SCOTTISH PLANT BREEDING STATION

PENTLANDFIELD, ROSLIN, MIDLOTHIAN

RECORD

1962

CONTENTS

PAGE

STAFF 4

DIRECTOR'S REPORT—

Brassica Crops 5
Herbage Plants and Genecology 7
Oats 13
Potatoes 17
Sugar Beet 24

PUBLICATIONS 25

OCCASIONAL PAPERS—

C. M. DRIVER. Breeding for disease resistance. . 28

G. COCKERHAM. The status of the X^D strain of potato virus X 39

D. A. GOVIER. The reaction of seventeen potato varieties to tomato black-ring virus 49

The International Code of Nomenclature for cultivated Plants 56

D. J. HARBERD and P. J. WATSON. A Note on segregation ratios in tetraploid grasses . . 58

E. W. TISDALE. The ecotype concept in range management 61

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DIRECTOR'S REPORT

Brassica Crops.—When assessing yield of the "leafy" brassicas it has been routine practice to separate stem and leaf for the very good reason that leaves and stems are not equally acceptable to the grazing animal. Some observations on the feeding habits of sheep during the period 27th December 1960, to 22nd February 1961, illustrate this point. One-year-old lambs running on a pasture and supplied with cake and hay were regularly offered fully-grown plants of kale and kale hybrids and it was found that they consumed only 1½ to 2½ lb. per head per day during the first week, a diet which consisted almost entirely of leaves, whereas in the last three weeks consumption had risen to 5 or 6 lb. and included as well as leaves, the more succulent parts of the stem. When deprived of grass by snow-falls consumption rose to 7½ lb. per day, but even then a considerable amount of stem of both marrow-stem and thousand-headed kale remained uneaten. Comparison of long and short-stalked lines of marrow-stem indicated that the proportion of stem rejected was the same in each case. On the other hand, some cabbage × kale hybrids with short stems were completely eaten. From these observations it would seem that when assessing the productivity of these brassicas in terms of dry-matter, yield of leafage is a much more reliable criterion than that of stem. But even so the dry-matter percentages of small samples of leafage can be extremely variable. This seems largely to be due to the differences in the ratio of lamina to petiole, for laminae are relatively high in dry-matter though ratio differences can also be affected by age of leaf and growing conditions.

Parts of leaves were analysed separately in the case of *B. campestris* ssp. *chinensis*, a virtually stemless type with thick fleshy midribs and petioles. Midribs and petioles, structurally mainly parenchyma with little fibre, were very low in dry-matter, 3·5 per cent in contrast to 8 per cent for laminae. When whole leaves were compared the oriental ssp. *chinensis*, *nipposinica* and *pekinensis* proved to be about 5 per cent lower in dry-matter than turnip-rape, reflecting the relatively high lamina : petiole ratio of the latter. In the case of *B. oleracea* var. *capitata* a further complication arises for when heart leaves and outer leaves were separately analysed the former consistently gave the lower dry-matter percentages. In addition to the foregoing tests a number of colchicine induced autotetraploids of thousand-headed kale, Scotch kale, cabbage, broccoli and kohl rabi were grown along with well-known diploid cultivars and it was found that in respect of the dry-matter of leaf laminae these tetraploids did not differ significantly from that of the corresponding diploids.

From the above observations it is evident that when dealing with the "leafy" brassicas the criterion of total dry-matter yield cannot be regarded as a satisfactory basis for varietal comparisons since differences in the digestibility of dry-matter samples from different parts of the plant—*e.g.*, parts of the stem, may well be very considerable. In this connection the recent development by Raymond and his associates at the Grassland Research Institute, of an *in vitro* technique for the determination of digestibility of the dry-matter in herbage plants is noteworthy as it is probable that it will also be applicable to brassica crops. In that event the assessment of the feeding value of dry-matter samples derived from different parts of the plant and from plants at different stages of development would become a practical proposition.

During the year a number of recently obtained F_1 hybrids were observed under field conditions. Hybrids between *B. campestris* ssp. *nipposinica* and ssp. *rapa* 'Gelria' were vigorous and leafy; there was no tendency towards early flowering, and leaf retention was good until late November when the plants were severely damaged by frost. Hybrids between ssp. *nipposinica* and ssp. *chinensis* were only moderately leafy and flowered early. F_1 plants of ssp. *nipposinica* ssp. *pekinensis*, crossed at the tetraploid level, were of interest because of their abundant leafage as well as the size and thickness of the leaves. Pollen fertility of this combination was almost 100 per cent and fairly good seed setting was obtained on selfing.

Derivatives of a synthetic swede were also grown in the field. This swede was the result of a cross between diploid 'Bruce' turnip and a hybrid thousand-headed kale × kohl rabi and subsequent treatment of the hybrid with colchicine till a fertile racema appeared. Though some plants had fair-sized bulbs they were mostly fang rooted and long necked.

Preliminary field observations in respect of flowering time, growth habit and hardiness were made on forty-five forms of *B. campestris sensu lato*. Oil seed varieties were early flowering and poor in leafiness. All oriental forms were highly susceptible to frost.

The search for a source of club-root resistance is continuing. The more recent material to be tested included *B. campestris* ssp. *nipposinica* and two forms of *B. tournefortii*, allegedly immune to club-root. The tests revealed ssp. *nipposinica* to be susceptible to relatively low spore concentrations, and both forms of *B. tournefortii* to be highly susceptible to the particular race of *Plasmodiophora* used.

In response to the increasing demand for a swede capable of being mechanically harvested easily and without undue waste a Station product possessing a high degree of uniformity in respect of growth-habit has been named ' Pentland Harvester '; a name which has been registered and the cultivar described in compliance with the provisions of the International Code of Nomenclature for Cultivated Plants by the Department of Agriculture and Fisheries for Scotland acting in its capacity as the National Registration Authority. The official description of ' Pentland Harvester ' is as follows :—

Type :	Early maturing swede.
Botanical Characteristics	*Bulb :* spherical ; flesh yellow ; ' top ' light purple ; ' bottom ' relatively free from side roots ; good hold of ground. *Neck :* light purple, very short. *Shaw :* small, somewhat prostrate. *Variability :* low.
Agronomic Characteristics	Particularly suitable for mechanical harvesting on account of erect and uniform growth habit ; cropping capacity equal to that of good early cultivars in current use.

Seed of the cultivar will not be available commercially until next year.

Herbage Plants and Genecology.—The improvement of hill land has been the subject of some controversy and many experiments for a considerable number of years but the increasing loss of thousands of acres of good arable land to urban development and other uses makes it a matter of urgent necessity. Improvement can be accomplished at considerable expense but the real need is for a simple method requiring little outlay of capital and low maintenance costs which will, nevertheless, be effective. The possibility of economically improving open hill grazings by irrigation flushing of limited areas with local supplies of water of suitable chemical composition was discussed in last year's Report. In order to appreciate the possible effects of irrigation upon the native vegetation a variety of natural flushes are now being surveyed, and certain of these areas have already been chosen for detailed examination. Most of the flushes which have been surveyed so far are in the Pentland Hills where the springs have been found to be relatively high in minerals compared with many of those in the Moorfoot Hills and other parts of Scotland. The pH values are mainly between 6·5 and 7·5 and correspond fairly closely to the concentration of calcium (10 to 80 parts per million) which is probably the most important single element so far examined. Figures for magnesium (3 to 10 p.p.m.), potassium (up to 1·3 p.p.m.) and sodium (up to 7 p.p.m.) have also been obtained. One of these Pentland flushes on the N.W. side of Carnethy Hill, was selected for intensive study, mainly because of its simple form. It is situated on an even slope and shows as a clearly marked area of bright green grassland amid a fairly uniform grass-heath with much *Nardus* and *Calluna*.

Using a tool which cuts a turf of $2\frac{3}{4}''$ diameter, samples of plants and soil were taken at 5 ft. intervals along a longitudinal transect of 100 ft., starting just above the origin of the spring. The spring water flows on the surface from a point 5 ft. from the top of the transect for about 35 ft. and then disappears underground, and samples were also taken at 2 ft. intervals along two 20 ft. transverse lines, at right angles to the main transect, at 30 ft. and 60 ft. from the top. It was anticipated that this method and pattern of sampling would furnish a considerable amount of information on the distribution of the plants as well as their variation and that of the soils in relation to the water, and hence mineral, supply.

