of Burkill (1953), Braidwood (1952, 1958) and Helbaek (1959) on the origins of cultivated plants, it is clear that the period during which plants have been introduced into cultivation has been a long one, lasting for thousands of years. Simmonds (1962a) speaks of a " continuum of domestication " extending from the days of the earliest neolithic men and the Jarmo and Bat Cave settlements to the very recent domestication of pasture grasses and clovers in Europe and of rubber in south-east Asia. " Probably," Simmonds suggests, " few centuries passed without one or two useful plants being added to the list." Indeed, the period during which man has been taking wild plants into cultivation may be even longer since, says

Simmonds, " the process of finding earlier and earlier dates (for the beginnings of cultivation) may go on for a long time yet and still not reach finality. Suppose, for example, that the earliest crops of all were starchy roots domesticated in the lowland wet tropics of south-east Asia: what chance would there be of obtaining unambiguous evidence of their cultivation? The arid climates of Iraq and New Mexico may have an undue influence on our ideas of chronology."

During the first stages of plant introduction and domestication the spread of cultigens was limited by tribal boundaries, and tribes, isolated from others by cultural, ethnic and topographical factors, subsisted on a limited number of cultigens which in all likelihood differed from those of neighbouring tribes. Only at a later stage, with the collapse of tribal barriers due to war and trade, could the distribution of cultivated plants begin to attain sufficiently wide a spread for the considerable variety of formerly local cultigens to become apparent. The extent of this variety is only now beginning to be understood. Writing long before the completion of his world collections for the Institute of Plant Industry in Leningrad, Vavilov (1922) spoke of " 3,000 Jordanons of *Triticum vulgare* Vill., perfectly recognisable morphologically and physiologically." Later (1935, 1951) he said that " this number must be increased manyfold, and we cannot determine it even approximately." Kupcov (1965) describes a number of well-defined stages in the growth of crop plant distribution, and admirably demonstrates the association between ' cultural-ethnic ' boundaries and cultigen boundaries. Burkill (1953) modifies proposals by Vavilov with regard to the centres of origin of some important crops on the basis of historical evidence of this type. Kupcov's fourth and last stage of the spread of cultivated plants, their world-wide distribution, corresponds to the present day, when " humanity has established world trade relations." This is a recently attained condition, and it is therefore only recently that a world-wide appraisal of the variety of man's crops, and his ancestors' successes in plant introduction, has been possible.

Once certain useful plants were domesticated and basic needs satisfied, the stimulus to continued domestication will have been replaced by the necessity—and indeed, given the operation of selection upon such crops as were sown from seed retained from previous harvests, inevitability—of the improvement of those crops already domesticated. There is considerable evidence for the belief that, with the breakdown of tribal isolation and the improvement of cultigens by selection, the number of cultigens may have been reduced over long periods. Godwin (1965) presents evidence which suggests "that the Danish Iron Age people collected seeds from plant communities resembling a weedy fallow, but the results (of research) also make us aware of the possibility that some of the plants now regarded as weeds may at that time have been deliberately cultivated." At the same time, it has been noted frequently that, as Müntzing (1959) says, "some species are continually coming into, and others dropping out of, cultivation." There is a continuous process of replacement, which Schwanitz (1959) refers to when he remarks that "many ancient cultivated plants have disappeared, or they are disappearing, like *Triticum monococcum*, *Triticum dicoccum*, *Triticum spelta*, most of the plants which were employed for dyeing, etc. Plants which are beneficial to man have been found and improved and are given preference to the more ancient ones which are no longer cultivated and have disappeared. . . . The better varieties of today push aside the good ones of yesterday (and) will often be displaced in a short time by the still more improved forms of to-morrow." Simmonds (*loc. cit.*) also makes the same point.

The spectrum of plant domestication is unlikely to have been extended until needs arose which could not be satisfied by existing crops. Such needs have probably mainly been associated with changing social conditions in human society. The rise of trading cultures and population migrations associated with them led not only to the transfer of the established crops of the migrants to new environments, but also to the domestication of yet further species in less developed areas by the immigrants, which in turn have been transferred, often on a massive scale, from continent to continent. Frequently these new introductions have been technical crops such as rubber, which served to supply raw materials for processing by developing industrial cultures. This is a process which can be seen to be actively in operation at the present day, and there is no reason to believe that modern man's activities in the field of plant introduction will not rapidly surpass both neolithic and recent man's record, impressive though it has been.

Further, new and pressing world agricultural problems have emerged in recent decades. The rapid development of advanced technological communities has made possible a relative growth of population which is comparable to that which marked the period of the neolithic revolution, and which is world wide, but world food production and the organisation of human society are not yet designed to satisfy the increasing demands being made upon them. Starvation is still common in countries which are colonial, and in the rest of the world undernourishment is still more common. World hunger has been further aggravated by destructive, expensive and futile wars. Bernal (1958) observes that " the task of getting enough food . . . still remains the major task of humanity even in this scientific age." Man has been brought again, urgently, for the first time since the neolithic era, to the very practical necessity for a much increased food production and extensive plant introduction.

Although there has been some improvement in nutritional levels since the world food crisis of 1946 and 1947 (United Nations: Food and Agriculture Organisation, 1946a, 1946b), hunger is still the everyday experience of more than half of the world population. Not only is this shown in a disparity of per capita calorie intake between the developed and the undeveloped parts of the world, but it is even more evident from comparisons of diet quality. In Asia, the Near and Far East, and in Africa, for those countries for which statistics are available the proportion of diet protein which is of animal origin rarely exceeds 10 per cent of protein intake. Protein intake itself is mostly not much more than, and is frequently less than half of the protein intake of non-Mediterranean Europe (United Nations, 1963). There is, therefore, a recognisable need for a shift in the emphasis of some agricultural patterns in the direction of increased pastoral utilisation, or improved pastoral efficiency, as well as a need for a basic increase in total agricultural productivity. It may be noted in passing that in those countries of South America where livestock products play an important rôle in the economy are to be found the only populations in that continent with diets which show a tolerable adequacy and balance.

In the past, the settlement of new regions and continents has created the demand for new types of crop with desirable characteristics in the new environment. The migrations which led to the settlement of America and of Australia were accompanied by the transfer of large amounts of seed of crops which, with the passage of time and generations of selection, have yielded highly adapted varieties of considerable local and even international importance. In Australia immigrants found a continent which, according to Frankel (1957), "was devoid of an economic flora which would satisfy the needs and aspirations of civilised man. Every plant used in any of the more intensive types of land-use has come from beyond the sea." This circumstance led to an early recognition there of the importance of plant introduction. In future, the development of the desert and unproductive parts of the earth, as in the case of the present settlement and development of the Soviet Arctic and the Israeli Negev, will depend vitally upon similar broadly based plant introduction as in Australia, and will gain much from the rapidly growing experience of plant introduction at the present time and upon the strengthening of its scientific bases.

The importance of plant introduction does not cease with the establishment of viable human communities, but rather increases as society attains its highest development. There is a sequence in the process of domestication and introduction of crop plants, types of crop having their place in the sequence according to the sophistication of the needs which they satisfy. Burkill (1953) has applied this view to a consideration of the early stages of plant domestication, but it is equally applicable, suitably modified, to modern conditions. Basic food and fodder crops are followed by vegetable and fruit crops, and by decorative, aromatic and technical and medicinal crops for industrial processing. As stated at the United Nations Scientific Conference on the Conservation and Utilisation of Resources (UNSCCUR) in 1949 (United Nations, 1950), "there is a logical sequence in the development and application of new resources. New knowledge reveals new possibilities of satisfaction, creates new needs. Scientists must continue to search for new resources . . . in order to enrich our social environment."

Frankel (1957) describes plant introduction as "the transposition of a genetic entity from an environment to which it is attuned to one in which it is untried." He sees this to include techniques as chromosome transfer, such as the chromosome substitutions of Gerstel (1945), the segment transfers of Sears (1956) and the chromosome additions of Riley and Chapman (Chapman and Riley 1955, Riley 1956, Riley and Chapman 1958), and it may be extended to include the technical devices by means of which such transpositions may be effected, among them being gene and genome mutations and the techniques of embryo culture—the last of which has the effect of widening the range of genetic material available to the plant breeder (Harland 1955 ; Weiss 1961 ; Ivanovskaya 1962) and makes possible the introduction of a " vast new source of germplasm " into commercial crops. Using Frankel's definition, plant introduction may be extended to include even so widely employed a technique as the backcross, introduced into breeding practice by Harlan and Pope (1922) and extensively developed by Briggs (1930 ; Briggs and Allard 1953) and by Harland (1932, 1936), a technique which permits the maintenance of the genetic balance of the recurrent parent in the later generations of hybrids following wide crosses, and thus enables genes to be introduced—provided they fit in well enough to function at all—into the genetic background of another variety or species. None of these techniques will be further considered except to the extent that they may fall within the scope of genecological considerations, other than to note, with Gorz and Smith (1961) that " progress in the utilisation of diverse germ plasm depends not only upon the accumulation of genetic materials but also upon the development of new methods of utilising genetic mechanisms," including " radical approaches to the problem of crossing widely divergent strains (which) will greatly increase the available genetic variability."

If, making a distinction of convenience, we regard primary plant introduction as concerned with the introduction of new crops, and secondary plant introduction to be concerned with the introduction and utilisation of genetic variability for the improvement of existing crops, it is possible to observe that while much of plant introduction has to do with the latter, with the search for increased disease resistance and improved crop quality, much work is directed at the same time to primary introduction and its problems. Clearly, only primary introduction can serve to extend agriculture into the arid zones, and may also be of decisive importance in the establishment of tropical and sub-tropical pastures in the low-precipitation areas of Africa, Asia and Australia, and in the amelioration of high-altitude pastures on the Andean and Himalayan plateaus (Whyte, Nilsson-Leissner and Trumble 1953 ; Whyte, Moir and Cooper 1957 ; Crowder and Echeverri 1961).

Primary introduction may also be dictated by the necessity of social and economic changes in areas even where agricultural patterns are well developed. In India, where livestock density is the highest in the world, to the extent that there is semi-starvation among cattle and destructive over-grazing of grasslands (Whyte 1957), there is a need to consider plans for the cultivation of fodder crops under irrigation, which may be expected to lead to such alterations of the environment that it will be necessary to introduce and evaluate quite new fodder species. In Scotland, where the structure of agricultural practices appears to be deeply and unalterably imprinted upon social thinking, it may also be that primary introduction will be equally important in meeting the needs for a much-enhanced land-use even in so characteristic a field as her established grassland eco-systems, when the serious intent fully to exploit these resources as pasture rather than as playground emerges.

Primary plant introduction includes not only the transfer of crops to new environments " in which they are untried " but also the initial domestication of plants not previously cultivated by man. Whenever systematic investigations have been made, the domestication of wild plants has been shown to have great potential value : its possibilities are discussed at length in a series of publications by the Komarov Botanical Institute in Leningrad (Sokolov 1958, 1959, *inter alia*). Also in the USSR, Vavilov (1935, 1951) states, " It is possible to create entirely new plants out of old forms, as, for example, the alkaloid-free lupines developed in recent years. We have seen that an unlimited field for experiment is open in this direction in work with forage plants . . . . not only of plants utilised for grazing and for hay, but also of those grown for the grain. The Institute of Plant Industry has succeeded in discovering a lupine containing 21 per cent of fat and 30 per cent of protein, *i.e.* a lupine which equals the soy bean in food value and at the same time is adapted to light soils." The potential represented by wild species of legume, and their performance under different conditions of cultivation, has been recently surveyed by Mulyarchuk (1959), Miroshnichenko (1960), Shinkus (1960) and Sinskaya (1960). Garanina (1961) examines a collection of vetchlings from the wild and finds that some of these yield up to 33.6 per cent of protein in their seed, and 26 per cent as hay. Other recent surveys merely indicate the dimensions of a virtually untouched field of exploration. Hodge (1957) briefly discusses the need for a co-ordinated and concerted effort to discover new sources of utility in plants, noting that plants are a source of fibres, proteins, latex and waxes, vitamins, alkaloids and glucosides, pigments, tannins and oils, and refers also to the recent search for cortisone precursors in plants. Tukacov (1958) describes a survey of medicinal and aromatic plants in Yugoslavia following which more than 30 species from a total of 86 species collected have been successful in trial cultivations. Seelkopf, Rodriguez-Sanchez and Corothie (1959) describe a paper pulp derived from a mixture of sugar-cane bagasse and herbaceous plant fibres which gives a paper superior to that prepared from Canadian pine. Jones and Wolff (1961) examine 1,500 introductions, find them to yield a number of chemicals including long-chain organic acids and epoxidised oils, and report that 292 have an oil content of more than 20 per cent, 85 a protein content of more than 40 per cent and 189 a combined oil and protein content of more than 60 per cent. Even making allowance for rejections following more extensive and detailed assessment trials, such results are well within the 1 in 250 ratio of successful to unsuccessful introductions which Brock and Frankel (1963) regard as satisfactory, or the 1 in 360 which Barnard (1964) speaks of as the average ratio in North America and in Australia.

The task here, however, is to consider the forces which operate on and within plant populations under the conditions of cultivation to make them what they are, and to relate these forces to the circumstances of plant introduction. The transfer of a number of genotypes representing a sample of a population from the environment of which the population is the adaptive consequence (Turesson 1922, 1925; Stapledon 1928; Gregor 1930, 1938, 1944, 1946; Vavilov 1940, 1960; Clausen, Keck and Hiesey 1940, 1948; Sinskaya 1942, 1958, 1961, 1963; Clausen and Hiesey 1958; Stern 1964; Bennett 1964; Heslop-Harrison 1964) to another environment differing from the first to a greater or lesser degree will result in correspondingly larger or smaller changes in the nature and intensity of selection pressures acting on the sample. The effects of such changes may be considerable and may be variable in expression, depending on any of a number of factors, most important among them being the extent of climatic and agricultural dissimilarity and the latitude difference between the localities, and—in the crop—the nature of the breeding system and its influence on the degree of homozygosity or heterozygosity, the effectiveness of physiological and genetic homeostasis, and the magnitude of sampling error.

Selective forces and race formation

In equilibrium situations under natural conditions selection pressures acting upon a population are normally regarded as predominantly stabilising, but in the presence of long-term environmental trends a directional element will also be present (Mather 1953, 1955). Adaptive genetic responses to short-term environmental fluctuations will be avoided through the agency of physiological homeostasis and phenotypic plasticity (Mather 1953; Thoday 1953). Under cultivation the situation may differ considerably from this. The directional element in the selective forces will be greatly enhanced. However, this is so only with respect to those characters undergoing artificial selection, and will, nevertheless, continue to operate within the context of a broader stabilising selection. "The action of natural and artificial selection is quite often inseparable," states Vavilov (1940, 1960)—" It is often difficult to say what is the result of natural selection and what of artificial selection." He describes how, under the powerful selective action of the monsoon climate, beardless and short-bearded forms of barley evolved in which these characters are correlated with such features as grain size, economy in the use of structural substances, and accelerated development of the reproductive organs, and observes that "what is usually ascribed to the action of artificial selection is, to a considerable extent, the result of natural selection." Correlated responses to selection (Mather and Harrison 1949; Lerner 1954, 1958; Cooper and Edwards 1960; Falconer 1960; Cooper 1963; Edwards and Cooper 1963) may tend to obscure the discrete manifestation of responses attributable to one or other group of selective forces, and introduce an additional element of complexity to the analysis of the final products of selection.

Disruptive selection may also occur in at least the initial stages of domestication in outbreeding crops, as shown by Doggett (1965a), whose studies on sorghum show the effect of selection by man "operating in the direction of cultivated characters, and natural selection operating to hold the species in a form suited both to survival in the wild and to persistence as a weed of cultivation." "For plants which outcross at all freely," states the same writer (1965b), " the situation at the initiation of crop development must have been analogous to that in Thoday's disruptive selection experiments ; substantial gene flow between the improved and the unimproved plants will have occurred, becoming less as the plots became larger." In the case of the forage grasses, a crop in the initial stages of its domestication (Whyte 1958), a strong outbreeder, and extensively associated with its wild relatives, it would be surprising if a similar situation cannot be shown to exist, as indeed the evidence of introgression in grasses and other crops (Anderson 1949 ; Harlan 1951, 1961) indicates is likely, with considerable implications for man's understanding and effective direction of evolution in this group of crop plants.

" Compared with natural conditions," states Frankel (1959), " the ecosystem under domestication is partly controlled. Domestication reduces the infinite diversity of natural environments to simpler dimensions, it also changes the type of environments : in plants by cultivation, nutrition, irrigation, drainage, control of competition and parasites. . . . Control measures reduce not only the number of effective components of the environment, they tend to reduce the environmental variation within comparable areas." Schwanitz (1959) observes that " the amelioration of the external conditions by agriculture leads not only to a promotion of the phenotypes which under favourable conditions show a higher performance and bring higher yields, but reduces on the other side, more or less, the effectiveness of natural selection." At the same time, however, differences in environment under cultivation are sufficient to permit the emergence of a rich variety of what Gregor (1933) called ' agro-ecotypes,' to the extent that many scores of thousands of land-races have been collected and described, and countless more remain undiscovered, their genetic potential unexploited. The collection of the Institute of Plant Industry at Leningrad, established by Vavilov, now contains more than 160,000 living specimens of crop forms, excluding tree fruits (Sidorov 1962). Lehmann (1963) reports that more than 23,500 species are held in the Gatersleben collection. Mao (1959) lists more than 390,000 strains, varieties and cultivars which are held in other collections throughout the world.

Since the early work of Turesson and Gregor the occurrence of race formation within species of wild plants has been generally established. It is clear from the extent of the existing collections that evidence of the evolution of ecological races in crop plants is no less general. Stapledon (1928) and Gregor and Sansome (1927, 1930) describe heritable habitat modifications in populations of economically important grasses. Innumerable later studies have amply confirmed that every habitat factor, and every combination of habitat factors, calls forth adaptive and heritable responses in crop populations. Vavilov (1940, 1960) found that "data obtained in the study of world ecotypes of different crops which were sown under different conditions from the near polar region (67° 44′ N) to Transcaucasia, Central Asia and the Far East, have shown on the whole the persistence of ecotypes. . . . As shown by experiments and observations carried out over many years, the distinct ecotypic properties of the crops we studied manifested themselves graphically under field conditions everywhere in the USSR from the far south to the far north." Commenting on the summer and winter performances of European pasture grasses, Borrill (1960) notes that his observations "reveal the close genetical adaptation of the wild grasses to the seasonal fluctuations of climate in the places where they grow wild." This view is confirmed by other work on intra-specific races in grass species by McMillan (1959), Tisdale (1961, 1962), Knight (1962), Newell *et al.* (1962) and Cooper (1963, 1964, 1965). Chatterjee (1961), who studied net assimilation rates in ecotypes of *Festuca arundinacea* found inter-racial differences for this character. The present importance attached to physiological rather than morphological differences between ecotypic races was stressed by a number of early workers in genecology such as Turesson (1928) on transpiration rates, Beliakov (1930) on assimilation rates in barley, and by Langlet (1934) and Gregor and Horne (1935) and has considerable relevance to contemporary crop problems, but was long neglected by genecologists in favour of characters more easily measured in ecotypic studies, though in forestry, concern with the physiological properties of tree provenances is deeply rooted and has been investigated from the time of Kienitz in the late nineteenth century. Schülte (1963) describes inter-racial differences in the minimal germination temperature of seeds of *Lolium perenne*. Photo-periodic differences between races of alfalfa have been demonstrated by Barheine (1960), and Feofanova (1962) has shown the existence of differences in respiration rate between northern and southern races of legume crops. Land-races of red clover (*Trifolium pratense*) which have developed under the selective action of local environments described by Nüesch (1960) in Switzerland, and by Bingefors and Åkerberg (1961) in Central, Northern and Southern Sweden, show many distinct differences in useful physiological characters. Sotiriadhis (personal communication) maintains in Greece a collection of several hundred land-races of *Vicia sativa* which exhibit very marked inter-racial differences.

It has been noted often that, among the crops cultivated by man, the forage crops—grasses and legumes—are raised and managed under conditions less uniform than is the case with other cultivated groups, and this no doubt contributes in part to the considerable variation they exhibit. Racial differentiation occurs, however, scarcely to a lesser extent in other crops, as is indicated in fact by the extensive crop collections referred to above. Yamashita and Tanaka (1960) and Yamashita (1963) record large numbers of ecotypes of wheat species collected in the Mediterranean region. Nagata (1960, 1961a, 1961b) has examined in some detail the genecological differentiation of Japanese, Asian and American races of soya-bean. Jánossy (1962) describes the Hungarian collection of land-races of maize at Tapioszele which have been used as initial material in the creation of more than 800 new lines, many of which display superior yield and disease resistance characteristics, and the general importance of land-races in maize breeding programmes is discussed by Tavchar (1962). Arinshtein and Lyushinsky (1962) compare the qualities of a number of races of hemp and discuss their value as initial breeding material. Lysenko (1963) notes that in spring wheat-winter wheat conversions, the types produced resemble the existing locally adapted forms. In Ethiopia, Vaysière (1961) has reported a wide diversity of heritable local forms of *Coffea arabica*, and Anderson (1961), Écochard (1963) and Kuckuck (personal communication) comment upon the striking diversity of type in Ethiopian grain fields.

It is unnecessary to labour the point further that the evolution of adapted forms is a necessary consequence of any environmental fractionation, however slight. The problem is to develop methods which will enable more accurate and quantitative observations of its effects to be made. The point is to make use of natural selection and to direct it to man's ends. As Morley (1959) remarks—" Today, since serious and competent students of biology no longer debate the reality of natural selection, the demonstration that this character or that is subject to natural selection is of little interest. Therefore studies of the effects of natural selection on plants should attempt not only to demonstrate . . . but to evaluate selection intensities, to specify mechanisms of adaptation." He adds, " Further, we must consider the impact of that most important biotic factor, man, on the future evolution of plants. For man now controls, to an increasing degree, the distribution and abundance of plants over a very substantial part of the earth's surface." In the examination of crop plant adaptation, as in the case of natural populations, Morley (*loc. cit.*) states that " the materials studied may be of two kinds : (*a*) races (ecotypes, strains, cultivars, etc.) adapted to particular habitats; (*b*) populations, natural or artificial, in the process of becoming adapted to habitats to which they have not been long exposed. The examination of the adapted material may be termed the survey approach ; of the latter the experimental population approach."

The rate of adaptive change

Considerable evidence has been accumulated from studies of experimental populations—such as are represented, indeed, by almost any crop population—and it carries important implications for breeding and plant introduction techniques. In the past, discussions on the objectives and techniques of plant breeding have too often assumed that adaptive processes in crop populations are slow-acting, and for this reason are unlikely to offer striking short-term advantages as a breeding method. A great deal of work on experimental populations has indicated to the contrary that adaptive responses may be unexpectedly rapid.

The effect of natural selection on experimental populations of cultivated plants was first effectively demonstrated by Harlan and Martini (1938) who grew equal mixtures of eleven barley varieties for 13 years in ten different experimental centres in North America. Results which emerged from this work indicated that environmental differences between centres led to changes in the final composition of the mixtures which were considerable, and which differed from one centre to another. Many varieties failed to survive at any centre, or did so only in small amounts. At some centres one variety dominated the final mixture, at others several. A few varieties were successful in dominating the final mixture at more than one centre. Morley and Frankel (1959) and Morley *et. al.* (1962) describe a similar series of studies on experimental populations of *Trifolium subterraneum* in Australia. They ask (1962)—" (1) Will there be a clear indication of adaptation of strains to different localities? (2) In any locality will one strain predominate, or will there be a balanced mixture of strains? (3) Do changes in population composition take place rapidly, or are they gradual, implying low selection coefficients? (4) Are there some strains adapted to many environments, others to a narrow range of environments?" The results of this work indicate a close parallel with Harlan and Martini's conclusions, though proportions in the mixtures in certain populations fluctuated very much from year to year except under seasonally uniform environments. Most striking, however, was the evidence that " changes in population composition can take place very rapidly." Over the three years of the experiment some mixtures approached purity for one variety. Over a six-year period, Pal *et al.* (1960) showed similar significant changes to have occurred in mixed populations of wheat in India. McLennan, Greenshields and MacVicar (1960) report a pronounced shift in the proportions of seed yield from a constituted clover variety following only one generation of cultivation outside the region of adaptation. In a synthetic variety of red clover, Laude and Stanford (1960) observed that " flowering behaviour differed between first and second generation seed lots" produced in a locality differing by 8 degrees of latitude from the region of adaptation. Suneson, Ramage and Hoyle (1963), applying evolutionary techniques to barley mutation breeding, show significant evolutionary shifts in mutant-non-mutant mixtures in three to four years.

Observations on the rate of adaptive changes in single strain populations provide an even more impressive demonstration of the rapidity of evolutionary change. Although Kiesselbach and Keim (1921), Frankel (1954), Suneson (1956, 1963), Bal, Suneson and Ramage (1959), Simmonds (1962b) and Suneson and Weibe (1962) describe the evolution of distinct races in various crops in from 12 to 100 generations, other work shows distinct genetic shifts in much shorter periods. Sylvén (1937) found measurable adaptation to occur in a number of herbage species in Sweden within a few years, an experience which led to the development of natural selection breeding in forage crops at Svalöf, as described by Umaerus and Åkerberg (1963). Smith (1955, 1958) observed that " distinct changes occurred in the very winter-hardy Narragansett and Vernal varieties (of alfalfa) following one generation of seed increase in areas considerably south and also north of the production area of the original seed." Nagamatsu (1962) examined 7 varieties of rape grown for 10 years at a number of centres in Japan and found these " continuing to differentiate to new ecotypes, reconstructing their genetic constitutions to adapt to their new habitats," and he emphasises that the fact should be remembered that varieties " are not static but dynamic." The remark made by Huxley (1942) comes to mind, in which he refers to the maintenance, despite extensive gene-flow, of ecotypic distinctness over very short clines in the work of Gregor (1938, 1939). These findings " indicate that the clines *are produced anew in each generation* * by selection from among a wide range of ecotypes present in the species—an important general conclusion." The similar maintenance of ecotypic identity within clines of interpollinating populations of birch, described by Stern (1965) is equally significant, and Kuckuck has drawn the attention of the writer to similar evidence of the effectiveness of natural selection and the rapidity of its action in the work of Baur (1932) with *Antirrhinum* ecotypes growing at different altitudes. Extreme uniformity characterised populations growing at 1000 m. despite considerable gene-flow from lower and more variable populations effected by insect swarms. Seed samples, when grown in an experimental garden, exhibited wide genetic diversity. The uniformity of these 1000 m. populations may thus be attributed to the action of selection, being " produced anew in each generation."

Much interest in genetic shift in crop populations has stemmed from the concern of breeders to maintain purity of type in their stocks during multiplication, particularly when this stage is carried out in regions or under conditions to which the crop is not adapted. It is unfortunate that the knowledge of the rapidity of adaptive changes in crops that has been accumulated in this way, and from work on experimental populations, has not been applied more extensively in other fields at present dominated by factorial concepts of inheritance, such as disease-resistance breeding.

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* My italics. E.B.

Scottish Pl. Breed. St. Rec., 1965, pp. 27-113

Variability, adaptive change and the co-adapted gene-complex

In a discussion on variability in crop plants which must be considered as a major contribution to thinking on the subject, Simmonds (1962b) points to a number of possible reasons for this state of affairs. Using the phrase 'genetic base' as a "convenient collective term for the immediately available materials of adaptability," he shows that "the narrowly based crop responds slowly, if at all, to selection and is liable to crises brought on by its inability to adapt quickly to changing circumstances." Simmonds notes that adaptability, or the capacity for genetic response to selection, depends upon the provision of variability. "As has often been pointed out," he states, "there is a conflict between adaptation and adaptability, for closeness of the former implies restriction of the latter," and he comments that "advanced agricultures are characterised by a great increase in adaptation, associated with a decline of locally adapted variability. . . . In advanced crops the incorporation of new locally adapted variability is, in practice, negligible for it is rigorously culled out." "Often the adverse effects of a narrow genetic base," remarks Simmonds, "will be apparent only in a slow response to selection and may excite no comment beyond the observation that the breeders and varieties of the past were wonderfully good or perhaps that the upper limits of performance of the crops have been reached."

Conversely, rapidity of adaptive change depends on variability. Evans, Davies and Charles (1960) consider the problem of genetic shift in stocks of some herbage species during multiplication, and find that "selection pressures during multiplication are entirely different" from those for which the crop has been selected, and "during three or four generations might considerably change the nature of the variety." They add that "variability within the variety may have a very marked influence on its stability." Hutchinson (1940) observes that "there can be no response to selection unless the material is genetically variable. The relation of variability to rate of change under selection, and the effect of selection in reducing variability are therefore fundamental factors in breeding theory."

Variability itself depends upon a number of genetic factors, among them the nature of the breeding system. The view that "in the majority of cases outbreeders are significantly more variable" is well documented by Stebbins (1950, 1957) and Baker (1953). Gregor and Lang (1950) demonstrate that differences in sample variance between populations of *Plantago maritima* can be correlated with breeding behaviour. Cooper (1951) finds that there is less release of variability under selection from inbred than from outbred species of the same genus. The situation may be more complex, however, than the simple view might indicate.

Using one of the barley composite crosses—Composite Cross V—as a predominantly self-pollinating closed population, Jain and Allard (1960) find evidence for the occurrence of a "low incidence of intercrossing among the many diverse genotypes contained in the population" and the persistence of a degree of heterozygosity which is actively maintained by heterozygote advantage. The discovery that a degree of hybridity is maintained in these experimental inbreeding populations is reinforced and given a more general relevance by the further discovery by Imam and Allard (1965) that between 1 and 12 per cent of outcrossing occurs in the natural populations of *Avena fatua* examined by these workers. Heterozygote advantage is seen as a factor contributing to this effect, and enhancing it appreciably. Baker (1959) makes the point that there is probably no inbreeder which does not ever occasionally outbreed. Simmonds (1962b) states that such a situation is probably particularly conducive to crop evolution. "Perhaps," he says, "the most favourable situation for the evolution and detection of newly evolved variability would be the casually outpollinated inbreeder."

In experimental work on variability and crop adaptation "most of the adaptive characters which have been investigated genetically," states Cooper (1965), "show continuous variation and, as might be expected, prove to be polygenically controlled," or are—to use Sumner's (1930) phrase—"due to the action of a large number of synergistic genes of individually small effect."

Polygenic inheritance possesses a number of distinctive features. On the one hand, polygenic variability reacts with selection in such a way that samples from a population exhibit variance for any given adaptive character, and its class frequencies present a more or less normal distribution in the sample. Variation in the intensity of stabilising selection has the effect of increasing or decreasing the range of distribution for values of the characters upon which selection is operating, and for such other characters as show correlated responses. Changes in the type of selection acting on the sample will affect the distribution by imparting a skew if selection is directional, or bimodality if disruptive. It is a consequence of continuous variability that the sensitive and rapid responses to small habitat differences that are observed in crop populations take place, such that—as Cooper (1965) remarks—even "different farming systems can impose their own selective effects on the primary climatic adaptation" of crops.

On the other hand, polygenic inheritance permits the storage of enormous reserves of variability, as discussed in some detail by Mayr (1963). Wright (1965) points out that "ten alleles at each of 100 loci provide the potentiality for 10^{100} different homozygous genotypes." Heterozygosity for more or less numerous alleles and gene complexes, for which Sokal (1962) remarks that "recent work indicates near-universality," increases potential variability, and also permits its retention in the genotype in a concealed or latent form. Further, the work of Dobzhansky and many others (summarised in Dobzhansky 1955, 1959) leading to the balance concept of the genotype, and of Chetverikov (1926), Harland (1932, 1936), Mather (1953) and others on the co-adaptation of the gene-complexes which constitute the genotype—the genotype milieu of Chetverikov—shows that adaptive response, the reaction between polygenic variability and selection, depends "on the fitting together of favourable complexes from genes which cannot in themselves be described as either favourable or unfavourable" (Wright 1955). Lerner (1958) defines some of the characteristics of polygenic inheritance, among them that "the phenotypic effects of substitution at different loci are interchangeable, in the sense that identical phenotypes may be produced by a large variety of genotypes, even in the absence of dominance, epistasis, and environmental differences," that "the phenotypic expression of polygenic characters is subject to considerable modification by differences in the intangible environment to which the members of a given population are exposed," and that "most populations carry great reserves of hereditary variability with respect to polygenically inherited traits; that is, they are genetically heterogeneous."

When Wright (1965) comments upon the very large number of genotypes made available by the polygenic organisation of the genotype—a number greater than the calculated number of protons in the universe, even in the simple model he describes, and so truly astronomical !—he observes that among them " there may be expected to be an enormous number of favourable recombinants of unfavourable mutations." " The task of the breeder," concludes Dobzhansky (1959), " is more intricate than the classical hypothesis would lead us to believe. It is not isolation of some one genotype which engenders superior qualities in its carriers. It is rather the construction of a new balanced gene pool of the population in such a way that the processes of Mendelian segregation and recombination usually yield highly productive genotypes and phenotypes." Bodmer and Parsons (1962) similarly see the breeders' problem as " to achieve that rearrangement of linked balanced complexes which best suits his selection aims," and they continue—" It is disconcerting that standard textbooks on quantitative genetics make practically no mention of the significance of linkage and interacting polygenic complexes, and assess the results of selection by a measure of response based on heritability, which is completely ineffective in the face of the disruption of polygenic complexes by recombination."

At the level of the genotype—the level at which Bodmer and Parsons concentrate their discussion—polygenic variability is controlled by a balance between factors permitting genetic recombination and factors tending to restrict it, within the limits of the breeding system, and these factors contribute in large part to what Darlington (1939, 1956) calls the genetic system. Darlington observes that the history of the evolution of genetic systems is the history of the control of recombination, and has shown that a number of components contribute to this control, among them chiasma frequency and chromosome number. These components are expressed in the ' recombination index,' and this reflects the degree of stability or variability in the gene pool, that is, its degree of adaptation on the one hand, or of adaptability on the other. Thoday (1953) expresses the balance in this way : " fitness depends not only on the adaptation to present environment, but adaptation to changes in that environment. Short-term survival depends upon adaptation and stability ; long-term survival upon short-term survival and upon variability, the capacity to change." Grant (1958) enumerates the factors controlling recombination, remarking that " one of the main functions of the apparatus of heredity and variation is the striking of a balance between constancy and variability in reproduction."

Bodmer and Parsons (1962) point out that "cytological phenomena must be considered when discussing the over-all fitness of a species." Linkage conserves adapted gene-complexes, and Mather (1953) indicates that chiasma frequency is itself subject to selective adjustment. Similarly, the work of Rees (1955, 1957), Rees and Thompson (1956, 1958) and Rees and Naylor (1960) and of the Cambridge team of Riley (1956), Riley and Chapman (1958) and Kimber (1961) points to the importance of genetic control of chromosome, or genotype, behaviour. Adapted gene-complexes may also be protected from disruption by structural heterozygosity for chromosome interchanges and inversions as shown by Mather (1956), Carson (1958, 1959), Grant (1958), White (1962) and the extensive work of the Dobzhansky school, and may be regarded as functioning as 'super-genes.' Mather (1953) suggests that such super-genes could be built up under the action of selection pressures, and points to the importance of linkage and the control of recombination in serving to conserve or modify these. Hybridisation may also serve, according to Stebbins (1956, 1959), as a mechanism permitting a drastic increase in recombination leading to new gene combinations, some of which may be stabilised by the incidence of polyploidy. For outbreeders, the problem, Baker (1953) points out, "is how to retain adaptive stability. . . . Adaptive success goes to those outbreeders, therefore, with reduced recombination, thus retaining heterozygosity while restricting variation." Grant (1958) shows, conversely, that there is a correlation between inbreeding and a high chiasma frequency, so that as a result of rare outcrosses "a self-pollinated species will release its variability in periodic bursts alternating with generations when little or no recombination occurs."

Finally, under domestication, the very dimensions of recombination undergo a major change. "Under domestication," states Frankel (1959), "recombination is broadened and, to a degree, directed. Human migration and, recently, systematic collection of genotypes throughout the world have greatly increased the opportunities for recombination in cultivated organisms. . . . At the same time the choice of parents entering into recombination is directed with ever-increasing precision and significance." The effects of this may be seen in the extensive production of new varieties originating to a greater or lesser extent from introduced material, and the consequent release of variability may particularly be seen in transgressive segregation, such as reported by Govorov (Vavilov 1951) and Clausen (1952, 1953, 1958), *inter alia*, following the hybridisation of distantly related genotypes. The most striking example of the release of variability following directed recombination of this type is to be found in the composite cross populations of barley which are reported by Harlan, Martini and Stevens (1940), Harlan (1956), Suneson (1956), Suneson and Weibe (1962) and others. Here the release of variability has been described as explosive, and there is also evidence of mutagenic interaction between mutually unadapted or unaccustomed genotypes. The exploitation of the considerable genetic variability made available in this way will depend, however, on the success of measures on an international scale to conserve genetic resources and to explore them adequately, and upon the creation of reservoirs of variability more comprehensive, and more effective, than the present type of breeders' collections. Simmonds describes these as a wasting asset, neither effectively preserving nor exploiting variability. He suggests that the composite cross populations themselves may be utilised as " mass reservoirs of variability."

Effects of Environmental change

It has already been noted that polygenic inheritance enables the production of similar phenotypes by different genotypes, composed of genes " which cannot be described in themselves as either favourable or unfavourable." If, however, the selection pressures acting on a population of uniform phenotype are altered by the transfer of the population from one environment to another the different genotypes composing the population may be distinguished and separated from one another. Cooper (1965) points out that " selection in a particular environment is of necessity phenotypic only, and if an adapted population is transferred to a different environment considerable genetic variation between individuals may be revealed." He refers to experiments with Irish perennial rye-grass " which flowers very uniformly after an autumn sowing, (but) reveals a wide range of heading and non-heading types when sown in early spring, and lines differing greatly in inductive requirement

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can be selected " (Cooper 1960). Considerable evidence of this effect is presented in the work of Cooper and his associates (Cooper 1951, 1954, 1959, 1960; Peterson, Cooper and Vose 1958; Harrington 1965) and certain aspects of its practical significance are discussed by them. Peterson, Cooper and Vose, for example, describe a segregant of a rye-grass variety which remained completely vegetative in high-temperature, short-day conditions differing from the environment in which the variety originated, and suggest that the valuable objective of completely vegetative pasture grasses might be consciously attained by breeding in one climate for utilisation in another. Hertzsch *et al.* (1964) make a similar suggestion. Harrington (*loc. cit.*) draws attention to the importance of the fact to plant introduction that " population samples may show unexpected morphological and physiological traits not evidenced in their original habitat " when transferred from one region to another.

It is necessary to distinguish several types of environmental effect upon population samples, however, as pointed out by Heslop-Harrison (1959), Sinskaya (1958, 1960, 1961, 1963) and Cooper (*loc. cit.*). We may describe the release by environmental change of a genotypic diversity concealed in the native environment under the cover of a uniform phenotype as environmental segregation, and distinguish it from enhanced variation which is a result of the collapse of homeostatic mechanisms, though a distinction might not easily be demonstrated in the imaginable circumstances of environmental segregation in populations heterozygous for factors controlling homeostasis.