The plant samples were separated into individual "tillers" of the constituent species (mostly grasses) and established in a greenhouse, pending a field trial to obtain genecological information.

Although the "flushed" grassland has a fairly uniform appearance, except for the wettest areas, examination of the greenhouse material has shown that most species have a fairly clear zonation which can be related in a general way to the soil conditions, physical and chemical (see Table I).

TABLE I

Species	*Range on Transect (ft. from top)*
Poa annua . . .	10 → 35
Poa pratensis . . .	10 → 55
Holcus lanatus . .	10 → 40
Festuca rubra . . .	35 → 85
Agrostis spp. . . .	20 → 40 (v. few)
	60 → 95
Festuca ovina . .	70 → 90
Deschampsia flexuosa .	85 onwards

Poa annua is dominant where there is standing water and is virtually confined to these areas. Below is a zone, with running water at the surface, occupied predominantly by *Poa pratensis* and *Holcus lanatus*. This is followed by an extensive area dominated by *Festuca* species, where *Festuca rubra* is most widespread. Within this area *Agrostis tenuis* (with other *Agrostis* spp.) is most common in the centre, while *Festuca ovina* (tetraploid) is confined to the lower half. Finally the *Festuca* zone merges into the surrounding acidic grassland with *Nardus* and *Deschampsia flexuosa* dominating.

pH values were obtained for the fresh soils and a representative series (starting just below the point of disappearance of the water) was analysed for calcium, magnesium, potassium and sodium (see Table II). These results show that only

TABLE II

Position on transect (ft.)	mg. ions/100 g. dry soil				
	Ca.	Mg.	K.	Na.	pH.
30	4·47	0·78	0·28	0·33	6·8
45	5·45	1·32	0·37	0·41	6·75
55	6·33	1·26	0·26	0·43	6·2
65	6·87	1·28	0·36	0·43	6·0
75	5·95	1·08	0·33	0·39	6·2
85	4·49	1·20	0·42	0·39	5·6
95	1·52	0·90	0·60	0·30	4·6

calcium and pH show any significant variation and indicate that in subsequent investigations other minerals and also the physical characteristics of the soil must be taken into consideration. Nevertheless, some tentative conclusions may be drawn. Using the number of tillers of each species isolated from each sample as a crude measure of frequency it is possible to show that: (1) the frequency of *Festuca rubra* seems to follow the level of exchangeable calcium, (2) the total number of tillers (all species) isolated per sample is maximal in a zone with a high calcium level and with a pH of about 6·0, (3) this zone corresponds with the zone within which maximal root development was observed in the fresh samples, and where *Agrostis* spp. occurred in highest frequency with *Festuca ovina* in moderate frequency. It therefore appears that the most productive conditions, in terms of density of sward and number of species, are to be found on well-drained soils of pH around 6·0, with a high level of exchangeable calcium. In attempting to improve grassland by irrigation techniques these would, therefore, be the conditions at which to aim.

It has already been said that the flushed grassland has a fairly uniform appearance and the zones become apparent only upon minute examination. It is possible, however, that the bryophytes which grow in and around springs may provide a means of making a much quicker and reasonably reliable estimation of the mineral quality of the spring water.

One or two experimental irrigation systems using polythene pipes have been planned for use at selected sites and the early effects upon plants and soils will be investigated whilst further surveys are carried out on the various aspects of natural flushes.

The hope of finding a relatively inexpensive method of improving hill grazings serves to intensify interest in the genecological studies of individual species native to uplands, particularly those likely to be most frequently encountered. The *Agrostis*-fescue sward is undoubtedly of major importance but although *Agrostis* and *Festuca* spp. are the main constituents of the better grazings they are also to be found in relatively poor habitats and on that account the relationships between plant populations and the conditions of their respective habitats are of some interest. The following data have been obtained from collections of tillers and seed taken at random from three contiguous, recognisably different, habitats, together occupying an area of not more than three acres, in Central Scotland about ten miles north of Blair Atholl :—

A. Area of species-rich *Agrostis* fescue sward, fairly well drained and closely grazed by sheep ;

B. Rather wet, stony area intermediately situated between A; and

C. Large area covered by birchwood with a grassy flora including *Agrostis* and *Festuca*.

No attempt was made at the time of collection or when planting to separate *Agrostis tenuis* from *A. canina montana* and different proportions were naturally found in the different habitats for it is well known that in general *A. tenuis* is more frequent in drier, more fertile conditions whilst *A. canina* tolerates poor edaphic conditions and a certain degree of wetness. Both the tillers and the plants from the seed collected were planted in a single block per habitat without replication. The *Festuca ovina* plants were not cytologically examined and though the region is likely to support only diploids, there may have been a very few tetraploids present.

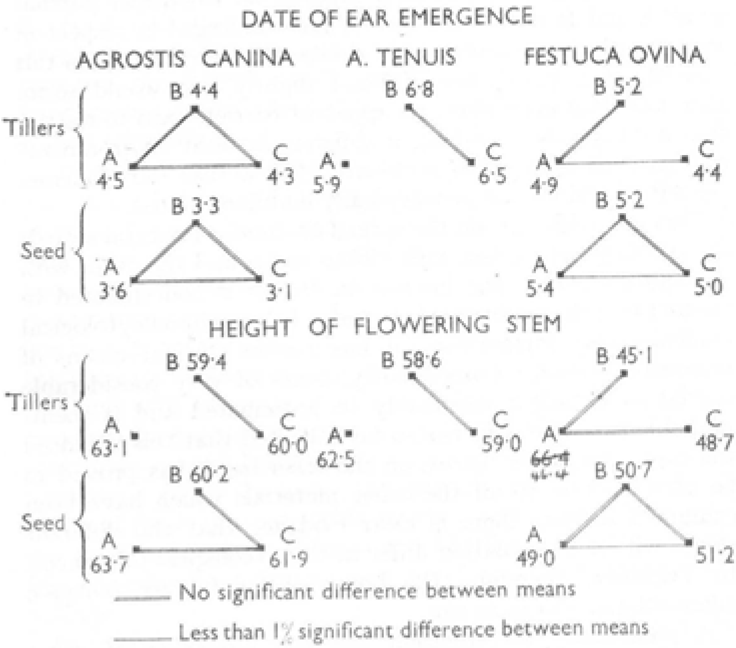

FIG. 1.—COMPARISON OF POPULATION MEAN VALUES.

Two characters, time of ear emergence (EE) and length of the flowering stem at maturity (SL) were considered to be reliable, EE in particular, since it is unlikely to be influenced by any edaphic irregularities in the trial area. Time of ear emergence is closely correlated with time of flowering in all three species and is much more accurately scored than the latter. Pairs of population means for both these characters were compared and the results are given in Fig. 1, where an increase of 1 in the EE mean value for a population indicates that the population was half a week later in time of ear emergence. Not sufficient plants to justify making comparisons were obtained from the seed collections of *A. tenuis* and for that reason these comparisons are omitted from the diagram.

Since the individuals of each species in the wild were neither spatially nor temporally obviously isolated it is reasonable to assume that populations A, B and C constitute in each species a single gamodeme. Nevertheless, the evidence suggests that despite the coincidence of their times of ear emergence populations A and B of *Agrostis canina* have diverged in respect of stem length. *A. tenuis* shows a similar tendency though in this case the EE values also differed slightly. It would seem, therefore, that even where no apparent barriers exist to restrict free intra-specific breeding, if different habitat environments are involved it does not necessarily follow that the ecodemes concerned will remain genotypically undifferentiated.

Two investigations on the spread of clones in natural swards are still in progress, one with *Holcus mollis* and the other with *Trifolium repens*. The interest in *Holcus* is concentrated in the fact that the material is believed to be ancient on cytological evidence, and, furthermore, it has a most efficient means of vegetative spread. Consequently clones of very considerable spatial cover might reasonably be anticipated and it seems probable from the evidence so far collected that this is indeed the case. *Trifolium repens*, on the other hand, has proved to be an exception to all the other materials which have been examined in that there is clear evidence that the different clones within a population differ in their ecological tolerances. In *Trifolium*, therefore, the potential for further ecotypic differentiation exists *in situ*.