The effect of changes in the external environment in altering the phenotypic expression of genotypes is well known and has been described by many genecologists. Hiesey (1953), Clausen and Hiesey (1958) and Watson and Clausen (1961) have particularly examined this effect. Clausen (1953) suggests that " some genes express themselves only in certain environments, so that both the morphological and especially the physiological differences (between ecological races) are regulated by an even more intricate system of genes than the analysis in one environment would suggest. . . . It is obvious that the interrelationships between the genes that regulate any one character in wild populations are very intricate, that the expression of any one genotype may change with the environment, and that apparently not all of the genes of a biotype are able to express themselves in any one environment but that new environments may call other genes into action." Knight (1954) describes environmentally correlated changes in the expressivity of certain genes in cotton as does Druger (1962) in *Drosophila*. Hédin (1961) remarks that many crops having a wide climatic distribution may develop differently in different parts of their range, and quotes the case of crops which are grown in Brittany for forage, but in Rumania are best grown as oil seed crops. Vavilov (1940, 1960) notes that the influence of environmental conditions upon phenotypic changes is particularly marked latitudinally as a photo-periodic response, finding that there was evidence in his experiments of a "sharp increase in the height and foliation of plants, as we moved north within the boundaries of the European part of the Soviet Union."

"In adapted genotypes," states Langridge (1963), in a discussion on the genetic basis of climatic response, "single genes which govern the organism's response to particular climatic components have often been recognised. In general, however, the genetic basis of an organism's adaptation to climate rests on a co-ordination of very many, if not all, of the constituent genes, the relationship between genotype and phenotype being mediated by many processes collectively comprising the epigenetic system"; that is, climatic response is polygenic as a general rule. Cooper (1954, 1963) has shown experimentally that "even where a character shows an 'all or nothing' response, the underlying genetic control proves to be based on a continuous distribution, truncated by a threshold which permits the expression of the character." He refers to such variation as 'quasi-continuous' and describes how environmental segregation into flowering and non-flowering types in rye-grass ('all or nothing') as a result of sowing in the spring instead of the autumn is dependent upon the degree of induction given to the segregating progeny (underlying continuous variation). In general, says Mather (1953), major genes are of some importance if they relate to physical environmental factors but, "in all the cases so far examined it has been shown that the adjustment of the types depends on, and has been achieved by, balancing of the rest of the genotype." Hutchinson (1959, 1965) notes that in one sense major genes have been instrumental in the attainment of important evolutionary changes in crops, referring to the genes for spinnable lint in cotton, brittle rachis as against tough rachis in the cereals, and the dwarfing gene in the sorghums—but, he continues, " a major change in any important character is rarely adequate in itself. . . . whatever major changes may arise from simple gene differences, the establishment of a new and superior stock is unlikely to occur unless the minor gene constitution of the material is also subjected to selection." Clear-cut effects due to monogenic differences may therefore be modified and obscured by changes in the internal, the genetic, environment. Cooper's (1963) quasi-continuous variation is such an effect.

Apart from the effect of changes in the external or the internal, genetic, environment leading to changes in phenotypic expression, environmental change may also result in the manifestation of increased variance within transferred samples of populations, which may be due either to environmental segregation or to a breakdown of homeostatic control in the individuals of the sample. Environmental segregation has been widely observed, particularly—though not exclusively—when changes of latitude are involved. Olmsted (1944) examined a number of latitudinal races of the forage grass, *Bouteloua curtipendula*, and discovered that considerable intra-strain genetic diversity became evident in material which had been transferred over a range of 17 degrees of latitude. Lawrence (1945) demonstrated environmental segregation in the grass *Deschampsia caespitosa*. When samples of this grass were transferred from latitudes 56°N, 60°N and 68°N to latitude 38°N, populations which were uniformly flowering and non-viviparous in their native habitat segregated into a number of types, ranging from strongly viviparous to completely non-flowering types of the sort later reported by Peterson, Cooper and Vose and referred to above (p. 55). Ludwig, Barrales and Steppler (1953) find environmental segregation for light intensity responses to take place when *Trifolium pratense* is transferred from native long-day to short-day conditions. Varieties of swede- and turnip-rape which flower uniformly when sown in their normal season, are shown by Fábry (1963) to segregate into several biotypes under the unaccustomed environmental conditions which follow sowing at a series of dates commencing in early spring.

Differences in cultivation methods are particularly effective in producing environmental segregation. Examining heterogeneity in natural and cultivated plant populations, Sinskaya

(1960b, 1961a, 1961b, 1963), Sinskaya and Borkovskaya (1960) and Sinskaya and Vorob'eva (1961) make use of spaced plant sowings and unusual vernalisation and sowing conditions to impose environmental changes on experimental populations and find that " all the agricultural plants studied have proved to be complex populations in respect of the biotypes they comprise." " In the region where a variety is formed," states Sinskaya (1958), " the heterogeneity of the population composition appears only within definite and narrow limits. . . . Thus the environmental complex of regional conditions where the given ecotype or cultivar (variety) has been created, appears stabilising for the given variety." However, " the transferring of the cultivar (varietal) population or the ecotype into extremely different conditions," she continues, " often leads to its completeness being broken with a consequent loss of uniformity " into its component biotypes, or ' ecoelements,' which are defined (Sinskaya 1942, 1963) as " groups of biotypes comprising plants possessing several adaptive features more or less firmly fixed hereditarily." Ecoelements are regarded by Sinskaya as the lowest order of adaptation, and she sees them as the consequence of positively correlated responses to selection of groups of characters selected together " either because they are all adaptive or are genetically linked," normally arising by selection, though cases are known of the mutational origin of groups of adaptive features characteristic of ecoelements. The evolution of ecoelements may be compared with the origin of what Darlington and Mather (1949) call ' genetic inertia ' which is " due to the integration, the building up of an adaptive system providing the very properties which have been responsible for its past success," and with the ' cohesion ' of Anderson (1949), Clausen (1958), Clausen and Hiesey (1960) and Hiesey (1964). When, however, " the complex of environmental factors is very unfavourable to all, or to the great majority of the biotypes of the population," Sinskaya (1958) points out, " visible differences among the components of a population usually diminish."

Kuckuck (1959, 1962) observes that wheat crops grown under irrigation in Iran show a striking diversity of types, while under dry farming conditions populations are uniform. This effect is considerable and distinctive even when climatic conditions are identical—to quote Kuckuck, " Während die Population unter Bewässerung sich fast immer durch eine auffallende

Vielförmigkeit von Typen auszeichnet, sind die dry-farming-Populationen auffallend einförmig. . . . Die Selektionswirkung durch die vom Menschen angewandte Anbaumethode ist bei sonst gleichen klimatischen Bedingungen sehr gross und unterschiedlich." The genetic uniformity of the dry farming populations is confirmed by growing the progeny of individual plants selected from such populations under irrigation, which then show a uniformity similar to that of the parent population. Kuckuck reports that crop yields under dry farming conditions are—with few exceptions—poor, and crops have often failed completely, and it would appear that the intense selection pressures operating under dry-farming conditions may impose not only phenotypic but also a degree of genetic uniformity, which may only be distinguished by progeny testing, while the variation evinced under irrigation regimes reflects reduced selection pressures. Schwanitz (1959) notes that " variability becomes reduced very much if cultivated plants escape from cultivation and become wild again. . . . Increase in natural selection (upon tomato escapes) has the same effect in very different regions ; the size of the fruits of the cultivated plants and their variability vanishes rather quickly and uniform types arise which are very similar to those of wild plants."

The release of variability which follows the reduction of selection pressures is described by Hutchinson (1958) who refers to the introduction of eucalypts into East Africa, and notes that when seedlings are raised under favourable nursery conditions " a range of diversity is evident in such plantations that could not be expected to persist, even for a generation, in natural woodland." Non-brittle mutants of barley were, says Zohary (1960), " the crucial step, and most likely the starting step in the process of domestication " in this crop ; he points out that the change " to harvesting and threshing by man corresponds in fact to a ' jump ' into a new adaptive range. This done, the whole ensemble of characters associated with fruit dissemination became functionless and lost its adaptive value. It is the relaxation of this pressure that facilitated, to a large extent, the burst of a wide range of ear and spikelet variations encountered among cultivated barley lines." " It appears," states Hutchinson (*loc. cit.*), " that uniformity is a function not so much of the genotype as of the selection pressure of the environment."

In a discussion on some of the practical consequences of environmental segregation Gregor (1956b) describes results he obtained when plant populations were transferred from their native habitat to the environment of the experimental garden: such samples " are often found to possess much higher genetic variances than is suggested by the character expressions appearing on the phenotypic surface in the original habitats." Linking these results with the work of Waddington (1952—but see 1957 for full discussion) on genetic assimilation, Gregor suggests that it is possible to select for the capacity to respond to a novel environment since—quoting Waddington—" selection will not act solely on fortuitous variants resembling the form produced by the environment, but on the sensitivity of normal individuals to the environmental stimulus." Gregor then makes the point that published information regarding strain performances " implies a knowledge of varietal response to agronomic environments that is seldom if ever realised," and suggests that a distinction should be drawn between ' potentiality ' and ' agronomic ' crop trials. Gamble (1963) discusses evidence of genotype-environment interactions in maize trials, and also concludes that there is a " need for many tests over a series of environments when studying quantitative variability in corn."

Sinskaya (1958) distinguishes environmental effects arising from environmental segregation from those which are caused by a collapse of homeostatic mechanisms. She describes a case in which the oil plant, *Perilla ocymoides*, grown in short-day conditions as seedlings for 15 to 20 days and then transferred to either natural or 24-hour photoperiods, " shows a very striking picture of a fabulous disintegration into several morphobiological types . . . beyond the limits of our present-day knowledge of the variability of the species or even family." " Such a mode of disintegration," she says, " should be distinguished from the state of falling into ecoelements." In a later publication (1963) she again draws attention to the need for such a distinction. " Changes in plants grown in unusual habitats may result from interference with homeostasis; it may also result from latent heterozygosity." Sinskaya restricts the use of the term ' disintegration ' to the latter type of change, that is, to the environmental segregation of populations " into the ecoelements which are the initial points or nodes of natural selection activity." She makes use of ' disintegration ' in practice to ' analyse ' cultivar populations into their ecoelements, which may then be employed in breeding programmes. Dolgushin (1963) has also made use of disintegration in this way. The term 'forced selection' is applied to a similar situation by Waddington (1957) who suggests that "one might apply environmental stress for the purpose of forcing into expression genetic factors which, although present in the population remain imperceptible under normal circumstances and therefore inaccessible to selective pressures."

It is possible that enhanced variance exhibited in the clonal transplant experiments of Hiesey (1953), Clausen and Hiesey (1958b) and in the apomictic lines in the *Poa* trials described by Watson and Clausen (1961) and Watson (personal communication) is due to a greater or lesser degree of interference with homeostasis, rather than to the suggestion by Cooper (1963) that "different sets of genes were operating in the different environments." Such a mechanism may be involved in the modification of phenotypic expression under the different selection pressures of different environments, but it can hardly account for increased intra-clonal variance in any one environment. Extreme homeostatic collapse in a number of varieties of rice introduced into Italy is described by Piacco (1960), who reports that some were so seriously disturbed that they failed to reach maturity, and in others maturity dates and yields were seriously retarded. Heslop-Harrison (1959) describes the breakdown of homeostasis in a fibre hemp (*Cannabis sativa*) following changes of photo-period. The same writer later discusses the increased phenotypic variance which indicates interference with homeostatic control, which occurs "when genotypes are carried so far out of their norms that developmental regulation is disrupted." "Here," he says, "it is not a question of the exposure of genetical heterogeneity —the effect may be seen in what is effectively a pure line— but rather the amplification to a phenotypically obtrusive scale of developmental noise" (Heslop-Harrison 1964). Langridge (1963) reviews some recent experimental evidence of homeostasis in a discussion of the genetic basis of climatic response, and notes that "there are considerable differences in homeostatic efficiency with respect to temperature in homozygous genotypes of different races." In the future the investigation of the genecology of homeostasis and related characters may do much to clarify the relationship between phenotypic plasticity and the genetic adaptation of populations on the one hand, and homeostasis on the other, by explaining the extent to which the ability of some plants endogenously to stabilise their phenotypic expression in varying environments to a greater degree than others affects the capacity of populations to respond adaptively to externally imposed environmental changes. The practical implications for plant introduction are obvious.

There is some evidence that homeostasis is dependent upon heterozygosity. Haskell (1952) showed that maize hybrids exhibit more stable responses to environmental adversities than inbreds. Increased variance which has been observed in diplo-haploids of maize and iso-genic lines of other species may also be due to reduced homeostatic efficiency, though there is no direct evidence at present to indicate that this may not also be due to recombinational (p. 52) or to mutational (p. 72) effects in the newly constructed genotype. Robertson and Reeve (1952) showed that environmentally induced variance in populations of *Drosophila melanogaster* frequently decreased as heterozygosity increased. Dobzhansky and Wallace (1953) found that " heterozygotes (of four species of *Drosophila*) are more uniformly successful in a variety of environments than are homozygotes ; this suggests that the heterozygotes are better able than homozygotes to cope with these different environments and to maintain their internal milieu in functional order." Mather (1956) also believes that homozygotes are " less able to withstand the vagaries of environmental upset and developmental accident." Allard (1961) finds that " genetic diversity consistently endowed populations (of lima beans) with stability, more or less irrespective of the number and characteristics of the components involved." Waddington (1957), however, queries the simplicity of these views, believing that the three concepts of fitness, homeostasis and homeorhesis have been to some extent confused and need " to be grasped separately before their interrelationships can be discussed with clarity," though he also indicates that semantic differences exist in the use of the term homeostasis. It is still true, as Langridge (1963) observes, that the concepts which have emerged from recent work—heterosis, homeostasis, flexibility, coadaptation, genetic assimilation and epigenesis—" lack exactness of definition, are difficult to test experimentally, and are largely incapable of interpretation in terms of current information on gene behaviour." With this challenging statement of the situation, however negative it may at first appear, we must for the moment leave the discussion.

Climate and environment

Although it is true that minor local and agricultural differences sufficiently alter selection pressures acting upon crop populations to effect significant changes in their genetic constitution, the most important environmental factor in the complex of selective forces acting upon both crop plants and crop populations leading to the evolution of locally adapted races or ecotypes is climate. Climate itself is a composite of a number of distinct components. Discussing the determinants of plant distribution, Good (1931, 1953) stresses that edaphic and biotic factors in the environment are secondary to climate since they are themselves also in large part the consequences of climate. Nuttonson (1957) states, "It has long been recognised that climate decides what can be cultivated, whereas soils indicate merely to what extent climatic opportunities can be realised. . . . It is rather common knowledge that temperature conditions and the complex accumulations of temperature, duration of daylight, intensity of radiation in certain special regions, and soil moisture are among the major factors in plant growth and plant yields." Wilsie (1962) devotes the larger part of his treatment of crop adaptation and distribution to a consideration of climatic components. The use of vegetational data in the construction of so many climatological classifications—such as those of Köppen (1923) and Trewartha's (1954) modification of it, the systems of Thornthwaite (1948), of Emberger (1956) and of others surveyed and discussed by Whyte, Moir and Cooper (1959)—also serves to confirm the importance of the climatic components of the crop-environment system.

Some effects of environmental, and particularly climatic, change upon crops have been considered sufficiently to indicate that their genetic consequences may be considerable. For this reason, plant introduction in the past has been concerned with the problem of assessing climatic similarities so as to minimise the consequences of changes of environment following crop transfer, and work in plant exploration and collection as well as in plant introduction must still, as Whyte (1960) remarks, "consider the environmental conditions of the sites of collection and introduction." In selecting suitable plant material for introduction, states Hartley (1961, 1963), " the main basis of selection must be the knowledge that the plants have been able to develop and reproduce satisfactorily under comparable conditions elsewhere. Thus the comparison of environments, especially in regions which are widely separated geographically, is an important aspect of pasture plant introduction." Leon (1961, 1963) discusses plant introduction in Latin America and remarks that the rules which have been proposed to determine optimum conditions for introduced plants in their new areas are based on the hypothesis that a species has definite requirements, particularly of climate, analogous to those which exist in its centre of origin, which may be defined in terms of temperature, precipitation, etc. It is evident, however, from the multiplicity of proposals which have been made for the determination of climatic analogy that the problem remains, " *How* are climates to be compared ? "

One approach to the problem has concentrated on the comparison of those physical environmental data which are considered to affect crop behaviour and distribution. Hanson (1949) points out, however, in a short but excellent review of work on ' agro-climatic analogues,' that " one of the major difficulties in making such climatic classifications is the selection from a wide variety of environmental factors of those that exert the greatest influence upon the important plants." Vavilov (1935, 1951) observes, " In selecting species and varieties for the U.S.S.R. one has to take into account the climatic conditions under which the plants introduced were growing and, whenever possible, to select varieties from regions more or less similar climatically to our country. . . . However, it must be borne in mind that the question of climatic analogy cannot be disposed of as readily as it has been in the recent past. A study of the distribution of plants shows the complex nature of this process." Vavilov (1940, 1960) sets out a classification of world ' agro-ecological regions ' based upon climatic statistics from a number of centres within each region, including a month by month record of precipitation, average temperature, and—as far as data are available—absolute minimum temperature, number of frost-free days, number of days above 5° C, etc. He also (1940) describes the preparation of an ' ecological passport ' for crop varieties, based upon " ' geographical sowings ' in different regions, studying the same varieties (collected from all parts of the world) under different conditions, examining their reaction to different parasites and to various environmental conditions." From his surveys of the world resources of cereals, leguminous seed crops and flax (*loc. cit.* 1940, 1960) it is clear that crop varieties differ widely in climatic response, and even the rather detailed climatic sub-divisions used by Vavilov show themselves to be inadequate. Walter (1955) makes use of a wider range of data relating to climate and the seasonal distribution of its components, and proposes the construction of detailed climatic diagrams as a means of comparing climates. Ferguson (1957) similarly proposes the preparation of diagrams called 'photo-thermographs' for comparative climatic studies. Nuttonson (1947, 1949, 1956, 1957, 1962) has made a notable contribution to the use of physical data for climatic comparison. He employs what is basically a temperature-summation technique, in which climate is expressed in degree-days above a selected base temperature which is altered according to the crop species under consideration. The purpose of his investigations, states Nuttonson (1957), " is to formulate an agronomic approach to bio-climatology and plant-climate studies, and to promote research along the lines of agricultural bio-climatology and crop ecology as it affects plant adaptation, plant introduction and the exchange of . . . plant materials among the various agricultural areas of the world." Despite the detail of his work, however, accurate climatic comparison remains as elusive as ever.

Hartley (1961, 1963) considers that the broad climatic classifications of Köppen and Thornthwaite " are too generalised for the comparison of climates within smaller and more intensively studied regions "; Cooper (1959) and Major (1963) nevertheless show that in grassland comparisons under certain conditions at least the water-balance diagrams of Thornthwaite can be useful in defining in general terms the characteristics of a habitat. Recognition of a number of inadequacies in purely physical climatic comparisons led, however, to the construction of many classifications which have been based particularly upon climatic factors assumed to be of special importance to crop performance. Thus Nuttonson, in the series of papers referred to above and in others (1948, 1953, 1955, 1957) attaches great importance to crop phenology. He has in mind (1948) such phenological data as " dates of sowing, or planting of crops, dates of germination or emergence, dates of stooling or tillering, dates of leaf-bud opening, dates of shooting, dates of blossoming or heading, dates of terminal bud formation, dates of various distinct stages of biological or market maturity of genetically homogeneous clones or pure-line horticultural varieties." Azzi (1956) considers the environment as divisible into positive and negative components which, acting together, determine the direction of the total effect of the climate on the crop. Papadhakis (1952, 1964) observes that many attempts have been made to express a crop's requirements in terms of climatic factors (minimum temperatures, hours of cold, length of day, sums of temperatures, millimeters of rain, etc.). The results have been disappointing. "The figures vary considerably from one instance to another, depending on other factors," he comments (1964), and suggests that "the order in which (different) cultivars are classified in respect of one factor (winter resistance, cold requirement, heat requirement, effect of variation in daylength, etc.) is much more constant." But, states Hartley (*loc. cit.*), "these very different approaches produce equally divergent results, and the indices (of comparison) differ much more than do those derived on a broad basis from simple climatic data," and their usefulness is limited to the "study of relatively localised botanical and agricultural problems."

The problem of climatic comparison may be approached from a second direction, by the use of vegational and floristic data, such as are represented by the life-form classification of Raunkaier (1934) and Cain (1950), the 'agrostological index' of Hartley (1954), and the crop indices of Nuttonson. Hartley's agrostological index is based upon the percentage frequencies of groups of grass species of certain tribes in the total grass flora of different regions of the world. Kerguélen (1963) proposes a similar method of floristic comparison of climates, which is based on the determination of areas which have a maximum frequency of naturalised plant species originating from a given area. Such systems suffer from a lack of the published data on which they depend, and both Hartley and Kerguélen note that there are imperfections in floristic methods of climatic comparisons. Hartley (1961, 1963) concludes his review by observing that "none of the methods of comparison approaches in universality the direct climatic classifications.

Hartley and Neal-Smith (1961, 1963), commenting upon the necessity for plant introduction programmes to be closely integrated with regional needs so that " all plants introduced must be grown and tested under the conditions and in the areas in which they are most likely to succeed," also remark that " it does not appear that the ' universal ' climatic classifications which have been proposed can be used without qualification as a guide in plant introduction." " The snag to Hartley's agrostological index," Whyte (1964) notes, " is the shortage of available information." This is as unfortunately as true of meteorological as it is of floristic data. In addition, both Nuttonson (1957) and Perrin de Brichambaut (1961, 1963) emphasise that not enough attention has been paid to the differences between macro-climate and micro-climate. Nuttonson states that " there may be a marked difference between climatic conditions as measured in a standard weather shelter 5 or 6 feet above the ground, and those immediately within the plant habitat. . . . The often-heard suggestion that temperature records for the purpose of agriculture be taken at the level of the plant habitat and not in enclosed screens at a fixed height above the ground appears to be very sound and, if carried out, would no doubt yield more valid data for studies of climate-plant relationships." From the paper of Penman (1962), for example, it is clear that differences between micro- and macro-climate exist which are not reflected in standard climatic determinations.

In one of a series of studies in which he examines the relationships between crop development and various climatic factors, Junges (1962) analyses the relationship between the photo-periodic responses of crop species and their centres of genetic diversity, and remarks that, " Wenn es bisher hiess ; erst hohe Erträge, dann klimatische Angepassheit, so sollte es vielleicht besser heissen : erst klimatische Angepassheit, dann hohe und wertvolle Erträge." Such climatic adaptation is a major aim of plant introduction. But it is clear that up to the present, inadequate knowledge of climatic homology can do little to predict the responses of complex population gene-pools to climatic conditions other than those in which they have arisen by adaptive evolution. Until such time that climatic homology has a wider and sounder basis than at present, undue reliance upon it can lead only to the waste of valuable scientific effort in plant introduction, a field which is seriously short of qualified workers.

The distribution of variability

"Plant introduction may be said to have passed through two major phases," states Whyte (1959)—a first which "began with the initial domestication of crops and inspired selection by primitive peoples (which) lasted for centuries if not millenia," and a second phase, the present, marked by the planning of expeditions similar to those first planned and led by Vavilov, and the organisation of plant introduction services. There is a need, however, Whyte emphasises, "for a careful consideration of the scientific bases for a third phase"—equipped with a real knowledge of the autecology, genecology, and taxonomy of the genera and species to be collected, and of the ecology of vegetation types and climatology of the regions to be explored—" in which more attention would be given to the preliminary stage . . . perhaps involving a preliminary field reconnaissance before the actual collection is made, and to the technique of sampling a population so that the swamping of introduction services may be avoided."

The third phase of plant introduction will rest upon—indeed will require as an essential prerequisite—the extensive development of many practical and theoretical disciplines, ranging from the establishment of adequate climatological services which are designed to provide data useful to crop ecologists, agronomists and breeders, to comprehensive measures for genetic conservation. It is possible also that it will depend upon a major reconsideration of the principles and techniques of plant breeding itself.

Vavilov, in the course of his monumental work on the origin and distribution of cultivated plants, reached certain challenging conclusions which must take our attention today. He states (1951) that "Evolutionary principles permeate the whole science of plant breeding." Plant breeding itself "is evolution directed by the will of man . . . in which *the study of the original material*, and of the origins of cultivated plants, are fundamental requisites. . . . In this sphere there is abundant scope for work of such importance as would serve even the highest aims of the plant breeder. As a rule, in the past, he dealt with parts of species; the near future holds promise for a synthesis of scientific knowledge that will throw light on the range of variation within the species, the systematics of species, the extreme variants, and the range of physiological, chemical and other properties. As a result of the investigation which we have begun along these lines in recent years, it has been clearly demonstrated that the old ideas which were concerned with fragments of species and the incidental material with which the breeder worked, must be changed at the root. *From now on, the basis of scientific breeding should consist of phyto-geographical information relating to varietal potentialities of species and breeds.*" The accumulation of such information is carried out, according to Vavilov, by making use of the 'differential phyto-geographical method,' the successive steps of which may be briefly stated as: (1) The classification of plant collections into species and genetic groups using all the available criteria of morphology, genetics and physiology. (2) The location of the original areas occupied by these groups in the past. (3) The determination of the total genetic variability within each species. (4) The determination of the areas in which the intra-specific variability of the species is to be found, and particularly the geographical centres in which the variability is concentrated and in which numerous endemic characters are found. (5) The determination of similar patterns in related non-cultivated and cultivated species (Vavilov 1926, 1935, 1951; Whyte 1958; Kuckuck 1962).

Vavilov found that "the geography of plants shows definitely that in modern times the distribution of plant species on the earth is not uniform," and that an extraordinary concentration of crop varieties "lies in the strip between 20° and 45° north latitude, near the higher mountain ranges, the Himalayas, the Hindu Kush, those of the Near East, the Balkans, and the Apennines. In the Old World this strip follows the latitudes while in the New World it runs longitudinally, in both cases conforming to the general direction of the great mountain ranges" (1935, 1951). Vavilov named eight 'centres of origin' or 'centres of varietal diversity' of which the second, the Indian, centre was further divided into two and the eighth, the South American, into three. The centres were distributed as follows: I. China; II. India; IIa. Indo-Malaya; III. Central Asia; IV. The Near East; V. Mediterranean; VI. Ethiopia; VII. Southern Mexico and Central America; VIIIa. Ciloe; and VIIIb. Brazil-Paraguay. "We can speak with a degree of exactness that was unthinkable ten years ago," says Vavilov (1935, 1951), "of eight ancient main centres of origin of world agriculture or, more exactly, of eight independent regions where various plants were first cultivated."

In each centre, a number of endemic species of cultivated plants are marked by a degree of varietal diversity not found in the same crops in other centres. For each crop there is a concentration of dominant genes in its particular gene-centre, states Vavilov, and recessive characters become more evident at the periphery of a species' distribution, a concept resembling the biotype depletion theory of Turesson (1930) and Baker (1953). Vavilov attributes the distribution of genetic variability in gene-centres to the effects of both cultural and topographic isolation ; his great attainment was to map the distribution of the variability upon which the future of all plant breeding depends.

The scale of Vavilov's work has never been duplicated, and is so monumental that, according to Harlan (1951), "it stands today neither substantiated nor disproved by subsequent research." "Wohl selten," observes Kuckuck (1962), in a thoughtful critique of Vavilov's theory, "hat eine Theorie auf so vielen Gebieten der Wissenschaft anregend und befruchtend gewirkt." Details of the theory have been criticised and modified, however, by a number of writers in recent years on the basis of a more extensive knowledge of the distribution of variability in some cultivated species than was available in Vavilov's time. Both Burkill (1953) and Helbaek (1959) believe that Vavilov did not sufficiently stress the rôle of cultural factors in defining gene-centres ; Burkill, in the light of more detailed evidence from cultural history, divides Vavilov's Indo-Malay centre into Indian, Indo-Chinese and Malaysian centres. Schiemann (1932), and later Harlan (1951, 1961), Harland (1955) and others, have questioned whether centres of genetic diversity are necessarily centres of ancient origination of crops—though this does not, says Harlan (1961) 'make the concept less useful.' More recent work on the distribution of varietal diversity in wheat by Gökgöl (1941) and Kuckuck (1962, 1963), based on their very impressive collections, has led them to consider Turkey as the gene-centre and also the centre of origin of *Triticum monococcum, Triticum durum*, and *Triticum aestivum* (*vulgare*), whereas Ethiopia and Central Asia were considered by Vavilov to be the centres of diversity for *durum* and *aestivum* (*vulgare*) wheats respectively. Similarly the work of Schiemann (1932) and Aaronsohn (Oppenheimer 1957, 1961, 1963) on wild emmer (*Triticum dicoccoides*) has challenged Vavilov's belief that the centre of origin of this species was Ethiopia.

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Hutchinson (1951, 1958) has shown that the breeding system of a crop is an important determinant of the distribution of variability throughout its range and that the diminished variability in peripheral areas which Vavilov describes (the Vavilov Effect) occurs in inbred crops only. "By contrast," states Hutchinson (1958), citing cotton and sorghum as examples, "there is no irrevocable loss of variability during the spread of an outbreeding plant."

Kuckuck (1962) relates some of the shortcomings of the earlier gene-centre theory to sampling effects. Is it possible, he asks, to determine the gene-centre of *Triticum aestivum* (*vulgare*), for example, so accurately as to be certain of an exact centre of dominant genes, or the location of a peripheral area marked by the occurrence of recessive characters, or even the exact centre of greatest varietal diversity, in an area so vast as southwest Asia, the gene-centre of the species, when the area which it is possible to sample is so small a part of the total? Further, the detection of varietal diversity is dependent upon the intensity of sampling, so that the localisation of gene-centres is also likely to be related to sampling activity rather than to the objective existence of genetic diversity.

Nor can the effects of the activities of early man upon the distribution of crop diversity be minimised. Kuckuck speaks of a sample of *Triticum polonicum* collected from an area in which the species had not been previously recorded, and traced it to a sample which had fallen by chance into the hands of villagers who, impressed by its size and quality, multiplied and grew it. Such exchanges of seed have probably been greater in former times when caravans plied extensively with many halts than at present when many areas are traversed rapidly, if at all. The same writer has shown that variability in crops can be considerably affected also by cultural techniques. Brieger (1961, 1963) has reported that there is evidence that indigenous plant breeders in South America long before the present epoch extensively used synthetic maize varieties, and may therefore be expected to have greatly controlled variability in the indigenous crop.

In recent years, evidence from two separate lines of research has indicated a further source of genetic variability which has a fundamental bearing upon the nature of gene-centres and the future utility of the concept. In the first place, the occurrence of unusually large numbers of mutants in the progeny of hybrids of maize and its relative teosinte—species sharing a high degree of chromosome homology—which have been backcrossed to maize, is reported by Mangelsdorf (1958); in some cases mutants amount to between 7 and 9 per cent of the total progeny (Mangelsdorf 1965). Mangelsdorf attributes this effect to mutagenic activity of teosinte chromatin upon the maize background of the hybrid genotypes. Stable and unstable mutations occur, the latter segregating more or less normally in some outcrosses but disappearing completely in others. In the latter case they resemble, therefore, the paramutations which have been described by Brink (1958) and more recently by Linden and Rodriguez (1965), and Mangelsdorf believes that the effects are related, suggesting that "it may be that the expression of some genes is as dependent upon the internal environment as is the expression of the genotype upon the external," or—we might add—as are some genes upon the external environment, as noted already (p. 56). The view is consistent with the long-standing evidence of modifier complexes, suggested by Harland (1932), and by the modern view of the genotype as a co-adapted polygenic system. Mangelsdorf (1965) himself refers to the development of modifier complexes in maize which affect the expression of the Tu-tu locus "until the point has been reached where the homozygous pod corn of the genotype Tu-Tu is, on most modern genetic backgrounds, monstrous and sterile." "The fitness of a gene," says Hutchinson (1958), "must be considered in relation to the external environment on the one hand, and to the internal gene balance on the other." Casperi (1963) also states 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 the other genes with which it is associated."

In the second place, it has been shown by Harlan, Martini and Stevens (1940) that one of the consequences of composite crosses in barley, in which a number of barley varieties of widely differing origins are crossed in all possible combinations, has been the emergence, in addition to new recombinants and transgressives, of extremely diverse segregants resembling mutants. Harlan (1956) describes the persistence of mutant forms in composite cross populations in unexpectedly high numbers as far as the F_8 generation. "If at any time these populations had been irradiated," he observes, " we would have been profoundly impressed by the power of irradiation to produce not only freakish mutations but desirable agronomic features as well. But these populations were *not* irradiated. The same sort of things that occur in irradiated populations occurs also in non-irradiated populations and sometimes at a very high frequency. It may be necessary to manipulate the population to some extent as was done here, but these variants occur naturally and frequently in suitable hybrid material."

Can it be that mutation is a more general consequence of hybridisation, particularly wide hybridisation, than has been supposed ? Darwin (1875) remarked on the appearance of " atavistic " forms following wide crossing. Darlington (1939) refers to the " vast array of segregates " which resulted from wide crosses within the genus *Hordeum* which are not observed when species from the same geographical area are crossed, reported by Karpechenko (1935). Clausen (1953) notes that " very extreme types of transgressive segregation " result when " parental populations of contrasting races are crossed." Is it enough to say that transgressive segregation alone is involved ? MacKey (Harlan 1956), quoting his own data and the data of Kajanus (1923), states that as much as a 50 per cent increase in mutation frequency occurs in the F_1 of some wheat crosses. Evidence has been reported from time to time that extreme changes in external as well as internal environment are mutagenic, and some of this will be referred to below. It is interesting, however, to note that Sobolev (1963) has reported a large increase in the incidence of mutations in wheat when embryos are removed from their endosperm and raised in culture.

With the experimental evidence in mind of Harlan and Martini's (1938) barley mixtures, and Harlan, Martini and Stevens' (1940) composite cross populations of barley with their high incidence of variant forms, Harland (1951) states that " it seems readily possible to distinguish populations representing mechanical mixtures from those which are to some extent at least actively interbreeding." He uses this possibility to examine the structure of wheat populations in the Turkish gene-centre. " Most wheat populations throughout Turkey," he states, " belong to the first category, being simple mechanical mixtures resulting from primitive husbandry." The wheat populations of Turkish Thrace are of a different order, however, " and represent a remarkable accumulation of variant forms."

He refers to such local centres within a gene-centre which possess a high incidence of variants as gene micro-centres, and believes that they indicate that gene-centres may be heterogeneous and their structure amenable to analytical study.

Harlan also further suggests that while it may be characteristic of some gene-centres that they are isolated or ecologically fragmented as conceived by Vavilov, this is only partly so and does not necessarily represent a general rule. It is not so in Thrace, part of which is an open plain " and can lay no claim to ecological diversity, remoteness from civilisation, isolation, nor even exceptionally primitive husbandry. Steel plows, grain drills, windmill-type binders, are commonly used in Thrace. Agriculture here is as highly developed as anywhere in Turkey, but the unique wheat populations are maintained. Many other sections are agriculturally far more primitive and ecologically much more diverse and yet contain a comparative paucity of genetic variants." Popov (1950) is reported by Raikova (1960, 1962) to have observed a comparable condition of spontaneous hybridisation and repeated secondary hybridisations between species in the Pamir region, which give rise to small secondary centres of origin and which enrich the species composition of the area.

" An examination of a wheat field in Turkish Thrace," says Harlan, " provides an education in crop evolution. The typical wheat field here contains a wonderful mixture of forms which according to some classifications would comprise a number of species, many botanical varieties, and dozens if not hundreds of agronomic varieties. . . . Around the borders of the fields, in the weedrows, the roadsides, the waste spaces, and to some extent in the fields themselves, the wild wheat relatives are found in abundance. The remarkable array of variants closely resembles certain composite cross populations artificially generated by some of our agronomists." Anderson (1961) states that in fields of *Triticum durum* in Ethiopia extreme variability is observed, and is " of another order of variability from any grain fields I had previously seen." "Some of the wheats from such fields are segregating markedly," he continues— " It is now evident that our classification of the small grains (including the great Russian collections) are more largely based on isolated samples carried back to herbaria than on the fluid populations from which such individuals come." There is little doubt that in such centres interbreeding and evolution are actively taking place. "The fundamental character which is common to all centres," states Harlan (*loc. cit.*), "is that evolution is proceeding at a rapid pace *now*."

The commonest result of hybridisation observed by Anderson and Hubricht (1938) in species of *Tradescantia* which they studied was that "through repeated backcrossing of the hybrids to the parental species there is an infiltration of the germplasm of one species into that of another," and the term 'introgressive hybridisation' was applied by them to such a situation. Anderson (1949, 1953) discusses and develops the concept of introgression. Summarising some of its important features, he states (1953) that "introgression is proportional to the selective advantage conferred by the foreign germplasm and within wide limits is independent of the strength of internal barriers to hybridisation." Grant (1958) notes that "the outcome of hybridisation in a cross-fertilising group is more likely to be introgression than the formation of new homozygous biotypes or micro-species. . . . Outcrossing by hybrids will normally take the form of backcrossing to the parents, rather than intercrossing with sister hybrids, because of the higher fertility and greater abundance of the parental individuals." In circumstances such that parental species predominate, and where reproductive barriers are strong, states Stebbins (1959), introgression is likely, and "the fact must be emphasised that the products of introgression are permanent additions to the gene pool of the recurrent species." Among inbreeders an appreciable amount of gene exchange has been shown to take place by Jain and Allard (1960) and Imam and Allard (1965). Zohary (1960), discussing the evolution of the barleys, stresses that "few if any workers have realised the full evolutionary implications of the fact that self-pollination here is incomplete and is accompanied by occasional cross-pollination." Introgression, therefore, may be expected to be equally significant in the evolution of inbreeding as of outbreeding crops.

"The effects of hybridisation under natural conditions are cryptic," Anderson (1953) observes. "Backcrosses tend to resemble the recurrent parent so strongly as to pass unnoticed." In a series of publications (1949, 1956, 1961), he has developed and applied various techniques for the detection of the effects of introgression in interbreeding complexes, most notably the 'pictorialised scatter diagrams,' which have been of considerable practical importance in plant breeding "(1) in the overall orientation of breeding programmes, (2) in the analysis of multiple-sense-impression data, and (3) in their locating and defining complexes of associated characters in cultivated plants" (Anderson 1956). More recently Alston and Turner (1962) report the use of chromatographic data in the analysis of complex hybridisation and this also may prove to be a useful tool in defining the complexes of relationships which have been shown to exist in gene micro-centres.