A preliminary investigation into the possibility of using miniature swards as a method of testing Italian ryegrass progenies has now been completed. In this experiment the yields of six diploid cultivars of Italian ryegrass planted at 2" spacing in small boxes containing forty-two plants per box were compared with the yields of the same material sown broadcast in the field. Both types of sward were given identical fertiliser treatments and it seems that at high fertiliser levels at least, yields from small " box-swards " correlate well with the yields from field sowings and may provide a satisfactory method of progeny testing during the early stages of a breeding programme. Material from the boxes was analysed by the *in vitro* digestibility technique by the staff of the Grassland Research Institute at Hurley. The digestibility percentages obtained range from 74·3-78·0, differences between fertiliser treatments being very small.

Oats.—In 1953 selection-centres were established in Argyll and Inverness-shire for the purpose of making selections and conducting trials in the early generations of hybrid material with a view to obtaining new cultivars particularly suited to the type of environment in which they were selected. Testing of selections within their respective regions of origin is continuous, with interchange of material between regions in the later stages giving information on versatility as well as on special suitabilities.

Since establishing the selection-centres the pattern of cereal cultivation has undergone considerable change. For example in 1953 the Scottish acreage of oats was 887,930 and that of barley 194,562 ; by 1961 oats had fallen to 632,000 while barley had increased to 321,000 acres, some 30 per cent above its war-time maximum. The acreage of oats, therefore, is now less than twice that of barley. This decline in oat cultivation has been particularly marked in the more productive areas of Scotland with the result that the marginal and less favoured areas of the country where oat yields are relatively low now contribute a much higher proportion to the total acreage than formerly. As it happens Inverness-shire has consistently returned the lowest oat yields of any county in Scotland with the exception only of Orkney and Shetland, while the yields from Argyll are at least 3 cwt. per acre below the national average.

In 1961 sixty fixed lines representing 10 families of selections made in Inverness-shire in the period 1953 to 1955 were included in a preliminary trial at Daviot, the Inverness-shire centre, and the same 60 lines were grown at Pentlandfield. Seed for both areas was provided by multiplication plots at Pentlandfield in 1960. The main difference between the results obtained at the two centres was the very much lower grain yields at Daviot, while the straw yields were for the most part slightly higher at that centre. The reduction in grain yield in the less favoured environment varied in the different selected lines, and many selections which had similar grain/straw ratios at the one centre were widely separated at the other.

A study of the 60 lines, family by family, allowing for the variation to be expected in a group of selections from hybrid material, showed each family to have a characteristic response to change of environment. When the selections within a family were placed in order according to their grain/straw ratios at the two centres the majority of them occupied the same relative positions in the list.

That a consideration of the grain/straw ratio, as a measure of the influence of the environment, can be applied to the evaluation of a series of trial results is borne out in a series of trials of another group of fixed lines at the different selection centres between 1959 and 1961. At Pentlandfield the mean ratios in the years 1959, 1960 and 1961 were 74·3 per cent, 81·6 per cent and 99 per cent respectively, and for the same trial material 73·5 per cent, 77·9 per cent and 43 per cent in Inverness-shire. The year 1959 was a drought year and lines derived from selections made in Inverness-shire gave the highest grain yield at both Pentlandfield and Daviot, while at both centres those from the difficult Argyll and Inverness-shire environments gave the highest straw yields. In the following year the grain/straw ratios were higher at each centre and differences in grain yield between lines of different origin were slight, neither group having the advantage at either centre. At Daviot in 1960 the control cultivar 'Blenda' was exceeded in grain yield by all the Pentlandfield and Inverness-shire lines and at Pentlandfield by one only, a Pentlandfield selection. As in 1959 the most straw at both centres was produced by lines from Inverness-shire and Argyll.

In 1961 at Daviot, environmental effect was particularly severe due, in the main, to prolonged and severe frost at the end of May, the effects of which were to be seen throughout the summer in the large areas of scorched larch and spruce plantations. The effect of this frost on the oat plots was to check the growth when the plants were at a particularly vulnerable stage in their development. This check is reflected in a general lowering of grain yields to about one-half of those at Pentlandfield, the later maturing types being relatively more successful. At Daviot in 1961 only one of the fixed lines of Daviot origin yielded more grain than 'Blenda' while other two of the same origin had straw yields which were exceeded only by the long strawed cultivar 'Albyn Bard.' In the Pentlandfield trial in 1961 the four highest grain yielding lines were of Pentlandfield origin, all four of them outyielding 'Blenda,' while the highest straw yields were again given by selections made in Inverness-shire or Argyll.

Resulting from these various tests some 28 potential new varieties have been retained for further trials in the Inverness-shire environment, and the best of these will be available for College trials throughout the area within the next two years.

A further stage has been reached in the breeding of oat varieties resistant to the stem eelworm, *Ditylenchus dipsaci* (Kühn), 96 highly resistant selections having been included in a yield trial in 1961 on eelworm free land at Pentlandfield with 'Blenda' as control. The trial consisted of a number of beds with the selections distributed at random in single rows, of which every sixth row was 'Blenda.' The grain yield of each row was compared with the average grain yield from the 'Blenda' rows on either side of it, and 13 of the selections gave yields equal to or better than 'Blenda.' These with an additional 20 have been retained for further trial.

Satisfactory confirmation of the relationship between the laboratory inoculation test for resistance, and resistance to attack in the field was obtained in 1961. Seed of 50 resistant selections and of the cultivars 'Milford,' 'Manod' and 'Early Miller' was sown in alternate rows with a susceptible variety in a heavily infested plot. Observations made throughout the season showed that none of the resistant selections from the inoculation tests nor 'Milford' and 'Manod' was damaged. 'Early Miller' showed its characteristic moderate dilation at the base of otherwise normal plants. All rows of the susceptible control variety were severely attacked, few plants reaching the heading stage, while those which did generally broke over at the base before maturity due to rotting of the crown of the plant as a result of eelworm attack.

Experience in earlier years having indicated that a relationship existed between severe attack in the field and rainfall in the months of April and May, a test plot was watered twice weekly at a rate equivalent to half an inch of rain per week from sowing until the commencement of earing. As a result obvious symptoms appeared earlier in the test plot than in neighbouring field crops in 1961, a year in which few stem eelworm-damaged crops were reported, and symptoms were more severe in the test plot than in the previous year in which there was no supplementary watering.

Laboratory testing of hybrid material derived from crosses with *Avena ludoviciana* (Dur.) continues, with the most resistant selections being set aside for further back-crossing to their high-yielding recurrent parent. Certain highly resistant selections derived from crosses between *A. ludoviciana* and unfixed *A. sativa* hybrids, have been used as parents in a new series of crosses since they appear to be as resistant as *A. ludoviciana* without its serious agronomic disadvantages. Additional sources of resistance have been found in the cultivar 'Bidi' (Reference No. Aa 137), and the selection Caffrey's No. 1 (Aa 33), the latter, with only slight symptoms in the inoculation tests, being the better of the two.

Inoculation experiments have shown that at least two types of resistance are involved distinguished in the laboratory by a tolerant reaction in which the plants, while becoming dilated at the base, can support large numbers of eelworm in the tissues without being seriously retarded in their growth, and by an inhibitant reaction in which, though severely stunted initially, the plants subsequently grow away with no other external symptoms of attack. In the latter case multiplication of eelworm in the tissues takes place at a greatly reduced rate, if at all, compared to the rate of multiplication in a susceptible variety. 'Milford' is an example of the inhibitant reaction and 'Early Miller' of the tolerant, although in 'Early Miller' there is partial inhibition of multiplication. The species *Avena ludoviciana* (Dur.) and the resistant selections made at Pentlandfield from hybrids between *A. ludoviciana* and various *Avena sativa* varieties appear to possess both attributes, being neither stunted nor dilated in the laboratory tests, nor showing any symptoms of attack in the field.

Under field conditions over-wintered eelworm invade the young oat seedling. The larvae mature rapidly, eggs which hatch in 5-7 days are laid in the tissues, the new generation reaching maturity in 3-4 weeks when the cycle is repeated. In the autumn the eelworm return to the soil from the decaying plant tissue and remain capable of attacking a suitable host for periods variously estimated of from one to five or six years, many of the common weeds of cultivation being alternative hosts. If the eelworm invades both resistant and susceptible varieties alike, then on theoretical grounds, the cultivation of varieties possessing the inhibitant type of resistance will have the effect of removing the eelworm from the soil, and, by preventing their multiplication, so eliminate them. Experiments are now in progress to determine the effect on eelworm population density of repeated cropping with such a resistant variety in the absence of weeds, and to determine how soon after such cropping susceptible varieties may again be grown on infested land with reasonable prospects of success.

Potatoes.—An early maturing seedling, Reference No. 2299 (10), has successfully completed the Merit Trials conducted by the Department of Agriculture and Fisheries for Scotland and has received "Commendation." It has been named 'Pentland Envoy' a name that will be registered by the National Registration Authority.

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

Maturity . First Early.

Tuber . . Kidney (long oval to pear-shaped), thick, often pointed at heel ; skin white, fairly smooth ; flesh white, crisp ; eyes, shallow on the point ; sprouts blue.

Foliage Type Ulster Chieftain.

Foliage . Haulm low to medium in height, fairly bushy, compact ; stems few to average, fairly thin, mottled purple at bases and in leaf axils ; wings of medium width, straight, green ; leaf fairly large, drooping, close ; leaflets large, medium-green, matt, thick, margins slightly waved, terminal broad, tapering ; secondary leaflets frequent, fairly large, rounded, occasionally borne on leaflet petioles.

Flower . White, infrequent, fairly large ; anthers orange, regular ; inflorescence stalks fairly long, bronzed ; buds yellow-green ovoid ; sepals long, dark purple ; berries not observed.

Remarks . Cropping : very good ; cooking quality : fairly good ; keeping quality : satisfactory ; field-immune from virus C, appears to have more resistance to leaf-roll than the average commercial variety and to have good resistance to virus Y ; susceptible to gangrene ; average susceptibility to blight ; moderately susceptible to dry rot and skin spot.

A Virus Tested Stock of 'Pentland Envoy' amounting to 3 tons has been distributed to specialist growers by the Department of Agriculture and Fisheries for Scotland. The Department also arranged for the distribution of virus-tested units to producers of virus-tested stocks.

Another seedling Reference No. 1565(4), which is grown commercially in Kenya under the name Roslin Sasumua has completed the Department's Wart Immunity and Identity Tests and the name 'Roslin Sasumua' has now been registered and the cultivar described as follows :—

Maturity . Maincrop.

Tuber . . Oval to long oval, slightly flat ; skin white, occasional faint pink at heel and eyes, pink colour develops on exposure, fairly smooth ; flesh white, fairly firm ; eyes on the point, shallow to medium ; sprouts pink.

Foliage Type Craigs Defiance.

Foliage . Haulm of medium height, bushy, rather straggling ; stems fairly numerous, medium thickness, branching, faintly mottled ; wings slightly waved ; leaf of medium size, fairly open, drooping, midrib faintly coloured red in the young leaves ; leaflets small to medium, narrow, dark-green, glossy, margins waved, faint colour in petioles and mid-veins of immature leaflets ; secondary leaflets infrequent, small, oval, often borne on leaflet petioles.

Flower . White, faint purple on backs of petals, fairly frequent ; anthers orange, regular ; inflorescence stalks mottled red-purple, cork-ring red ; buds oval, faintly mottled ; berries occur.

Remarks . Field-immune from viruses X, A and B ; foliage appears to have good resistance to blight.

In recent years, this cultivar has also given promising results in trials conducted by the National Agricultural Advisory

Service in South West England where it is now being grown commercially on a limited scale.

The Scottish Department's 1962 Merit Trials include eighteen of the Station's seedlings, ten in the 1st Year, five in the 2nd Year, two in the 3rd Year and one in the 4th Year of trial. In addition samples of five Station products have been supplied to the Department for inclusion in pre-registration Official Wart Disease and Identity Tests.

All the seedlings entered for the official trials in 1961 were tested under greenhouse conditions for their reactions to infection with potato viruses A, B, C, X and Y. In addition some 400 seedling selections were examined under similar conditions for their responses to infection with potato viruses X and Y, as a further aid to selection. Leaf samples were also taken from the named cultivars and advanced seedlings growing at the Station's isolation centre at Blythbank and tested serologically for freedom from viruses X and S. No X or S infections were detected and no virus Y infections were observed.

In order to test the possibilities of mechanical harvesting by a method involving pulling, seed tubers of twelve cultivars and unnamed seedlings were supplied to the National Institute of Agricultural Engineering in 1961. The results indicated that 'Pentland Envoy' and seedling 2191k(3), were fairly well adapted to this method of harvesting. They will be tested again, together with other seedlings, in 1962.

Investigations into the nature of "field resistance" to blight were continued during 1961 using detached leaves from 26 clones (including the seven tested in 1960) and infecting them with race 1, 2, 3, 4 of *Phytophthora infestans*. As in 1960, the number and size of the lesions and rate and amount of sporulation were found to be correlated; few, slow spreading lesions with slow, sparse sporulation were characteristic of the resistant plants. The order of susceptibility of the seven seedling clones used in 1960 was confirmed. Most clones showed increasing susceptibility as the season advanced, and the increase was more rapid in some than in others. The resistance of the clones was closely correlated with their assessed "field resistance." In the course of these "field resistance" studies inoculum of the blight race 1,2,3,4 was produced on leaves of the genotype $R_1R_2R_3R_4$, a genotype exhibiting no "field resistance." It was observed that the virulence of the fungus was reduced when it was transferred to, and repeatedly cultured on, certain of the potato clones under test. Indeed, after only two transfers the inoculum failed to infect some clones, though surprisingly enough such transference did not prevent the successful infection of the $R_1R_2R_3R_4$ genotype. All treatments were carried out under standard conditions, and standard concentrations of inoculum were applied; the number of lesions produced per leaf, the rate of spread of the fungus, the rate of sporulation and the number of spores produced were recorded. It is perhaps significant that loss of virulence was most evident when transference happened to be through clones showing the highest degree of "field resistance."

The identity of many of the races of *P. infestans* maintained in culture at Pentlandfield was checked. Included with the leaves of the usual differential host series (based on four R genes) were leaves of two clones of *Solanum demissum* (C5 and C6) from Canada, each containing an additional R gene, and *S. stoloniferum* (S6) from East Germany containing an R gene which differs from the six in *S. demissum*. The number and source of the isolates which caused blight on the clones with additional R genes is shown in the Table. The Table shows that such isolates have a wide distribution and, with two exceptions, they were isolated from potato.

Clone(s)	*No. of isolates causing disease*	*Original host*	*Source of isolate*
C5	14	Potato	Brazil, Canada, Holland, Italy, S. Rhodesia, Scotland.
C6	36	Potato	Brazil, Canada, Holland, Italy, S. Rhodesia, Scotland.
,,	1	Tomato	S. Rhodesia.
S6	20	Potato	Brazil, Canada, Holland, Italy, S. Rhodesia.
,,	1	Tomato	Brazil.
C5 + C6	6	Potato	Brazil, Canada, Holland.
C5 + S6	5	Potato	Canada, S. Rhodesia.
C6 + S6	11	Potato	Canada, Holland.
C5 + C6 + S6	2	Potato	Canada.

The racial constitution of samples of *P. infestans* received in tubers was determined. Race 3,4 was identified in 'Pentland Beauty' and the red variant of 'Pentland Beauty' from Perthshire, and race 1,2,4 was obtained from a seedling from Blythbank. Sporulation on C5 and C6 took place with the isolates from red 'Pentland Beauty' and the Blythbank seedling respectively. Three isolates from tomatoes and two from potatoes in S. Rhodesia were also received. The former were identified as race 3 and the latter as race 4; the isolates from potatoes also caused sporulation on leaves of C6.

The common scab trial, commenced in 1960, was continued. Seedling progenies which had no damage or very slight damage due to scab in 1960 were grown on in the greenhouse along with 60 cultivars and seedlings, including those used in 1960. All were grown under normal conditions in 6-inch pots embedded in soil inoculated with *Streptomyces scabies* Waksm. and Henrici. Similarly, 1,328 seedlings, the progenies of 11 crosses, were grown in 4-inch pots. The 60 cultivars and seedlings were also grown in the field on land known to produce potatoes with severe scab, and to which a quantity of soil inoculated with *S. scabies* was added. The seedling progenies which had moderate to severe scab in 1960 were also grown in the plot, with a view to contaminating thoroughly the soil and establishing a "scab garden." The field and greenhouse trials gave comparable results, and the order of susceptibility shown by some of the named cultivars agreed with that indicated for them in the literature. Greatest resistance was shown by five related seedling varieties which had extremely little or no scab; four of these had russet skin which has frequently been associated with resistance to common scab by other investigators.