Anderson's concept of introgression sheds a valuable light on the genetic relationships which exist not only between crop species, but also between crop plants and their related wild and weed species. It permits a genetic analysis of the long-recognised 'contamination' of crop plants by weed pollen, of which the occurrence of fatuoid types in oat and rice crops is a well-known consequence. Evidence of the extensive interfertility of wild, weed and cultivated rice species is presented by Kihara (1959) and Richharia (1960). Zohary (1960) says that "a small percentage of cross-pollination or 'contaminations' between cultivated varieties has been repeatedly observed by barley breeders." A striking feature of a recent series of essays on crop plant evolution by Dodds (1965) Mangelsdorf (1965), Bell (1965) and Doggett (1965a), it is noted by Hutchinson (1965), is that all stress "the great importance of the continuing genetic contact between the crop plant and its wild relatives." Zohary (*loc. cit.*) demonstrates introgression between wild and cultivated barleys in Israel; he also comments upon the association of the incidence of introgression with disturbance of the habitat. The concept of introgression provides, at the same time, a remarkable instrument for investigating the genetic structure of gene centres.

The possibility that just as in cultivated plants, gene centres of wild species exist was first suggested by Turesson (1932). If this were so, the knowledge of such centres would be of great value, since the grasslands of the world are composed of species as yet scarcely domesticated. Hartley and Williams (1956) extensively examined the distribution of the principal pasture grass species used in world agriculture. They report that three major regions contain particular concentrations of these species; these regions are the Mediterranean, East Africa and sub-tropical South America. The factors contributing to this distribution bear some resemblance to those which determine the distribution of other crop species, namely the selective action of man, the operation of such ecological components as soil moisture and fertility, the effects of taxonomic relationships and patterns of evolutionary development particularly in relation to the co-evolution of grasslands and grazing animals, a factor also recently stressed by Hédin (1961, 1963). Harlan (1959) reports the occurrence of Vavilovian centres of diversity in grasses, being " relatively small areas in which are concentrated enormous variability" which " exhibit marked introgressive hybridisation as well as the appearance of new and original variants." Harlan (1963) describes gene-centres of two kinds in a number of grass species of the *Bothriochloinae* in the Western Ghats in India. He describes these as ' endemic centres ' and ' gene-microcentres,' and they compare with the similar divisions found by the same writer in the Turkish gene-centre. As in Turkey, populations in the micro-centres are marked by the presence of extreme polymorphism and extensive introgression. They are associated also with habitats recently disturbed by man and by the presence of ruderal species.

Evidence has been referred to above (p. 72 *et seq.*) that mutation is a source of the enhanced genetic variation which is seen to follow wide hybridisation. Anderson (1953) questions this. Plants used in genetic research, he points out, have generally been such as to indicate that " their origin, where known, is a consequence of introgression, frequently multiple introgression. In such material crossing over in short heterozygous introgressive segments could be distinguished from gene mutation with great difficulty or not at all." However, recent views indicate that crossing over may occur within the gene. " The total number of mutational sites separable by recombination within a section of chromosome in which recessive mutants are allelic to each other (a cistron, or gene for short)," states Pontecorvo (1959), " may well be in the order of hundreds or thousands." Pontecorvo adds that " a change of bases, or loss of one nucleotide pair or a rearrangement, including deletion, in the sequence of nucleotides, either minute (*i.e.* within the cistron) or gross (*i.e.* with one break within the cistron and one elsewhere) would constitute a mutation." Sax (1931) noted a high degree of correlation between cross-over frequency and the frequency of mutation in *Drosophila* and suggested that most of the mutations observed resulted most probably from the occurrence of unequal crossing-over leading to minute duplications and deficiencies. The condition described by Anderson to be a consequence of extensive introgression would be peculiarly conducive to changes of this type. So also with the material described by Mangelsdorf (1958). With maize, he says " we are here dealing with . . . a complex hybrid resulting from repeated introgression of teosinte into maize which has been going on for centuries and perhaps for as long as 2,000 years."

Danert (1962) observes that there is a greater tendency in many of our cultivated plants to give rise to new forms than is the case among wild species. This observation may also have its basis in the type of situation which Anderson and Mangelsdorf describe. Braidwood (1958) attaches importance to the occurrence of what he refers to a ' permissive mutation ' in the early evolution of the cereals. Helbaek (1959) suggests that the first cultivators of barley and wheat in the hills of northern Iran were forced, probably under the pressure of an increasing population and a shortage of tillable land, to move into the lower valley areas and that " one of the consequences of this forced movement of the grain beyond its natural habitat by human transplantation was presumably the emergence of mutations, hybrids and freaks in the wheat crop." Danert (1962) remarks that early man's successes in crop domestication relied to a degree on the fact that " durch den Anbau unter veränderten klimatischen und edaphischen Bedingungen die Mutationsrate gesteigert wurde." To what extent these observations and others of a similar kind referred to in this discussion—as far as they can be confirmed by present-day experience in evolving crop populations—may be explained by environmental segregation or by the reduction of selection pressures in the new environment, as Zohary (1960) and Danert (*loc. cit.*) suggest, or by the mutagenic effect of altered environmental conditions or extensive introgression, certainly cannot be answered at the present time. It is clear that there is a need for an intensified examination of the origins of genetic variability. We may say, with Anderson (1961) that " the whole subject is one demanding collection and analysis, rather than discussion and debate. The only point which seems reasonably well established is that here is something which needs looking into." This said, we may nevertheless note that the synthesis of the concept of introgression and the phytogeographic method and its product, the gene-centre theory, has been extraordinarily fertile. There can be no doubt about the enormous contribution studies on introgression have made to knowledge of the origins and distribution of genetic variability so impressively begun by Vavilov. That the dynamic view of the gene-centre and of the origin of variability which has emerged is entirely in keeping with the views of Vavilov himself is confirmed by reference to his own work; of the Transcaucasia-northwest Iran-northeast Turkey region, for example, we may note his observation that " here the process of *species formation* in such plants as wheat, alfalfa, pear, almond and pomegranate is strikingly in evidence. It seems that one can trace here, *in statu nascendi*, the process of segregation of species and of larger genetic groups of these plants " (1935, 1951). Kuckuck (1962) notes that it is upon the work of Vavilov in plant breeding, and on the systematics, the evolution and the origin of cultivated plants that the world-wide activity of the present day in the field of plant exploration, collection and introduction is founded, activity which is playing a decisive rôle in the development of agriculture. Invigorated by its fusion with recent ideas, the work which Vavilov began is now entering a stage which brings plant introduction to the third, scientific, phase described by Whyte, and brings man to a fuller understanding of the mechanisms underlying the origins of genetic variability, and to the possibility of its knowledgable conservation and effective utilisation.

Genetic conservation and the future of plant breeding

Progress in plant breeding, states Simmonds (1962b), " is wholly dependent upon the provision of variability, whatever its source. . . . Whether the aim of breeding is better adaptation to existing conditions or new adaptation to an altered environment, success or failure depends on the adaptability of the crop, that is upon the provision of recombinational variability." Sylvén (1937) compares the response to rather severe natural selection of unselected and of highly inbred strains of *Trifolium repens* grown at Svalöf in Sweden. Directly imported seed, and first and second generation seed were sown and their yields compared. In a highly-bred strain the relative yields were 100, 100.3 and 102.4 against relative yields of 100, 129.1 and 137.2 in an unselected strain. " There can be no response to selection," states Hutchinson (1940), " unless the material is genetically variable. The relation of variability to rate of change under selection, and the effect of selection in reducing variability, are therefore fundamental factors in breeding theory." Mather (1953) says, that "in discussing the adjustive properties of populations, we must pay special attention to the conservation of variation actually present, as it is on this variation that rapid adjustment will depend." In its turn variation will depend upon the amount of variability available in either the free or latent state. Mather and Harrison (1949) note that "the limit of advance under continued selection will be determined by the total amount of variability initially available, whether in the free state or in the potential state but capable of being freed. The rate of advance towards this limit will depend on the relative proportions of free and potential variability, and also on the rate at which the latter becomes freed." "Changes in the mean of a trait under selection are theoretically accompanied by a reduction in variability," Lerner (1958) observes—"After a population has been under fairly intense pressure for a number of generations, it is not uncommon that response to further selection becomes erratic. Gradual decay of additive genetic variability and the consequent increase in the importance of complex non-additive interactions may in part explain this fact"; among such factors may be the force of genetic homeostasis, the number and size of the effective units of segregation, their linkage relationships, and the means by which they are protected from disintegration. In general, "selective advances in an isolated population, when it is viewed as a closed system which lacks sources of variation provided by mutation or immigration, are made at the cost of additive genetic variance" (Lerner *loc. cit.*). Grasses as a crop still possess considerable genetic heterogeneity, and Cooper (1961) describes rapid and extensive response to selection for date of ear emergence in the Irish (early) and Kent (late) strains of perennial rye-grass (*Lolium perenne*). By the fourth generation the full normal range for date of ear emergence of the Irish strain had been obtained from Kent and *vice versa* but, Cooper points out, the selection potential is greater in the Kent strain than in the Irish and he attributes this to the fact that there is a history of less stringent selection in Kent than in Irish strains. In short, as Frankel (1950) says, "without variation there is no adaptability."

Plant breeding, however, for long has neglected the conservation of variability—indeed the reduction of variability in breeding stocks and crops alike has been deliberately sought. The concept of uniformity in crop varieties, now stronger than ever before, states Jensen (1952), " is everywhere written into variety and crop trials. It is reflected in the thinking at all levels of crop improvement, in the pride that the seedsman takes in his product and the grower in his crop." In plant breeding, Simmonds (1962b) observes, " there is a general tendency towards the rapid elimination of variability and, coupled with this, the notion that strictly uniform crop populations are a universal ideal to be aimed at whenever possible. . . . Plant breeding, in proportion as it is successful in producing highly adapted stocks, automatically tends to restrict subsequent adaptability."

Clearly, the breeding system of a crop is also a major factor determining the amount of genetic variability available for adaptive responses to selection, and in the cotton crop residual heterozygosity has been shown to persist (Manning 1955, Justus 1960) despite inbreeding and selection, even in the case of the Uganda Upland cottons which have a very narrow genetic base. Here, nevertheless, Manning (*loc. cit.*) notes that " it is likely that the genetic variation remaining within the inbred lines may soon become too small to justify continued selection among sister lines as the major breeding programme." Among inbreeding and clonally propagated crops loss of genetic variability is even more marked. In general, and as has been noted above (p. 49), Simmonds (1962b) states " the narrowly based crop responds slowly, if at all, to selection and is liable to crises brought on by its inability to adapt quickly to changing circumstances." Referring to loss of variability in potatoes, he remarks that while European breeders " raise well over two million seedlings annually most of the leading maincrop varieties are 30 or more years old. . . . It is true that conservatism may be partly responsible ; and it is also true that the survival of old varieties is a tribute to modern methods of phytosanitation. But the conclusion seems inescapable that the north temperate potatoes are so narrowly based that they are capable of little response to selection even in enormous progenies."

" It is not generally realised," states Whyte (1959), " on what a narrow genetical base many of our well known crops are founded." A mere handful of parent wheat lines have contributed to the gene content of all the Australian wheats (Frankel 1954, Whyte 1958). It is probable that the entire acreage of the grass *Digitaria decumbens* in Central America and the West Indies originates from a single clone introduced in 1940. Of the three crops—potato, banana and sugarcane—none is represented in cultivation by more than a few hundred genotypes and even these are often inter-related (Simmonds 1961). The great majority of the trees of the *Coffea arabica* crop in South America are derived from a few seedlings produced by a single mother tree in the Amsterdam botanical garden early in the eighteenth century (Simmonds 1962b). Weiss (1961) says that " the inadequate breadth of the genetic base, a significant limitation of many crops, is particularly evident in a number of forage species. Thus a very substantial percentage of the intermediate wheat grass acreage in the United States is planted with strains that trace to a single introduction." In perennial crops the importance of growing well-adapted, high-yielding and disease resistant strains or clones in each area is still more evident than with annual crops, Krug (1961, 1963) observes, yet " one of the handicaps for many breeders has been the rather limited amount of basic germplasm available for their work, often compelling them to deal with a narrow range of genetic variability, hence considerably reducing the probabilities of success. Sometimes, selection and breeding work has been restricted to the original plant material with which the crop has been established and to occasional introductions."

"The effects of a narrow genetic base are nowhere more apparent," states Simmonds (1962b), "than in the relation between a crop and its pathogens." Lacking the genetic variability of more broadly based crops, and of natural populations, the narrowly based crop population is peculiarly susceptible to pathogen attack. Already, Whyte (1959) points out, it is becoming necessary to spray *Digitaria decumbens* pastures in Central America as a protection against aphids and fungal diseases. Leaf spot disease of bananas reduced the Mexican production of the Gros Michel strain by 50 per cent in two years. Coffee rust in East African plantations commonly causes a harvest loss of 30 per cent, and the cost of chemical protection for the total East African crop, it has been estimated, would be about £10 million. In the United States alone, the cost of crop losses due to disease in the period 1951-1960 has been estimated to be more than 3,250 million dollars (Barnes 1964). This itself is probably considerably less than the cost of chemical protection for crops too narrowly based to carry adequate resistance genetically.

The responses of uniform highly-selected and highly-adapted crop populations to sudden environmental changes tend to be all-or-nothing responses. Lacking polygenic variation, the range of distribution for values of any given character is extremely narrow, and even minor shifts in selection pressure are sufficient to override the close limits of variation in the population. Its adaptive tolerance is low. If such a crop lacks resistance to a pathogen or, more commonly, to a new race of pathogen, and if conditions permit pre-epidemic foci to develop (van der Plank 1960, 1963; Zadoks 1961), epidemic will destroy the crop on a wide scale. Resistance breeding does little to allay this situation for, since the discovery of Biffen in 1907 that resistance to *Puccinia glumarum* could be inherited as a simple Mendelian recessive, it has concerned itself wholly with the search for such monogenic factors. In the flush of Mendelian ardour during the first decade of this century it was not surprising that resistance breeding should take this course. If it was an unfortunate choice, states van der Plank (1963), it was also understandable—"Vertical (monogenic) resistance has an immediate appeal which horizontal (polygenic) resistance has not. It is easy now to be wise after the event. What is less understandable is that later, as the shiftiness (of pathogen races) became glaringly apparent, knowledge of this shiftiness was used to intensify and support breeding for vertical resistance—the opposite strategy from what one would have expected; the strategy that allows the enemy to reap the maximum advantage from shifting." It is astonishing, Becker (1959) observes, that after 30 years of development in which genetics has come to regard evolution as a problem of the genetics of populations and has rejected the misleading simplicity of the early explanations offered by factorial genetics, this same development has passed plant breeding theory by. This is all the more astonishing since even in Darwin's day it was clear that breeding itself is an evolutionary process. At the beginning of the century the new factorial genetics was applied to plant and animal breeding, and the breeding principles which were laid down conformed to its precepts: breeding procedures still clearly bear this character. What is inconceivable, however, states Becker, is that this outlook has not altered to the present day—"Wenn man damals in der ersten Periode der Genetik so verfuhr, ist das nicht verwunderlich. Völlig unbegreiflich aber ist es, dass sich an dieser Betrachtungsweise bis heute nichts geändert hat." It is as tragic, indeed, as it is astonishing that, with the enormous genetic potential available, the most permanent achievement of modern plant breeding with all the equipment of genetics at its disposal appears to be the loss or destruction of much of the world resources of genetic variability.

In the first place, one consequence of monogenic resistance breeding is that plant breeding devolves into a game of cat and mouse with rapidly evolving pathogen populations, seeking only a step by step evasion of each new and more virulent pathogen race, and offering only a perspective of perpetually limited scope. Another consequence is continuous and heavy disease losses in crops. "One can aver," states van der Plank (1963), "that there is no evidence in history to show that vertical resistance breeding was able to reduce the frequency of first class epidemics." During the 1947-48 wheat stem rust epidemic in New South Wales, Vallega and Chiarappa (1964) report, "the wheat loss represented food for 3 million people for one year." The same writers also note that annual losses in sorghum and millet in Africa are equal to the effect "of not harvesting sorghum and millet from an area of nearly 5 million acres. If these disease losses did not occur in Africa, there would be . . . enough to feed more than 5.5 million people" each year. Annual disease losses in basic crops are high, rarely indeed falling lower than 10 per cent even in countries with favourable facilities for controlling disease incidence by crop hygiene and other methods, yet in many parts of the world a loss of between 5 and 10 per cent may represent a disaster owing to the difficulty in meeting even essential nutritional requirements. "Disease outbreaks in cereal crops," state Vallega and Chiarappa, "have often had a profound impact on food-supply with far-reaching effects on the social well-being of entire populations."

A third consequence of major gene resistance breeding is that the stimulus to establish a broader genetic base in crops is absent. Simmonds (1962b) shows that breeders' collections carry "virtually the whole load of future adaptability" of a crop. Yet, "traditionally they are regarded as sources of 'characters,' generally oligogenic, which may be detected by suitable screening techniques" and extracted by backcrossing programmes. Residual variability is broken up and destroyed or discarded. Hutchinson (1958) remarks that "close examination of any breeding programme devoted to the exploitation of useful major genes reveals the existence—and importance—of numerous minor genes whose segregation is generally regarded as an undesirable complication of an otherwise clear issue." He later adds that "it is interesting to note that the establishment of resistance to bacterial blight in American Upland cottons can be traced to cross-contamination between Upland and *punctatum* cottons in the breeding plots of pioneer cotton workers in India and in Africa. Had they maintained the standards of purity in their stocks that modern plant breeders require, the establishment of resistant Upland cottons would have been postponed indefinitely." To a plant breeding long accustomed to thinking in terms of monogenic effects and Mendelian segregations, the quantitative variation which results from the adaptive responses of a broadly-based crop population to the selective forces of its environment, and its inevitable association with characteristics as much those of the population as of any individual plant, must seem to be an unfortunate complication disturbing the computations of an orderly segregation, and the uniformity that results from a narrow genetic base a quality devoutly to be wished. But the cost to mankind of the luxury of such thinking is enormous, and more than mankind can afford in the present situation.

It is well to ask how plant breeding has come to be dominated by concepts and methods which seek to eliminate rather than conserve variability in crops, and a number of workers have cogently done so. Harland (1944) reports on selection experiments with Tangüis cotton in Peru which, using methods which were a "radical departure from current methodology," attained very rapid improvements in the crop. He states that "after 1900, the methodology of cotton breeding soon became dominated by the 'Pure Line' concept of Johannsen," according to which "a pure line is completely homozygous for all its measurable characteristics (and) something as definite as a chemical compound and as unchangeable. . . . Once a good variety was obtained, it was good for ever. The fetish of pure lines spread to most cotton-growing countries, and 'like the letter H, is treasured by many who formerly knew it not.'"

Harland shows, in a lengthy critique of the pure line concept, that while for fine cottons it had a certain though overworked value, its advantages in other directions were illusory and indeed, from the standpoint of the grower or the breeder, harmfully so. Hutchinson (1940) shows that the effect of natural selection on populations of cotton in India is the establishment of a well-adapted population consisting of a great range of types. " If variability, and not uniformity, is the natural characteristic of crop populations, the breeder's ideal must be reconsidered. Selection for uniformity should not proceed beyond the stage needed to ensure a satisfactory grade in the product." Nevertheless, " in early line breeding work it was assumed that the ideal was a ' pure line,' and once this was established all that was necessary was to preserve it from contamination by mixing or hybridisation and it would remain pure indefinitely." It may be noted in passing that if the genetic contact between crop populations has the significance in evolution in crop plants that has recently been suggested by a number of workers, and discussed already (pp. 73-77 ; also Harlan 1965 ; Harlan and de Wet 1965), and the evidence is increasingly in support of this view, the maintenance of such pure lines effectively isolates the crop from further evolutionary advance. " The dominance for so long of breeding techniques that involve the deliberate reduction of variability in breeding stocks has come," according to Hutchinson (1958), " from the influence of Johannsen's pure line theory, the accident that many of the temperate region crops are self-fertilised in western Europe and America, and the convenience of inbreeding techniques for the exploration of genetic principles." He adds that " it is perhaps a by-product of the practice of working with ' pure ' or nearly ' pure ' stocks that so much time and effort has been devoted to the search for single genes of large effect." Frankel (1950) echoes the present views of a growing number of workers when he remarks that " the ' purity concept ' has not only been carried to unnecessary lengths, but it may be altogether inimical to the attainment of highest production." As Suneson (1960) pungently observes, " modern plant breeders and plant pathologists may have over-extended the logical applications of the pure-line theory and become enslaved by the uniformity and conformity conventions their over-indulgence produced."

In complete contrast to the factorial concepts which have dominated plant breeding for so long stand the views of Vavilov which have been discussed above (p. 68 *et seq.*). In his essay on " Plant Breeding as a Science," published a generation ago, he states that " as a result of the investigations which we have begun . . . it has been clearly demonstrated that the old ideas which were concerned with fragments of species . . . must be changed at the root. From now on, the basis of scientific breeding should consist of phytogeographical information relating to varietal potentialities of species." In practice, acceptance of the basic truth of Vavilov's thesis is implied in the wide use by plant breeders of breeding material collected from the world's gene-centres. It has been pointed out, however, that such material serves mainly as a source of monogenic 'characters' (p. 84), and the great bulk of the varietal potential which such collections represent—its adaptive variability—is eventually lost or discarded. This is borne out by Rodenhiser's (1961) observation that although numerous varieties have been developed through the use of the germplasm available in the world collections, " it is generally recognised that success may be temporary and that the future value of a new variety depends on the breadth of its genetic base." Thus in general, plant breeders continue to work with " fragments of species "—supplemented by new genes to a greater or lesser extent, it is true, but fragments of species nevertheless.

In the field of resistance breeding in recent years there has been an increasing tendency to intensify the search for more permanent forms of disease resistance. It has been argued (van der Plank 1949 ; Harland 1955 ; Zhukovsky 1959, 1960 ; Simmonds 1962b ; Bennett 1964) that when a pathogen is part of the total environment of a plant population, the population may be expected to show adaptation to this as to any other environmental factor. Exposure of a species population to a novel pathogen in a new area, states Harland (1955), " will bring into play a potent screening mechanism which will push the whole population in the direction of resistance." Adaptive resistance of this type has been described as field resistance, and the search for field resistance to blight in potatoes has been described by Gallegly and Niederhauser (1959) and by Black (1960), and by a number of other workers (Toxopeus 1959, 1960 ; Driver 1962 ; Simmonds 1962b ; Umaerus 1963, *inter alia*). Arnold (1963) describes the breeding of bacterial blight resistant cottons in Uganda, and points out that natural selection, acting in an environment which favours the disease, has served progressively to increase the incidence of resistance genes and gene-complexes in the crop. He shows that the utilisation of this type of resistance depends upon the systematic exploitation of the genetic variability of locally adapted populations. Graham and Hodgson (1965) show that breeding techniques of the type used to transfer major genes in breeding stocks tend to destroy the gene-complexes controlling adaptive resistance. The extension of the search for adaptive resistance in cereal crops is described by Bell and Macer (1962), who stress the need to develop techniques of screening for field resistance.

Vavilov set out certain stages in the development of scientific breeding, of which the accumulation of information on varietal potentialities by the phyto-geographic method formed the first. This is followed by the study of variation, and this by the study of the interrelationships of the species and the environment. The next stages are the study of inheritance and hybridisation, and of the theory underlying these, and the final stage consists of the study of special breeding for specific needs, such as the development of special industrial crops. The phyto-geographic basis " provides the starting point for breeding investigations," according to Vavilov. Hutchinson (1958) states that " the distribution of the variability in a crop plant is of considerable importance both in genetic studies and in plant breeding practice. . . . It is with variability, and the distribution of variability, that genetic studies begin." The emergence of a new attitude to the search for adaptive disease resistance has brought with it a new recognition of these principles. It remains for this search to continue and to broaden its scope to include all the objectives of plant breeding. There is evidence, also, in the work of Harlan, Suneson, Weibe and others that the limits of utilisable variability are not reached with the completion of a world survey —if this is ever likely to be possible, since evolution is certainly taking place rapidly at the present time and will continue to do so. Indeed, Hutchinson (1958) comments that if the assessment of the existence and extent of genetic diversity in natural populations is accepted " the effort that has been devoted to the creation of diversity for plant-breeding purposes by physical and chemical means in recent years seems somewhat unnecessary."

Seen in such a context, Vavilov's work—his unparalleled explorations of the world resources of crop plant variability, his studies on the agro-ecological regions of the world and the relationship they bear to the distribution of adaptive genetic variability, and his discovery of the centres of genetic diversity —need to be regarded, therefore, not so much as the great attainments of an outstanding explorer, as they tend to be, but rather as first steps in the painstaking construction of a new science of plant breeding, in which the dynamic interaction of the environment and the adaptive capacity of crop populations is seen to be the creative factor in the evolution of crop forms. Such a view is also the view of genecology.

But at this point it is necessary for us to direct our attention to a new and serious danger. Gene-centres are the richest sources we possess of genetic variability. Countless land-races of crops throughout the world are a scarcely less valuable resource. Plant introduction has drawn upon them extensively in the past, even before their true significance as reservoirs of adaptive variability was recognised. Simmonds (1962b) remarks that "the contribution of foreign genes to locally adapted variability has been profoundly important at every level of crop evolution, alike on the grand scale of the creation of new cultivated species (as in the cottons) or of hybrid groups (as in the bananas), and on the smaller scale of innumerable contemporary plant breeding operations." But gene erosion, resulting from the improvident techniques of monogenic breeding and the replacement of land-races and local varieties by highly uniform crops (distributed all too often by agricultural extension services) on a world-wide scale, threatens these vital resources, despite the fact that, in the words of B. P. Pal, they represent "all the plant breeding work carried out by nature over thousands of years." Harlan (1956) describes how great acreages have been planted to a single variety of flax in Turkey, saying that "from one end of Cilicia to the other I could not find a single indigenous variety although this very area had at one time been a centre of diversity for flax." Kuckuck (personal communication) has observed that the replacement of local cereal varieties in Ethiopia by introduced and highly uniform varieties is progressing very steadily even in apparently remote regions. "The geographic centres of diversity upon which we have depended so much in the past for our sources of germ plasm," states Harlan (*loc. cit.*), "are in great danger of extinction . . . and time is running out faster than most of us realise." Action is urgently required now to conserve world gene resources.

Gene erosion is a dangerous and alarming feature of present-day exploitation of genetic resources. Many local races are becoming more and more difficult to find even within the gene-centres. Preservation is therefore becoming increasingly urgent. This is a problem of world-wide dimensions, however, and must therefore depend upon international co-operation if it is to attain success. Without such co-operation the enormous promise which plant introduction holds out for mankind, and upon which man depends for food and technical raw materials, must be diminished in its effectiveness. The need for international scientific co-operation on a broad front has already led to the planning of a long-term International Biological Programme and the establishment of International Co-operation Year. In the light of these plans the recommendations of the F.A.O. Technical Meeting in Rome in 1961 (United Nations 1963) assume a new significance. "Recognising the great importance to this and future generations of preserving the gene pool of genetic variability which now occurs in the major gene-centres of the world, but which is threatened with destruction," the F.A.O. Meeting takes a number of decisive steps in the direction of world genetic conservation.

In the first place, the F.A.O. world catalogue of genetic stocks is to be enlarged considerably. It must also, however, be extended to include land-races and local ecotypes of wild forms. Genecological considerations indicate that the genetic value of land-races and local forms is very great, and probably greater than that of highly-bred varieties, since the latter mostly lack the reserves of adaptive variability which an enlightened plant breeding will wish to use for the improvement of plant stocks.

Living collections of local ecotypes, land-races and cultivated varieties should be increased, and should be held by all research institutes, botanical gardens and national and regional plant introduction services. But it must be recognised that such collections cannot be maintained for more than short periods outside their regions of original adaptation, except as seed or in the vegetative state, because adaptive responses of the populations under environmental conditions to which they are not adapted can lead to rapid changes in the balance of the gene-pool of the population. Local and national collections, therefore, must be regarded as relatively short-term reserves of genetic variability, depending upon material derived from basic collections maintained within the gene-centres.

In the gene-centres the population-environment complex within which the interaction of natural selection and adaptive genetic variability has given rise to and is continuing to give rise to new evolutionary forms, must be preserved. This can only be done by the creation of areas of natural conservation within the centres of genetic diversity, where plant communities may be maintained entire and *in situ*. The F.A.O. Meeting recommends the establishment of International Crop Research Centres *within* the gene-centres with the task of fully exploring the genetic potential of their respective regions on the basis of detailed local knowledge, of assessing and maintaining basic collections of crops and local races and of wild forms, and of setting up areas of genetic conservation to be managed in such a way as to preserve the evolutionary potential of local population-environment complexes. The F.A.O. 1961 meeting welcomed the establishment of an International Institute with such terms of reference at Izmir in Turkey, for the study of the Mediterranean and Near East gene-centres. Institutes of this type represent an essential stage in the development of a co-ordinated world genetic conservation programme based upon the genecological concept stressed by Vavilov and later workers that the potentialities of species are determined by the potentialities of the local populations of which the species are composed ; population gene-pools are associated with particular localities and are the consequence of the continuous interaction of adaptive, quantitative, genetic variability and the selective forces of their environments.

It is deeply disturbing to note, however, that a great danger to the Izmir project exists which may seriously undermine the vital work not only of this but of later international projects of the same type which it has already been proposed should be established at Peshawar and on the South American continent. This danger lies in the inability of remote administrators to understand the genecological principles upon which the project was founded, and in their attempt to impose upon the institute at Izmir a national rather than an international character, based upon orthodox plant breeding and empirical plant introduction, ignoring the fact that for many genera and species of cultivated plants Turkey can in no way be compared with other countries which do not possess the same genetic diversity. The interests of Turkey herself depend upon the exploration, recording, and systematic utilisation of her extraordinarily rich genetic resources, rather than the empirical introduction of uniform varieties which can only hasten the process of gene erosion.

From their earliest stages, discussions on the Izmir institute emphasised the paramount importance of genetic conservation, and of the exploration, cataloguing and evaluation of the valuable genetic resources of the Mediterranean and Near East gene-centres. "The old technique of collecting material in large amounts and in a haphazard way," states an early discussion document on the project (1959), "must be replaced by one based on a full appreciation of the ecological requirements and distribution of the individual genus or species being collected," in order to prevent a swamping of plant introduction services with genetically unrepresentative material. "This demands as complete a knowledge as possible of the natural vegetation and primitive crops of a region, of the flora and the ecological habitats of the important genera and species." Such detailed local knowledge can best be served by the creation of skilled teams of crop ecologists, taxonomists and genecologists based in the regions concerned. Upon these considerations the Izmir project was conceived, and they form the basis of the final agreement signed by U.N. Special Fund, Turkish Government and F.A.O. representatives in 1963. Erkun (1961, 1963) admirably summarises the proposed functions of the Izmir institute, and correctly stresses the importance of its rôle as an international plant exploration centre. Attempts to impose a change, and to create at Izmir a national plant introduction centre, neglect alike the necessity of genetic conservation and the fact that if plant introduction is to enter a planned, scientific, phase then it can only do so upon the basis of systematic exploration of the world centres of genetic diversity. Plant introduction must of course be developed in Turkey as in every country, but the Izmir project must remain the international exploration centre it was designed to be.

The 1961 recommendations observe that "inadequacy of fundamental research on the origin, genecology, adaptability, variability and distribution of plants of economic importance is hindering the development of practical work in the study of utilisation of the world's genetic resources." Genetic conservation and plant introduction will therefore depend upon the supply of trained scientists specialising in these subjects. It is suggested that universities should consider opening specialist research departments. There is an urgent need to establish training facilities in every country. The Izmir project, by accumulating experience of the problems in this field, can materially contribute to such training.

In addition to the shortage of specialists, a lack of adequate floristic knowledge of the gene-centres is hindering the development of fundamental research, so that the publication by Davis *et al.* (1965) of the first volume of a Flora of Turkey may be regarded as of the greatest importance. This, and other works of the same type in other gene-centres, should receive every possible assistance towards rapid and effective completion.

The full implementation of the programme outlined in the F.A.O. recommendations requires a major, co-operative world effort. Without such an effort, much of the work of those who have indicated by their researches the nature of the mechanisms by which genetic diversity is created, and who have pointed to the great value to man of the existing genetic resources in the world, will have been in vain. It remains for the scientists and governments of every country fully to recognise this fact and to support the F.A.O. 1961 recommendations, hardly more appropriately than through the present projects for international co-operation—the International Biological Programme and International Co-operation Year, and through the F.A.O. itself and the Izmir project.

Urgent action is needed immediately to prevent irreparable loss to the world of its genetic resources. These resources are a human heritage, amassed and created by man himself, however unconsciously, in the long and painful course of his rise from savagery to civilisation. In conserving and utilising these resources, we will truly be laying the foundations not only for a new plant breeding, but for a richer human society. Here indeed, in the sphere of "the study of original material, and of the origins of cultivated plants," there is truly, in the words of Vavilov, "abundant scope for work of such importance as would serve even the highest aims of the plant breeder."

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GENECOLOGY, AGRICULTURE AND COMPUTERS

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Introduction

At the risk of oversimplification, it may be said that the principal aim of classical plant breeding is the production of constant varieties which, when cultivated under conditions in which competition from other plants is reduced to a minimum, will give the best yield of food for human consumption, or, less frequently, for the consumption of animals which will themselves provide human food.

Although there are obvious exceptions (e.g. fruit trees), most such plants are grown as annuals, being cropped only once, and cropping may remove any possibility of reproduction. Even where it does not, the reproduction of the plants that are cropped is generally of little or no useful significance ; on the contrary, it may sometimes lead to one year's crop becoming the next year's weeds, and this is something to be avoided. Desirable varieties are usually maintained by cultures grown, perhaps under special conditions, solely for the purpose of producing seed or other instruments of propagation.

Sometimes, where it is the vegetative part of the plant which is cropped, reproductive capacity and crop yield may be in direct conflict ; early flowering (bolting) of such plants as lettuces or beetroot provides a well-known example of this. One of the problems of the plant breeder is then to strike a proper balance, for the ability to reproduce remains essential if the variety is to be maintained.

Forage Crops

The application of plant breeding methods to perennial forage crops presents a somewhat different picture. Here the plants, usually grasses or clovers, are cropped many times, and the pasture may be required to last for many years. Initially, the ground will have been cleared before sowing, and the crop will start off relatively free from competition. But the normal wild inhabitants will sooner or later begin to invade and re-establish themselves. In general, in any situation which is reverting to more natural conditions from active cultivation, the wild plants will tend to be the better adapted, and will be able to compete successfully with the cultivars.

Unless the pasture is to be short-lived, the plant breeder will now have to give at least some consideration to the ability of his products to compete. This competition needs to be effective not only at the vegetative level, but it will be advantageous if it can also be effective at the reproductive level. If, as plants die, they can be replaced by new plants coming from seed produced within the existing crop, this will clearly stiffen the resistance which natural invaders will have to face. Reproductive capacity of the crop may therefore be of some importance, but it is not just a simple matter. The breeding system of the plant may be a key factor, for an outbreeding species may, because of pollination by wild relatives, produce seed which is genetically inferior. Putting this another way, the wild plants may invade not merely directly, but more insidiously through reproduction.

The situation becomes much more complicated when pastures are designed to be mixed, of two or more species. Here, competition between the chosen species has to be taken into account. Unless the constitution of the pasture is to change considerably with time, there must be a balance not only in the vegetative competition of the species concerned, but between their reproductive capacities. Moreover, this balance is liable to change with time.

Hill pastures

Leaving traditional aspects of plant breeding, we come to an almost virgin field in which many of the problems are completely different, and call for very different methods of solution.

So far, we have considered the situation where land can be cultivated, constantly where the crops permit or initially where they do not. But there are vast areas where even initial cultivation is impracticable or its cost prohibitive. These are the hill farming areas where the pastures are poor to very rough, and where the nature of the ground or its topography make it practically or economically impossible to clear the land and follow the ley farming methods of less hilly regions. Scotland in particular has a large amount of such country. If some economical way could be found of improving the quality of Scottish hill pastures, this could have a profound effect on the welfare of Scottish agriculture.

But the problems are immense, they will take a long time to solve, and the practical application of the solutions is likely to take even longer. If anything is to be done, these problems should be considered now, and from many points of view. Whether the ideas which follow have any practical possibility, I do not know, but I hope that they may perhaps give some stimulus to those who have a more direct familiarity with this aspect of Scottish agriculture than I have, and lead to better answers to the problems than I can give.

One obvious approach to the improvement of hill pastures is the use of fertilizers, to increase the total productivity. But this is little better than a negative approach, unless fertilizers can be found which preferentially encourage the more desirable species. More positive would be attempts by the use of selective weed-killers to improve the balance between the desirable and undesirable components of the natural hill pasture vegetation, and if this were combined with the use of fertilizers it might well be effective.

But such effects would be temporary, and treatment would need to be constantly (and perhaps expensively) repeated.

Has the plant breeder anything better to offer? The difficulties are considerable, and arise from two main reasons. Not enough of agricultural significance is known of the ecology of hill farming areas. The orthodox approach of the plant breeder is inapplicable.

Broadly speaking, there are two ways of approaching the problem. We may try to produce improved strains of fodder species already existing in the pastures, or we may try to produce strains of other species which we would hope later to introduce successfully into the pastures.

There are also two ecological possibilities. We may have to take the pastures as we find them, and our new forms will have to be adaptable to the prevailing conditions; this will probably be the usual state of affairs. Or in some cases it may be economically possible to alter the environment, by changing the drainage, for example, or by introducing fertilizers by irrigation methods, or by planned grazing management; the aim would be to integrate plant breeding and ecological manipulation.

From the genetical point of view, the more difficult (and more interesting) problem is the improvement of already existing species in pastures which it is either impracticable or uneconomical to modify ecologically. The remainder of this essay will concentrate on this problem, and will consider it primarily with regard to the grasses in the pastures.

The primary plant-breeding aim would be to produce improved grasses which are ecologically well adapted to hill farming conditions. We will usually have to start from scratch, by drawing on the genetical variation already present in natural populations. Our starting material will have to be selected carefully, and this will require a genecological understanding of the communities from which this raw material is to be drawn.

But the production of improved forms is only the beginning of the problem. Success achieved, we would then be faced with the difficulty of introducing our new varieties into the existing communities.

Where we are unable to obliterate the present communities by ploughing or other means, and replace them by our own creations, any improved varieties will have to penetrate those communities by active and successful competition, and establish themselves permanently. Such penetration will have to be not only by vegetative competition, but by reproductive competition as well. Now, reproductive capacity comes to be of prime importance, in terms both of seed production and of the ability to compete aggressively through hybridization with the existing forms in the community. We shall have to consider how far we can actively assist such competition.

This complex and challenging problem calls for the practical application of a theoretical understanding of population genetics and of the ecological problems which are involved.

If introduction in the first place is to be by seed, we are faced with the difficulty that in a closed community, only a small proportion of such seed is likely to germinate, grow and

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reach maturity, though a maximization of the ability to do this would be one of our objectives. Unless the resultant plants have a strong competitive advantage, this method will often be ineffective.

Alternatively, it might be practicable to clear strips of ground and grow relatively pure stands of the desired strains, and hope that seed from these strips would eventually allow a gradual penetration of the pastures. We should have to make sure that our strips were not preferentially grazed.

Since grasses are wind-pollinated, another, more subtle, method of introduction could be by pollen, putting new genes into the existing population by way of hybridization. Artificial distribution of pollen would require accurate timing, and would also have the difficulty that grass pollen is often very short-lived. Again, growing the desirable variety in cleared strips would allow penetration by pollen, and over a wider range than penetration by seed. For this purpose, pollen production higher than that of the normal wild form would be one of the qualities the plant breeder would need to produce. But there is a more subtle possibility, by way of an attack through the breeding system.

The pollen approach is only applicable to species which are largely outbreeding. If it were possible to produce a variety which was largely self-fertilizing yet continued to shed plenty of pollen, and if any effect of inbreeding depression could be satisfactorily minimized, we would have a situation essentially like that postulated by Crosby (1960) for the primrose in S.W. England, where the self-fertilizing homostyle form, because it can still outcross onto one of the heterostyle forms, is at a considerable advantage over the heterostyle forms and is slowly replacing them.

Whatever method we choose to employ in introducing our new varieties into the existing habitat, there may often be the opportunity at the same time of helping them by suitable ecological action, modifying the habitat and altering the competitive balance between wanted and unwanted in favour of the former. Where it is known in advance that such action will be possible, this should be taken into account by the plant breeder, who will aim to produce varieties which will take the maximum advantage of such ecological assistance.

One special example of ecological action would be an attempt to eliminate unwanted (weed) species from the pastures. A novel possibility which might be put to the plant breeder would be that he should turn his attention to these weed species. The aim here would be to produce competitively ineffective forms whose pollen could be used to weaken genetically the natural forms; or, better still, which would on crossing with the natural forms produce sterility and so reduce their reproductive capacity. Closely related species which produce sterile hybrids may in some cases already be available. Would this be an effective method of reducing the competition from unwanted species in hill pastures?

One question which would need to be answered is this. If a proportion p of the total seed production of the weed species normally grows and develops to maturity, then if we introduce sterility in the way suggested and so produce a much lower quantity of viable seed, does the same proportion p of this seed develop to maturity, or is there a compensating increase in p? On the extent to which there is such an increase, the effectiveness of the technique suggested partly depends.

The theoretical attack

The ideas which have been put forward in this essay are born not so much of an intimacy with the problems involved, as of a broad interest in the fields of population genetics and genecology. Other, and better, ideas should come from those more closely concerned. But whatever may be the merit of any suggestion, before its practical application can be instigated careful consideration will have to be given to the underlying genetical and genecological theory, so that we may have sufficient understanding of the problems we are trying to solve.

The situations we have been considering, involving as they do problems of vegetative and reproductive competition, population genetics and ecology, are highly complex, and their theoretical investigation by the more usual mathematical methods would be a matter of great difficulty, even if it were possible, calling for a high degree both of mathematical and biological competence—a rare combination. It would probably require too great an element of simplification to have much general validity.

An easier and more satisfactory approach would be by way of exploiting the new techniques of computer simulation, in which abstract models of genetical systems are set up, and allowed to evolve according to whatever conditions we choose to prescribe.

Such models can be of two kinds. One has a fundamentally mathematical basis, a complex mathematical model being devised which can rapidly be dealt with by a computer. This has been successfully used, for example (Crosby, 1960), to study simultaneous evolution in a number of primrose populations separated in space but partially interbreeding ; this particular model was eventually developed to deal with an area containing 150 such populations in various habitats, and it was followed for a simulated 200 years.

A second method eliminates the mathematical basis, substituting a direct simulation by patterns within the computer of the genotypes of the organisms to be considered (Crosby, 1963). The computer, as it were, contains one or more populations of electronic plants, and these can (among other things) be made to reproduce and compete with one another according to any rules we choose to apply. These rules may correspond closely to what we consider to be the " rules of nature ", or they may take any form, however fanciful, which we may choose. This technique is being used at the moment to study the population genetics of the situation where two related subspecies, capable of interbreeding but with low hybrid fertility, have ranges which partially overlap. 300 generations can be produced in an hour of computer time.

Both of the experiments given as examples have features which would be relevant to the agricultural problems I have been discussing, and there is no doubt that similar techniques could be used equally successfully here. Not only would this approach be practicable, but it is probably the one most likely to succeed.

Computers and biologists

Perhaps the biggest difficulty would arise from the curious (and erroneous) belief which many biologists seem to have that computers are things they could never understand and use, and to which they therefore close their minds.

The attitudes of biologists to computers vary greatly. There are some who take the view that it would take too much of their time to learn how to programme a computer ; but it takes time and experience to learn how to use any complicated piece of equipment properly, even a microscope. Perhaps there is an illogical resentment against having to go to the time and trouble of learning to use a machine which itself performs highly complicated operations in little time and with no trouble.

In fact, it is not difficult, does not require much knowledge of mathematics, and does not take very long to learn how to programme a computer ; after that, programming experience is the teacher, and the more experienced the programmer becomes the more competent will he be, and the greater the complexity of the situations with which he can deal.

At the other extreme are those people who say "I have a very interesting problem, do you have a programme which will solve it for me ? " imagining that in some miraculous way computers are equipped with a large stock of programmes capable of solving off-hand any problem which may arise.

Any problem requires to have its own programme, specially written for it. Although many different programmes will have features in common, where similar processes are involved (e.g. reproduction and selection), yet the ways in which these processes are used and put together must vary from programme to programme, having regard to the special features of the different problems.

Although to some biologists the need to undergo the labour involved in writing programmes seems to be a formidable deterrent, it is one of the strong points in the application of computer techniques to biological problems. Paradoxically, one may get as much benefit from producing a computer programme as from a study of the results coming from it. This is because you cannot effectively simulate a biological system which you do not understand, and you may not realise that you don't understand it until you start writing a programme. Programmes which may be correct from a computing point of view may produce results which are biological nonsense ; if the biology of the programme is not understood, the conditions set initially in the programme, and the methods used, may have been biologically nonsensical. During the struggle to produce biological sense, a great deal may be learnt about the problem, and one may be brought face to face with important aspects of it which have been overlooked or which had not been thought worth considering.

Even if a programme never produces a sensible result, its construction will almost certainly lead to a much better understanding of the problem than would have been achieved in any other way. Travelling may be more rewarding than arriving, although, of course, one usually does arrive eventually.

It seems clear that the application of computer techniques to the genetical and genecological problems involved in the improvement of hill pastures would lead to a clearer understanding of the principles involved, and would greatly increase the possibility of practicable solutions being found within a reasonable time.

The solutions may be slow to arrive ; their effective application must, because of the nature of the problem, take even longer. But the beneficial effect on Scottish agriculture should, eventually, be considerable. The sooner an attack is begun along these lines, the sooner may we see an improvement in the productivity of Scottish hill farming.

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INTERACTIONS IN MIXTURES OF HERBAGE GRASSES

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Summary. The performance of four herbage grasses, two cocksfoot varieties and two ryegrass varieties was compared in pure stand in all possible 50 : 50 mixtures at two densities (2 in. spacing and 4 in. spacing) and under two different cutting régimes. Under one cutting regime (HS 1) the material was kept vegetative, in the other (HS 2) the plants were allowed to pass out of the vegetative phase before the first cut but were frequently defoliated thereafter. Neither density nor cutting treatment had any effect on total yield but cutting treatment had a marked effect on competitive performance of the different components and also on the relationship between pure stand and competitive performance of individual components. Under the cutting treatment HS 1 the two ryegrass varieties showed greater " competitive ability " than the two cocksfoots and competitive ability tended to be associated with vigorous performance in pure stand, under the conditions of HS 2 the cocksfoot varieties were competitively superior, one of them markedly so, and there was no obvious relationship between mixture and pure stand behaviour. In general the effects of density on competitive behaviour were slight, being negligible in HS 1 and non-significant in HS 2. Mixture yields tended to exceed the yields of the mid-pure stands. The use of V_r/W_r graphs in interpreting the behaviour of mixtures is discussed.

Introduction

This paper deals with the behaviour of four herbage grasses when grown alone and in mixture with each other. The term element has been used when referring to any single component of a mixture ; this has been done since some taxonomically neutral term seems desirable when referring to single components of a group which may consist of say, different genera and different species within genera.

The assumption is often made, implicitly if not explicitly, that any one element will perform in similar fashion in pure stand as in mixture. The validity of this assumption is of obvious interest to plant breeders, especially those dealing with outbreeding species; in the case of the herbage grasses the question is also of importance to the agronomist since it is common practice to grow mixtures of varieties, species and genera of herbage plants.

Most studies of the behaviour of mixtures have been conducted on plants grown primarily for their seed yield, mostly cereals and usually the characters measured have been those of the mature plant, either grain yield or plant weight, tiller number etc., when the plant was " ripe to harvest ". There have been relatively few investigations based on vegetative behaviour of plants in mixture.

The most comprehensive series of experiments comparing the behaviour of elements in pure stand and in mixture have been carried out by Sakai and his co-workers. Sakai (1955) found that elements which performed well in pure stand did not necessarily do well in mixture with others and in some cases found the exact opposite. Sakai also found that increases in plant density, while tending to increase the magnitude of competitive effects, did not alter the relative performance of elements. Sandfaer (1954) working with two element mixtures of barley and oat varieties also found no effect of density on competitive ability.

Allard (1961) found that mixtures of three pure lines of Lima beans tended to give lower seed yields than the mean of the pure stands and attributed this to a negative correlation between seed yield and vegetative vigour, so that in mixture the vegetatively vigorous but low seed yielding lines were suppressing their less vigorous but better seeding associates.

Hanson, Brim and Hinson (1961) investigating seed yields of Soybean found that the competitive advantage gained by one of a pair of competing units tended to be the competitive disadvantage for the other. Eberhart, Penny and Sprague (1964) report a similar effect in maize.

The performances of mixtures as such compared with pure stands have been reported on by a number of authors, Simmonds (1962) has reviewed the literature up to that date and summarises the results of most workers by saying ". . . the general conclusion that emerges may be stated thus: the performance means of mixtures are often equal to the means of components but they sometimes exceed them and occasionally even exceed the higher components; they are rarely inferior to the mean of the components ". Work carried out since Simmonds' review tends to confirm this summary although Allard's findings quoted above give one reason why the reverse may hold when competitive vigour depends on some character of the plant which shows a negative correlation with the character under consideration.

Materials and Methods

The four herbage grasses concerned were Ayrshire perennial ryegrass, Scotia perennial ryegrass, Daeno II cocksfoot and Scotia cocksfoot; these are identified as elements A, B, C and D respectively. Ayrshire ryegrass is an early flowering indigenous commercial variety, it is not particularly leafy and does not recover well after cutting; Scotia ryegrass is a variety selected from Scilly Isles material, it is rather similar in flowering time and growth habit to S.23 and is much later flowering than the other three elements. Scotia cocksfoot is a variety selected from plants growing in a small woodland clearing and might be expected to be more shade tolerant than the other three elements, there is some evidence from agricultural use that this variety does not persist or yield well in mixture with other grasses. The mean ear emergence dates for these elements at Edinburgh are :—

A	Ayrshire Perennial Ryegrass	15 May
B	Scotia Perennial Ryegrass	12 June
C	Daeno II Cocksfoot	6 May
D	Scotia Cocksfoot	8 May

Seed of all elements was sown in seed pans on 8th May, 1963, and seedlings were pricked into boxes 17 in. × 17 in. × 3¾ in. deep (43.2 × 43.2 × 9.5 cm.). The plants remained in these boxes for the remainder of the experiment. The plants were set out in a square grid arrangement with uniform and equal spacing between and within rows; three densities were employed having 1 in. (2.5 cm.), 2 in. (5.1 cm.) and 4 in. (10.2 cm.) between neighbouring plants but the behaviour of the material at the 1 in. spacing is not dealt with in this paper since it proved very difficult to harvest separately the individual elements of the mixtures at this spacing. Each replicate consisted of ten boxes, four of them containing the pure stands of the elements and six containing one each of the possible two element mixtures; in the "mixed" boxes plants of the two elements were planted alternately so that a plant of one element had as its closest ("square") neighbours plants of the competing element and as its diagonal neighbours plants of its own element. Within each density four replicates were used, two being used for each of two different cutting régimes differing in times of cutting, these cutting régimes are referred to as "Harvest Series" 1 (HS 1) and "Harvest Series" 2 (HS 2). All boxes were harvested three times in 1963 and five times in 1964, only the results for 1964 are discussed in this paper, the 1964 harvest dates are given in Table 1. At each harvest the plants were cut at ½ in. (1.25 cm.) above the soil surface, oven dried and the dry weights recorded. In the "mixed" boxes, the two elements were harvested separately and in 1964 the pure stand boxes were treated in an analogous fashion, *i.e.* alternate plants were harvested separately to give two "dummy" elements for each pure box. Immediately after each cut each box received 6.5 gms. (≏ 3 cwts/acre) of general fertiliser containing 12 per cent N. Details of the yields are given in Tables 2(*a*)-(*d*).

TABLE 1

DATES OF HARVEST FOR EACH HARVEST SERIES

HARVEST	HARVEST DATE	
	HS 1	HS 2
1	2 May	20 May
2	18 June	3 July
3	21 July	28 July
4	25 August	28 August
5	28 September	4 October

TABLE 2(*a*)

DRY WEIGHT YIELDS IN GRAMS/½ BOX FOR EACH HARVEST AND EACH REPLICATION IN 1964 FOR HS 1. LOW DENSITY

Assoc. / Element		A		B		C		D	
		Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
A	1	15.4	21.7	18.7	29.1	19.1	26.1	22.8	28.5
	2	49.5	51.6	48.3	51.6	64.6	55.4	60.8	72.6
	3	9.3	8.0	9.4	9.7	8.9	7.4	12.4	7.8
	4	16.5	14.6	14.4	10.7	14.5	6.6	17.5	17.9
	5	12.4	12.8	9.1	9.0	7.9	6.7	12.3	14.1
B	1	11.4	15.0	11.3	17.7	18.7	18.3	16.7	22.9
	2	53.4	62.8	57.9	65.1	77.0	76.3	65.3	101.1
	3	14.7	7.2	11.9	8.8	15.2	8.4	12.5	11.7
	4	25.3	17.9	20.2	18.0	21.7	16.2	16.9	24.0
	5	14.0	16.7	11.7	12.8	13.6	12.0	13.5	15.2
C	1	9.2	13.2	11.6	15.3	13.2	19.6	16.3	27.4
	2	26.3	36.5	30.4	28.6	34.3	34.7	43.8	39.3
	3	12.7	17.0	10.9	11.4	11.8	11.6	17.4	13.8
	4	15.9	18.5	13.5	16.6	13.7	13.9	19.2	18.0
	5	11.9	17.2	9.9	11.5	10.6	10.0	14.0	14.3
D	1	8.0	9.9	11.2	10.8	7.8	18.7	14.4	17.1
	2	29.4	26.9	34.6	22.3	25.9	35.6	38.6	42.7
	3	10.2	7.2	12.3	7.7	6.9	8.8	12.3	9.6
	4	13.0	11.7	13.7	11.4	6.7	11.7	14.3	13.6
	5	11.5	8.8	12.5	9.2	4.8	7.5	8.6	10.0

TABLE 2(*b*)

AS 2(*a*) BUT FOR HS 1. HIGH DENSITY

Assoc. / Element		A		B		C		D	
		Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
A	1	19.0	24.9	23.7	26.8	24.3	26.8	22.2	41.8
	2	46.3	43.6	60.6	51.9	59.6	59.2	65.2	81.6
	3	12.0	10.6	10.6	8.7	11.4	10.4	16.1	9.3
	4	18.7	18.4	12.4	15.7	12.1	11.5	17.0	13.8
	5	16.2	15.5	12.1	10.7	9.1	9.2	14.8	9.2
B	1	10.0	18.4	12.1	19.3	16.3	22.6	15.5	24.5
	2	51.5	76.3	54.5	74.1	84.9	97.2	80.9	96.4
	3	12.0	11.0	13.5	10.5	13.5	11.5	15.3	11.2
	4	17.9	25.1	17.6	17.6	18.2	17.1	21.9	18.6
	5	15.1	5.9	15.1	14.7	13.0	13.7	17.8	13.2
C	1	10.5	12.7	10.8	15.4	14.8	21.9	14.4	26.0
	2	29.4	25.8	27.5	29.3	37.3	34.3	38.8	43.6
	3	16.2	14.7	11.5	13.7	13.6	14.0	8.1	18.5
	4	17.5	17.7	13.0	16.4	13.8	14.8	17.9	19.9
	5	15.6	12.8	10.8	11.6	9.6	10.8	14.0	14.4
D	1	7.5	13.4	9.9	13.9	11.6	13.4	16.8	20.2
	2	26.7	36.1	32.9	25.9	37.8	25.2	45.1	33.5
	3	9.6	15.1	8.1	12.1	14.7	10.2	10.9	12.0
	4	11.8	22.0	8.4	15.7	9.4	9.8	13.3	13.3
	5	11.4	16.9	7.5	11.6	7.5	6.4	10.5	9.6

TABLE 2(*c*)

AS 2(*a*) BUT FOR HS 2. LOW DENSITY

Assoc. Element		A		B		C		D	
		Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
A	1	47.9	67.0	46.5	69.6	65.4	55.5	53.4	54.8
	2	24.5	22.9	24.4	18.9	26.0	13.7	31.5	18.0
	3	9.3	10.0	9.1	7.0	5.2	7.9	9.1	6.9
	4	12.6	13.2	10.8	11.0	7.4	6.0	10.4	8.6
	5	13.6	13.0	11.0	11.3	5.0	4.5	7.8	7.6
B	1	28.4	41.0	35.0	43.8	27.1	44.4	37.9	47.3
	2	37.8	23.3	30.5	26.7	27.3	24.7	41.5	27.6
	3	11.6	9.9	10.6	10.1	6.9	7.5	11.1	9.9
	4	16.4	18.1	12.1	15.2	6.8	8.3	10.9	12.0
	5	16.2	16.3	13.1	13.3	5.1	6.0	10.9	10.3
C	1	33.7	57.4	58.5	91.1	52.8	52.7	66.7	54.7
	2	29.0	28.1	28.0	30.6	26.5	17.7	33.4	20.4
	3	13.9	13.0	15.8	14.0	9.9	10.3	13.1	11.9
	4	19.8	23.8	20.6	23.3	12.6	13.1	16.7	15.5
	5	17.2	19.7	19.3	15.9	11.5	10.7	16.1	13.2
D	1	33.2	54.3	33.9	36.6	28.3	48.8	45.7	45.5
	2	22.7	23.9	18.7	18.8	16.1	14.8	22.6	18.5
	3	12.6	13.4	11.3	11.5	6.3	8.2	11.1	9.7
	4	16.1	19.3	13.8	15.9	7.7	10.4	13.0	13.3
	5	14.8	16.6	14.0	14.3	7.0	8.7	12.0	10.0

TABLE 2(*d*)

AS 2(*a*) BUT FOR HS 2. HIGH DENSITY

Assoc. / Element		A		B		C		D	
		Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
A	1	49.9	62.8	51.7	54.3	79.1	76.6	72.7	74.8
	2	24.9	29.1	45.1	23.6	40.1	16.0	32.8	26.4
	3	11.3	11.6	12.8	6.2	10.1	6.5	8.5	8.6
	4	17.4	17.1	15.7	7.5	9.9	5.8	10.4	9.6
	5	14.7	15.5	13.3	8.0	7.3	3.9	7.1	8.5
B	1	22.9	43.8	29.2	43.8	36.3	35.1	43.4	60.9
	2	42.6	39.4	50.3	29.8	27.5	28.6	36.6	36.0
	3	9.9	13.4	10.5	10.1	8.6	9.9	11.9	12.9
	4	14.9	16.5	15.2	15.0	10.1	9.3	15.5	12.6
	5	13.3	17.9	14.5	13.9	7.4	8.5	11.6	11.4
C	1	26.4	59.7	38.8	50.7	44.1	41.3	56.0	59.3
	2	26.8	29.0	24.7	22.5	25.9	19.6	37.7	30.1
	3	14.3	18.4	14.8	10.7	9.6	10.2	17.5	15.2
	4	23.7	22.5	15.3	17.9	14.1	12.8	21.5	17.3
	5	16.3	17.1	16.9	14.9	10.4	9.2	16.4	13.8
D	1	23.7	39.7	24.0	32.7	23.9	33.0	27.3	37.4
	2	30.1	22.7	21.2	18.9	16.8	15.2	19.7	22.5
	3	13.9	15.1	9.5	11.0	6.7	8.6	9.9	10.3
	4	19.9	17.5	12.6	13.9	8.1	9.7	11.7	12.5
	5	16.0	14.9	11.8	12.8	5.9	7.3	9.0	9.0

In general the statistical symbols used are those employed by Eberhart *et al.*, (1964), but for convenience of presentation the following symbols are used when describing the performance of specific elements :—

AA mean whole box yield of pure stand of element A. Similarly BB, CC, DD.

Aa	mean $\frac{1}{2}$ box yield of pure stand of element A. (Each box gives two estimates of Aa; their sum = AA). Similarly Bb, Cc, Dd.
AB	mean whole box yield of elements A and B in mixture. Similarly AC, ..., CD.
Ab	mean $\frac{1}{2}$ box yield of element A when grown with element B. Similarly Ac, ..., Dc. Ab + Ba = AB.

The layout of the experiment is analogous to a genetic diallel containing all reciprocal progenies and parental lines. One obvious approach to the analysis of the results is to set them out in a two-way table so that the element arrays occupy the rows and the associate arrays the columns for each replication, the pure-stand yields (reduced to the same basis as the mixed yields, in the present case to half plot yields) then occupy the NW-SE diagonal. The table can then be analysed for row (element) effects; and column (associate) effects; their interaction and the interactions of these three with replications. There are two main objections to this approach, in the first place the model on which it is based can only include an estimate of competitive effects of the one element from its effect on the other elements, it provides no estimate of the comparison between the behaviour of one element in mixture and in pure stand; a further objection in the present case is that the design is not strictly orthogonal since the pure-stand yields are derived from whole plants and may be expected to have reduced variances from the mixed-stand yields which are derived from half plots.

Williams (1962) has published an analysis based on the analogy with the genetic diallel using plot sums and within plot differences and involving weighting the yields of pure stand plots in inverse proportion to the variances of pure stand plots and mixed plots. He goes on to compute an index of competition for each element based on the average effect of each element on all the others. Eberhart *et al.*, (*loc. cit.*) point out that the model on which this and similar diallel analyses are based is incorrect if the data are available for each individual entry. Eberhart *et al.*, have produced a model which in effect measures deviations about the pure-stand mean and it measures competitive effects of an element as average increments from the pure-stand mean of that element; these authors define three types of competition effect :—

$\hat{k}$	the general competition effect, the average difference between all mixed plots and all pure stand plots on a single entry basis, positive if on average elements yield more in mixture than in pure stand.
$\hat{sk}_i$	the element by general competition effects, positive if the i^{th} element performs better in mixture than in pure stand after allowance has been made for $\hat{k}$.
$\hat{c}_{i(i')}$	specific competition effects accounting for any further deviation in the yield of the i^{th} element grown with the i'^{th} element, not explained by $\hat{k}$ and $\hat{sk}_i$.

The difficulty with this model is that in the presence of numerous significant specific competition effects it is difficult to interpret the values of $\hat{sk}_i$. In this situation it seems better to adopt a quasi-split plot analysis for the calculation of whole and sub-plot errors and then make such particular comparisons as seem useful. Such an analysis has been devised for the present experiment by Sampford (private communication). A worked example is shown in Tables 3 and 4. Since there are only two replications the error items are based on replication differences. The differences between two halves of the same pure-stand plot have been treated on exactly the same basis as the other within plot differences, this tends to reduce the variance due to within plot differences but gives a slightly better estimate of the within plot error.

Writing M_1 and M_2 for the whole plot and within plot error mean squares respectively standard errors can be calculated as in Table 5.

In this paper Eberhart's analysis has been used but for the reasons given above certain comparisons have been made on the basis of Sampford's quasi-split plot analysis.

Results

All data for 1964 were first analysed by the method of Eberhart *et al.* Data for the two harvest series were analysed separately. In Hs 1 there were no significant interactions between element effects and density, in HS 2 significant interactions were present but inspection of the data indicates that they are mainly due to differences in behaviour of the pure

TABLE 3

DATA ON WHICH EXAMPLE OF QUASI-SPLIT PLOT ANALYSIS (IN TABLE 4) IS BASED. HALF-PLOT YIELDS FOR SECOND HARVEST HS 1. LOW DENSITY. (GMS. PER HALF-BOX)

	$Y_{i(i')}$ = HALF PLOT YIELDS				$Y_{i(i')} + Y_{i'(i)}$ = PLOT TOTALS				$Y_{i(i')} - Y_{i'(i)}$ = WITHIN PLOT DIFFERENCES			
	REP. 1		REP. 2		REP. 1	REP. 2	1 + 2	2 − 1	REP. 1	REP. 2	1 + 2	2 − 1
	$Y_{i(i')}$	$Y_{i'(i)}$	$Y_{i(i')}$	$Y_{i'(i)}$								
Aa	44.8	54.1	54.1	49.1	98.9	103.2	202.1	4.3	−9.3	5.0	−4.3	14.3
Ab	48.3	53.4	51.6	62.8	101.7	114.4	216.1	12.7	−5.1	−11.2	−16.3	−6.1
Ac	64.6	26.3	55.4	36.5	90.9	91.9	182.8	1.0	38.3	18.9	57.2	−19.4
Ad	60.8	29.4	72.6	26.9	90.2	99.5	189.7	9.3	31.4	45.7	77.1	14.3
Bb	49.5	66.2	68.4	61.7	115.7	130.1	245.8	14.4	−16.7	6.7	−10.0	23.4
Bc	77.0	30.4	76.3	28.6	107.4	104.9	212.3	−2.5	46.6	47.7	94.3	1.1
Bd	65.3	34.6	101.1	22.3	99.9	123.4	223.3	23.5	30.7	78.8	109.5	48.1
Cc	36.2	32.3	30.6	38.7	68.5	69.3	137.8	0.8	3.9	−8.1	−4.2	−12.0
Cd	43.8	25.9	39.3	35.6	69.7	74.9	144.6	5.2	17.9	3.7	21.6	−14.2
Dd	43.5	33.6	45.3	40.1	77.1	85.4	162.5	8.3	9.9	5.2	15.1	−4.7
	533.8	386.2	594.7	402.3	920.0	997.0	1917.0	77.0	147.6	192.4	340.0	44.8

TABLE 4

SAMPLE QUASI-SPLIT PLOT ANALYSIS OF VARIANCE FOR DATA IN TABLE 3

		df.		SS		MS
Between whole plots						
	Replications	$r - 1$	1	$(997.0 - 920.0)^2/40$	148.23	
	Mixtures	$\frac{1}{2}rp(p + 1) - 1$	9	$(202.1^2 + \ldots\ldots + 162.5^2)/4 - CF$	2778.18	308.69**
	Plot error	$\frac{1}{2}rp(p + 1) - 1$	9	$(\ 4.3^2 + \ldots\ldots + \ 8.3^2)/4 - REPS$	134.20	$14.91 = M_1$
Plots		$rp(p + 1) - 1$	19	$(\ 98.9^2 + \ldots\ldots + \ 85.4^2)/2 - CF$	3060.61	
Within plots						
	Differences	$\frac{1}{2}p(p + 1) - 1$	10	$(-4.3^2 + \ldots\ldots + \ 15.1^2)/4$	7798.85	779.89**
	w/i plot error	$\frac{1}{2}p(p + 1) - 1$	10	$(\ 14.3^2 + \ldots\ldots + -4.7^2)/4$	1013.17	$101.32 = M_2$
Total		$2rp(p + 1) - 1$	39	$(\ 44.8^2 + \ldots\ldots + \ 40.1^2) - CF$	11872.63	

TABLE 5

FORMULAE FOR CALCULATION OF STANDARD ERRORS OF MEANS FOR CERTAIN COMPARISONS; BASED ON QUASI-SPLIT PLOT ANALYSIS

	SE one value	SE difference of two values
1. Using recorded plot totals		
(a) Mixture means	$\sqrt{2M_1/r}$	$2\sqrt{M_1/r}$
(b) Mean of all plots containing a particular element	$\sqrt{2M_1/rp}$	$\sqrt{4(p - 1)M_1/rp^2}$
(c) Whole plot competition effects, e.g. AB − ½(AA + BB)	$\sqrt{3M_1/r}$	$\sqrt{6M_1/r}$ with one element in common $\sqrt{5M_1/r}$ no elements in common
2. Using sub plot totals		
(a) Effect of competition on performance of one element when grown with another, e.g. Ab − ½AA	$\sqrt{(M_1 + \frac{1}{2}M_2)/r}$	———
(b) Average effect of competition on performance of one element when grown with all others, e.g. ⅓(Ab + Ac + Ad) − ½AA	$\sqrt{(pM_1 + M_2)2r(p - 1)}$	$\sqrt{\{(p^2 - p - 1)M + pM_2\}/r(p - 1)^2}$

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stands at the two densities, the general competition by element by density effects and the specific competition by density effects being negligible. The results of the analyses of variance are summarised in Table 6, the estimates of pure stand yields $(\widehat{\mu_o + s_i})$, element by general competition effects ($s\hat{k}_i$) and specific competition effects for the total season's yield for each harvest series separately are shown in Table 7. As already mentioned the $s\hat{k}_i$ effects are difficult to interpret in the presence of numerous specific competition effects but four useful points emerge. Firstly, the largest estimates of $s\hat{k}_i$; for Scotia cocksfoot (D) in HS 1 (− 22.6) and Danish cocksfoot (C) (+ 25.7) in HS 2 account for nearly all the variation in these two instances, the associated specific competition effects all being non-significant ; the same applies to Ayrshire ryegrass (A) in HS 2. All other $s\hat{k}_i$ effects are associated with two relatively large specific competition estimates. Secondly, in HS 1 the relatively high values of specific competition estimates for all other elements in association with Scotia cocksfoot are noteworthy. The third and probably most important point is the change in the estimates of the $s\hat{k}_i$'s between the two harvest series, the two ryegrasses being on average relatively "good" competitors in HS 1 and the two cocksfoots being relatively poor, in HS 2 almost the reverse situation applies. Fourthly, in HS 1 the higher values of $s\hat{k}_i$ tend to be associated with the higher values of pure stand performance, i.e. the more vigorous competitors are those with the highest pure stand yields, the effect is not quite consistent, Scotia cocksfoot with a higher pure stand yield than Danish cocksfoot, is, nevertheless, considerably less successful than Danish. In HS 2 there is no obvious association between pure stand performance and average competitive behaviour.

The situation becomes somewhat clearer if we consider the actual behaviour of one element in mixture with another compared to its own pure stand performance (Table 8). In this table each off-diagonal entry represents the difference between the yield of the i^{th} element when grown with the i'^{th} and the yield of i alone (i.e. it is equal to the sum of $\hat{k}$; $s\hat{k}_i$ and $\hat{c}_{i(i')}$). The diagonal entries are the mean pure stand yields gms./half plot. In Table 9 the differences of these values for the two harvest series are shown, a positive (negative) value indicating that element i with element i′ performs competitively better (worse) in HS 2 than in HS 1.

TABLE 6

SUMMARY OF ANALYSES OF VARIANCE FOR FIVE HARVESTS SEPARATELY AND FOR THE SUM OF FIVE HARVESTS FOR EACH HARVEST SERIES

		HS 1						HS 2					
		HARVEST						HARVEST					
Source of variation		1	2	3	4	5	Σ	1	2	3	4	5	Σ
Densities	D	*	NS	NS	NS	NS	*	NS	**	*	NS	NS	NS
General mixture effect	K	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Element Arrays	S (unadj. S)	**	**	**	**	**	**	**	**	**	**	**	**
Elements × Gen. mixture	SK (adj. S)	**	**	NS	*	*	**	NS	NS	**	**	**	**
Specific mixture effect	C	**	**	NS	**	*	**	*	*	**	**	**	**
Density × Elements	DS	*	NS	NS	NS	NS	NS	**	NS	NS	NS	*	**
Density × SK	DSK	—		Not calculated			—	NS		Not calculated			NS
Density × specific	DC	—					—	NS					NS

TABLE 7

ESTIMATES OF PURE STAND YIELDS AND COMPETITION EFFECTS. AVERAGED OVER DENSITIES FOR EACH HARVEST SERIES SEPARATELY. (GMS. PER HALF-BOX)

	HS 1						HS 2					
	$\hat{c}_{i(i')}$				$\widehat{sk}_i$	$\widehat{\mu_0+s_i}$	$\widehat{\mu_0+s_i}$	$\widehat{sk}$	$\hat{c}_{i(i')}$			
$i \backslash i'$	A	B	C	D					A	B	C	D
A	—	-10.2^*	-8.3	$+18.5^{**}$	$+8.0^{cd}$	109.1	122.0	-11.2^{a}	—	-0.3	-1.8	$+2.1$
B	-19.8^{**}	—	$+6.2$	$+13.5^*$	$+15.4^{ad}$	120.9	110.6	-8.7^{a}	$+7.5$	—	-19.6^{**}	$+12.1^*$
C	-4.7	-12.6^{**}	—	$+17.3^{**}$	-0.8^{c}	89.5	103.7	$+25.7^{b}$	-5.9	$+2.7$	—	$+3.2$
D	$+3.5$	-0.3	-3.2	—	-22.6^{b}	92.0	92.6	-5.9^{a}	$+19.3^{**}$	-1.5	-17.9^{**}	—

$\widehat{sk}_i$ estimates having a superscript in common do not differ significantly.
* and ** indicate that the estimates of $\hat{c}_{i(i')}$ are significant at the 5% and 1% levels respectively.

TABLE 8

DIFFERENCE BETWEEN YIELDS OF EACH ELEMENT IN MIXTURE WITH EACH OTHER ELEMENT AND YIELD OF ELEMENT IN PURE STAND (e.g. Ab − Aa) GMS. PER HALF-BOX. PURE STAND YIELDS ARE SHOWN IN NW-SE DIAGONAL. WITHIN EACH CELL OF THE TABLE THE UPPER LEFT FIGURE REFERS TO THE VALUES FOR HS 1 AND THE LOWER RIGHT TO HS 2. IN EACH CASE AVERAGED OVER DENSITIES

ELEM. \ ASSOC.	A	B	C	D
A	**109.1** **122.0**	+ 1.7 − 7.5	+ 3.6 − 9.0	+ 30.4** − 5.1
B	− 0.6 + 2.9	**120.9** **110.6**	+ 25.5** − 24.3**	+ 32.7** + 7.5
C	− 1.6 + 23.8**	− 9.6 + 32.4**	**89.5** **103.7**	+ 20.4** + 33.0**
D	− 15.3* + 17.5*	− 19.1** − 3.4	− 22.0** − 19.8*	**92.0** **92.6**

* and ** indicate significance at 5% and 1% levels respectively.

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TABLE 9

DIFFERENCES BETWEEN MIXTURE AND PURE STAND DIFFERENCES BETWEEN HS 1 AND HS 2. A POSITIVE (NEGATIVE) VALUE INDICATES THAT THE ith ELEMENT IN MIXTURE WITH THE i'th DOES RELATIVELY BETTER (WORSE) IN HS 2 THAN IN HS 1

Assoc. / Elem.	A	B	C	D
A	+ 12.9	− 9.2	− 12.6	− 35.5**
B	+ 3.5	− 10.3	− 49.8**	− 25.2*
C	+ 25.4*	+ 42.0**	+ 14.2	+ 12.6
D	+ 32.8**	+ 15.7	+ 2.2	+ 0.6

* and ** indicate significance at 5% and 1% levels respectively.

In Table 8 a positive value is matched by a negative value for the diagonally opposite entry, i.e. in this experiment, if one element of a mixture does better than the same element in pure stand, then its associate does worse; but in general positive values are of greater magnitude than negative, i.e. any advantage of yields of mixture over pure stand in general is due to the advantage to one element of the mixture being greater than the disadvantage to its associate.

In Table 9 there are six significant changes of competitive behaviour between HS 1 and HS 2. Four of these occur in pairs of opposite sign (i.e. one element in a mixture performing better (worse) and its associate worse (better)), these are the elements of the combinations AD and CB, the remaining two significant changes are also associated with fairly large though non-significant changes of opposite sign, Bd (cf Db) and Ca (cf Ac) the change in behaviour of Bc and Bd is matched by corresponding changes in the behaviour of the pure stand of B and is probably due to factors affecting B as such whether in pure stand or in mixture. The large change in the behaviour of A and D in mixture with each other and the change in the relative behaviour of Ac and Ca do not obviously correspond to changes in pure stand performance.

The relationship between pure stand and competitive performance is shown graphically in Fig. 1 for HS 1 and Fig 2 for HS 2. These diagrams show the differences between pure stand and mixture yield for each element with each associate, compared with the pure stand difference from the mid-pure stand. In HS 1 there is a fairly clear relationship between the relative pure stand performances for the elements in each mixture and their behaviour in mixture with each other, although elements C and D when grown together depart from this trend. In general when two elements are grown together the heavier yielding in pure stand increases its yield and the lower yielding suffers a decrease, these increases and decreases being roughly proportional to the pure stand differences between the elements, although on average the increases are slightly larger than the decreases, which is reflected by the regression line cutting the vertical axis above the origin and, of course, means that mixtures have slightly higher yields than the pure stand yields would imply. In HS 2 there is no similar relationship apparent at either density although certain elements do show a degree of consistency in their behaviour, the concentration of points for element A, for example, in the "S-E" sector of Fig. 2 shows A to be a poor "competitor" despite its relatively good pure stand performance, conversely C is a strong "competitor" in spite of its relatively low yield in pure stand.