In dealing with resistance to potato root eelworm and the relationship between strains of the pest, the practicability of adopting the convenient type of nomenclature that is used in the international system for classifying strains of *Phytophthora infestans* is being examined.

As a first step towards such a classification the dominant resistance genes of *S. tuberosum* subsp. *andigena* and *S. multidissectum* have been provisionally labelled H_1 and H_2 respectively. Strain 1 of the eelworm then encysts in plants of genotype H_1 but not H_2 and strain 2 *vice versa*. Strain 1,2 should theoretically encyst in plants of either genotype and the combination H_1H_2 in addition. An attempt to breed such a strain by giving strains 1 and 2 (as represented by the Duddingston and Boghall populations, respectively) an opportunity to interbreed on recessive potatoes failed in the first or F_1 generation in that no F_1 cysts were detected on plants of genotype H_1H_2 suggesting either that aggressiveness was recessive or failure of the two strains to interbreed in the first place. It should be possible to decide between these two alternatives in the F_2 generation.

Nearly four hundred seedlings with the desired combination of H_1 and H_2 remained virtually free from cysts of strains 1 and 2 in 3" pots in the greenhouse. They were then transplanted into 6" pots and later selected in shape of tuber, leaving just over a hundred for further selection in 3-tuber plots at Blythbank this year. The potential usefulness of this material depends on whether or not biotypes of strain 1,2 already occur in the field and how widespread they are. This problem is being investigated in conjunction with workers at the Plant Breeding Institute, Cambridge, the Nematology Department at Rothamsted and in the National Agricultural Advisory Service.

Although the diploid specis *S. sanctae-rosae* is resistant to all populations of potato root eelworm, it was apparent that most of the resistance to strain 2 had been lost in the second backcross to commercial varieties of *S. tuberosum* whilst the resistance to strain 1 remained and segregated as if conferred by a single, dominant gene. As such, it would be indistinguishable from the gene H_2 of *S. multidissectum*. *Solanum vernei* subsp. *ballsii* is usually held to have a polygenic form of resistance equally effective against all populations of potato root eelworm but a batch of hybrids (× *tuberosum*) included some which appeared to be more resistant to strain 1 than strain 2 or *vice versa*, indicating a qualitative as well as quantitative aspect of resistance in this breeding line.

The collection of tuber-bearing *Solanum* species received from Professor Hawkes in 1958 was re-grown for maintenance but no investigational work was carried out on the material during the period under review. Work was resumed when glasshouse accommodation became available in winter, however, and further studies of the reactions of particular clones to X, Y and S viruses are now in progress. In connection with this material it was erroneously stated on page 21 of last year's Report that the two lines of *S. brachycarpum* examined were diploid, when in fact both were hexaploid with $2n = 72$.

Breeding for the combination of resistances to different viruses was continued and over 7,000 seedlings were passed through the initial stages of selection in the glasshouse for resistance to X and/or Y viruses. Further selection in the field, on the basis of economic characters, reduced the number to about 600 clones for extended trial and further breeding. These included selections from two new breeding lines derived, respectively, from *S. chacoense* and from hybrids between *S. acaule* and *S. stoloniferum*. A fertility barrier had held up progress in the development of this latter material but this was overcome by inducing polyploid hydrids by colchicine treatment of germinating seed. Four of the polyploids so produced were crossed successfully with cultivars of *S. tuberosum* and it is from this material, now in the third generation of out-crossing with *S. tuberosum*, that the present selections were derived.

A point of interest which came to light in the general breeding programme was the fact that "Collajera," a clone of *S. tuberosum* subsp. *andigena*, is duplex for a gene controlling immune reaction to virus X.

In field trials carried out at Cambridge, in 1960, and evaluated at Pentlandfield in 1961, the new potato cultivar 'Pentland Envoy' proved to be well above average in its field resistance to both the leaf roll virus and virus Y. The cultivar contracted 33 per cent infection with leaf roll as compared with 44 per cent in 'Pentland Crown,' 96 per cent in 'Dr McIntosh' and a mean value of 72 per cent for the whole trial of eight entries. With virus Y the infections were few in number and they amounted to 2 per cent in 'Pentland Envoy,' 4 per cent in 'Pentland Crown' 8 per cent in 'Dr McIntosh' and 7 per cent for the whole trial. The cultivar 'Roslin Riviera,' also included in the trial, contracted 64 per cent leaf roll and 2 per cent virus Y, amounts which confirm the moderate resistance recorded in previous years.

Investigations into the relationships of genes controlling reactions and resistance to X and Y viruses are in progress with diploid, tetraploid and hexaploid species as experimental material. Hybrids between *S. chacoense*, *S. simplicifolium* and *S. sparsipilum*, with *S. phureja* as a bridging species, have provided basic material for investigations at the diploid level. A first outcome of these investigations is evidence that a gene controlling reaction to virus Y in *S. chacoense* is either identical with or is an allelomorph of a gene controlling necrotic reaction to virus Y in *S. simplicifolium*.

In tetraploids, genes controlling reactions to X and Y viruses in the two sub-species *tuberosa* and *andigena*, of *S. tuberosum* and in *S. acaule* are being studied. The prevalence of autotetraploidy in this material is proving to be a severe handicap in the interpretation of the results obtained. To overcome this difficulty, attempts are being made to produce and assemble a collection of haploids carrying genes of interest. Twenty-seven haploids are now available and they are under test for gene content.

In *S. stoloniferum* (tetraploid) a fourth gene controlling necrotic reaction to part of the virus Y complex was discovered and breeding was carried out to permit the examination of the relationship of this gene to the others already identified.

Interest in the hexaploid series is centred upon *S. spectabile* and the relationship between the genes controlling reactions to virus Y in the species and the allelomorphic series of genes already disclosed in the related species *S. demissum*. Breeding difficulties between the two species were encountered but sufficient material was obtained and examined to provide evidence of the dominance of high level resistance to virus Y in *S. spectabile* over the whole range of reactions in *S. demissum*. Whether the genes concerned are independent or allelomorphic is yet to be determined.

Results of investigations with the beet ringspot strain of tomato blackring virus, made over the past three years, are reported in an occasional paper on page 49.

Sugar Beet—Continuing the programme undertaken at the request of the Sugar Beet Research and Education Committee, tests for bolting resistance were carried out on a number of lines bred by the Plant Breeding Institute, Cambridge, for whom unbolted " stecklings " were also selected. Non-bolting strains of sugar-beet generally exhibit a somewhat small " top." In Scotland, however, a large bulk of leafage is desired for stock-feeding, and attempts have been made at the Station to combine a large-foliage type with high resistance to bolting and good yielding capacity. So far the progenies of selections have proved in yield trial to be lacking in one or other of these qualities.

In 1950 a gift of seed of biennial male-sterile sugar-beet was received from Dr F. V. Owen of Salt Lake City, and stocks were propagated by planting male-steriles alongside lines of several non-bolting families. After two or three generations of pollination by members of the same family, the male-sterile stocks were showing some similarity to their pollen-parents. Monogerm plants have been selected from the segregating derivatives of American monogerm × non-bolting sugar beet.

Publications

CICCARONE, A., BLACK, W., and MALCOLMSON, JEAN F. (1961). Identification of races of *Phytophthora infestans* (Mont.) de Bary on potatoes and tomatoes, from four Italian regions. *Phitopathologia Mediterranea*, **2**, 49-53.

Cultures of *Phytophthora infestans* (Mont.) de Bary were obtained from potatoes and tomatoes in Sicily, Apulia, Campania, and Emilia. From 183 multispore isolations, 193 race determinations (129 from potatoes and 64 from tomatoes) were made.

Race 4 was identified in 89·89 per cent of the cultures obtained from potatoes, while races 0 and 4 were found in 60·93 per cent and 31·25 per cent respectively, of those from tomatoes. Both races were present in all the regions investigated, and on five occasions they were obtained as mixtures in one culture. Eight cultures consisted of mixtures of races 0 or 4 with race 3 or 3,4 and one, from tomato, was a mixture of the three races 0, 3, and 4. One culture from potato was a mixture of races 2,4 and 2,3,4 and another was race 3,4 alone. The presence of the race 4 characteristic in these cultures was noted.