The reasons for the differences in relationship between pure stand and mixture performance for the elements in HS 1 and HS 2 are not obvious, but are probably accounted for by the fact that the cutting regime in HS 1 tended to maintain the plants in a much more vegetative condition than was the case in HS 2; in HS 1 competitive behaviour would be largely a reflection of vigour "*per se*", in HS 2 it would be the result of a complex series of interactions between "vigour" and such factors as maturity as determined by time of flowering and regrowth after a "hay cut". The lack of relationship between pure stand and mixture performance in HS 2 is con-

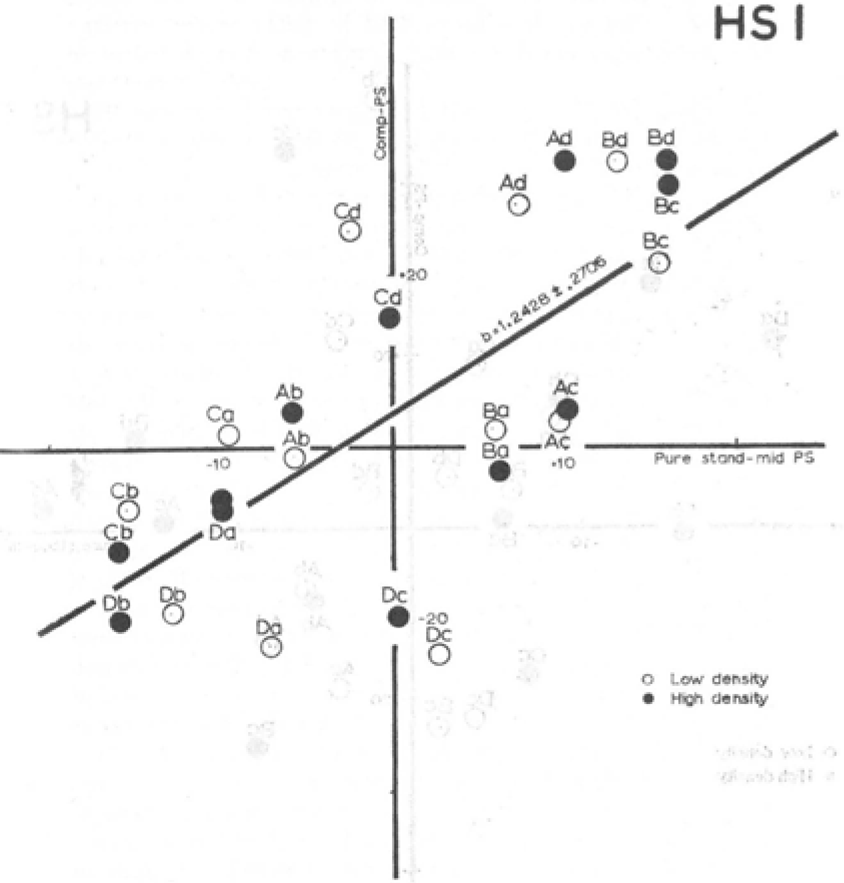

FIGURE 1

HS 1. Sum of five harvests. Relationship between pure-stand deviation from mid-pure-stand (horizontal scale) and competitive yield minus pure-stand yield (vertical scale) for each element in each mixture. Gms./half-box. *e.g.* $\{\tfrac{1}{2}AA - \tfrac{1}{4}(AA + AB)\}$ *v.* $\{Ab - \tfrac{1}{2}AA\}$.

The straight line joining the two points for the two elements in a mixture, *e.g.*, Ab : Ba cuts the vertical axis above (below) the origin by half the amount by which the mixture yield is more (less) than the mid-pure-stand.

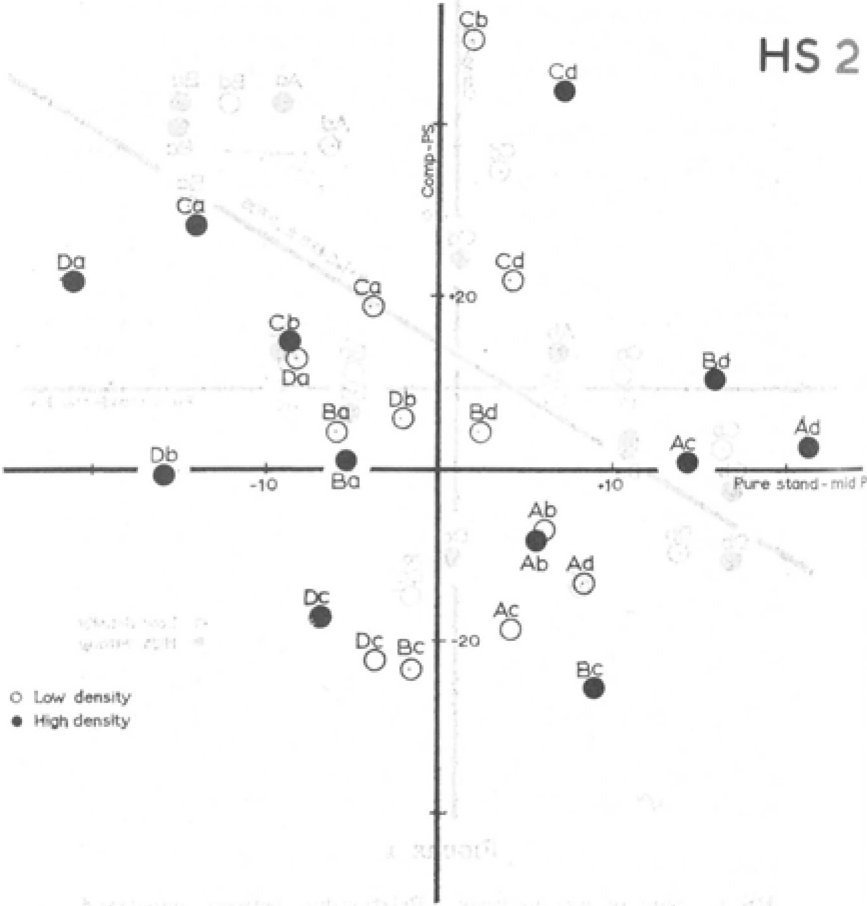

FIGURE 2

HS 2. Sum of five harvests. Otherwise as Fig. 1.

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sistent with the findings of workers with mixtures of cereal varieties where yields of both grain and vegetative parts at maturity do not, in general, show much correspondence with pure stand yields.

Harper (1964) has suggested the use of V_r/W_r graphs for detecting ecological effects analogous to the various dominance relationships in a genetic diallel. Statistically the analogy seems quite justifiable, but the interpretation of V_r/W_r graphs is much more speculative in the case of the mechanical diallel since there is no widely accepted hypothesis about the relationship of pure stand performance of an element to that of its performance in mixtures and its effect on the performance of the mixture as such. In certain limited cases it may be that V_r/W_r graphs do detect an analogue of genetic dominance, this will be so if, in 50 : 50 mixtures, the differences between the departures of each element from its own pure stand performance are in the same direction as the differences between the pure stands; even so, the precise meaning of "dominance" in this context is difficult to visualise; it is easy, for example, to imagine a situation in which the changes of behaviour of elements due to mixture are exactly compensatory so that the mixture yields are the same as those of the mid-pure stands, in this case the V_r/W_r graph would detect no dominance and yet those elements which showed the greater increases (or smaller decreases) in mixture compared to pure stand would be showing "dominance" in an ecological sense.

Despite these limitations, V_r/W_r graphs may be useful when only the mixture yields are available and not the yields of the separate elements, particularly when they reveal a change in "dominance" relationships associated with a change in environment. Harper quotes an example in which at low density a situation akin to full dominance obtains whereas at higher density certain elements show strong interactions.

V_r/W_r diagrams for the total (season's) yields for the present experiment are given in Fig. 3, they show that in HS 1 "partial dominance" without interaction obtained at both densities, in HS 2 this was true at the higher density but at lower density strong interactions were present, the elements in HS 2, therefore, show a reversal of the behaviour of the *Linum* varieties in the experiment quoted by Harper.

Comparison of the graphs in Fig. 3 with Figs. 1 and 2 shows that in HS 1 the order of "dominance" on the V_r/W_r graphs

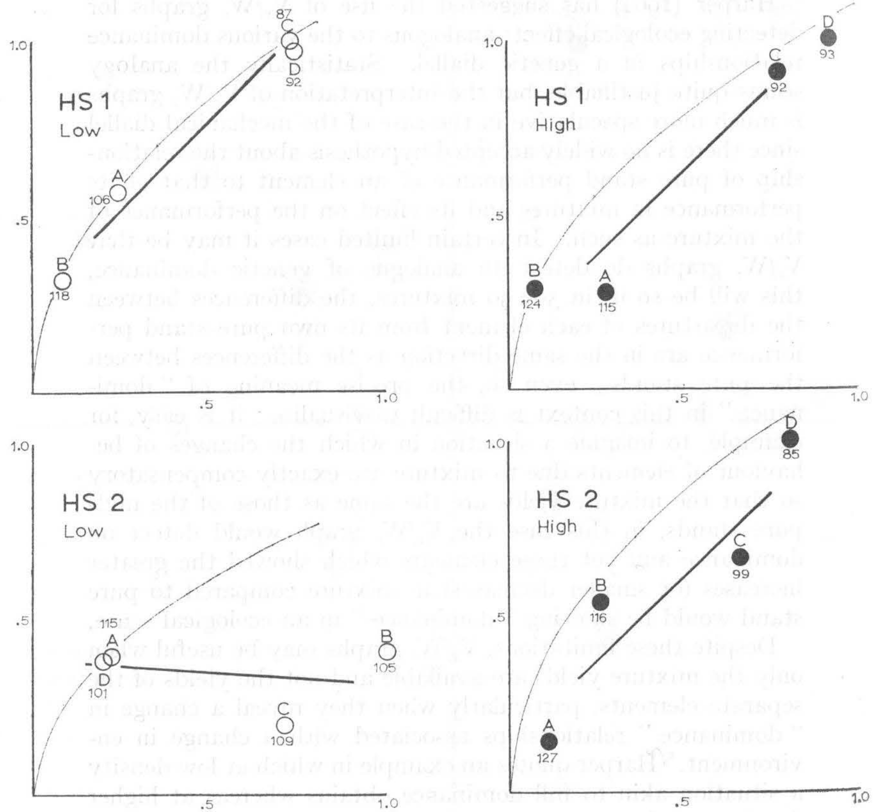

FIGURE 3

V_r/W_r graphs for total (season's) yield for each harvest series and density. The number below each point gives the mean pure-stand yield for the element.

corresponds to the order of " ecological dominance " as shown by the distribution of points in Fig. 1 and is also in the order of pure stand yields. In HS 2 at high density the V_r/W_r order of dominance is still in the order of pure stand yields but does not now correspond to the ecological dominance indicated in Fig. 2. The apparent dominance of element A, for example, is due to deviations in yield of mixtures containing A from their mid-pure stands in the direction of pure A which are attributable to small decreases in the yield of A being more than compensated for by larger increases in the yields of the associates of A. In these circumstances it is difficult to attach any meaning to the statement that A shows " dominance " in mixtures with the other three elements. In all these cases where " V_r/W_r dominance " is indicated, the apparent dominance of those elements having the highest pure stand yields is an inevitable consequence of increases due to competition being greater in magnitude than are decreases.

The comparisons between the yield of each mixture and the mid-pure stand yields are shown in Table 10. In most cases mixture yields exceed mid-pure stand yields for the reasons already given, but the increases are rarely significant, although in some cases quite large ; nearly 15% in one case. There are no significant values in the data for HS 1 but the behaviour of mixtures is consistent over both densities. In HS 2 there are quite large differences between the same mixtures at different densities, in particular mixtures BC and CD show marked contrasts in the data for total yield. Reference to Fig. 2 indicates that this difference in behaviour at the two densities is in both cases due to the behaviour of element C which at low density yields particularly well when grown with element B and at high density when grown with D.

Conclusions

Although the conditions under which the experiment was conducted are not directly comparable to those of the field, the behaviour of the material suggests that under conditions of vegetative growth competitive behaviour is mainly a reflection of vegetative vigour as assessed from pure stand performance, nevertheless, elements which differ only slightly in pure stand performance may show quite marked differences in competitive behaviour when grown together. When plants pass out of the vegetative phase the relationship between

TABLE 10

EXCESS OR DEFICIT OF MIXTURE YIELD COMPARED TO MID-PURE STAND GMS. PER HALF-BOX,
e.g. $\frac{1}{2}AB - \frac{1}{4}(AA + BB)$

	HS 1						HS 2					
MIXTURE	PEAK HARVEST = 2nd		SUM OF 5 CUTS				PEAK HARVEST = 1st		SUM OF 5 CUTS			
	Low Density	High Density	Low Density	%	High Density	%	Low Density	High Density	Low Density	%	High Density	%
AB	− 3.9	+ 11.0	+ 0.9	+ 0.4	+ 1.5	+ 0.6	− 4.0	− 6.4	− 2.6	− 1.2	− 6.7	− 2.8
AC	+ 6.4	+ 6.3	+ 5.5	+ 2.9	− 1.4	− 0.7	− 4.2	+ 21.9*	+ 0.5	+ 0.2	+ 29.2*	+ 12.9
AD	+ 3.7	+ 20.6	+ 4.5	+ 2.3	+ 25.9	+ 12.6	− 5.2	+ 16.9*	+ 0.1	± 0.0	+ 24.9	+ 11.8
BC	+ 10.3	+ 19.5	+ 14.6	+ 7.2	+ 17.4	+ 8.0	+ 18.5	+ 1.3	+ 26.8*	+ 12.5	− 10.4	− 4.8
BD	+ 9.6	+ 14.1	+ 13.9	+ 6.7	+ 13.4	+ 6.2	− 7.1	+ 11.7	− 1.5	− 0.7	+ 9.9	+ 4.9
CD	− 2.8	− 2.4	+ 1.0	+ 0.6	− 4.0	− 2.2	+ 1.0	+ 11.1	− 0.3	− 0.1	+ 26.8*	+ 14.6

* indicates significant values at 5% level.

competitive and pure stand behaviour is markedly disturbed even when the character being measured is forage yield. The implications are that while testing under pure stand with frequent cutting would permit the detection of competitively vigorous progenies for, say, use under grazing managements, this would not be the case for hay or silage management. The problem is considerably more complicated if one considers the difficulties of breeding " compatible " varieties for " grazing " conditions since even when pure stand performances are similar competitive behaviour will probably differ ; this problem might be partly overcome by adjustment of proportions of the elements in a mixture.

In terms of agronomic practice the extensive use of mixtures would appear to be justified because apart from the extra flexibility conferred by their use it seems likely that overall yield will generally be increased.

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ASPECTS OF THE MINERAL NUTRITION OF HILL PASTURE GRASSES

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Summary. 1. A preliminary account of the possible relative importance of various mineral nutrients in determining the micro-ecological amplitude of hill pasture grasses. 2. In *Festuca rubra* from a small flushed area on the Pentland hills there is apparently wide genetic variation in Ca and Mg uptake. 3. In eight species variation in soil N induces a wide variation of uptake of P and K; Ca and Mg are little affected. 4. These and other data indicate that extreme care must be exercised in interpreting habitat-correlated variation. 5. It should not be assumed that species showing similar ecological behaviour do so for similar reasons, and the modifying effect of competition between species cannot be ignored.

The concept that a species is the same wherever he sees it is basic to an ecologist's thought and yet there is overwhelming evidence, recently reviewed by Heslop-Harrison (1964) that what the ecologist conveniently thinks of as one entity can be very different both morphologically and physiologically in different places as a result of the selective effects of various environmental factors—in other words, it is several entities. On the other hand, he knows that his "species" behaves as one entity in being consistent in its habitat preferences, i.e. the breadth of its inherent environmental tolerance (its ecological amplitude) is limited. This, however, implies that a given species is more suited, or *adapted* to one type of environment than another. There can be no doubt that limitation of the ecological amplitude of a species is due to the operation of the same selective processes which also cause morphological and physiological divergence within the species as the ecologist knows it. One can only presume that the divergences which the genecologist can demonstrate fall within the ecological amplitude of the ecologist's "species", though this cannot invariably be true for this would preclude any progressive evolutionary process.

The ecologist is, therefore, interested in factors determining the ecological amplitude of a species as a whole while the genecologist is concerned with " distinguishing genetical divergence in consequence of selection " (Heslop-Harrison, 1964). At the practical level, however, both must derive their information from populations of species and both are concerned with the adaptive responses of their material. Both approaches give information of great relevance to the problems of the improvement of hill pastures. It is of no importance in this context whether the intention is to introduce exotic species or to breed or select native species which are more productive, for in either case factual information is required on (i) the ecological amplitudes of the species concerned, (ii) the nature of the environment which they will experience and (iii) the fitness of the species for that particular environment.

The major problem is to distinguish adaptive responses from phenotypic plasticity and random variation of various kinds and though a great deal of genecological work has been directed towards habitat correlated variation both in morphological and physiological features (Bradshaw, 1959, 1960 ; Snaydon, 1962 ; Snaydon & Bradshaw, 1961, 1964) only in certain " all or nothing " cases such as adaptation to lead-containing soils (Wilkins, 1960) is it possible to be certain of the precise environmental factor involved and to say that it is exerting a selective effect leading to an adaptive response.

Previous work at the Scottish Plant Breeding Station has demonstrated the presence of habitat-correlated morphological variation in hill pasture species (Harberd, 1961) but it has not so far proved possible to identify any precise factor in the environment having a selective effect. One of the reasons is that measurement of individual environmental factors, and their expression in terms which bear a relationship to their effect on the plants, is not easy. Indeed, the major difficulty is likely to be that several factors are interdependent and that plant populations are adapted to a complex of factors. Nevertheless, measurements of individual environmental factors must be made and an understanding of their effect on plants achieved before an evaluation of their selective effect can be made.

The work described below is a preliminary report on the problems encountered in investigating the relation between mineral nutrient levels in the soil and the distribution of a number of hill pasture grasses on a flushed site on the Pentland hills. This site has been described by Ratcliffe (1963) and has been shown to have a gradient of soil pH from about 4.0 to 7.0 with parallel variation in availability of Ca and Mg and little variation in K and Na. It has not proved possible to demonstrate significant variation in soil P availability but there is as yet no satisfactory method by which this can be measured easily. There is, of course, a gradient of soil moisture, but over that part of the flushed area under consideration, and bearing in mind the species involved, this is probably not an important factor. Over a distance of 40 feet there is a change in the vegetation from a close-grazed turf dominated by *Festuca rubra* to an almost ungrazed turf among *Calluna/Vaccinium* heath. Data for 5 sites along a transect down the centre of the flushed area are summarised in Table 1.

TABLE 1

VEGETATION AND SOIL GRADIENTS ON A FLUSHED AREA

			Soil cation level % of C.E.C.			
	Vegetation	*Surface pH*	*Ca*	*Mg*	*K*	*Na*
Site 1	*Festuca rubra* dominant	6.5	54	19	1.1	1.7
Site 2	*Festuca rubra/Agrostis tenuis*	6.1	55	14	1.3	1.5
Site 3	*Festuca rubra/F. ovina/Agrostis tenuis*	6.0	53	13	1.3	1.4
Site 4	*Festuca ovina/Agrostis tenuis*	5.5	46	13	1.5	1.4
Site 5	*Deschampsia flexuosa* dominant	4.5	25	10	1.7	1.3

Ideally it would be possible to identify a precise environmental factor determining the " upper " and " lower " limits of the species between which each is growing in more or less optimum conditions. The general correlation between the change in soil pH, Ca and Mg over the length of the above transect and the change in the dominant species at first sight suggests that soil nutritional factors are likely to be most important, but departure from the above simple situation is very likely as a result of interspecific competition and the modifying effect of grazing on the latter. In addition it is entirely possible that there is genecological adaptation within each species to soil conditions at the extremes of range. It follows that any correlation between the presence or absence, or frequency, of a species at a given site and soil nutritional factors is not in itself adequate evidence of any real relationship. This point has been made very clearly by Ellenberg (1964b) who has shown that along a gradient of depth of water-table maximum growth of certain grass species occurs at different parts of the gradient according to whether they are growing as pure stands or under competition with other species. Further, Grime (1963) suggests that on an area in which *Deschampsia flexuosa* is spreading owing to progressive leaching of an initially calcareous soil *Festuca ovina* is being eliminated from soils on which it would otherwise grow successfully through the competition of *Deschampsia*.

Any investigation of the factors limiting the range of individual species on the flushed area under consideration must, therefore, take into account these possible effects and it seemed likely to the author that measurement of the nutrient level in leaf material under various conditions would provide information not only on the relationship between soil nutrient levels and uptake by the plant but on the relative requirements of different species and/or genotypes. This aim has not in fact yet been realised but the results are, nevertheless, instructive.

Experiment 1

To give information on the usefulness of the analytical techniques and on the variability in nutrient levels within a single species leaf material cropped from 260 spaced plants of *Festuca rubra* in a uniform manner on the same day, was dried, milled and analysed for Ca, Mg, K and Na. The range of the results is shown in Table 2.

TABLE 2

VARIATION IN CATION CONTENT OF *FESTUCA RUBRA*

	me/100 g. dry wt.	
	Highest	*Lowest*
Ca . .	39.20	7.13
Mg . .	37.19	5.72
K . .	102.32	47.58
Na . .	4.90	0.69

The ranges of Ca and Mg are very much greater than anticipated. There is no reason to doubt the analytical techniques, in fact there was considerable duplication of genotypes and in several cases it was possible to pick out a series of results with similar levels of Ca or Mg and check that these were plants of the same genotype, as reported by Smith elsewhere in this *Record*. There were three main groups of results: (i) High Ca, low Mg ; (ii) Low Ca, high Mg ; (iii) Average Ca and Mg—into which group most results fell. K is not so variable but, nevertheless, rather more than might be expected. The difficulty is to be certain to what extent this variation in nutrient levels is due to random variation, soil variation or genotypic variation, though the latter is apparently very important.

Experiment 2

It appeared desirable to take two precautions in a preliminary experiment attempting to compare several species. (i) Plants were grown from seeds rather than tillers, in order to include a range of genetical variation ; (ii) the experiment was conducted in pots in the greenhouse in order to eliminate soil variability as far as possible.

Twenty pots of five seedlings per 5-in. pot of *Agrostis stolonifera, Festuca ovina, Festuca rubra, Festuca vivipara* and *Anthoxanthum odoratum* of various origins were cropped at intervals and analysed for N, P, K, Na, Ca and Mg. The soil used was John Innes compost No. 1 with no added fertiliser. Growth was at first normal but within six months it virtually ceased and by July 1964 all plants were more or less chlorotic. Additions of N, P or K, as ammonium nitrate, potassium sulphate or superphosphate, were made to groups of five pots leaving five as a control. The results are shown in Table 3 as means for all species, space not permitting full exposition.

TABLE 3

RELATION OF MINERAL NUTRIENT UPTAKE TO N, P AND K SUPPLY

Analysed	N	P	K	Na	Ca	Mg
1963 Autumn . . .	3.96	78.44	100.27	1.85	23.17	15.97
3 : 8 : 64 before treatment .	1.51	29.69	40.00	0.90	21.10	15.43
27 : 8 : 64 24 days after application of—						
N	4.82	46.27	72.12	2.83	22.81	16.88
P	1.78	39.48	44.73	1.67	23.87	12.77
K	1.54	34.85	49.85	1.77	21.28	12.57

N : percentage dry weight.
P, K, Na, Ca, Mg : me/1000 g. dry weight.

There was insufficient growth on the control to enable full analyses to be carried out but the remaining results were very similar to those for material cropped on 3rd August 1964.

It is clear that nitrogen deficiency was the cause of cessation of growth, this being accompanied by reduction in the uptake of P and K independently of the soil availability of these elements.

The general conclusions were :—

(i) N nutrition is very important in controlling the uptake of P and K.
(ii) Ca and Mg were little affected by the nitrogen level.
(iii) Na appears to be taken up in greater amounts when K is deficient.

Experiment 3

Experiment 2 was followed up along the same lines but using seeds from plants obtained from the Pentland hills flushed area and given an arbitrary range of N treatments to find out whether different species reacted differently at different N levels. There were 4 plants per pot and 5 pots per treatment. Previous to the nitrogen treatment an application of P and K, as superphosphate and potassium sulphate, was given to all pots. To date only one nitrogen addition has been given and the experiment is continuing but the results are shown in Table 4.

Again before treatment N, P and K levels were low rising considerably after addition of N but little after addition of P and K. In fact K is considerably lower. On the other hand, in this experiment the PK addition (which includes Ca and Mg) has resulted in all species in a rise in Ca and Mg giving normally higher values than after N treatment, suggesting that Ca and Mg are influenced more by soil levels of these elements than by the nitrogen status of the plants. At this stage it is not possible to know the significance of the differences between the species.

Experiment 4

Parallel to the above investigations croppings were made from the flushed area itself. Wire letter-trays were inverted and pegged down at 5 sites on the area in the spring of 1963 and the herbage plucked by hand to simulate grazing when sufficient growth had occurred. This was continued for one year after which there was no obvious effect of the treatment

TABLE 4

RELATION OF MINERAL NUTRIENT UPTAKE TO N SUPPLY

			Before treatment	3 months after treatment	
				+PK	+NPK (Mean of all N levels)
Agrostis stolonifera	N%	dry weight	3.08	3.78	5.56
	P	milli equivalents /100 g. dry weight	45.8	55.5	86.3
	K		81.8	61.4	93.7
	Na		2.3	2.0	3.2
	Ca		18.5	23.7	20.7
	Mg		18.6	27.5	26.3
Poa pratensis ssp. *subcaerulea* (infected with *Erisyphe*)	N		1.82	1.82	3.64
	P		53.2	52.7	80.3
	K		81.8	60.0	85.9
	Na		1.5	3.5	3.8
	Ca		24.2	41.3	32.6
	Mg		13.6	30.0	30.2
Poa trivialis	N		1.68	1.82	5.07
	P		50.5	41.0	82.9
	K		85.9	73.2	116.5
	Na		1.5	5.8	5.8
	Ca		43.5	65.5	34.9
	Mg		37.9	68.7	49.0
Festuca rubra	N		1.96	2.10	3.92
	P		62.1	60.5	70.5
	K		93.6	76.7	98.3
	Na		1.0	2.7	2.7
	Ca		22.1	32.0	27.4
	Mg		11.4	17.2	18.4
Festuca ovina	N		2.24	2.38	4.27
	P		53.7	50.5	61.0
	K		69.6	56.3	64.5
	Na		0.9	2.7	2.6
	Ca		22.8	37.2	29.4
	Mg		12.9	47.6	30.6
Agrostis tenuis	N		2.10	1.54	4.79
	P		61.0	74.7	120.9
	K		73.1	62.9	63.8
	Na		1.48	5.30	2.06
	Ca		22.8	34.2	21.9
	Mg		30.7	55.0	41.5
Anthoxanthum odoratum (infected with *Erisyphe*)	N		2.38	3.07	5.70
	P		51.0	80.0	59.1
	K		93.6	79.8	109.8
	Na		2.2	7.3	4.6
	Ca		20.0	32.5	27.8
	Mg		13.6	36.0	22.6

on the cropped areas compared with the surrounding vegetation. The sites are those for which data are given in Table 1 and the results are given in Table 5. Site 1 has slightly anomalous figures probably because the year was extremely wet and the site was waterlogged for a long period and growth was rather slow. There is a clear gradient in uptake of all elements, from the site with the highest pH to that with the lowest, which might be expected for Ca and Mg but not necessarily for N and not for P, K and Na. In view of the results of Experiments 2 and 3 the most likely explanation is that the level of Ca and Mg in the soil is controlling the level of these elements in the plant material and the soil N level is controlling the plant level of N, P and K. It must be borne in mind that not only is there a change in the species representation from site to site but a change in leaf-stem ratio related to the amount of grazing, though the figures in Table 4 do not indicate any gross differences between species. However, soil nitrogen availability was measured using the technique of Waring and Bremner (1964) in which a soil sample is incubated under waterlogged conditions for two weeks at 25°C. and NH_4 estimated. In addition estimations were made of NH_4 in unincubated soil. These results are also shown in Table 5. N is clearly more available on the soils of higher pH, falling as the pH falls except in the upper, humus-stained 5 cm. at site 5; here apparently it is present as ammonium N, little more being released on incubation. These data support the hypothesis that N is limiting P and K uptake on this flushed area.

TABLE 5

MINERAL NUTRIENT UPTAKE BY THE SWARD ON A FLUSHED AREA

Site	N	P	K	Na	Ca	Mg	†Incubated	†Non-incubated
1	2.69	29.7	50.9	6.26	31.2	18.7	3.20	0.60
2	3.01	31.5	56.8	7.24	33.4	18.8	3.26	0.55
3	2.72	28.5	47.9	4.01	32.1	17.4	2.15	0.65
4	1.97	20.4	41.3	2.89	29.7	13.6	1.94	0.70
5	1.57	16.2	29.3	2.06	19.5	12.0	*2.06/0.70	*1.80/0.65

* Upper figure: top 0.5 cm. (humus-stained); lower figure 5-10 cm.

† N_4 in soil; arbitrary units.

Discussion and conclusions

It seems reasonable to conclude from Experiments 1 to 3 that

(i) At least in *Festuca rubra* and possibly in other species there is considerable genetic variation in the level of Ca and Mg in the leaves though not necessarily so in K.

(ii) Soil Ca and Mg levels have a considerable effect on uptake of these elements by the species concerned, irrespective of genetic factors.

(iii) Variation in soil N induces a wide variation in uptake of P and K to a greater extent than variation in the soil P and K levels in the experiments.

(iv) The data from the flushed site confirm the hypothesis that these effects also operate in the field.

It should be made clear that the plant nutrient levels refer in all cases to the proportion in the dry material as milliequivalents/100 gm. dry weight (except N which is given as % dry weight) and, therefore, independent of the amount of growth; indeed if the total uptake were to be calculated the effects would be even more striking particularly in relation to N nutrition.

The problem is (as stated earlier) to interpret the relationship between the changes in soil nutrient levels, nutrient uptake and the correlated changes in species representation—there are several possible hypotheses, not mutually exclusive.

(i) The species differ in nutrient uptake, those with the lowest levels occurring on the most acid soils: the figures in Table 4, though variable, do not support this view.

(ii) A change in "leaf"/"stem" ratio causes a spurious gradient in uptake which would not be present if only green leaves were sampled—in other words, the gradient in leaf nutrient levels does not follow the soil gradient: the dry matter production does in fact follow the soil nutrient gradient and the combined effect would be a steeper gradient in total uptake.

(iii) Following from (ii) each species could be confined to that part of the soil nutrient gradient on which "normal" nutrient levels in the leaves could be maintained; this infers that the least productive species would occur on the poorest soils.

(iv) In addition to (iii) interaction between species could produce a situation in which each species is confined to a particular part of the soil nutrient gradients within which it can compete most effectively for soil nutrients.

(v) The range of genetic variation in requirements for and/or ability to take up nutrients within each species would determine the precise range of each species.

These hypotheses take no account of the interaction of nutrients: while it is perfectly acceptable to study the effect of Ca and Mg in isolation on various species, e.g. Bradshaw *et al* (1958, 1960), the situation is not nearly so simple for N, P and K because whether P and K are limiting factors will depend on (*a*) the total supply of each in the soil, (*b*) the rate of release in the soil of relatively unavailable forms, combined with (iii) the rate and amount of growth, which will be related to N levels in the soils and rate of mineralisation of organic nitrogen. Nevertheless, except on soils derived from rocks extremely deficient in P, such as ultrabasic rocks (Ferreira, personal communication) or K (extremely unlikely), N is likely to be the most important factor in the first instance. The results for soil N level in Table 5 show that there is a steep gradient of non-ammonium N correlated with soil pH, ammonium nitrogen being the principal form of N on the acid soil (it must be presumed that the ammonium-N produced under incubation would have been oxidised to NO_3 under aerobic conditions). Similar gradients in soil N have been demonstrated by Ellenberg (1964a).

The author's conclusions are that extreme care must be exercised in interpreting habitat-correlated variation. The preceding experiments have shown that soil N, P and K cannot be separated as possible selective factors in the soil environment, and though the relationships between soil Ca and Mg and plant uptake is apparently simpler it must not be assumed that these are the primary selective factors for they in turn are strongly correlated (albeit fortuitously) with pH which has far reaching effects on the availability of such elements as iron and manganese. Further, the modifying effect of competition of any kind cannot be ignored, and here nitrogen can again be implicated: Bradshaw *et al* (1964) have shown that in sand culture different species have maximum growth at different levels of nitrogen. Further results from Experiment 4 indicate a similar effect. Finally, it should not be presumed that species showing similar ecological behaviour do so for similar reasons.

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THE ASSESSMENT OF PATTERNS OF VARIATION IN *FESTUCA RUBRA* L. IN RELATION TO ENVIRONMENTAL GRADIENTS

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CONTENTS

Summary. A genecological investigation of *Festuca rubra* from a flushed hill community has shown that there is considerable variation in morphological characters, physiological characters including uptake of certain minerals, and breeding systems. As a result of a number of tests, contrasting genetic types are indicated to occupy different positions on a series of environmental gradients allied to a transition from poor to fertile soil. Such *genodemes* could commonly be made up of two or more comparable genotypes which are so similar in their physiologies that they occupy the same small niche in the environment. If the present arrangement of genodemes is an outcome of each being adapted to its particular part of the environment, such orderly arrangement could have arisen by selection from an array of genotypes or perhaps by an amoeboid type of vegetative spread to result in a re-arrangement of them. The place of adaptation is discussed in relation to possible ways of agricultural improvement.

Introduction

Hill sheep production is faced with many problems, one of the most outstanding being the difficulty of providing an adequate supply of nutritious herbage all the year round in the poorer areas. The situation is commonly one of imbalance between summer and winter plant growth, in which a shortage of winter keep may impose limitations on the stocking rate and so prevent the complete utilisation of the abundant summer yield. Recent research has indicated that the efficiency of the process of animal production is greatly influenced by the rate of growth of the stock, and the greater economic return will occur when the diet is so good that there is a speedy turnover. The provision of better hill pastures is therefore of paramount importance.

The introduction of good herbage varieties to hill areas can often produce impressive results, but because introduced varieties usually require the better soil and climate of the lowland, their establishment is costly, in a large measure due to the initial necessity of upgrading the hill soil by the application of fertilisers. Furthermore, these types are often less able than the existing species to withstand the rigours of the climate, and so competition may tend to favour a reversion to the original vegetation, particularly if the soil minerals lost as a result of leaching are not replaced.

There is clearly the need to exploit the better components of the natural vegetation in order to take advantage of their adaptation to the local environment. It is desirable to obtain a better understanding of the underlying causes of this adaptation and how it operates. Knowledge of fundamental properties of hill vegetation, particularly where it involves the effects of soil fertility on variation, may make it possible for new ways of pasture improvement to be envisaged.

Flushes are useful areas for this kind of work because they contain an area of fertile soil produced by mineral-rich spring water surrounded by poorer soil. There are differences in a wide range of environmental factors connected either with grazing intensity or with the moisture, temperature, aeration, mineral content, macro-biological and micro-biological relationships of the soil. Flushes thereby present a complex series of environmental gradients.

One such area was selected for detailed study because of its symmetrical shape and good contrast with the surrounding hillside. The soil mineral composition has been described by Ratcliffe (1963) and the object of the present investigation is to examine the variation of the grass species of the area and the interaction between them. Representatives of *Festuca rubra* and *Agrostis tenuis* in the flush were transplanted to form a spaced plant field trial and an examination was made of certain morphological and physiological characters and of their breeding relationships. A less intensive study was made with *Festuca ovina*, *Anthoxanthum odoratum*, *Agrostis stolonifera*, *Poa trivialis*, *Poa annua*, *Poa subcaerulea* and *Holcus* sp. which

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were less frequent in the sward. The present paper is a preliminary account of the findings in *Festuca rubra*.

The flush from which material was obtained is situated on a N.W. slope of Carnethy hill, in the Pentland hills. Spring water flows down the hillside for about 30 feet and gradually disappears into the substratum. Associated with this there is a strip of *Agrostis-Festuca* pasture approximately 20 feet wide and 90 feet long (down the slope). Starting from a point just above the spring a transect of sampling points at 5 feet intervals was taken down the centre of the flush. With sampling points 2 feet apart, two transects at right angles to this were taken at positions 30 feet and 60 feet down the original transect. The positions of the sampling points are given in Figure 1 in which it will be observed that an additional sample was taken near to that at 60 feet.

At each sampling point a cylindrical core of turf with underlying soil, approximately 3½ inches in diameter was taken. The soil was removed for analysis and the plant material was separated into single tillers (' isolates ') and planted in boxes of sterilised soil. Where the core of turf yielded too many isolates for study, a random sample was taken. Most of the specimens were too small for identification at the time of collection.

Sampling took place in late October and early November 1961 and the plants were grown in a heated greenhouse during the following winter. In the spring the isolates of *Festuca rubra* were divided into portions of approximately equal size and one portion was assigned to each of five plots (replicates) of a spaced plant field trial. It was not possible, owing to shortage of space, to put a representative of every isolate in each plot. A random selection was therefore made so that some of the isolates were assigned to all five plots (replicates A, B, C, D and E) while others were placed in only two plots (A and B). The plants were grown at a spacing of 2½ and 3 feet (two directions at right angles).

The plants were positioned in replicate A so that those isolated from the same core of turf occurred side by side to facilitate comparisons to be made between them. In all other replicates the plant positions were randomised. There were in all 639 plants derived from 249 isolates. Virtually none of the plants flowered in 1962. Each plant produced a tussock about 30 cm. high and 30 cm. in diameter from which a sample

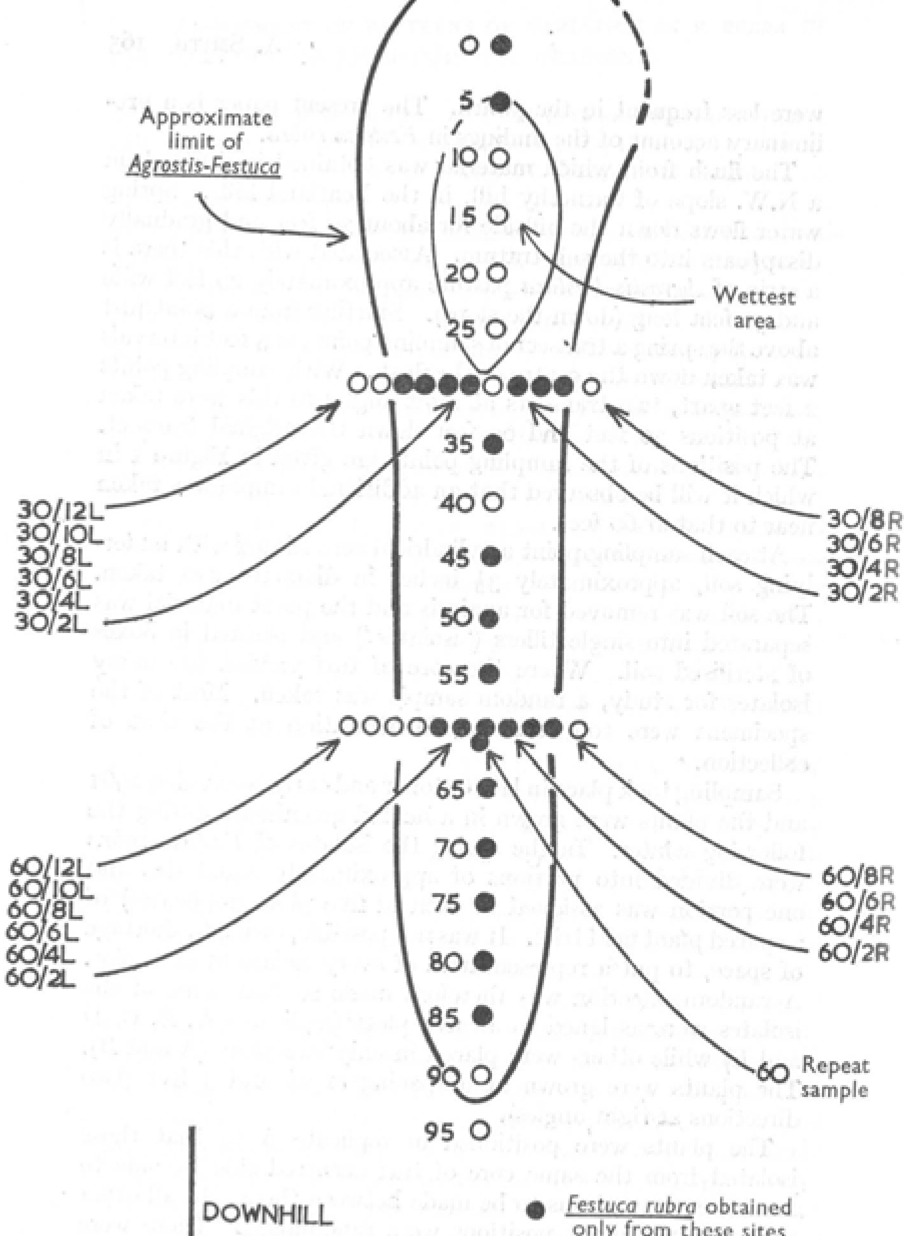

FIGURE 1

Positions of the sampling sites in the original habitat. On the central transect the numbers indicate the distance in feet from the origin. On the transects crossing this at the 30 and 60 feet points, the numbers denote the distance to the right and left of the central line.

of leaf material was removed, oven-dried and then analysed by Dr D. Ratcliffe for the content of potassium, calcium, magnesium and sodium. Milled material was digested in a perchloric/sulphuric/nitric acid mixture, and estimations made of Ca and Mg by an ethylenediaminetetra-acetic acid titration technique, and of K and Na by flame photometry.

The somatic chromosome numbers of some isolates were counted before the field trial was laid down. Tillers were also removed from the spaced plants, established under glass as pot plants, and the chromosome numbers counted. Chromosome numbers were thus obtained from a random sample of 175 isolates. Other series of tillers were removed from the spaced plants from time to time in order to provide material for crosses as described later. In every case, the amount of tissue taken from the spaced plants was so small that it did not constitute a disturbance. Single tillers were obtained to avoid uninterpretable results arising if any plant contained a contaminant. The trial was given the minimum of hoeing simply to prevent the spread of weeds, and an attempt was made to give similar treatment to all plots.

The plants were cut down and weighed in October 1962 and again in March 1963 to record the regrowth after a particularly severe winter. The panicles were cut off in July 1963 for counting and to prevent self-seeding, and the plants were cut down and weighed in September 1963. The panicles were removed in July 1964 but the plants were not cut in autumn 1964 with the result that the performance of the foggage could be observed in the following winter.

Variation of plants from the natural habitat

It was clear from the outset that there was a great deal of variation among the plants of the field trial. This variation was either in qualitative characters such as the colour of leaves and panicles, quantitative characters such as leaf length and panicle length, and what are here called ‘ quasi-quantitative ’ characters such as the degree of compactness of panicles. The latter often appear to be discontinuous yet the presence of intermediate phenotypes has necessitated the treatment of the whole range of expression as though it were a continuous variable. There was no variation in chromosome number which was $2n = 6x = 42$.

A survey of the extent of variation of the majority of the characters used is given in Table 1. Leaf measurements, mineral analyses, plant fresh weights and percentages of dry matter were recorded late in 1962. Metric data on panicles and culms were obtained in 1963 and infection with *Puccinia festucae* was scored in 1964. All other characters in Table 1 for which the year of recording is not given were examined frequently during the course of the trial. The values given are the means of replicates A and B (all available replicates in the case of mineral analyses) of all the isolates in the groups referred to later. For quantitative characters, the lower extreme consists of values equal to or less than the lower quartile while the upper extreme implies the upper quartile and above. Quartile values are approximate. The selection of characters for study at particular times depended to a certain extent on the fact that almost all the plants did not flower in the first year, and vegetative characters were then more amenable.

Now although, as may be seen from Table 1, there is variation in a large number of characters, certain plants in the field trial seemed to be identical to others. This was particularly noticeable when plants originating from the same or adjacent cores of turf were compared. Because the flush was sampled intensively, taking many tillers from a small piece of turf, the same original plant could be expected to be represented more than once. The fact that certain plants looked alike was felt to be due to reduplication of certain genotypes.

A consideration of the overall variation in characters from point to point in the flush would, therefore, involve the combined effects of differences between genotypes on one hand and changing proportions of these genotypes on the other. It was desirable to be able to separate these two factors by working out which isolates were from the same original plant. This has been done by first classifying the isolates into groups of similar plants and finding whether or not each of the groups is likely to consist of a single genotype by investigating their self- and cross-incompatibility relations.

The programme of work was as follows :—

(1) The characters were recorded by a series of measurements and other observations.

(2) A survey was made of which plants appeared to be identical without attempting to give reasons for this

TABLE I

Characters of *Festuca rubra* involved in this work

Quantitative Characters

Character	*Lower extreme value*	*Upper extreme value*	*Units*
Culm length	400-464	592-657	mm.
Panicle length	55-66	87-98	mm.
Number of panicles produced	3-91	268-357	per plant
Plant diameter			
1962	35-40	52-58	cm.
1963	57-63	74-79	cm.
Plant height			
1962	17-19	24-26	cm.
1963	23-27	34-37	cm.
Plant dry weight			
1962	6-19	44-56	gm.
1963	38-71	138-172	gm.
Plant winter dry weight yield	0.7-2.7	6.8-8.8	gm.
Plant fresh weight	21-69	164-212	gm.
Plant dry matter content	25.2-28.4	34.7-37.8	%
Leaf length	138-175	250-287	mm.
Leaf width	1.7-2.1	2.9-3.3	mm.
Leaf index	0.8-1.0	1.6-1.8	$\frac{\text{width}}{\text{length}}$ %
Potassium content	67.3-75.1	90.9-98.7	milli-equivalents per 100 gm. dry matter
Calcium content	7.4-13.6	25.9-32.1	
Magnesium content	7.4-14.4	28.4-35.4	
Sodium content	1.4-1.7	2.4-2.7	

Qualitative Characters

Character	*Average Phenotypes*	*Extreme Phenotypes*
Leaf colour	Intermediate green	1. Light green 2. Dark green 3. 'Oily' dark green
Panicle colour	1. Normal (dull greenish-purple) 2. Normal with red tinge 3. Normal with 'golden green' tinge	1. Green or khaki-green 2. Bluish-purple 3. Purple 4. Whitish-pink
Colour of nodes on culms	Nondescript (greenish-purple)	1. Bright green 2. Green 3. Purple-brown
Winter greenness	Dead to dull green	Bright green
Infection with *Epichloe typhina*	Not infected	Infected

Quasi-quantitative Characters

Character	*Extreme in one direction*	*Average*	*Extreme in opposite direction*
Degree of infection with *Erysiphe graminis*	Not infected	Moderate infection	Severe infection
Degree of infection with *Puccinia festucae*	Not infected	Moderate infection	Severe infection
Degree of compactness of panicle	Virtually closed (lowest branch c.0 degrees)	(Lowest branch c.45 degrees)	Virtually open (Lowest branch c.90 degrees)
Date of ear emergence (a)	(Early)		(Late)
1963	3 to 5		10 to 12
1964	7 to 12		22 to 27

(*a*) Recorded as the number of days elapsed from an arbitrary origin immediately prior to the first emergence, before which eleven or more panicles had become visible excluding any which may have burst through the side of their leaf sheaths. The origins were 27/5/63 and 3/5/64.

('assessments of similarity') and of all plants which appeared to be different ('assessments of difference'). These assessments were largely subjective.

(3) Crosses and tests of self-compatibility were made with isolates which were likely to be of the same genotype. Following from the work of Harberd (1961), and as discussed later, these tests could greatly influence the conclusion as to whether genotypic reduplication was present in the material. Information obtained in (2) formed a guide to the most profitable arrangement of crosses which were carried out at a time when there was insufficient objective data for classifying the plants.

(4) Formation of groups. Using the information from (1), the isolates were divided into groups and, where appropriate, statistical tests were made of the validity of differences between groups.

(5) Each group was tested for homogeneity by statistical tests on measured characters, and by comparison with the results of the incompatibility experiments in (3) conclusions were drawn concerning the number of genotypes in each group.

(6) The subjective impressions (2) and the objective approach (4) were now compared to see whether they agreed.

(7) The relation between the distribution of these groups on the original flush, and the variation in known environmental factors was examined.

It should be noted that the arrangement of the present paper does not strictly follow the above order.

Although an inspection of the spaced plants by the writer and independent observers can produce the very strong conviction that certain plants are identical, while others are completely different, it is often difficult to give precise reasons and so the conclusions are without proof. Yet it should be acknowledged that the human eye is often able to appreciate morphological features which tend to become nebulous when they are measured objectively. It was therefore considered to be of value if these subjective impressions were recorded and later compared with an objective classification of the plants.

The degree of similarity which is observed depends on how much detail is ignored, for clearly all plants differ in some small feature, yet they are all the same in many other respects. A compromise was therefore reached in which two plants recorded as similar were thought to be portions of a common original plant. Similar plants were allocated the same assessment number. A new series of numbers was used for each occasion when scoring was carried out, and each number was used for only one observed similarity. As a result of scoring on several occasions during the season, each plant received more than one assessment number, such as 103, 697, 1242. The data were then sorted by using edge-punched cards so that plants having the same assessment number were grouped together. Since all scoring was done without knowledge of previous results, there were many instances where the findings at one stage of growth were confirmed at a later stage.

The assessments of similarity were most conveniently done in replicate A where each isolate was more likely to be close to a similar one. The general impression on looking at the other replicates was that all the plants appeared to be different from their neighbours. Assessments of difference were more readily achieved within these replicates. Each plant was compared with all plants adjacent to it and where it was obvious that a pair were different they were both allocated the same number, but with the prefix + and − respectively. None of these numbers was employed for the assessments of similarity and new series were used for each session of scoring. As before, the data were processed on edge-punched cards.

It will be shown later in this paper that these assessments broadly agreed with the objective classification of the plants.

Division of plants into groups

The task was essentially that of classifying 249 isolates into homogeneous groups being sure that each group was distinct from the others. They were first arranged according to the qualitative and quasi-quantitative characters previously described. Where intermediates were apparent, separation rather than combining was purposely adopted so that each group would be likely to be homogeneous and it was anticipated that certain groups might have to be merged if additional evidence was not obtained to support them. For example, isolates with intermediate leaf colour were kept separate from ones with dark green leaves or light green leaves. While it was certain that 'dark' groups were distinct from 'light' groups, it was possible that any 'intermediate' group might have to be combined with any of the 'dark' or 'light' ones when the final analysis was complete. On the other hand, it was conceivable that plants which could only be denoted as 'intermediate' possessed a completely different quality of colour which could not be described in simple terms. The 'intermediate' classification consisted of plants recorded as 'dark' on one occasion and 'light' on another, plants designated 'intermediate' because of indecision when scoring, and all instances where the records conflicted between replicates. As a result of this approach it can be assumed that groups ultimately described as having dark green leaves, or light green leaves, have been consistently scored for the character for several seasons, and variation was not encountered between replicates. The term 'oily' dark green denotes a colour which is different from all others but difficult to describe concisely.

With all characters, variation between replicates has been taken into account when forming the groups. This variation is attributed to various degrees of phenotypic plasticity, experimental error, random variation and lack of uniformity of the trial area. Environmental differences were undoubtedly present, chiefly involving soil fertility and drainage, and exposure to wind and sun.

If the characters used in forming the groups were reliable then little confirmation would be required. Yet it is commonly known that there are very few truly discrete characters in biological material. The presence of intermediates is part of the natural state of affairs, yet is to a certain extent due to errors of observation and the near-impossibility of recording qualitative characters in an unbiased objective manner. It was felt that comparisons should be made between every possible pair of groups to see whether there were clear qualitative distinctions or acceptable differences when other metric data were considered in addition to the characters already used. A significant difference in an analysis of variance of a character which had been taken into account in forming two groups was, however, treated with great caution. For reasons which are discussed later, confirmation of groups was sought in characters which had not been exploited hitherto.

There were initially 57 groups which necessitated 1,596 different comparisons. The results of these were entered in the cells of a 57 × 57 matrix, indicating clear differences in qualitative characters and significant differences in quantitative and quasi-quantitative ones. Most of the cells were filled-in. Those which were not were taken to imply that the respective groups ought to be merged and this was done.

There were entries in some cells which implied that certain groups had only minor qualitative distinctions and/or metric differences which could not be satisfactorily tested statistically (or if tested, the differences did not reach significance). Judgment had to be exercised in these instances and the conclusions taken as provisional for it is possible that further work in progress will clarify the situation. These groups, involving a proportion of comparisons made by inspection, are indicated separately on the map (Figure 2) which is described in a later section. Other groups on the map are regarded as distinct because virtually all comparisons involving them gave apparently reliable differences.

Analyses of variance were carried out for many measured characters to discover whether there was any heterogeneity within each group. Although the majority of tests showed lack of significance, in a few cases there were significant differences within a group in one or more characters, and it was clear that the group needed to be subdivided. This was done without theoretical difficulty except in some groups where the heterogeneity could not be removed by further reorganisation. Such groups might therefore be expected to contain more than one genotype, but the presence of negative crosses within many of them tends to reject this idea and favour the alternative that the heterogeneity is a demonstration of phenotypic plasticity. For the time being therefore it has been noted that there is heterogeneity within groups 31, 46, 501, 60, 61 and 65 and possibly within groups 44, 502, 62, 63 and 67.

Groups which occurred on more than one site in the flush were similarly tested for heterogeneity between sites, and in one case this led to a subdivision of the group.

As a result of the confirmation and appropriate modification of the original groups, an acceptable classification was achieved, a synopsis of which is given in Table 2. The terms 'low,'

TABLE 2

SYNOPSIS OF THE SALIENT CHARACTERS OF GROUPS OF *FESTUCA RUBRA* ISOLATES

066	Light green leaves, moderate to severe *Erysiphe* and *Puccinia*, many panicles, short leaves, highest leaf index, high calcium.
202b	Light green leaves, severe *Erysiphe* infection, no *Puccinia*, self-compatible, longest panicles, few panicles, 'difficult' ear emergence, high dry weight (1962), highest dry weight (1963), high fresh weight, low leaf index, no mineral analysis data available.
22	Light green leaves, bright green nodes, moderate *Erysiphe*, moderate *Puccinia*, late, high winter weight, high potassium, low sodium.
24350	Light green leaves, green nodes, moderate *Erysiphe*, moderate to severe *Puccinia*, many panicles, tall plant (1963), high winter weight, broad leaves, high leaf index, low potassium, low sodium.
24355	Light green leaves, green nodes, moderate *Erysiphe*, moderate to severe *Puccinia*, lowest potassium, lowest calcium, highest magnesium, low sodium.
27	Light green leaves, purple panicles, purple-brown to nondescript nodes, moderate to severe *Erysiphe*, no *Puccinia*, joint earliest (1963), many panicles, low leaf index, low sodium.
292	Light green leaves, moderate to severe *Erysiphe*, no *Puccinia*, late, longest culms, long panicles, tall plant (1962), largest plant diameter, high dry weight, high fresh weight, low sodium.
30	Light green leaves, green nodes, moderate *Erysiphe*, moderate *Puccinia*, joint latest, short culms, few panicles, high potassium, low sodium.
31	Light green leaves, purple-brown nodes, virtually no *Erysiphe*, moderate *Puccinia*, late (1964), large plant diameter (1963), tall plant (1963), high dry weight (1963), low sodium.
352	Light green leaves, khaki-green panicles, moderate to severe *Erysiphe*, moderate *Puccinia*, self-compatible (low level), many panicles, tall plant, high winter weight, low leaf index, high calcium.
361	Light green leaves, khaki-green panicles, severe *Erysiphe*, severe *Puccinia*, slight *Epichloe* not detected until 1965, tall plant (1963), narrow leaves, high calcium, high sodium.
362	Light green leaves, khaki-green to red-tinged panicles, moderate to severe *Erysiphe* and *Puccinia*, few panicles, smallest plant diameter (1962), small plant diameter (1963), shortest plant (1962), lowest dry weight (1962), low dry weight (1963), lowest winter weight, lowest fresh weight, short leaves, narrow leaves, high magnesium.
371	Intermediate green leaves, moderate to severe *Erysiphe*, no *Puccinia*, late, few panicles, compact panicles, small plant diameter (1963), narrow leaves, low leaf index, low potassium.

372 Intermediate green leaves, heavy *Erysiphe* infection, no *Puccinia*, late (1964), shortest culms, short panicles, few panicles, most compact panicles, 'difficult' ear emergence, small plant diameter (1963), narrow leaves, low leaf index.

373 Intermediate green leaves, severe *Erysiphe*, no *Puccinia*, late (1964), fewest panicles, short panicles, 'difficult' ear emergence, small plant diameter (1963), short plant (1962), shortest plant (1963), low winter weight, highest dry matter content, short leaves, narrowest leaves, high calcium, low sodium.

374 Intermediate green leaves, severe *Erysiphe* infection, no *Puccinia*, late (1964), short culms, few panicles, 'difficult' ear emergence, small plant diameter (1963), short plant (1963), low winter weight, longest leaves, low leaf index, low sodium.

381 Intermediate green leaves, green nodes, moderate to severe *Erysiphe* and *Puccinia*, self-compatible (low value), few panicles, low leaf index, high calcium.

382 Intermediate green leaves, bright green to green nodes, moderate *Erysiphe*, moderate to severe *Puccinia*, self-compatible, late (1963), long panicles, small plant diameter (1962), high winter weight, high potassium, low sodium.

391 Intermediate green leaves, green nodes, moderate *Erysiphe*, no *Puccinia*, tall plant (1963), high winter weight, low sodium.

392 Intermediate green leaves, green nodes, moderate to severe *Erysiphe*, no *Puccinia*, few panicles, highest score for opening-out of panicle, tall plant (1963), high calcium, low sodium.

401 Intermediate to light green leaves, bright green nodes, none or slight *Erysiphe*, no *Puccinia*, late (1963), joint latest (1964), few panicles, smallest plant diameter (1963), low dry weight (1962), lowest dry weight (1963), low fresh weight, high potassium low sodium.

402 Intermediate green leaves, bright green nodes, moderate *Erysiphe*, no *Puccinia*, joint latest (1963), late (1964), few panicles, tall plant (1962), high winter weight, high potassium.

43 Intermediate green leaves, whitish-pink panicles, bright green nodes, virtually not infected, one plant emerged in 1962 (other plants in the trial did not), early (1963), short culms, shortest panicles, many panicles, small plant diameter (1963), highest winter weight, high fresh weight, high calcium.

44 Intermediate green leaves, bluish-purple panicles, purple-brown nodes, severe *Erysiphe* infection, no *Puccinia*, late (1964).

46 Intermediate green leaves, khaki-green panicles, green nodes, moderate to severe *Erysiphe*, intermediate self-compatibility, small plant diameter (1963), narrow leaves, low leaf index.

47 Intermediate green leaves, khaki-green to red-tinged panicles, moderate *Erysiphe*, moderate *Puccinia*, early (1963), short culms, small plant diameter, short leaves, narrow leaves, highest calcium.

501 'Oily' dark green leaves, normal to golden-green panicles, purple-brown to nondescript nodes, moderate to severe *Erysiphe*, no *Puccinia*, female-sterile, male-fertile, many panicles, tallest plant (1962), high dry weight (1962), high fresh weight, long leaves, high potassium.

502 'Oily' dark green leaves, purple-brown nodes, moderate to severe *Erysiphe*, no *Puccinia*, markedly winter-green (uncut foggage), few panicles, 'difficult' ear emergence, lowest sodium.

512 Intermediate green or 'oily' dark green leaves, virtually no infection, few panicles, tall plant (1962), high dry weight, high fresh weight, long leaves, low leaf index, highest sodium.

52 Intermediate green or 'oily' dark green leaves, purple-brown nodes, moderate to severe *Erysiphe*, no *Puccinia*, short culms, open panicles, tall plant (1962), highest dry weight (1962), high dry weight (1963), highest fresh weight, long leaves, low leaf index, high potassium, high sodium.

53 Intermediate green leaves, normal to bluish-purple panicles, purple-brown nodes, moderate to severe *Erysiphe* infection, no *Puccinia*, earliest, long culms, long panicles, greatest number of panicles, tall plant (1962), tallest plant (1963), high winter weight, broadest leaves.

55 Intermediate green leaves, green nodes, moderate *Erysiphe*, no *Puccinia*, joint latest (1963), late (1964), few panicles.

60 Light green leaves, moderate *Erysiphe*, virtually no *Puccinia*, self-compatible, low potassium, low sodium.

61 Light green leaves, moderate *Erysiphe* infection, severe *Puccinia*, tall plant (1963).

62 Light green leaves, purple-brown to nondescript nodes, khaki-green to red-tinged panicles, moderate to severe *Erysiphe*, moderate *Puccinia*, small plant diameter, short plant (1962), low dry weight (1962), low winter weight, low fresh weight, short leaves, narrow leaves, high calcium.

63 Light green leaves, purple-brown nodes, moderate *Erysiphe*, early, long panicles, long leaves, low leaf index.

64 Intermediate to dark green leaves, green panicles, moderate to severe *Erysiphe* infection, no *Puccinia*, conspicuous *Epichloe* infection, the only case of vivipary occurred in this group, many panicles, tall plant (1963).

65 Dark green leaves, virtually not infected, late (1964), low leaf index.

67 Intermediate green leaves, moderate to severe *Erysiphe*, no *Puccinia*, few panicles, small plant diameter (1962), short plant (1962), low winter weight, low fresh weight, shortest leaves, narrow leaves, high potassium, low sodium.

72 Light green leaves, moderate to severe *Erysiphe* and *Puccinia*, compact panicles, high dry weight (1962), narrow leaves, lowest leaf index, highest potassium.

NOTES

(*a*) 'Difficult' ear emergence means the protracted production of very few panicles in 1963, on most plants.

(*b*) Since almost all of the groups have a low magnesium content and a low dry matter content, the synopsis of their characters only records the occurrence of high values.

(*c*) Where the year is not specified, all years of recording are implied.

'high,' etc., are the extreme values given in Table 1. It will be seen that every group has some extreme characters compared with the rest.

It is of interest at this stage to see how the classification compares with the subjective assessments of the plants made by field observation of their general appearance (paragraph 2 of the 'programme of work'). The result is that in no cases have closely similar plants been divided between groups. Each group contains one or more series of similar plants, which could be taken to imply that the assessments of similarity were too detailed, or that they have detected valid differences which are reflected by the heterogeneity indicated by statistical tests. Unfortunately, there is not usually a clear relation between the heterogeneity pin-pointed by the two methods.

All plants which were subjectively assessed to be different were later found to occur in separate groups.

Previous work by Harberd (1961) has shown that the study of the incompatibility relationships of a population sample of *Festuca rubra* can be an invaluable aid to deciding whether genotypic reduplication is present. This method is particularly appropriate to the present problem, and it was largely for the same purpose that investigations of the breeding systems of the plants obtained from the flush were made.

Harberd's rationale is essentially as follows. Cross-incompatibility between two plants which are functionally fertile and self-incompatible could be explained in two ways: that the two plants result from clonal propagation arising from a single zygote, in which case they are of identical genotype, or alternatively that the plants are different genotypes which possess the same incompatibility alleles. Work on the distribution of incompatibility alleles in populations has demonstrated that the chances are low of encountering two different genotypes having the same incompatibility alleles, and so if the two plants are morphologically similar, the first alternative appears to be the most probable explanation. It is therefore expedient to carry out incompatibility tests if a group of similar plants is suspected to consist of a single genotype. Conversely, cross-compatibility between morphologically different groups of plants supports the validity of the group differences.

In the present work, because isolates which are of the same genotype are likely to occur in the same group, negative crosses are expected only to occur within groups, and positive crosses between groups. In addition to the need to confirm the present classification of *Festuca rubra* in this manner, it was desirable to characterise the breeding systems of the plants from the area of hillside under study to augment the knowledge of intraspecific variation.

As stated earlier, several series of pot plants were derived from the plants of the field trial. In order to stimulate flowering one series was kept at a higher altitude on a field plot in the Pentland hills for almost two months during one spring to ensure that they would have a cold period. Flowering performance each summer was found to vary between the series. The condition of some of them appeared to be particularly good for seed setting in the summer of 1964, and so the data from these plants are given separately, and results from other crosses are given in brackets in the Tables.

Tests of self-compatibility were carried out by excluding foreign pollen from a group of panicles with a 25″ × 8″ semi-transparent bag made of a kind of paper which has a high wet-strength yet allows the passage of water vapour and gases to take place. The bag was normally supported internally by a wire frame, was shaken several times each day during anthesis, and was cut open to allow better aeration when the seed was developing. Crosses were conducted in the same way as for selfs using panicles from two adjacent plants and verifying as far as possible that there was coincidence of anthesis.

Certain of the crosses were arranged in a series of rings in which each plant was crossed with the two on either side of it, care being taken to place plants which were expected to be cross-incompatible side by side. This resulted in a rather greater yield of information than from isolated pair-crosses. In many cases, all the isolates from one core of turf could be placed together in a single ring, which was joined to the rings of plants from other cores of turf, so that the crossing-pattern resembled a chain.

Other schemes were arranged so that morphologically-different isolates were crossed in anticipation of seed setting. Many plants were divided into two portions to facilitate several combinations of crosses. Panicles which were not used in crosses or selfs gave information of seed yield under open-pollination. When the results were known at the end of the season, virtually all isolates which were apparently cross-incompatible were known to be functionally fertile on account of the seed set in open-pollination or in other (compatible) crosses.

After harvesting, the panicles of each female parent were kept separately and subdivided according to the apparent presence or absence of seed on them. In the case of a compatible cross, the object was that the panicles which had a low yield due to their having largely escaped from cross pollination would not decrease the average seed-setting figures for the panicles taken as a whole and so obscure the fact that certain panicles had a high yield.

The yield in self-incompatible plants was rarely found to exceed two seeds per panicle after selfing, and so the most appropriate way of subdividing the panicles from a cross was those having (*a*) no seeds, (*b*) one or two seeds, and (*c*) three or more seeds, the first two categories being considered to have escaped cross-pollination. The grading was not done in detail because all that was required was an approximate indication of the range of variation between panicles.

Panicles of categories (*a*) and (*b*) were subjected to a germination test and the number of seedlings counted. Since panicles of category (*c*) contained abundant seed, most of it was counted and retained for further use, and to save time the chaff was subjected to a germination test and the number of seedlings added to the number of seeds.

The system is illustrated by the following example :—

In cross 1101, *between plant* 1342 *F and plant* 482 *F*

The ten panicles used on plant 1342 F were graded as follows :—

(*a*) 2 panicles probably having no seeds. A germination test gave 4 seedlings, that is 2.0 per panicle.

(*b*) 4 panicles probably having one or two seeds each. A germination test gave 25 seedlings, that is 6.3 per panicle.

(*c*) 4 panicles which had abundant seed. 172 seeds were counted and a germination test on the chaff gave an additional 8 seedlings. Average yield 45.0 per panicle.

The germination tests were conducted with a control sample of 50 seeds taken out of the counted batch and 94 per cent germination was obtained. There was thus a total yield of 209 seeds (for brevity the term 'seeds' implies seeds + seedlings in the rest of this paper). The final value is given as 20.9 (2.0 to 45.0) seeds per panicle. The seed setting of 482 F as female parent was 36.0 (13.0 to 47.5) seeds per panicle.

Because this system necessitated carrying out a large number of germination tests (over 1,500 resulting from some 500 crosses and selfs) a rapid method had to be devised as follows. Each sample was stored in a paper bag having one surface of cellophane, and the germination test was started by placing the bag with the paper side downwards on a layer of moist soil and covering with muslin to prevent drying. Germination in a warm greenhouse commenced after about one week, and the seedlings could be easily counted (or large numbers estimated) through the cellophane.

Most of the isolates tested were found to be self-incompatible, 11 others had varying degrees of self-compatibility, and others were intermediate. Table 3 gives the seed yield figures for the three types, with data for crosses and open pollination of self-incompatible plants for comparison. It will be seen that although there is variation between the results of several tests on the same type of material, there are clear differences between the self-compatible and self-incompatible groups.

It has been found a workable plan to designate the term 'self-incompatible' to average yields of under 3.0 seeds/panicle in individual tests (not exceeded by any group of panicles which are components of that average), and 'self-compatible' to average yields of 5.0 or more seeds/panicle. 'Intermediate self-compatibility' refers to average yields of between 3 and 5 seeds per panicle, with the extension that plants with an average yield which would normally result in their being classed as self-incompatible are placed in the intermediate category if any panicles or groups of panicles which are components of the average yield have 3.0 or more seeds/panicle. For example, group 63 of Table 3 is described as an intermediate in view of the value 4.0 seeds/panicle, whereas group 46 is a *bona-fide* intermediate. The reason for the caution with group 63 is that individual tests of material with a low level of self-compatibility may occasionally give unusually low values as seen with group 381 of Table 3.

Table 4 gives a survey of the breeding relationships of the groups of isolates which have already been described. Five groups are self-compatible, 27 are self-incompatible, 1 is

TABLE 3

SEED SETTING PERFORMANCE OF SELF-COMPATIBLE, INTERMEDIATE AND SELF-INCOMPATIBLE PLANTS OF *FESTUCA RUBRA*

Item to be illustrated	*Type of test*	*Group*	*Number of isolates tested*	*Results of individual tests* (average number of seeds per panicle)	*Overall Mean* (*c*)
Performance of self-compatible groups	Self pollination	202b	1	21.1	21.1
		352	1	5.0	5.0
		381	1	2.8 (? to 7.0), 5.9 (0.0 to 6.7), 5.3 (2.0 to 6.4)	5.1
		382	1	11.1 (5.0 to 13.1)	11.1
		60	7	5.3 (1.0 to 8.0), 14.8 (3.0 to 15.1), 13.1	9.5
				4.0 (? to 9.0), 7.7 (3.0 to 8.3), 3.0, ≥ 7.7	9.5
Performance of groups classed as intermediate self-compatible	Self pollination	46	11	1.7 (0.5 to 4.0), 3.7 (0.0 to 5.5), 2.5, 3.2 (2.0 to 3.7), 0.6 (0.5 to 1.0), 2.3 (1.5 to 4.0), 0.0, 2.5 (1.0 to 5.0), 0.2 (0.0 to 1.0), 2.0, 1.2 (0.0 to 4.0), 0.5, 1.3, 0.0, 2.0, 0.8 (0.7 to 1.0)	1.7
		63	2	0.0, 1.2 (1.0 to 1.2), 0.0, 1.2 (0.0 to 4.0)	0.9
Performance of a self-incompatible group for comparison with the above two categories	Self pollination	31	6	0.0, 1.0, 0.4, 0.0, 0.8	0.7
	Crosses within the group	31	9	0.0, 0.6, 0.3, 0.3, 0.6, 0.5, 0.0, 0.4	0.3
	Open pollination in greenhouse	31	5	10.8, 24.0, 13.9, 21.0, 4.6, 13.0	12.9
	Outcrossing	31	8(a)	7.0, 0.4(b), 8.4, 17.9, 2.7(b), 15.2 8.5, 27.0, 6.0, 9.6, 24.5, 10.9, 36.0	10.2

(*a*) Only data for group 31 as ♀ parent given.

(*b*) Abundant seed on the other parent so the particular combination of plants is correctly defined as cross-compatible.

(*c*) Weighted by the number of panicles used in each test.

TABLE 4

SURVEY OF THE SELF- AND CROSS-INCOMPATIBILITY RELATIONS OF GROUPS OF *FESTUCA RUBRA* ISOLATES

GROUP	NO. OF ISOLATES	NO. OF ISOLATES TESTED FOR BREEDING SYSTEM (*a*)	BREEDING SYSTEM (*c*)	SIZE OF CROSS-INCOMPATIBLE CLUSTERS	NO. OF POSITIVE CROSSES WITH OTHER GROUPS (*d*)	POSITIVE CROSSES OBTAINED WITH THE FOLLOWING GROUPS (*d*)
066	8	4(4)	SI	(2)+(2)=4(4)	1(1)	(60)
202b	1	1	C	—	3	27, 502
22	2	1	SI	0	2	292, 65
24350	4	3	SI	3	11	24355, 381, 402, 43, 60, 61, 62
24355	2	1	Int.	0	2	24350, 72
27	2	2	SI	2	9(3)	202b, (31), 44, 502, 60, (67)
292	2	1	SI(*b*)	0	2	22, 512
30	1	1	Int.	—	2	391, 43
31	21	7	SI	7	12(1)	(27), 372, 374, 43, 46, 60, 61
352	2	1	C	—	2	361, 64
361	5	4(2)	SI	2	8(1)	352, 46, 501, 61, 62, 64
362	1	1(1)	SI	—	0	
371	2	2	SI	0	9	402, 44, 46, 47, 62, 64
372	3	1	SI	0	2	31, 46
373	1	1	SI	—	6	402, 44, 46, 55, 61
374	2	2	SI	2	4	31, 382, 67, 72
381	5	1	C	—	4	24350, 46, 61
382	1	1	C	—	6	374, 46, 53, 61, 62, 65
391	2	1	SI	0	3	30, 512, 60
392	1	1	SI	—	3	55, 60, 64
401	1	1	SI	—	2	44, 53
402	1	1	Int.	—	4	24350, 371, 373, 44
43	5	5	SI	5	15(5)	24350, 30, 31, 501, 65
44	10	6(2)	SI	4	7(1)	27, 371, 373, 401, 402, (501)
46	25	17(2)	Int.	15+(2)=17(2)	21(1)	31, 361, 371, 372, 373, 381, 382, 47, 501, 62, 63, 64, 65
47	1	1	SI	—	5	371, 46, 62, 63
501	19	18(10)	♀ Sterile	—	20(7)	361, 43, (44), 46, 502, 53, 61, 62, 64, 67
502	9	3	SI	2	7	202b, 27, 501, 60, 61, 62
512	1	1	SI	—	2	292, 391
52	1	(1)	SI(*b*)	—	0	
53	3	3(1)	SI	2	7(2)	382, 401, 501, 61, 64, (65)
55	1	1	SI	—	2	373, 392
60	19	7	C	—	19(2)	(066), 24350, 27, 31, 391, 392, 502, 61, 65, 72
61	24	14(2)	SI	14(3)	15(1)	24350, 31, 361, 373, 381, 382, 501, 502, 53, 60, 65
62	10	10(5)	Int.	5+(5)=10(5)	14(1)	24350, 361, 371, 382, 46, 47, 501, 502, 63
63	3	2	Int.	2	3	46, 47, 62
64	6	5(1)	SI	2+2=4	10(2)	352, 361, 371, 392, 46, 501, 53, (65), 67
65	34	16(8)	SI	8(1)+(2)+(2)+(2)+(2)=16(9)	15(5)	22, 382, 43, 46, (53), 60, 61, (64)
67	5	4(2)	Int.	(2)+(2)=4(2)	5(1)	(27), 374, 501, 64, 72
72	2	1(1)	SI	0	4	24355, 374, 60, 67

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NOTES

(*a*) Includes a few isolates which although having no self test *per se* were concluded to be self-incompatible on the basis of cross-incompatibility within the group.

(*b*) No seed set on this isolate so the conclusion is subject to assumption of female fertility.

(*c*)
C = self-compatible.
SI = self-incompatible.
Int. = intermediate.

(*d*) In the case of self-compatible groups, conclusions are drawn from their behaviour as male parent only.

— means 'inapplicable.'

One additional unclassified isolate was obtained from site 55.

Numbers in brackets are part of any adjacent number, *e.g.* 15(5).

female sterile, and 7 are intermediate. Of the intermediate groups, only 46 is truly intermediate, while the others are virtually self-incompatible. In the case of self-incompatible and intermediate groups, the number of isolates which have been crossed with others of the same group varies from 2 to 17. The actual number depends on chance, for it may be recalled that the crosses were carried out before the groups had been derived. These intra-group crosses have given negative results. It was frequently found that two or more plants within a group could be linked together as a 'cross-incompatible cluster' on the basis of negative crosses between them, and the sizes of these clusters are given in Table 4. Certain groups possess more than one cluster because the crosses necessary for linking them were not carried out. The presence of these negative crosses within groups is consistent with the theory that each group is a single genotype, or very few genotypes.

It will be seen from the table that crosses between many of the possible combinations of groups have given positive results. In the case of groups with intermediate self-compatibility such results are concluded from seed yields which are far in excess of the expectation from selfing. These findings suggest that there is a genotypic difference between the groups.

Particular interest rests with group 501 which is apparently female sterile but male fertile. It has been found that in self-pollinations the plants seemed to be self-incompatible until it was clear that there were no instances of seed having been set on them in open pollination or in crosses with other groups. In these compatible cross-combinations, seed was always formed on the panicles of the other parent (Table 5), and tests of germination showed that it was normal in that respect. Group 501 did not seem to be outstanding in the time of anthesis of greenhouse plants, and Table 2 shows that the plants in the field were not extreme in that character. The failure to set seed was not due to paucity of panicles, and it appears to be a case of functional sterility the cause of which has yet to be investigated.

The data so far are in accordance with what was originally anticipated, that crosses between similar self-incompatible plants are negative, and crosses between morphologically different plants are positive. If they occurred, exceptions to this pattern would take the form of positive crosses between morphologically similar plants, and the converse.

Positive crosses between morphologically similar plants, provided they were not due to technical failings, would indicate that the plants were two different genotypes. They might differ in only a few alleles, including those for incompatibility, or in a large number of genetic factors thereby emphasising that the characters used in this study are very few and are imprecise compared with the vast number of traits and processes which living plants possess. Failure to detect differences is only a crude inference of homogeneity, and one could imagine that certain plants which are described as similar within the limitations of the present work could differ in a wide range of physiological and cryptic morphological characters.

This state of affairs cannot be common or a large proportion of the intra-group crosses would have given positive results. There has been only one case, a positive cross between two isolates of group 502. Seed setting occurred only on some of the panicles of one parent and so the cross will have to be confirmed.

Negative crosses between morphologically distinct plants are thought to be most probably explained by faulty technique or chance factors such as a failure to cross-pollinate. Confirmation is vital in these cases. There is, however, one well-substantiated case which cannot be dismissed in this way. It is between group 371 and 372. One isolate of group 372 was crossed with two isolates of 371 and both crosses were negative. All plants set seed freely in crosses with other groups carried out at the same time. There is no reason to suspect that anthesis did not coincide in these plants (the spaced plants had similar ear emergence dates) but it should be mentioned that it was not directly observed. Since the details of the incompatibility system of *Festuca rubra* have not been thoroughly investigated, these conclusions are subject to its ultimately being found to be conventional in its behaviour.

Distribution of genodemes in the natural habitat

The foregoing sections have demonstrated how the majority of plants of *Festuca rubra* have been arranged in groups of similar phenotypes whose incompatibility reactions suggest that each group is either a single genotype or two or more comparable genotypes.