The predominance of race 4 on potatoes and race 0 on tomatoes indicates that infection of potatoes is largely independent of that on tomatoes. The relatively high proportion of race 4 on tomatoes suggests that potatoes might provide a source of infection with this race, particularly where tomatoes follow potatoes.

The low frequency of specialised races indicates that the corresponding R genotypes are not common in the regions studied. Sufficient isolates of these races were not obtained to determine their geographical distribution.

GREGOR, J. W., and WATSON, PATRICIA J. (1961). Ecotypic differentiation: observations and reflections. *Evolution*, **15**, 166-173.

Observations on leaf length responses of *Plantago lanceolata* gamodemes to a range of habitat conditions indicate that it requires a considerable difference in phytosocial environment before exogenous adaptation becomes associated with detectable ecotypic differentiation.

Since ecotypic discontinuities are rarer than had initially been imagined, it would seem that a better understanding of ecotypic patterns could be achieved through the accumulation of records in which the emphasis has been transferred from the discrete ecotype to the trends of ecotypic differentiation. Such a change in emphasis would in no way invalidate Turesson's original concept. What does detract from its significance is the wrongful use of the term ecotype.

To facilitate the accumulation of information relating to ecotypic as well as to other micro-evolutionary patterns, it is suggested that the investigator should record in terms of demes whatever entities he is able to detect by the techniques he chooses to employ.

A merit of the deme terminology from the genecological point of view is that the categories are in no sense mutually exclusive, since the same population may be referable to several different categories according to which of its properties is taken into account, and the categories may be coincident or overlapping. Moreover, by avoiding absolute standards the flexibility of this terminology makes it useful over a wide range of genecological techniques.

HARBERD, D. J. (1961). Observations on population structure and longevity of *Festuca rubra* L. *New Phytologist*, **60**, 184-206.

Two collections of *Festuca rubra* from the local hills were involved. The one collection was of 1,481 plants all gathered from within a 100 square-yard quadrat ; the other of 340 plants was of wider distribution.

Detailed morphological examination of the material growing as spaced plants suggested that relatively few genotypes were present. Further work, involving a replicated field trial and an investigation of self- and cross-incompatibility corroborates this view. One of the genotypes occurs abundantly within an area of more than 240 yards diameter.

Among the genotypes there were considerable differences of colony size and density. There were also indications of differences in ecological requirements.

A consideration of the presumed age of the genotypes and the vigour of their vegetative spread suggests that very little ecotypic differentiation can be taking place in *F. rubra* at the present time. Any observable differentiation must have taken place either before colonization or during its early stages.

RATCLIFFE, D. (1961). Adaptation to habitat in a group of annual plants. *J. Ecol.*, **49**, 187-203.

Shallow soils on slopes with a southerly aspect on the Derbyshire limestone are characterized by a community of small annuals.

These species have identical life-cycles, germinating in autumn and flowering in spring. This life-cycle is remarkably constant, being little upset by abnormal climatic conditions.

These annuals are an ecological group found in similar habitats over much of Europe and have a centre of distribution in mediterranean and sub-mediterranean areas.

The seeds of all the species need to after-ripen before rapid germination of a high percentage of seeds is possible. The length of the after-ripening period varies from species to species in such a way that whatever the time of flowering normal germination is possible in September.

Germination of all species is better in light than darkness. This may help to prevent premature germination.

Soil moisture is important in determining the exact time of germination.

Lack of flowering in the autumn is not due to curtailment of the growing period or unfavourable daylength.

In constant high temperatures no species flowers normally, if at all. A period below 15° C. brings about normal flowering.

The behaviour in the field is considered in relation to the experimental data and the origin of the groups discussed.

BREEDING FOR DISEASE RESISTANCE

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The production of our major food plants is continually menaced by diseases which can cause spectacular losses if allowed to develop unchecked. Their control has been attempted in two ways, by the use of therapeutants and by breeding for resistance. Therapeutants, such as Bordeaux mixture on potato blight, have retained their effectiveness for long periods, but some notable failures in breeding have tended to overshadow the successes and lead to a very pessimistic outlook by some breeders and geneticists, who have suggested that results have been in accord with genetics and that we could not expect to do better (Lewis, 1955).

Potato blight (*Phytophthora infestans*) is a disease which caused such serious losses in Ireland in the years 1845-47 as to influence the whole course of history of the country (Large, 1940 ; Salaman, 1949). Within a comparatively few years, reasonable control was obtained with copper based sprays which are still used on a large scale. No real progress was made in breeding until this century when blight resistance was found in a derivative of the Mexican species, *Solanum demissum*. Inheritance of resistance was simple and so attempts were made to incorporate this resistance into commercial varieties. Before any new varieties emerged a new race of blight appeared which could attack much of the previously resistant material (O'Connor, 1933). New resistance genes were found but ultimately new blight races appeared which could attack the new hybrids. This pattern has continued to the present day so that although at least six genes have been demonstrated which give resistance to various combinations of races, races of the fungus have been found which can attack any gene combination.

Breeders, then, have questioned the wisdom of continuing breeding, for it appeared as though, by presenting the organism with a new genotype, they were stimulating the evolution of the fungus, encouraging it to mutate and produce a more " virulent " race. Because new races could attack genotypes resistant to the old races, the assumption was made that they were more virulent, leading to the further assumption that they resulted from beneficial mutations. To counter the argument that genetics has shown the rarity of beneficial mutations (Dobzhansky, 1957), it was said that fungi reproduce at such a high rate that chances of beneficial mutations occurring were greater than with slower reproducing organisms. This explanation ignored the obvious conclusion that because fungi have reproduced at such a rate for a long time, there is a greater likelihood of beneficial mutations having occurred in the past and become established in the genotype and less likelihood of beneficial mutations occurring in the future.

Where a plant and an associated parasite have survived to present times it is because of a balance between the two genotypes. A beneficial gene change may make a plant more resistant but if it becomes immune the parasite dies out. On the other hand a change to too great aggressiveness in the fungus may kill out its food supply. If a fungus does little damage there may be no selective advantage in immunity. The position has been reached where surviving plant genotypes are immune to the vast majority of plant pathogens, but are susceptible to a relatively small number, the majority of which do so little damage that they are not thought of as diseases.

Fungus and plant can remain in balance for long periods of time and from a genetic viewpoint the balance changes only when there is some change in the relative relationships of the two genotypes. Such changes may be of three types :—

1. Climatic changes which selectively favour one genotype. Climatic changes are largely responsible for the variation in the incidence of a disease from year to year and for the different balance attained in different areas.
2. Other environmental changes such as changes in cultural treatments, and availability of alternate hosts.
3. Genetic changes in plant or pathogen.

Genetic changes can result from gene changes in plant or parasite, or by the introduction of a new genotype from elsewhere. Undoubtedly, most of the changes we see come from the introduction of new plant varieties which have frequently been bred without reference to the disease in question. A recent example seen by the author is leaf stripe of wheat which reached epidemic proportions on the new variety Omar in Washington State in the United States of America in 1961. The disease had been unimportant in the past because earlier varieties were highly resistant. *Alternaria* blight of potatoes is unimportant in many of the big potato growing areas, but most potato breeders will have had the experience of producing hybrids which were highly susceptible, illustrating the resistance of our common varieties. Potatoes were bred in Europe many thousands of miles from their centre of origin and without any reference to their late blight resistance for blight was not present in Europe. Consequently, when blight was introduced in the 1840's it quickly became epidemic on the very susceptible varieties commonly grown, with resulting famine in Ireland (*loc. cit.*).

A mutation to lower resistance in the host is unlikely to be of importance in upsetting the balance unless associated with some other beneficial character, for the resultant genotype would be eliminated in favour of the more resistant one. On the other hand, a mutation to higher pathogenicity of the fungus would be of great selective value. Only a slight change may make an organism more pathogenic, and as we have become accustomed to the idea of evolution proceeding by a succession of small, discrete changes, it is easy to envisage such changes occurring in fungi. Yet the author can find no example occurring in nature of a disease suddenly becoming more severe on a plant genotype which had served as its host for any length of time.

A familiar example is the potato blight fungus on non-immune varieties. These varieties can be rated in the same order and with the same degree of infection as when first introduced even though some are over one hundred years old. This is true throughout the world, so that there is no evidence of potato blight varying the balance between it and the field resistance of commercial varieties over the past century.