The deme terminology originated by Gilmour and Gregor

TABLE 5

BREEDING BEHAVIOUR OF TWELVE ISOLATES OF GROUP 501 WHICH IS CONCLUDED TO BE FEMALE-STERILE MALE-FERTILE

Code No. of the isolate under consideration	SELF POLLINATION	INCOMPATIBLE CROSSES (*a*)			COMPATIBLE CROSSES (*b*)			
	Seed yield	*Seed yield on isolate under consideration*	*Seed yield on the other isolate*	*Code No. of the other isolate*	*Seed yield on isolate under consideration*	*Seed yield on the isolate of the other group*	*Code No. of the isolate of the other group*	*The other group*
690	0.7	0.0 0.1	0.0 0.0	701 709	0.2 0.1 0.4	18.5 5.4 4.5	1429 1619 1675	361 61 61
709	0.4	0.0 0.1	0.1 0.1	690 719	0.1 0.7 0.3	1.6 26.2 3.1	1619 890 13	61 62 53
646	0.1	0.0 0.0	0.0 0.0	664 719	0.1 0.0	33.5 2.5	890 59	62 43
664	0.0 0.0	0.0	0.0	646	0.0 0.1	10.8 17.3	59 868	43 62
697	0.0 0.7	0.1 0.1 0.1	0.0 0.0 0.1	701 710 710	0.0	5.7	9002	502

Code No. of the isolate under consideration	SELF POLLINATION	INCOMPATIBLE CROSSES (a)			COMPATIBLE CROSSES (b)			
	Seed yield	*Seed yield on isolate under consideration*	*Seed yield on the other isolate*	*Code No. of the other isolate*	*Seed yield on isolate under consideration*	*Seed yield on the isolate of the other group*	*Code No. of the isolate of the other group*	*The other group*
701	1.7	0.0 0.0 0.0	0.0 0.1 0.1	690 697 710	0.2	13.5	1452	64
719	0.1 0.1	0.1 0.0	0.1 0.0	709 646	0.1 0.3	17.0 15.8	9002 594	502 67
710		0.1 0.0 0.1	0.1 0.1 0.0	697 697 701	(0.0)	(6.3)	74	43
716		(0.0)	(0.0)	717	(0.0)	(21.0)	1210	44
717		(0.0) (0.0)	(0.0) (0.0)	721 716	(0.0)	(11.0)	901	62
721		(0.0)	(0.0)	717	(0.0)	(18.6)	1436	361
685		(0.0) (0.0)	(0.0) (0.0)	640 647	(0.0)	(0.7)	590	67

(*a*) Results of crossing with other isolates of group 501.
(*b*) Results of crossing with isolates of other groups.
Yield figures are average number of seeds per panicle.

(1939) and further developed by Gilmour and Heslop-Harrison (1954) is a useful way of referring to these groups. It is proposed, therefore, to define a *genodeme* for the purpose of this paper only as

> 'a group of phenotypically similar plants which apparently consists of a single genotype or relatively few genotypes'.

The groups already described will now be denoted as genodemes. Where a genodeme is considered to be a single genotype, the term genotype has not been adopted since it cannot be proved with existing techniques, and is therefore liable to modification. The case for it is largely circumstantial and can always be improved by additional work. Table 6 is a list of genodemes and the sites from where they were obtained.

Figure 2 is a diagrammatic map of the positions in the flush occupied by the isolates of each genodeme. It shows the number of tillers (isolates) of *Festuca rubra* which were obtained at each of the sampling points already illustrated in Figure 1, except that the places yielding no specimens of that species have been omitted. Since an equal number of isolates was not recovered from each core of turf, the values have been weighted. This was done for each core by totalling the number of viable isolates of all angiosperms and calculating the factor to transform this to 100. The number of tillers of *Festuca rubra* in the core has been multiplied by this factor, so that the length of each histogram is a measure of the frequency in the sward. The actual number of tillers varied from 1 (30/8L, 30/6R, etc.) to 22 (core 60).

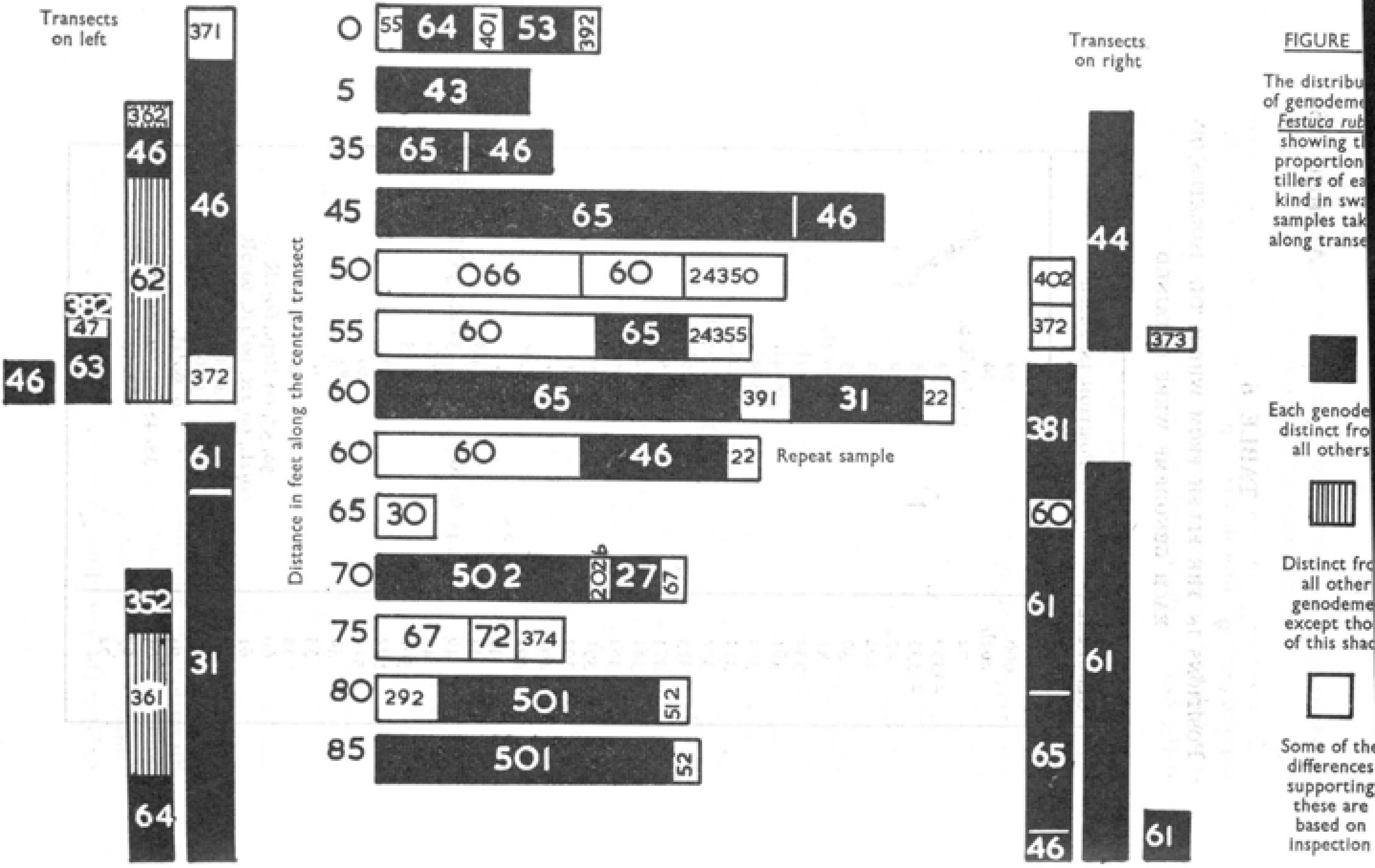
While the diagrams show the composition of the material removed from the flush, there are too few samples for this to be a true reflection of the vegetation as a whole. The lack of *Festuca rubra* at sites 30, 40 and 65 is probably due to chance. The difference between the genodemes occupying sites 60 and 60 Repeat would also have been attributed to chance if it were not known that 60 has in fact a higher pH and cation content. The occurrence of different genodemes could be a response to this environmental change.

It will be seen that some sampling points are dominated by a single genodeme while others have two or more. Some genodemes are localised on a single site, others occur on adjacent sites or are more widespread. The most ubiquitous genodemes 65 and 46 tend to occur together.

TABLE 6

POSITIONS IN THE FLUSH FROM WHICH THE ISOLATES OF EACH GENODEME WERE OBTAINED

GENODEME	POSITION IN FLUSH
066	50
202b	70
22	60, 60 Rep.
24350	50
24355	55
27	70
292	80
30	65
31	60, 60/2L
352	60/4L
361	60/4L
362	30/4L
371	30/2L
372	30/2L, 30/2R
373	30/6R
374	75
381	60/2R
382	30/6L
391	60
392	0
401	0
402	30/2R
43	5
44	30/4R
46	35, 45, 60 Rep., 60/2R, 30/2L, 30/4L, 30/8L
47	30/6L
501	80, 85
502	70
512	80
52	85
53	0
55	0
60	50, 55, 60 Rep., 60/2R
61	60/2L, 60/2R, 60/4R, 60/6R
62	30/4L
63	30/6L
64	0, 60/4L
65	35, 45, 55, 60, 60/2R
67	70, 75
72	75



FIGURE

The distribu
of genodeme
Festuca rub
showing t
proportion
tillers of ea
kind in swa
samples tak
along transe

The presence of genodeme 64 at sites O and 60/4L without being found at intermediate points is not easy to explain. It could have a more extensive spread around the periphery of the flush or the two patches might have arisen from viviparous propagules. This latter idea is not impossible in view of the fact that one plant of 64 has already given rise to viviparous progeny which have been successfully established. Furthermore, this group is also outstanding in being conspicuously infected with *Epichloe* which has been transmitted to the viviparous plantlets.

General discussion

It has been shown that the environmental gradients associated with the area under study are inhabited by *Festuca rubra* plants which represent a series of genetic types, and that different parts of the environment are usually occupied by different genodemes, while a small number of genodemes are more extensive. The accuracy of this conclusion lies in the validity of the genodemes, which is based on agreement of morphological and physiological characters with the results of investigations of their breeding relationships.

If there were no discrete characters, the present approach would not be possible and other ways such as those of numerical taxonomy would have been employed. It is conceivable, for example, that the analysis of other habitats could yield data which is continuous throughout, and which when illustrated diagrammatically would appear as a multi-dimensional 'spider's web' of similarities. Such cases would involve these other methods.

Where the distinctions between any two genodemes have required confirmation, significant differences in quantitative values have been sought as an assurance that there are in fact two groups, but this does not indicate that the demarcation between them is absolute, and so it is theoretically possible for there to be an interchange of isolates between certain genodemes. This statistical confirmation is meaningful where the quantitative values were not the basis of the initial delimitation of the groups. It would, however, be considered inadmissible merely to separate plants into, say, 'large' and 'small' and to assume that the two groups are necessarily valid if the size difference between them is statistically significant, because this can in certain cases be done erroneously with a single population of data.

It was stated earlier that each group was subjected to analyses of variance of measured characters to detect whether there was any heterogeneity among the isolates. Apart from the exceptions which were noted, there was lack of significance using $P = 0.05$ as the minimum level for significance. In the cases where the values of F were less than unity or approximately unity, heterogeneity is not suspected. But where the value of F corresponds to values of P between, say, 0.25 and 0.05, the odds are in favour of heterogeneity although these levels are not normally accepted as implying significant difference. The extent to which non-significant values of F can be taken to indicate homogeneity is a matter of interpretation based on a knowledge of the material in question. Using small samples, variations of F above and below unity might be expected to occur by chance, due to inaccuracies in the estimations of variances. Values obtained for cross-incompatible clusters of plants gave some support for this idea.

Although a large number of ramets of a single genotype may be found to be uniform in some characters (for example, date of ear emergence (Harberd, 1961)), this uniformity may not occur with other characters or in other more plastic genotypes. Knowledge of the variation between individuals of a known clone is essential for the judgment of the uniformity within a genodeme, and any measurement of this variation is improved by increased multiplication as spaced plants within each plot and as a larger number of plots. In this trial, however, to have increased the amount of replication would have reduced the acceptable number of isolates and so a compromise situation had to be reached. The conclusions are thought to be the most reasonable which can be achieved with these technical limitations.

Because so many of the genodemes consist of very few isolates, it may well be wondered whether the writer has tended to give importance to differences which should have been overlooked in view of the variability which is always apparent in biological material. However, the fact that almost all the larger groups have shown themselves to be heterogeneous in one or more characters, as suggested by analyses of variance, implies that whichever way the material is arranged there will inevitably be many groups.

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The heterogeneity within certain genodemes could be envisaged to indicate one of several alternative phenomena. Firstly, it could be that such a genodeme is made up of two or more comparable genotypes which are so similar in their physiology in this environment that they occupy the same small niche. Alternatively the genodeme could consist of a single genotype whose heterogeneity in the field trial demonstrates some facets of a phenotypic plasticity which has enabled it to survive in a region of spatially rapid environmental change. The heterogeneity could also be attributed to carry-over effects from the previous environment, shortcomings of the statistical tests applied, the use of ' bad ' characters or cryptic infections such as with *Epichloe typhina*.

The paucity of flowering on the flush owing to a high grazing intensity, and the lack of *Festuca rubra* in the surrounding ungrazed area would suggest that new genotypes are introduced to the flush only on rare occasions, perhaps if for some reason sheep were removed for a period of time. If the present arrangement of genodemes is an outcome of each being adapted to its particular part of the environment, such orderly arrangement could have arisen by selection from an original array of genotypes, or perhaps by an amoeboid type of vegetative spread to result in a rearrangement of them.

The situation can be contrasted with that in *Agrostis tenuis* because this species is present in the poorer soil surrounding the flush, where it is not prevented from flowering, and from which a supply of recombinants could reach the flush. When the work with *Agrostis* is complete it may well be found that there are overall differences between it and *Festuca rubra* which can be attributed to a long period of vegetative growth in the latter contrasted with a history of recombination.

It is possible that an analysis of many areas of *Agrostis-Festuca* will reveal a different picture in each case, and that there is no general rule to predict the extent of genetic variation. In his work with one such community, Harberd (1961) found that a small area was dominated by the extensive spread of a few genotypes. It is difficult to make a valid comparison of the genotype frequency in that case with the present flush, because of differing methods of sampling, and the presence in Harberd's collection of unclassified plants which might contain many genotypes. The impression is, however, that the present study shows a relatively greater number of genotypes, possibly as a consequence of the flush having a wide range of soil conditions.

The arrangement of the genodemes on the map (Fig. 2) may be orderly, fortuitous or intermediate between these two extremes. Examination of their characters is in progress to discover whether they parallel the known variation in the environment. At first sight there does not appear to be an obvious pattern for many characters, but it is possible that the most meaningful index of environmental variation would be derived from a complex integration of several parameters, and so the first impressions are to be taken with caution. It should be noted, however, that the lower part of the central transect is dominated by the genodemes with high potassium levels, and genodemes with 'oily' dark green leaves occur only in that region. Further work is contemplated to find whether genodemes are adapted to particular parts of the range of soil conditions.

Adaptation to the environment could be of ultimate agricultural value. A larger survey of many communities may, for example, show that genotypes from the periphery of populations possess qualities which would enable them to compete in rather poorer soil than the norm for *Agrostis-Festuca*. Such genotypes, if they exist, could be the progenitors of a type of *Festuca rubra* of value in reseeding areas of poor hill soil for which only a small degree of mineral upgrading is economically feasible. Any attention to detail of the classification of these plants is, therefore, eclipsed by the knowledge that there is genetic variation in physiological characters involving mineral nutrition. It is one step towards the ultimate aim of tapping the large reservoir of genecological potential to the benefit of agriculture.

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METHODS, APPARATUS AND MATERIALS EMPLOYED IN TESTING OAT SEEDLINGS FOR RESISTANCE TO STEM EELWORM *DITYLENCHUS DIPSACI* (KÜHN) FILIPJEV

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Summary. The procedures employed at the Scottish Plant Breeding Station in the course of testing oats for resistance to the stem eelworm *Ditylenchus dipsaci* are described in detail. Description of the special pieces of apparatus constructed to facilitate this work and the sources of the various materials used are given in Appendices A and B. Infested oat material collected in the field is fed into a Chopper (Fig. 1 (*a*)), the chopped material is placed on the eelworm Extractor (Fig. 1 (*b*)) and the eelworms so obtained are cleaned and stored. Seedlings to be tested are grown in slits in germination pads held in aluminium Pad Holders (Fig. 3) suspended in racks constructed for the purpose (Appendix A). The slits in the pads are cut by means of a Gang Knife (Fig. 2). The inoculum in which the nematodes are suspended in a solution of Carboxy-Methyl-Cellulose (Appendix B) is prepared and the inoculation procedure and subsequent evaluation of the test is described. The final assessment followed by the transplanting of resistance seedlings takes place six weeks after inoculation.

Since the severity of *Ditylenchus dipsaci* attack on oats varies from year to year under natural field conditions and depends on the soil moisture at and for a time after sowing, a technique suitable to the laboratory and glasshouse has been developed, based on that used by Dr J. W. Seinhorst (1952) for testing rye which enables large numbers of plants to be tested quickly within a limited space. The method used at the Scottish Plant Breeding Station for testing oat seedlings for resistance to *D. dipsaci* is described below, the apparatus used is detailed in Appendix A, and the materials in Appendix B.

The infested oat plants are collected once a week over a period of four weeks from about the second week of July, commencing when the basal parts are markedly swollen and beginning to show signs of decay. Experience has shown this to be the period for optimum yield of eelworm. The material is spread out while awaiting extraction in a cold room at a temperature of 40°-45°F. to prevent fermentation which, in stored material, appears to have a detrimental effect on eelworm survival.

The roots with any adhering soil are trimmed off after which the basal 6 in. of the plants, wherein most of the eelworm are to be found, is fed endwise into the Chopper (Fig. 1 (*a*)) from which it emerges as short, partly shredded pieces. When sufficient material has been chopped it is spread in a layer not exceeding 1 in. in thickness on the tray of the Extractor (Fig. 1 (*b*)) and continuously sprayed with water in the form of a fine mist. The water carrying the nematodes from the chopped material is collected by funnels into settling dishes *via* plastic tubes so placed to produce a swirl at the deep end of each dish. The effect of the swirl is to deposit the eelworms at that end of the dish and prevent their being carried by the current over the outflow. After spraying for 24-30 hours the accumulated nematodes are sucked into a wash bottle and the Extractor tray recharged with fresh chopped material. To prevent the accumulation of troublesome slime the extraction apparatus is thoroughly cleaned once per week. At all times care is taken to shade the nematodes from direct sunlight.

To clean and separate the nematodes from debris collected with them the contents of the wash bottle are filtered by means of a Buchner funnel and as the last of the water is drawn through the filter eelworms and debris are washed from the edge of the filter paper towards the centre by means of a fine jet of water. A perforated aluminium dome shaped like a watch glass and 12 cms. in diameter is placed in a 15 cm. diameter petri dish and the filter paper, eelworm side up, laid over the centre of the dome. Water is run in at the side of the dish until the level reaches the edge of the paper. At this point a film of water spreads over the whole surface of the paper enabling the nematodes to find their way down the incline into the dish leaving the bulk of the debris behind. Since a certain amount of debris is carried down by the nematodes the process of collecting on filter paper and running off into the petri dish is repeated. The nematodes thus cleaned are collected again on a filter paper which is then dried quickly at room temperature by hanging in front of a small fan. When thoroughly dry, the paper, covered with nematodes, is placed in an airtight jar and stored in a refrigerator at 2°C. until required.

A week before they are required for inoculation the nematode laden filter paper is taken from the refrigerator and again placed over the aluminium dome in a petri dish with water as described above. *D. dipsaci* which have been stored for periods of up to one year revive within twenty-four hours, but more time must be allowed if the period of storage is longer. As the storage period increases the percentage which revive falls off, a 10% survival after seven years having been noted. The revived nematodes are cleaned once more and are kept in the refrigerator overnight in shallow water before making up the inoculum. In the morning the dish containing the eelworms is removed from the refrigerator, the contents stirred, and the dish tilted to allow the eelworms to settle to one side. After 10 minutes they are drawn up into a sufficient number of 1 ml. syringes to hold the required volume of concentrated eelworm. The filled syringes are stood on their thumbpieces for 10 minutes to concentrate the eelworms on top of the pistons. A No. 5 needle, bent in the form of a semi-circle, is fitted to each syringe in turn. Without inverting the syringe the supernatent liquid plus a drop of the concentrated eelworm is expressed back into the dish. The rest of the concentrated eelworm is then ejected into a small specimen tube.

To prepare inoculum for about 1,500 doses, 1.4 ml. of concentrated eelworm is collected in the specimen tube to which is added 1.8 ml. of the stock solution of Carboxy-Methyl-Cellulose and .25 ml. saturated aqueous solution of Gentian Violet. The whole is thoroughly mixed by stirring gently with a small spatula taking care to avoid as far as possible the formation of air bubbles. Air bubbles being compressible give rise to variations in dose if present in the inoculum. The piston and needle joint of a clean syringe, fitted with a No. 1 needle, are liberally smeared with stock Carboxy-Methyl-Cellulose solution and the syringe is then filled by drawing the inoculum from the specimen tube. The Carboxy-Methyl-Cellulose seal prevents minute air bubbles from entering at the joints and becoming trapped in the suspension.

A No. 15 needle is substituted on the filled syringe and the piston depressed slightly to drive the air from the needle. The needle point is inserted into the orifice of the specially modified syringe in its holder (Cameron & Speed, 1963) which is stood mouth upwards, with the piston sealed as above in the withdrawn position. The inoculum is expressed through the needle to fill the barrel of the modified syringe, the needle being withdrawn as the filling is completed. The No. 15 needle is transferred to the modified syringe and the milled head of the holder turned to express any air which may have entered the needle during the transfer.

Turning the milled head through one division expresses .002 ml. of inoculum containing a minimum of 300 nematodes, the dose given to each seedling. Before commencing inoculation a series of counts is made under the low power of a binocular microscope. For this purpose the droplet forming the dose is expressed on to a slide, mixed with about 20 times its volume of water, and spread in a narrow band along the slide. While in the suspension medium the nematodes remain inert but within a few minutes of water being added they become very active. Counting is completed before this activity becomes excessive. Should the number counted be greatly in excess of 300 the syringe is emptied into the specimen tube, a calculated volume of stock Carboxy-Methyl-Cellulose is added and, after mixing, the number of nematodes per dose is checked.

To prepare oat material for inoculation the grains are husked in a machine based on the design of G. H. Willis and L. H. Scott (Love & Craig, 1944) and the kernels are placed in racks of glass tubes. Where a tube contains fewer than 20 kernels the number is made up by adding grains of polished rice. Into the mouth of each tube a small piece of blotting paper is inserted on which is placed a droplet (.004 ml.) of Panogen, a liquid organo-mercuric fungicide. The tubes are corked, left overnight and uncorked in the morning to allow surplus Panogen to evaporate. Twenty equally spaced slits, 1 cm. in length, are cut at right angles to and ½ cm. from one long edge of each germination pad using the Gang Knife (Fig. 2) and are numbered by means of a stamp to aid in the subsequent identification of plants. The pads and cover papers are heat sterilised overnight then the cut edge of each pad is dipped in sterile water to soften the area of the slits. The treated kernels are inserted in the slits using a pair of hollow tipped forceps (Seinhorst, 1952) so that the embryo lies on the numbered side and on germinating the coleoptile grows upwards towards the near edge and the roots grow downwards. Two cover papers of thin filter paper are placed over the numbered sides of the pads which are placed in aluminium holders (Fig. 3) which in turn are suspended in racks (Appendix A) in such a way that the lower edge of the pad dips into sterile water in the shallow tray. The racks are placed in a temperature controlled germination chamber at 59°F. with the front of the pads turned away from incident light. Seedlings are ready for inoculation when they are ¾ in. to 1 in. in height, normally after five days in the chamber. Any pads of seedlings which are in advance of their fellows or which cannot be inoculated on the appointed day are kept for up to 24 hours in a cold chamber at 40°F.

To inoculate, the needle is inserted into the coleoptile about ½ in. above and pointing towards its base so that the ground face of the needle point is towards and approximately parallel to the surface of the pad. With the needle orifice within the coleoptile the milled head of the syringe holder is rotated one division whereupon the violet coloured dose is seen to spread within the coleoptile. During the winter months the racks of seedlings after inoculation receive 18 hours per day illumination in a glasshouse heated sufficiently to prevent frost, and during the summer months in a controlled environment chamber at a temperature range of 50°-55°F. After inoculation the sterile water in the trays is replaced by Knop's nutrient solution.

A photographic record of each test series is made after 4 weeks followed at 6 weeks by a final assessment and the transplanting of selected plants. The plants, five to a 6-in. pot, are grown to maturity in the glasshouse.

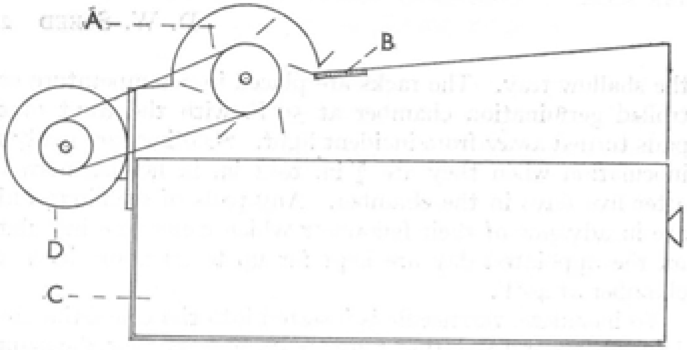

FIG. 1 (*a*)—CHOPPER

A. Cutting cylinder.
B. Adjustable steel plate.
C. Drawer.
D. Motor.

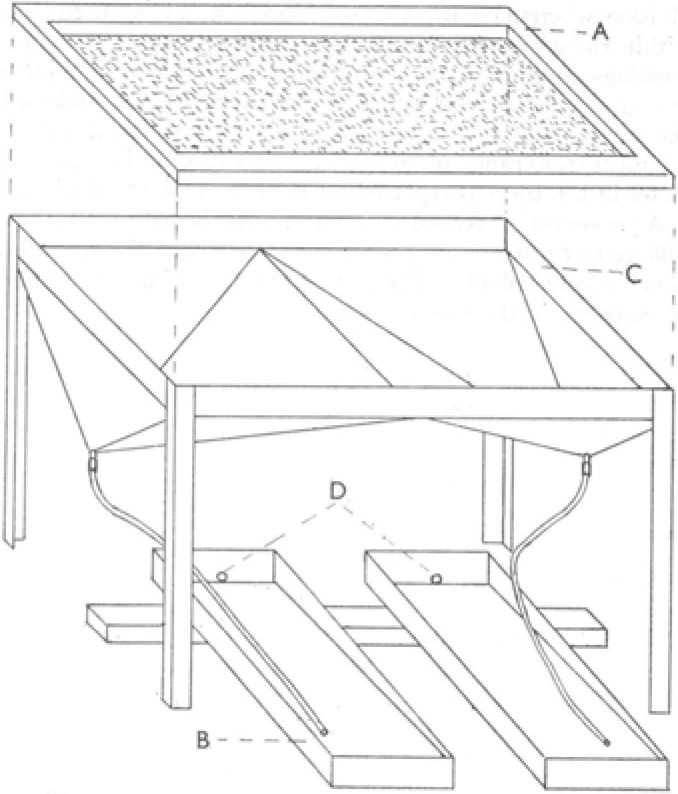

FIG. 1 (*b*)—EXTRACTOR

A. Frame covered with nylon mesh.
B. Collecting dish.
C. Double funnel.
D. Outlet

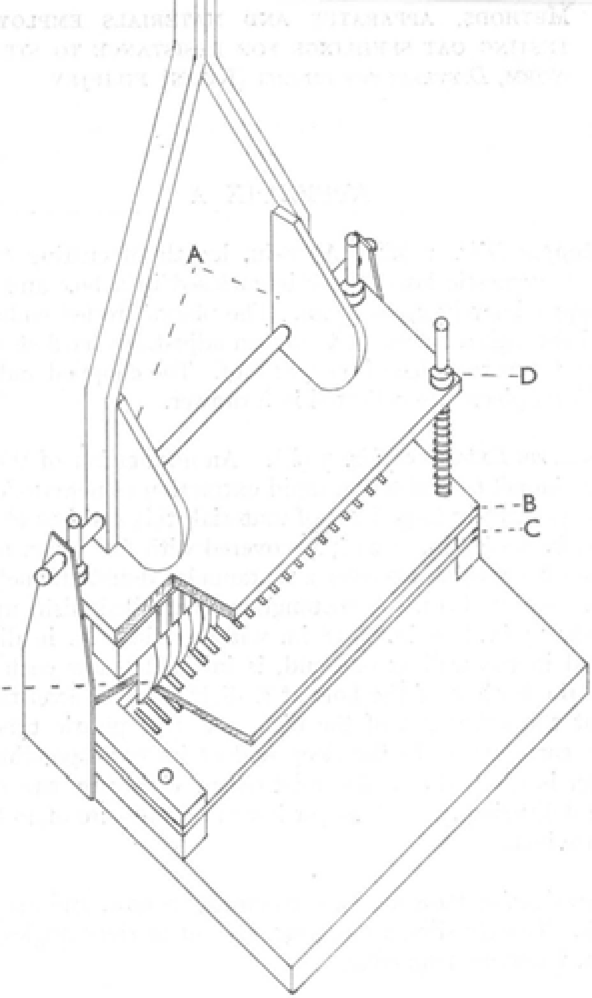

FIG. 2—GANG KNIFE

A. Lever operated cams.
B. Upper fixed plate.
C. Lower fixed plate.
D. Oilite bearing.
E. Scalpel blades.

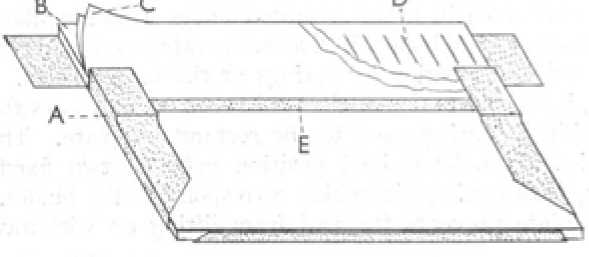

FIG. 3—PAD HOLDER

A. Pad Holder.
B. Germination pad.
C. Cover papers.
D. Slits.
E. Retaining strip.

APPENDIX A

Chopper (*Fig.* 1 (*a*)). An 8-in. length of cutting cylinder from a domestic lawnmower is enclosed in a box and driven at approximately 2,000 r.p.m. The plants are fed endwise by hand through a narrow slit over an adjustable hard steel plate which forms the edge of the box roof. The chopped and partly shredded pieces are collected in a drawer.

Eelworm Extractor (*Fig.* 1 (*b*)). An adaptation of the Baermann funnel to enable the rapid extraction of nematodes from a comparatively large bulk of material, this consists of a light wood frame (25 in. × 21 in.), covered with fine nylon mesh to form a tray which fits over a rectangular double funnel, made from copper sheet. A rectangular enamelled dish, approximately 1½ in. × 6 in. × 18 in. with a hole ½ in. in diameter drilled in the wall at one end, is inclined below each funnel with the bottom of the hole at a slightly lower level than the lip at the other end of the dish. A clear plastic tube leads from each funnel to the deep end of its corresponding dish. Water is sprayed as a fine mist over the tray by two nozzles, each delivering .99 gallons per hour at a pressure of 40 lbs. per square inch.

Germination Pads measure 16 cms. × 8 cms. and are 3 mm. thick. Twenty slits, 1 cm. long, are cut at right angles to and ½ cm. from one long edge.

Gang Knife (*Fig.* 2). Designed to cut parallel slits 1 cm. long at right angles to and ½ cm. from the long edge of a germination pad, the machine has twenty equally spaced scalpel blades which are pushed simultaneously through the pad. The scalpel blades are fixed in a bar mounted under a rectangular plate which is depressed by a pair of lever operated cams and returned to its original position by springs at the four corners. Each spring is mounted on a vertical guide rod which passes through an "oilite" bearing fixed to the rectangular plate. The pad occupies a pre-determined position between two fixed steel plates, both having slits which correspond to the blades. The upper plate prevents the pad from lifting on withdrawal of the blades. The space below the lower plate prevents the blades becoming clogged by an accumulation of fibres from the pads.

Pad Holders (*Fig.* 3). The Pad Holder used differs from that described by Seinhorst (1952) in that the lower edge is turned at right angles and all but the upper 1.5 cms. of the ends are turned through two right angles to form channels. The unturned portion of the ends project and are used as a support for the holder when suspended in the rack. The pad with the cover papers in position slips easily into the channels and rests on the turned lower edge. To prevent the cover papers from adhering to the back of the adjacent Pad Holder when in the rack a stiffened aluminium retaining strip is placed over the cover papers, the ends being held in the upper part of the channels which have been made wider to accommodate it. A former was constructed to facilitate the manufacture of the Pad Holders.

Racks. A rack consists of a rectangular frame with legs, standing in a shallow tray containing water or nutrient solution. The frame is made from ½ in. aluminium angle and the tray from 20 gauge aluminium sheet coated with non-phytotoxic paint to prevent corrosion.

APPENDIX B

Carboxy-Methyl-Cellulose

Manufactured by the Imperial Chemical Industries under the proprietary name of Edifas " A ", the stock solution is made by dissolving 13 gms. in 100 mls. water. This is allowed to stand for at least 10 days after which it is squeezed through a fine nylon mesh in about 20 ml. lots as required. The strained solution is allowed to stand for a further 7 days before use. Straining in this way is an essential part of the procedure as it removes any fibres and incompletely dissolved pieces of Carboxy-Methyl-Cellulose which, if left, would block the needle during inoculation. A useful guide to the correct viscosity of the inoculation medium is the rate at which any air bubbles formed when mixing the concentrated eelworm with the Carboxy-Methyl-Cellulose solution rise to the surface and burst. This should take place within 1-1½ hours of mixing.

Germination Pads and Cover Papers

Manufactured by Messrs J. Barcham Green Ltd., Hayle Mill, Tovil, Maidstone, they measure 8 cm. × 16 cm. The pads are 3 mm. thick, and the cover papers are Green's 401 filter paper.

Knop's Solution

10 gms. $MgSO_4$ in 1 litre water
40 gms. $Ca(NO_3)_2$ in 1 litre water
10 gms. KCl in 1 litre water
10 gms. KH_2PO_4 in 1 litre water
0.4 gms. $FeCl_3$ in 1 litre water

The nutrient solution is prepared by taking 50 mls. of each of the above and making up to two litres with water.

Filter Paper

Whatman No. 4 filter paper, 11 cms. in diameter is used in cleaning and storing the nematodes.

Scalpel Blades

Swann-Morton No. 24.

Panogen

Manufactured by Ab. Casco, Stockholm.

Nylon Mesh

For eelworm extractor 1/64-in. mesh—
Messrs Fothergill & Harvey (Sales) Ltd.,
Peter Street, Manchester.
For straining stock Carboxy-Methyl-Cellulose solution—
Messrs Pronk, Davis & Rusby Ltd.,
44 Penton Street, London, N.1.

Bitumen Paint

Briggsonite Black Bituminous Solution F. W. Grade—
Messrs William Briggs & Sons,
Dundee, Angus.

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Spray Nozzle

W. F. 80 Nozzle tip strainer adaptor assembly and Tip No. 2.50—

Messrs H. T. Watson Ltd.,
Croft Street, Widnes, Lancs.

ACKNOWLEDGMENTS

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SOIL-BORNE VIRUS DISEASES OF POTATO

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CONTENTS

Introduction

Some of the plant diseases now known to be caused by viruses with soil-living vectors have been familiar to many generations of farmers and gardeners. For instance, the internal brown discoloration of potato tubers known as spraing was, even in the late nineteenth century, " the potato grower's old acquaintance " (FINDLAY, 1905). Growers learned to associate some of these diseases with particular fields or soils and took advantage both of this and of varietal differences in susceptibility. The notion of soil-borne virus infection is not new: for spraing the work of Atanasoff (1926), Quanjer (1926, 1931), and Grieve (1934), all suggested it. But only recently has the natural history of these diseases begun to be understood: notably, about 80 per cent of the published work on soil-borne virus biology has appeared within the past decade (see Cadman, 1963). This quickening of interest started with important problems in a few crop plants which led up to and culminated in the discovery of nematode and fungus vectors.

Regarding the soil-borne virus diseases of potato, one can offer reasons for the long delay in coming to an understanding of them. They did not seem to fit with the criteria that suited the classic degenerative potato virus diseases: they tended to have obscure, variable and partial symptom expressions readily attributable to the weather or some other environmental cause; viruses could not be associated with symptoms; and diseased plants became healthy or produced healthy tubers. The purpose of this review is to summarise what is now known about these seemingly complicated diseases.

The different viruses and their main features in relation to potato

Cadman (1963) has placed the soil-borne plant viruses in two groups. Those of one group do not remain infective in soil samples allowed to dry, presumably because the vectors, free-living nematodes, do not survive this. Viruses of the second group are still infective in dry soil; certain of these are known to have a fungal vector, *Olpidium brassicae*, and it seems likely that at least one of them persists in the resting sporangia (Campbell, 1962). Within either group the viruses can be further classified according to the shape of the nucleoprotein unit—whether isometric or rod-shaped. Certain of each sub-group as follows, can infect potato: group 1 (isometric)—tobacco ringspot, tomato black ring, tomato ringspot (Samson and Imle, 1942); group 1 (rod-shaped)—tobacco rattle (potato stem mottle and spraing); group 2 (isometric)—tobacco necrosis; group 2 (rod-shaped)—tobacco mosaic. A soil-borne virus which resembles those of both rattle and tobacco mosaic, Rotterdam-B virus of tobacco occurring in Indonesia, can be inoculated to potato (Jochems, 1928; Thung and Hadiwidjaja, 1958). However this virus, and tomato ringspot virus, do not appear to affect potato in the field; accordingly they will not be considered further in this review.

The symptoms and main epidemiological features of soil-borne potato virus diseases are summarised in table 1.