It is useful to consider what is meant by the term " beneficial " gene, and if any gene which confers some apparent immediate advantage is necessarily beneficial in the widest evolutionary sense. Stebbins (1957) points out that an adaptive gene change may fit an organism for a special niche but not confer greater capacity for evolutionary development and may even be deleterious in the long-term view. He gives as an example the mutation to self-pollination in a normally cross-pollinated plant as an adaptive gene change which may fit a plant for a habitat where cross-pollination is difficult, if not impossible, but which lowers the capacity of the plant for further evolutionary development. On the other hand, a beneficial gene change should make an organism not only more successful in its present habitat but also confer a greater capacity for evolutionary development.

In the present instance, a beneficial gene change would make the potato blight fungus better able to attack existing susceptible varieties. A race of blight which attacked Majestic as severely as the present common race attacks the more susceptible King Edward, could be considered to have resulted from a beneficial gene change. On the other hand, a race which gave a lower level of attack could be classified as resulting from a deleterious gene change, even though the race may be better fitted in a narrow environment.

When a mixture of potato blight races is inoculated to a susceptible genotype and cultured on that host for several generations, the relative proportions of the races change. Some races are eliminated quickly and over a period the common race emerges as the dominant one (Black, 1952; Thurston and Eide, 1953; Thurston, 1958). Similarly, when a particular plant is rated for susceptibility to a number of races, it is found that the disease is less with the new races than with the old. On the earlier definition these races would be classified as deleterious. Yet these new races attack plants immune from the old races and so superficially appear more vigorous with the natural inference that they result from beneficial gene changes.

The clue to the situation is found in a study of the mechanism of resistance. To the plant breeder there appear to be two types of resistance to potato blight. The first has been called "hypersensitivity" and is considered by Müller, *et al.* (1955), to be "true resistance," whatever that may mean. Specific immunity to the different races is of this type. The second type has been called "field resistance" because it is a partial resistance only which gives some resistance in the field. It is a generalised resistance to all races and is expressed in varying degrees in commercial varieties. Plant resistance of the hypersensitive type comes from a high cell susceptibility, rapid cell death localising the infection. On the other hand, field resistance is an expression of cell resistance which hinders, though it may not entirely stop, the development and passage of the fungus (Gallegly, 1960).

Müller and Behr (1949), with narcotics, were able to slow up cell reaction to the stage where a hypersensitive genotype previously immune to a particular race of blight, became susceptible to that race. In like fashion, a new race may infect because the reaction of the cell to it is too slow to kill the blight before mycelium has penetrated adjacent cells. New races then are likely to be able to attack an immune genotype if they have a lower overall vigour, and can best be described as " adaptive " races. This agrees with the classification resulting from their reaction on susceptible varieties as mentioned earlier in this article. A similar situation appears to exist with tomato *Cladosporium* races. Day (1954, 1955) found his new races to be less vigorous on susceptible varieties and to be eliminated from mixtures. On crossing races he apparently recovered the common race as it could not attack genotypes susceptible to his other two races. In other words, it was more vigorous and so killed the cell too quickly to allow infection to become established.

If beneficial mutations occurred in fungi with the frequency needed to account for the arrival of new races of blight, we would be continually finding cases of diseases suddenly becoming more important on established varieties. No such case is known to the author, and this fact leads to the conclusion that beneficial mutations are rare and that fungi obey the normal laws of evolution. It is too much to think that fungi start to produce mutations when we start to investigate them, but more reasonable to assume that earlier interpretations of the origin of the races were in error.

The fact that therapeutants, such as Bordeaux mixture, which reduce but do not eliminate the fungus, remain permanently effective supports the viewpoint that beneficial mutations in fungi are rare. With an asexually reproduced organism such as potato blight, the common race is likely to contain the whole gene complex, so that a fungicide tested against a sample of the population would in effect be tested against the whole of it. Consequently, a fungicide found to be effective would remain that way until the arrival in the pathogen of a beneficial gene conferring resistance to it. So far this has not happened with blight. This is in contrast to the position with insecticides which are tested against a population sample which is unlikely to be representative of the whole gene complex as the insects are cross-breeding. Present testing methods select out resistant genotypes. On the other hand plant resistance to insects appears to be permanently effective because the plant is subject to attack by the whole insect genotype and resistance is determined by the capacity to attack of the most vigorous segment of the population. That resistance, once obtained, remains effective points to the paucity of beneficial gene changes in insects as well as in fungi (Driver, 1962).

All these facts support the view that the newer blight races arise from adaptive gene changes. The same races of blight arise quickly throughout the world wherever the appropriate plant genotypes are grown, suggesting that they arise purely by segregation from what is almost certainly a heterozygous—and probably heterokaryotic parent (Graham, 1955). Genetical theory suggests that there is no limit to the number of deleterious mutations that can occur and so we can expect no limit to the number of new blight races possible. At the present time, the number of races distinguishable on potatoes appears to be limited by the available differential potato genotypes, and what may appear to be a pure race on potatoes can be a mixture of races on tomatoes (Graham, *et al.*, 1961 ; Gallegly, 1960).

To the plant breeder, this means that breeding for blight resistance using the hypersensitive reaction alone is almost certain to end in failure, and at best can give only a temporary halt to the disease.

Field resistance is based on the capacity of the plant cell to reduce infectivity and to slow the growth and development of the fungus. Plants for selection are grown in the field and so are subject to the whole gene complex of the fungus. Resistance is determined by the reaction of the plant to the fungus genotype best able to attack and a more vigorous race would be needed to reduce the level of resistance. Because the common race gives the highest level of attack it can be considered to be the most advanced genotype and being asexually reproduced represents the whole gene complex. As there is no evidence of a change in pathogenicity of the blight fungus over the past one hundred years, it can be assumed that beneficial gene changes are so rare as to be virtually non-existent.

Field resistance to disease is extremely common and appears to be the normal type of resistance to those diseases which normally infect our crop plants but do little damage. It appears to be evolutionarily stable, not likely to be upset by changes in the pathogen, and so should be the type of resistance used by plant breeders. The breeder needs a stable type of resistance, expecially with an asexually reproduced crop such as potatoes in which a new variety takes so long to increase that new races can have arisen before it is established.

When starting a breeding project, then, it is important to study the whole plant-pathogen complex, including the mechanism of resistance, to give an idea of the type of change necessary in the pathogen to overcome plant resistance. If resistance is of the hypersensitive type with gene for gene relationship between fungus and host, it is most likely that we are dealing with a type of resistance which can be overcome by adaptive gene changes. No permanent solution is likely to come from breeding for this type of resistance. On the other hand where resistance is expressed not as complete immunity but as a high cell resistance to infection and to pathogen development, it is likely to need a beneficial gene change in the fungus to reduce the resistance. Such gene changes appear so rare as to be non-existent and so resistance is likely to be permanent.

It is possible that in some cases the two types of resistance could be combined. For instance hypersensitivity to the common race of potato blight could lower the requirement for level of field resistance to the less virulent newer races. The main difficulty in this type of approach is that of testing selections. Adequate field resistance to blight under the worst possible blight conditions has been obtained by Dr J. S. Niederhauser (1958) and his assistants of the Rockefeller Foundation in Mexico City as to make reliance upon hypersensitivity unnecessary. Some of the resistant selections were seen by the author in August 1961 growing in the Toluca Valley, quite unharmed when susceptible material was completely destroyed.

One difficulty in breeding for disease resistance is that of securing resistant parents. Yet any established commercial variety will have some degree of resistance to any disease present in the locality, though the level may be too low to give effective protection. Breeding trials show many hybrids to be much more susceptible than the parent varieties emphasising the fact that no variety would have survived without some resistance. Unfortunately, selecting for a level of resistance which varies with the physiological age of the plant and with the environment, is more difficult than selecting for immunity or susceptibility as expressed in the hypersensitive reaction. Consequently, there has been a tendency to look for the hypersensitive type of resistance especially as it seemed to be governed by single genes. On the other hand field resistance can best be considered as a physiological reaction which is increased or decreased by a number of genes. Because of this difference and because early geneticists tended to think in terms of single gene differences, the levels of resistance in our established varieties have been ignored, and it has not been appreciated that it is a more stable type of resistance.