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TABLE I

A SYNOPSIS OF SOIL-BORNE POTATO VIRUS DISEASES (Only key references are given: literature on generally-accepted facts is not cited in the table. Viruses marked with an asterisk are known to be associated with but have not been proved to cause the disease)

VIRUS	VECTOR(S)	DISEASE IN POTATO						
		Form	Common or applied name	Occurrence	Haulm symptoms	Tuber symptoms	Persistence in Stock	Transmissibility of virus to test plants
Tobacco ringspot*	Nematoda Dorylaimida *Xiphinema americanum* (Fulton, 1962)			U.S.A. (rare)	Yellow marks, sometimes ring-like, along leaflet margin and between veins; especially on lower leaves.	None	Symptoms and virus infection persist.	Regular, but some potato varieties resist inoculation.
Tomato black ring	Nematoda Dorylaimida *Longidorus elongatus* (Of Scottish beet ringspot strain, Harrison, Mowat and Taylor, 1961) *L. attenuatus* (Of English lettuce ringspot strain, Harrison, Mowat and Taylor, 1961)	Beet ringspot	None	British Isles	Frequently, not all stems show symptoms, but, except in the year of infection, symptomless shoots contain virus. The earliest, acute symptoms sometimes begin to appear in the year of infection but more often in the year following; reaction variable, according to variety, from symptomless to severely necrotic; on the leaflets small black spots to large blotches and rings sometimes forming chevrons; in some varieties shoot and bud necrosis. In later years, variable according to variety, from symptomless to some stunting with misshapen leaves, the leaflets rolled or spoon-shaped, often with necrotic streaks underneath the midrib. (Harrison, 1959; Govier, 1962)	None	Symptoms vary according to phase but virus infection usually persists.	Regular

Virus	Vector(s)	Disease in Potato						
		Form	Common or applied name	Occurrence	Haulm symptoms	Tuber symptoms	Persistence in Stock	Transmissibility of virus to test plants
Tomato black ring *contd.*		Bukett (Bouquet)	Bukettkrankheit (This disease and "Gelbfleckigkeit" at first attributed to tobacco ringspot virus infection : see Bercks, 1962)	Germany	Characteristically, not all stems show symptoms ; symptomless stems sometimes contain virus. In the first year, severe necrotic rings ; later leaves may show "oak leaf" pattern. In the second year, bushy stems with thick-set foliage (Bukettkrankheit) but these stems may later grow either symptomless or have some misshapen leaves, the leaflets rolled, spoon-shaped, sickle-shaped, often with necrotic streaks on the rachis. (Köhler, 1952, 1955 ; Gehring and Bercks, 1956)	None	Symptoms vary according to phase ; virus infection persists in shoots with symptoms but may not persist in symptomless shoots of affected plants.	Regular
		Pseudo-aucuba	Gelbfleckigkeit (Yellow spotting)	Germany (rare)	Course yellow spotting or general yellowing over a sector of the leaflet. (Köhler, 1940, 1955)	None	Persistence of symptoms and virus infection vary with variety ; can soon be lost. (Bercks, Gehring and Follmann 1958)	Regular ; potato could be infected but the yellow spotting symptom was never reproduced.
Tobacco rattle	Nematoda Dorylaimida *Trichodorus pachydermus* (In the Netherlands, Sol, van Heuven and Seinhorst, 1960 ; in Southern England, Gibbs and Harrison, 1964) *T. primitivus* (In English Midlands and Scotland, Harrison, 1961 ; Mowat and Taylor, 1962 ; n Germany, Sänger, 1961)	Stem mottle	Stem mottle Mop top Stengelbont Stengelbunt	British Isles Netherlands Germany Denmark	Characteristically, not all stems affected (hence the common name—not because of any mottling of the stems). Shoot symptoms seldom in year of infection.	Often misshapen ; some, in section, with brown flecks, spots, fine arcs and circlets up to a few mm. across in cortex and pith.	Symptoms generally most evident in year following infection ; when stock grown in non-infective soil usually a rapid decline in symptom expression and infection.	Occasionally easy but usually very irregular and uncertain ; sometimes regular from roots of plants grown in infective soil. (Cadman, 1959)
					Stems short ; paired leaflets sometimes unequal, misshapen, with distorted margins and venation, variously mottled ; or symmetrically con-			

VIRUS	VECTOR(S)	DISEASE IN POTATO						
		Form	Common or applied name	Occurrence	Haulm symptoms	Tuber symptoms	Persistence in Stock	Transmissibility of virus to test plants
Tobacco rattle *contd.*	*T. christiei* (In Florida, U.S.A., Walkinshaw, Griffin and Larson, 1961) *T. allius* (In Oregon, U.S.A., Jensen and Allen, 1964) *T. viruliferus* *T. teres* (In the Netherlands, van Hoof, 1964a)				stricted (guitar-shaped) often with a chlorotic or necrotic band across the constriction; or normally shaped with a broad chlorotic chevron.			
			Figuur-aucubabont (Figure aucuba) (Rozendaal, 1947)	Netherlands	Necrosis common; on stems and petioles externally as corky streaks, internally as brown spots and arcs in cortex and pith; on leaflets as fine flecks to irregular or V-shaped blotching. (A leaf symptom associated with stem mottle). Clear yellow stripes, arcs, rings and figures (as distinct from the opaque round spots of aucuba mosaic).			
		Spraing	Spraing Kringerigheid Concentric necrosis (Quanjer, 1931) Pfropfenbildung Kringerigheit Kringerkrankheit Corky ringspot	British Isles Sweden Denmark Netherlands Germany U.S.A. Italy (Gigante, 1963) Poland (Blaszczak, 1964)	Spraing tubers usually produce symptomless and virus-free haulm. Many investigators have suggested that there is no haulm symptom. At least in some circumstances, haulm symptoms can be associated, which resemble those of stem mottle. Lihnell (1958) describes symptoms which recall Rozendaal's figure aucuba.	Single or concentric brownish lines, streaks, arcs or circles sometimes evident on the surface but typically in section; often relatable to a focal point. Symptoms sometimes result from direct infection of the tuber. Microscopically, the discoloration is of the parenchyma cell walls extending to the cell contents. *Pfropfenbildung* similar, but lesions typically localised to to form a cork-like mass. (Braun, 1934)	Irregular; depending on variety and stage of infection, up to about 50 per cent transmission rate in families; usually a rapid decline in symptom expression and infection when stock grown in non-infective soil.	Usually very irregular and uncertain. Cadman (1959) transmitted from necrotic zones early in storage season only. Sänger (1961) transmitted by rubbing cut tuber surface on tobacco leaves. Walkinshaw and Larson (1959) transmitted readily from necrotic zones.

VIRUS	VECTOR(S)	DISEASE IN POTATO						
		Form	Common or applied name	Occurrence	Haulm symptoms	Tuber symptoms	Persistence in Stock	Transmissibility of virus to test plants
Tobacco rattle *contd.*						*Corky ringspot* similar but the arcs and circles of fairly small diameter ; surface rings strongly suberised, extending inwards for 5-10 mm.		
Tobacco necrosis *	Phycomycetes Chytridiales Olpiduim brassicae (Teakle, 1962)		ABC-ziekte (ABC disease)	Netherlands (Noordam, 1957) Italy (Gigante, 1959) Switzerland, (Salzmann, 1960) U.S.A. (Gold, 1960) British Isles (Calvert ; Todd ; unpublished)	None ; but Gigante (1959) reports the virus to be present in small amounts in leaves, petioles and stem and in large amounts in roots.	Infection localised to brown spots (either smooth or reticular), skin necroses and cankers variously resembling other diseases (*e.g.* common scab, gangrene). Sometimes lesions extend during storage to mummify the tuber. The Dutch name "ABC" connotes three kinds of symptom : A—brownish blisters ; B—dark sunken lesions ; C—light brown reticular spots.	Tuber symptom not persistent,but Gigante (1959) isolated tobacco necrosis virus from symptomless tubers derived from affected ones.	Regular from tuber lesions.
Tobacco mosaic	Not known		None	Germany (Kausche, 1938) Argentina (Hansen, 1960)	Severe reactions obtained experimentally (see Blodgett, 1927) but, as in the case described by Kausche, infections were frequently mixed. In Hansen's case, *Solanum commersonii* showed stunting, rather rigid leaves and diffuse interveinal mottling.	None	Hansen's isolate not persistent in varieties of *S. tuberosum* tested, but in clones of some other *Solanum* species.	Regular

<table>
<tr><th rowspan="2">Virus</th><th rowspan="2">Vector(s)</th><th colspan="7">Disease in Potato</th></tr>
<tr><th>Form</th><th>Common or applied name</th><th>Occurrence</th><th>Haulm symptoms</th><th>Tuber symptoms</th><th>Persistence in Stock</th><th>Transmissibility of virus to test plants</th></tr>
<tr><td></td><td colspan="8">The following symptom has been associated with an undescribed potato virus infection in the British Isles (Cadman; Calvert; Todd; unpublished). Although the natural means of transmission is not known the infection is included here because the symptom clearly resembles those described respectively for infection with tobacco ringspot virus, tomato black ring virus (" Gelbfleckigkeit ") and tobacco rattle virus (" Figuur-aucuba "). Similar symptoms have been associated also with the aphid-transmitted viruses of aucuba mosaic and lucerne mosaic.</td></tr>
<tr><td>Un-described</td><td>Not known</td><td></td><td>Yellow mottling</td><td>British Isles</td><td>Chlorosis conspicuous or vague, depending on variety and part of plant affected. If conspicuous, bright yellow, rather coarse chevrons, arcs, rings and blotches; if less conspicuous, soft green patterns of similar type but especially, vague chevrons coincident over all or some of the primary leaflets of a leaf. Conspicuous pattern usually on lower leaves, less conspicuous on upper.</td><td>Generally none; but spraing symptoms are sometimes associable with this infection. (Calvert, unpublished)</td><td>The haulm symptom can persist indefinitely.</td><td>Very irregular; tobacco varies either in susceptibility or in tendency to give symptoms.</td></tr>
</table>

Three distinctive haulm symptoms are evident from table 1 each of which may be caused by more than one virus. They are: (1) dwarfing, often affecting only part of the plant, with misshapen leaves and some necrosis (characteristic of beet ringspot infection, bukettkrankheit and stem mottle); (2) chevron patterns on the leaves, variously chlorotic or necrotic (beet ringspot infection—necrotic; stem mottle—necrotic and chlorotic; and yellow mottling virus infection—chlorotic); (3) yellow patterns on the leaves (tobacco ringspot infection, gelbfleckigkeit, stem mottle, yellow mottling virus infection, aucuba mosaic and lucerne mosaic virus infection).

The extent to which these and other symptoms are associated in Scotland with different viruses is indicated in table 2; this abstracts the appropriate results of several years' virus check tests on field samples many hundreds of which are made annually at East Craigs. White Burley tobacco is the standard test species inoculated but *Chenopodium amaranticolor* is also commonly used, especially when a soil-borne or unusual infection is suspected.

TABLE 2

ASSOCIATION OF VIRUSES WITH SYMPTOMS MAINLY OF THE "SOIL-BORNE" TYPE IN SCOTLAND: RESULTS OF SEVERAL YEARS' CHECK TESTS. Positive transmissions enumerated (columns 4-7), negative evidence evaluated (column 3)

SYMPTOM	GENERAL FREQUENCY IN SCOTTISH CROPS	USUAL REACTION FROM CHECK SAMPLES ON TOBACCO	NO. OF CASES FROM WHICH THE VIRUSES NAMED WERE ISOLATED			
			Ring-spot*	Rattle	Yellow mottling	Aucuba
Nil	—	Negative (many hundreds tested)	5	2	0	0
Stem mottle (dwarfing, misshapen leaves, etc.)	Occasional in many crops; common in crops recently grown on infective soil	Rattle virus or negative (a few hundreds tested)	0	49	0	0
Mild chlorotic chevron patterns on upper leaves	Common	Negative (a few scores tested)	0	2	2	0
Yellow patterns	Common; especially in early growth and in certain varieties (*e.g.* Craigs Royal)	Negative (a few hundreds tested)	3	3	3	2
Necrotic arcs, rings	Uncommon; in crops being grown on infective soil or in the year following	Ringspot (only one tested)	1	0	0	0
Vein clearing and banding,	Occasional	Virus Y; tobacco veinal necrosis virus (many hundreds tested)	7	5	0	0

* The host range tests indicated beet ringspot virus.

Scottish Pl. Breed. St. Rec., 1965, pp. 209-235

This analysis suggests that the symptom of dwarfing with misshapen leaves is in Scotland generally associable with rattle virus infection. And as rattle virus is at least not uncommonly sap transmissible from potato to tobacco it is possible that the few cases of association with the mild chevron and yellow patterns were fortuitous. Ringspot virus is thought to be easy to transmit to test plants, and so is rather unlikely to have caused the symptoms with which it was associated in these tests, except for necrotic arcing. The yellow mottling virus, besides being rather difficult to transmit, is now known sometimes to infect tobacco without causing symptoms (Calvert, unpublished) so that the tenuous association here between virus and symptoms might nevertheless be significant. The aphid-transmitted aucuba virus also is often symptomless in tobacco but it is easy to transmit and distinctive on *Capsicum annuum*; check tests with Capsicum have not suggested that the yellow arc and line patterns in potato are commonly caused by aucuba virus.

In the following general account the different soil-borne virus diseases are grouped in relation to virus and vector. Emphasis is on the history and economics of the diseases and the peculiarities of infection.

The ringspot group

Yellow patterns on the leaf were the first, and for many years the only symptoms associated in the field with ringspot virus infection of potato. In Germany the pseudo-aucuba or yellow spotting disease was ascribed to this group. Periodically in routine testing one isolates ringspot virus from yellow patterned leaves. However no one yet has clearly reproduced this characteristic expression with a ringspot isolate.

Tobacco ringspot virus was obtained by Johnson (1930) and Valleau and Johnson (1930) from Kentucky-grown Irish Cobbler with aucuba-like yellowing. They were unable to infect potato, which confirmed the experience of Priode (1928) and Wingard (1928) with this virus. Valleau (1932) repeatedly got tobacco ringspot virus from yellowed leaves of Cobbler; he could not infect this variety by leaf rubbing but succeeded by grafting. However, although they also were unable to infect Cobbler, Henderson and Wingard (1931) caused local necrosis but not systemic infection in several varieties by leaf rubbing.

Gelbfleckigkeit (yellow spotting) or *Pseudo-aucuba.* Isolates claimed to be of tobacco ringspot virus were obtained in Germany from occasional yellow mottled plants by Böhme (1933) and Köhler (1940). That they had actually caused the symptom was not directly checked by infection tests but Köhler (1940) was from his general experience impressed by the coincidence of having isolated ringspot virus only from yellowed plants. A later similar isolate of Köhler's studied by Gehring and Bercks (1956) gave necrotic lesions but never yellow mottling on a range of varieties; these authors suggested that yellow mottling might happen only in certain environments or from a mixed infection.

Yellow patterns different from those of the classic aphid-transmitted potato aucuba virus have occasionally been associated with ringspot virus in Scotland (table 2); but as already shown, the evidence is against accepting a cause and effect relationship. Another virus with some symptoms of the ringspot type but possibly belonging to a distinct group is more clearly linked with this kind of yellow mottling (Cadman; Calvert; Todd; unpublished). A fuller account is given later.

Bukettkrankheit (bouquet disease). According to Köhler (1955) plants with yellow spotting are not evidently different from normal ones in growth and development. Gelbfleckigkeit thus differed from another disease of potatoes in Germany also ascribed at first to tobacco ringspot virus and for which the term " bukettkrankheit " of Schander (1925) was reintroduced (Köhler, 1952; 1955).

Bouquet disease symptoms are of stem dwarfing, necrosis and leaf deformation. Badly affected plants hardly yield but what often happens is that symptoms appear on only part of the plant, the remainder growing well. As described by Köhler (1950) bukettkrankheit appeared after the 1939-45 war; he suggested that the more extensive cultivation of tobacco about that time might have enabled more virulent strains of tobacco ringspot virus to appear and that tobacco plants carrying the virus in the masked phase might be sources of infection for potato. However it became evident that bukettkrankheit did not spread in the manner of the aphid-borne virus diseases and differed remarkably from them in course and nature. Arenz and Elkar (1954) found that tubers from plants of Maritta with severe secondary bouquet symptoms could give rise under identical glasshouse conditions to both apparently healthy and severely-affected plants; the latter yielded at rates of 34-89 per cent of the former. In the field, 50 per cent of some plants of Ackersegen which had bouquet symptoms when young became apparently healthy, while about 20 per cent did not show any recovery. The infection rate in mostly symptomless clones can remain high (Gehring and Bercks, 1956; 1958) but it is also known to fall off considerably (Gehring and Bercks, 1958). Healthy-seeming stems of diseased plants are sometimes virus-free (Köhler, 1955). Apart however from the characteristic tendency of ringspot-affected clones to lose symptoms or even to throw off infection bukettkrankheit seems to be only an occasional phenomenon. The epidemic in North Germany subsided rapidly (Köhler, 1955). What truth there is in Köhler's early idea of a build-up following tobacco cultivation would have to be reconsidered in the light of what is now known about the identity of the virus and its means of transmission. The important features would be the extent to which tobacco favoured vector populations or helped to distribute infection by means of its seed.

Beet ringspot. As a result of research into soil-borne virus diseases of raspberry, a potato disease resembling bukettkrankheit was discovered in Scotland firstly in the variety Kerr's Pink (Cadman, 1956; Harrison, 1957; 1958a). The symptoms in tobacco resembled those of tobacco ringspot virus but Harrison (1957) showed that the two viruses were distinct. The Scottish virus was named after the crop plant in which it was first discovered. That ringspot virus infection could be symptomless in potato in Scotland was also established. In 1956 I discovered a stock of Craigs Royal of which 0.6 per cent carried a latent infection easily detectable by inoculating tobacco (cited in Harrison, 1958a); this latent infection persisted in all of several families observed over a few years. These observations suggested that varieties react differently, which was confirmed by Govier (1962). Differences were greatest in the acute phase of the disease just after infection and ranged from systematic necrosis and death of shoots (in Arran Pilot, Dr McIntosh and Home Guard, of the 17 varieties tested) to an absence of symptoms (in Craigs Royal, Pentland Beauty and Redskin); in later years infection mostly persisted but the plants seemed only slightly less vigorous than healthy controls. Nevertheless yields were surprisingly reduced in many varieties; in two successive years the mean reductions for twelve varieties were 24 per cent and 12 per cent respectively. Crop losses are bound to be greatest where a stock is grown continually on affected land and in such circumstances the disease would appear to spread and increase. On clean land however Harrison (1959) showed that the loss from an affected crop decreases slowly with time because infected plants produce fewer tubers than normal. With two stocks he studied which were grown for a year on affected land and thereafter for three and two years respectively on clean land Harrison (1959) estimated a total loss of 1 per cent for the first and of 5 per cent for the second, while they were held on the clean land.

In contrast to bukettkrankheit in Germany, beet ringspot infection in potato is hardly known to growers in the United Kingdom. Probable reasons for this are: except in the acute phase infection tends to be latent; shock symptoms in the acute phase often affect only part of the plant and resemble other more familiar diseases; infection does not spread from plant to plant and on unaffected land its incidence is gradually reduced; and the effect on crop yield is usually trivial. It is true that these characteristics apply almost equally well to bukettkrankheit so that the greater awareness of the disease in Germany may be attributable to agronomic, natural or other factors outwith the normal scope of phytopathological investigation. Finally, in Scotland at least, ringspot infection of potato is uncommon. During ten years of routine checking for potato viruses fewer than two dozen affected stocks have been discovered. As to the argument that these would carry a risk of rendering clean land infective (Cadman and Harrison, 1960) one would now have to prove that this exceeds the natural risk existing through the transmissibility of ringspot viruses in seeds of many common plants (Lister, 1960).

Affinities of ringspot viruses affecting potato. The German isolates from plants with gelbfleckigkeit and bukettkrankheit were for long thought to be strains of tobacco ringspot virus. Bercks and Gehring (1956) confirmed that isolates from both diseases were related but their serological and premunity studies indicated only a slight connection with tobacco ringspot virus. Similar work with Scottish isolates of beet ringspot virus showed that they were all related but suggested at first (Harrison, 1957) that this virus was not close to either tobacco ringspot virus or potato bouquet virus. Later tests confirmed the distinction from tobacco ringspot virus but indicated that beet ringspot virus, potato bouquet virus and English isolates from tomato and lettuce of the tomato black ring virus were all related (Harrison, 1958b). Following precedence, Harrison (1958b) proposed that the bouquet and beet ringspot viruses be regarded as strains of tomato black ring virus and this has been generally adopted. However, the type strain could not be made to infect potato systemically and was evidently more closely related to the bouquet isolate tested than was the latter to the beet ringspot strain. This led Harrison to think that there might be strong geographical variation in the group resulting from the seemingly restricted distributions of its members. However the serological evidence of Bercks (1962) that the two German potato strains could be grouped separately, one (bouquet) with the English type strain and the other (pseudo-aucuba) with Scottish beet ringspot, contradicted this hypothesis. Harrison (1964) now suggests that serological differences among strains correspond rather to differences among their vectors.

The tobacco rattle group

Difficulties similar to those that held up the finding of a virus cause for spraing have confused the connection between spraing and the other main form of rattle virus infection in potato—stem mottle. This section begins with an account of the relationship between these two main forms. Next the viral peculiarities are summarised. Because these features bear upon the practical importance of infection in potato this aspect is considered last.

The relationship between spraing and stem mottle. Spraing—the internal arc necrosis of tubers—is one of the classic diseases of potato. It is still confused with internal rust spot, the functional disorder manifested by corky spotting and cavitation, although Grieve (1934) clearly distinguished the two symptoms. Furthermore he added to Atanasoff's (1926) evidence that spraing could be transmitted by tuber graft but did not transmit internal rust spot by this means. Quanjer (1926) cured soil of its infectivity by steaming and so introduced the probability of a biological link between soil and disease. (Incidentally, Braun and Nienhaus (1962) obtained as much " Eisenfleckigkeit " (internal rust spot) in potatoes grown in sterilised as in unsterilised soil thus adding significantly to the evidence that this disease and spraing differ fundamentally.)

If moreover one considers the spraing symptom to be a three-dimensional representation of the ring and line patterns seen on leaves the grounds for ascribing spraing to soil-borne virus infection were already firm nearly forty years ago. Some reasons were suggested earlier why this was not decided then. Plainly the impermanence of spraing in stocks did not help and this feature meant also that any effects seen on the haulm were not associated.

Stengelbont (stem mottle—a haulm abnormality already recognised and so named by Dutch potato inspectors) was first investigated virologically by Rozendaal (1947) ; the associated tuber necrosis recalled spraing. Rozendaal transmitted a virus from stengelbont plants to tobacco in which the local necrosis that developed was like that of rattle virus. Rozendaal and van der Want (1948) transmitted local and systemic isolates from potato to tobacco and concluded that they were both of the rattle virus group ; potatoes planted in rattle-infective soil developed stem mottle in the following year and in the first year some of the tubers showed spraing. Spraing and stem mottle tuber necrosis were still thought of as distinct and van der Want (1952) suggested that stem mottle virus had mutated from that of spraing. Lihnell (1958) regarded stem mottle as a disease mainly of the haulm, its virus (rattle) being sap inoculable ; spraing was mostly a tuber disorder caused by a virus not transmissible in sap although it could be associated with a haulm expression like that of stem mottle.

Corky ringspot, the American tuber disease similar to spraing and caused by rattle virus (Oswald and Bowman, 1958 ; Walkinshaw and Larson, 1958 ; Walkinshaw, Griffin and Larson, 1961), was first stated to have no haulm symptom and not to persist in stocks (Eddins *et al.*, 1946). But Webb and Schultz (1957) found that some tubers produced haulm typical of stem mottle. Walkinshaw and Larson (1959) observed foliage symptoms from corky ringspot tubers grown in the glasshouse but partly because they seemed more severe than those of stem mottle, the authors felt that the two diseases were different. Other distinctions were that corky ringspot tubers do not produce affected haulm in the field in Florida ; the concentration of corky ringspot virus in symptom-bearing leaves seems much lower than that of stem mottle virus ; and the tuber necrosis of stem mottle infection is never superficial as corky ringspot often is. This last distinction was blurred however by what Walkinshaw and Larson themselves pointed out—that surface lesions did not appear on the tubers developed by an affected plant although they could show a severe internal necrosis extending from the vascular tissues. They suggested that superficial corky ringspot might result from direct infection of the tuber surface, the internal necrosis in progeny tubers being caused by virus entering from the stolon. Lihnell (1958) also ascribed differences in the localisation of necrosis in the tuber to how it was infected—either directly from the soil or secondarily from the stolon. Van Hoof (1964 b, c) caused spraing symptoms by rubbing tubers with infective tobacco sap and showed that the latter were most susceptible after reaching a fair size. However by inoculating roots Walkinshaw and Larson (1959) caused large suberized external lesions in some tubers as well as internal necrosis in others. Thus it seemed that not all externally localised lesions result from direct infection. But apart from this explanation it may be, as Walkinshaw and Larson (1959) also point out, that differences in tuber expression depend sometimes on the factor of the age of tissue when infected. Conceivably, tubers infected from the beginning show the fine-grain flecking of the stem mottle-type necrosis while those affected later, either from the stolon or the soil develop the arc necrosis of spraing. The other tuber symptom, irregular shape, is associated with flecking rather than with arcing and this supports the view that the stem mottle necrosis is laid down early.

Apart from symptoms, spraing has been thought of as different from stem mottle because for long no virus could be isolated from diseased tubers. However there have been several reports of rattle virus transmitted from the necrotic parts of spraing tubers (Oswald and Bowman, 1958; Walkinshaw and Larson, 1959; Cadman, 1959; Cadman and Harrison, 1959; Sänger, 1961; van Hoof, 1964b); transmission from normal-seeming parts of affected tubers is more difficult (Walkinshaw and Larson, 1959; Cadman, 1962). These isolates were typically of hard-to-transmit, unstable forms, but, as Sänger (1961) states, they fall within the range of variation of rattle virus. Similar forms are commonly obtained from stem mottle haulm and sometimes also from the stem mottle tuber necrosis (Cadman, 1959; Todd, unpublished).

Thus some of the differences between the stem mottle tuber necrosis and spraing are conceivably attributable to the circumstances of infection. Spraing tubers, possibly because they are infected late, may contain less virus than those with a stem mottle necrosis and so be less likely to produce affected haulm. Again the environment may determine to some extent whether a haulm symptom appears; in Florida where corky ringspot is not associated with stem symptoms it may be too hot for these normally to develop.

However the environment and the circumstances of infection do not explain everything. Although the spraing and stem mottle symptoms cannot be neatly separated on the basis of being caused by different viruses, van Hoof (1964c) has shown that rattle virus isolates do vary greatly in their ability to bring about infection in potato and to cause different symptoms.

Rattle virus infection in the potato host. Compared with the classic virus diseases of potato, rattle virus infection in this host has been hard to understand for two main reasons: infection does not normally persist in a stock; and potato-infecting strains are usually difficult to transmit. The host range of rattle virus is known to be very wide (Noordam, 1956; Uschdraweit and Valentin, 1956; Schmelzer, 1957). Many species tolerate infection well but potato seems rather sensitive and inhospitable.

In tobacco, infection is typically systemic; the virus can be readily subcultured, with consistent symptoms. Even in this host, however, the expression of infection varies remarkably. A common experience is that isolates from much diluted sap fail to become systemic. The dilution end-point in sap from systemically-infected tobacco exceeds 10^{-5} but at this level one is unlikely to find a strain able to infect tobacco systemically. I have isolated a systemic strain at 1/80,000 and from it obtained a further systemic culture at 1/32,000. These selected cultures did not behave differently from ordinary systemic isolates in further dilution tests. Köhler (1960) and Sänger (1961) report similar phenomena: systemic activity was maintained on slight dilution but beyond 10^{-4} (Sänger) isolates caused only local or half-systemic necrotic infection. A similar expression had been reported by Köhler (1956) as a seasonal development and termed "Wintertyp"; however Köhler showed that the seasonal influence was secondary by isolating "Wintertyp" forms in the summer. Much the same phenomenon was encountered by Walkinshaw and Larson (1959) who separated "etching" and "necrotic" isolates from tobacco plants growing on rattle-infective soil. Compared with the fully-systemic isolates the others were hard to transmit in sap from symptom-bearing plants (Walkinshaw and Larson, 1959; Sänger, 1961).

Both these kinds of isolate are transmissible from affected potato but mostly it is the form that multiplies only locally in tobacco and is difficult to transmit especially from potato. Experience in different countries varies a little. Like others in Scotland, I have periodically obtained from stem mottle haulm cultures that are full-systemic and easy to transmit in tobacco. But usually only locally or hardly multiplying forms are isolated with some difficulty and one cannot select better-multiplying cultures from them (Cadman, 1958; 1959; Cadman and Harrison, 1959); even after inoculating potato with stable strains, Cadman (1959) re-isolated only the locally-multiplying form. However transmission from tubers is almost universally difficult and the isolates are of the poorly-multiplying forms; American corky ringspot is exceptional in that rattle virus is sometimes easily obtained from necrosed parts (Walkinshaw and Larson, 1959).

Nevertheless one can select for easily transmissible stable forms of rattle virus in the potato. In 1958, I selected 17 stem mottle plants of Kerr's Pink growing in infective soil. Six of the 17 sets of tubers showed internal necrosis. Six tubers from each of the 17 families were planted in 1959. Rattle virus was isolated from one plant of one family and from two of another; all three had grown from necrosed setts and all had stem mottle. Five other plants showed mild symptoms but they did not yield rattle virus. The single plant from the first family gave some slightly necrosed tubers but these grew into normal plants in 1960. The two other plants yielded quite abnormally: there were very many small tubers with an internal necrosis of spots, arcs and circlets. Plants grown from these in 1960 had stem mottle and the tuber effect was repeated. Then and ever since it has been possible at will to transmit rattle virus to tobacco from leaves, whether symptom-bearing or not, and from the tubers. Leaf isolates are generally of the fully systemic stable form; tuber isolates are mostly of the local type but some give rise to systemic infection.

This unusual selection may have been fortuitous. But it is possibly significant that soils in the part of Morayshire where the original plants came from often yielded virus of the stable type (Cadman and Harrison, 1959).

The curious properties of diluted infective tobacco sap suggest that the two forms of rattle virus occur at different concentrations. Paul and Bode (1955) reported two particle lengths of around 70 and 180 mμ respectively. Brandenburg (1959), noting that about 80 per cent of the particles were short, suggested that when sap is diluted the long particles disappear and the necrotic local form, associated with the short particles, emerges. Köhler (1960) also speculated on the effect of dilution on different kinds of particle. However Cadman and Harrison (1959) could not see particles in sap from tobacco plants infected with non-multiplying forms whereas they were always to be found in sap from plants infected with multiplying forms. Brandenburg's theory ran into further difficulties when Harrison and Nixon (1959) and Sänger (1961) showed that the smaller particles were unlikely to be infective.

That the dilution effect is not a simple matter of different virus concentrations was demonstrated spectacularly by Sänger and Brandenburg (1961) and Cadman (1962). They independently showed that sap from plants infected with unstable forms could be made highly infective if extracted in the presence of phenol. The inference is that the cultural difficulties associated with rattle virus infection in potato derive from its nature : the virus exists in potato mostly as nucleic acid but not in the particulate nucleoprotein form normally experienced with viruses. Phenol extraction seems to expose the nucleic acid and protect it from ribonuclease. Possibly a part of the selective effect of dilution is through watering down this enzyme or other inhibitors.

Stem mottle and some other symptoms of infection with unstable variants can be severe and this presumably is coupled with or caused by high concentrations of viral nucleic acid (Sänger and Brandenburg, 1961). And yet the symptoms in potato are usually temporary and the infection disappears. How the potato plant achieves this is not understood.

Virus variation. Apart from the constitutional variation just described rattle virus isolates can differ serologically (Cadman and Harrison, 1959). Such features also as the existence of different vector species (table 1), and of various expressions of infection all suggest considerable variability (van Hoof, 1964c).

Economics. Rattle virus infection in potato is mainly important because of the tuber necrosis that can happen either when the stock is grown on infective land or in the season following this. Eddins *et al.* (1946) instanced as much as a 50 per cent loss in a part of Florida and Eddins (1959) stated that some fields in the area have had to be abandoned. The loss varies according to year and variety. Some varieties observed in Florida for up to eight years never showed more than one affected tuber out of several hundreds. Others varied in this respect from nil to around 70 per cent according to year. Complex varietal differences have been seen in Scotland; for instance both Kerr's Pink and King Edward show stem mottle but the former seems more likely to develop spraing. Similar variation occurs in the Netherlands (Rozendaal, 1947; van Hoof, 1964b). Losses may be avoided through the use of resistant varieties and the disease can be important enough locally to merit the attention of breeders. Beukema (1964) has developed a method of testing for resistance.

Presumably because of the time taken for a new infection to become established in a plant symptoms of stem mottle and to a lesser degree of spraing may first be conspicuous in a stock in the year after infection—possibly after it has been moved to non-infective soil. Away from infective soil, however, the disease usually declines rapidly. The following observations on a stock of King Edward are typical. In 1957, which was the first year of growth of the observed plants on non-infective land after an unknown history of exposure to infection, about 5 per cent of a plot of a thousand plants showed stem mottle symptoms and rattle virus was fairly readily isolable. In 1958 a plot of the same size was planted from the 1957 crop but only a few symptom-bearing plants were seen and rattle virus was not isolated in the course of sixteen tests. In 1959 stem mottle symptoms were not recorded and rattle virus was not isolated from representative progeny of nine plants which had shown stem mottle symptoms in 1958. The history of infection in Kerr's Pink detailed earlier in this section seems characteristic except for the appearance in that stock of a stable strain. Cadman (1959) gives further case histories which suggest that the virus seems to be inefficiently transmitted through seed tubers. Because of the severe effect the yield from individual stem mottle plants may on the average be little more than half that of normal ones (Cadman, 1959). Particularly regarding spraing, Oswald and Bowman (1958) found that 44 per cent of tubers from diseased plants were necrotic; Lihnell (1958) studied spraing transmission in 93 series of 10-15 plants each; in 16 series there was no transmission; in 48 series, up to 10 per cent of the progeny tubers developed spraing; in 16 series, 11-20 per cent; and in 13 series, more than 20 per cent. Lihnell found instances of spraing persisting over several generations and thought that in some it might have persisted indefinitely. Van der Want (1952) also noted that spraing was transmitted to progeny tubers at different rates. Such cases possibly indicate further that rattle virus infection is variously adaptable to the potato host.

Tobacco necrosis

Tobacco necrosis virus has previously been isolated incidentally from potato roots (*e.g.* Harrison, 1957). Even the associated tuber symptom seems hardly more than a curiosity and most of what is known about it is summarised in table 1.

In Northern Ireland and Scotland affected tubers were discovered recently in some observational plots (Calvert; Todd; unpublished). In Ireland several common varieties were attacked; in Scotland only two varieties, Aura and an unnamed seedling, showed lesions while other varieties growing nearby were untouched. In Aura, the lesions started as a superficial brownish scald but many of them progressed during storage to form blackish cankers which finally mummified the tuber. No fungal pathogen was isolated from them but tobacco necrosis virus invariably was, although not from unaffected flesh. Isolates were identified by their reactions on tobacco and *Phaseolus vulgaris*; these varied within the known range.

Some affected tubers were grown in sterilised soil and produced normal plants. Towards the end of growth samples from roots, stolons, underground stems and spent setts were tested for virus. Tobacco necrosis virus was isolated from rotted setts and occasionally from the roots but not from the other parts. Lesions were not seen on progeny tubers. So far then there is no evidence in Scotland for the apparent systemic infection obtained by Gigante (1959) in Italy.

Yellow mottling

All the viruses associated with yellow mottling of potato leaves were listed earlier. The authentic aucuba mosaic of opaque yellow spotting is occasionally seen in Scotland and characterises the old variety Ninetyfold. A much more common yellow mosaic is of streaks, arcs and line patterns; here the chlorosis is often less opaque than with aucuba mosaic in that it tends to merge from yellow to green.

Stem mottle plants sometimes have a yellow mottling of this sort. Rozendaal's (1947) figure-aucuba fits in here and Hunnius (1959) thought that yellowing was becoming more common as a manifestation of rattle virus infection. In Scotland, at least, rattle virus is not likely to be isolated from a yellow mottled plant that is not dwarfed or showing other acknowledged stem mottle characters. Transmission of any virus from normal-sized plants with yellow mottling is unpredictable but Cadman (unpublished) was the first to show that isolates could regularly be obtained in *Chenopodium amaranticolor*: the inoculated leaves become finely etched with an extensive necrotic scrawling. Calvert (unpublished) found that tobacco is also susceptible but rarely shows symptoms in the summer months. I have recently isolated from Arran Pilot a culture of this virus which multiplies fairly well in White Burley tobacco; the symptoms even in summer are of extensive etching, watermarking and oak leaf patterns. Patterns are usually rather inconspicuous; they tend to become less evident on the upper leaf surface but remain discernible on the underside. Some cultures are at least weakly systemic in tobacco but the most obvious patterns are formed on inoculated leaves. The susceptibility of potato to this virus has not yet been directly tested.

Yellow mottling may well be something of a generalised expression causable by several viruses. So far, however, except for aucuba virus none of those tried have been made to reproduce the potato symptom. Conceivably, the effect is complex and in this respect it may be significant that it is popularly attributed in Scotland to chilling.

The practical significance of soil-borne potato virus diseases

Because an affected crop is plainly unacceptable as ware, spraing or its equivalent is universally regarded as an important disease. Spraing can be sporadic but it is a constant risk with certain varieties on some light soils: in Scotland one could instance Kerr's Pink when grown in the sandy soils around parts of the Moray Firth. By exercising some selection over variety and field, experienced farmers try to avoid the disaster of finding themselves with an unsaleable crop on their hands.

Can anything more be done? At one time the problem seemed particularly difficult because so many crop plants and weeds are susceptible to rattle virus infection. But one now knows that populations of the Dorylaimid nematodes fluctuate and are influenced by cropping: and weeds can be controlled. However, although so much has been done qualitatively to reveal the nature of spraing and the like there is little quantitative information as to what kinds of eelworm population and cropping circumstances result in an outbreak.

Evidence of infection in other crops in the rotation may be a guide to the risk of getting spraing in potatoes but this would have to be regarded in the light of vector bionomics during the rotation. For what it may be worth, I found that rattle virus infection in oats grown in the sandy soils of Morayshire was accompanied by a conspicuous watermarking and eyespotting mosaic. This symptom is very uncommon elsewhere.

The complexity of varietal differences in susceptibility to spraing and stem mottle has been mentioned. In plots, for instance, it is sometimes only certain ones, or particular varieties, that are affected. Whether a plant or tuber is infected from the soil may depend only partly on its constitution: the growth stage reached when the infective eelworm feeds may well be of consequence. And the ultimate varietal property in respect of spraing is whether an infected tuber becomes necrosed.

Another point is the extent to which rattle virus infection becomes adapted to potato. One effect of an adapted strain would be to make the disease persist longer in the stock: a feature that would add greatly to its significance in seed potatoes. Adapted forms can be selected, as this review has shown. One aspect of the build-up of infectivity in agricultural land may be a natural selection of forms increasingly adapted to crop plants. The ready isolation of stable rattle virus from the Morayshire region (Cadman and Harrison, 1959) may be evidence of this.

Ringspot and, if soil-borne, yellow mottling virus infections are more of a challenge to the high-quality seed producer than a worry for the ware grower. However, the latter should not forget the potential losses in yield. The main responsibility here lies with the breeder or raiser of nuclear healthy stocks, to determine if possible that his land is not infective. Particularly yellow mottling is very widespread and common in some varieties. If it is mostly caused by the same virus then either the virus is freely transmissible above or below ground or it has been distributed widely from some original stocks that were infected.

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