In some ways it is fortunate that immunity was not found to some potato diseases, for in these cases breeding for field resistance is well advanced. Notable examples are for resistance to scab, *verticillium* wilt, ring rot, *fusarium* wilts and *rhizoctonia*, where the levels of resistance available in some breeding stocks is already high enough to make the particular disease unimportant (*e.g.*, Akeley, *et al.*, 1961). Some of the Mexican hybrids appear good enough to allow blight to be added to the list. Potato wart disease is one which has been dealt with satisfactorily by a single gene controlled immunity, though new races have arisen in Germany (Maris, 1961). It is possible that these new races, too, are adaptive races and further new races may arise, although the method of dispersal of the fungus may slow and restrict their appearance.

Resistance to the potato root eelworm is worthy of greater investigation before breeding and selection proceeds too far. Already a new race has arisen which can attack previously resistant genotypes (Jones, 1957), and it is possible that permanent results will come from exploiting differences in levels of susceptibility rather than from the immune reaction.

Present theories of evolution suggest that organisms evolve by the production of small discrete changes which make the organism better able to survive and so become established in the genotype. If, as it appears, there is no forward evolution in pathogenicity of fungi evident to-day, it is interesting to speculate on how they have evolved to their present level and how further evolution can occur. Can they evolve only along the lines of adaptive mutation or do they on occasion take a big jump forward by chromosome increase, nuclear fusion or grouping, followed by further dissipation of gene possibilities in adaptive mutation ?

Selection in the past appears to have favoured highly integrated, highly buffered genetic systems (Dobzhansky, 1956), which would militate against the occurrence and establishment of small beneficial gene changes. Yet a major change which circumvented the buffering system would have difficulty in achieving genetic stability because integration is likely to have been greatly upset. The small "adaptive" gene changes which occur in fungi indicate that the system is adjusted to these changes, suggesting that we are dealing with either a segregation of existing genes or with mutations which have arisen frequently in the past. Field resistance appears to be polygenically controlled, so that to overcome resistance, several gene changes may be necessary in the fungus. As the chances of these occurring at once are remote there is little chance of the fungus developing greater virulence in this way. Resistance is unlikely to break down unless there is a major change in the metabolic pathway through which the fungus attacks, perhaps by developing a completely new pathway.

To summarize, the following points emerge :—

1. Beneficial mutations in the widest evolutionary sense are extremely rare in plant pathogens so that if we include the right type of resistance to a disease, we can expect the resistance to be permanent.
2. Before commencing any programme of breeding for disease resistance the whole plant/pathogen complex should be investigated, including the mechanism of resistance to determine the type of resistance which requires a beneficial gene change to break it down.
3. Field resistance is the type of resistance to blight which can be broken down only by beneficial mutation in the fungus and such mutation is unlikely to occur.
4. Adequate field resistance to blight is available already in Mexican hybrids and resistance to most if not all potato diseases in stocks already available to breeders. Breeding techniques need to be improved but there is no genetic reason why success cannot be achieved if sufficient effort is put into a breeding project.

5. There is a wealth of field resistance to diseases in established varieties of all crops, for they would not have survived had they not possessed some resistance. With the development of appropriate breeding techniques the level of resistance can almost certainly be raised to the level at which diseases become unimportant.
6. There appears to be no reason from genetics why we cannot conquer plant diseases. With appropriate techniques and the selection of the right type of resistance, loss from disease can be banished from our crops.

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THE STATUS OF THE X^D STRAIN OF POTATO VIRUS X

G. Cockerham

Summary

The reactions of potato varieties and seedlings to infection with virus strain X^D are described. Material immune from other strains of virus X was also immune from X^D; material carrying the gene Nx was hypersensitive to X^D; material carrying the gene Nb but not Nx responded to infection by manifesting the non-lethal disease, foliar necrosis; and varieties carrying neither gene were either symptomless carriers of the virus or they evinced symptoms of mild mosaic disease. From the pattern of relationship thus established, the strain X^D conforms to a strain of Group 3 viruses in the classification of Cockerham (1955). It differs from other strains in Group 3 in causing foliar necrosis in the presence of the gene Nb and it is suggested that this relationship is indicative of its derivation from a strain of virus X in Group 1 of the classification.

The intensified, near-lethal foliar necrosis exhibited by the variety Catriona was ascribed to duplication of the Nb gene in this variety.

Introduction

Cultivated varieties of potato differ markedly in their responses to infection with strains of potato virus X, some being immune from all strains, others being hypersensitive to particular strains but susceptible and tolerant of many strains, and yet others are susceptible and tolerant of all strains. These distinctions are based on simple genetic differences between varieties involving genes controlling immunity and two pairs of genes, Nx, nx and Nb, nb, of which the dominant partners control lethal, necrotic responses to particular strains of the virus (Cadman, 1942; Cockerham, 1943a, 1943b, 1945; Black, 1956). The relationship between these latter genes and strains of virus X is regular and forms a pattern which enables a particular strain of the virus to be assigned to one of four groups according to its ability to cause lethal top-necrosis in the presence of either Nx or Nb (Group 1), Nb only (Group 2), Nx only (Group 3), or not to cause top-necrosis in the presence of either gene (Group 4) (Cockerham, 1955).

Of the many strains of virus X which have been examined personally or recorded in the literature, only two appear to contravene the pattern of relationship referred to. These are virus D (Bawden, 1934, 1936) and the strain X^N (Bawden, *et al.*, 1948) both of which were reported to have lethal necrotic effects on varieties possessing neither Nx nor Nb. A possible interpretation of these aberrancies from the established pattern is that there are, within cultivated potato varieties, additional genes which also control lethal necrotic reactions to parts of the virus X complex. It seemed desirable, therefore, to examine this possibility. Enquiries failed to locate any source of X^N, however, but sub-cultures of the oringinal virus D were finally obtained from Dr W. R. S. Wortley, Cambridge, and from Dr R. H. Larson, Madison, Wisconsin.

Although virus D was first recorded as a distinct virus with affinities to virus X (Bawden, 1934), it was subsequently accepted as an aberrant strain of virus X (Bawden, 1936; Salaman, 1938). It was differentiated from other strains chiefly by causing a destructive but non-lethal necrotic disease, foliar necrosis, on a range of potato varieties and by causing lethal top-necrosis on a wider range of varieties than the accepted strains of virus X. As will be shown, the sub-cultures used in the present work possessed the former but not the latter characteristic. Because of their derivation, however, they will be referred to as strain X^D.

Methods

The two sub-cultures were received in leaves of *Datura stramonium* from which they were immediately transferred to white Burley tobacco. After establishment in tobacco they were each inoculated, by lightly rubbing infective juice on leaflets dusted with carborundum powder, to a range of potato varieties and also to young plants of tomato var. Essex Wonder. The latter, in turn, provided scions for the graft-inoculation of potato material.

Parallel inoculations were made from each source of virus to 31 potato varieties and one X-immune potato seedling. In comparing the results of these inoculations there appeared to be no differences between the two cultures and subsequent inoculations were made with virus from the Wisconsin culture only. With this virus a further 36 cultivated varieties and 54 X-immune seedlings were tested for reaction to sap- and/or graft-inoculation. The total number of clones tested was thus 122 of which 79 were inoculated by both methods. In general, sap transfers were highly successful in establishing infection and graft transfers were made in special cases only. These included all X-immune material, varieties reported earlier to react with top-necrosis to virus D, some varieties which responded to sap transfers with local lesions only, and a few varieties which prior to test were already infected with virus X.

When symptoms of infection were not markedly evident, successful transfers of virus were identified, firstly, by serological agglutination with anti-virus serum prepared from strains of virus X in Group 3 (above), and secondly, by transfer to one or other of the varieties Arran Victory and Craigs Alliance, which usually responded by showing typical symptoms of foliar necrosis.

Experimental Results

Fifteen varieties carrying neither Nx nor Nb, that is varieties of the type nx : nb, were tested. These varieties are susceptible and, in varying degrees, tolerant of strains of X in Groups 1, 2, 3 and 4, and all were found to be susceptible and tolerant of the virus X^D. They showed only minor differences in the symptoms evoked. Thus a few necrotic spots occurred on the inoculated leaflets of Arran Banner, Arran Peak, Dunbar Rover and Up-to-Date, but none were observed on Di Vernon, Eclipse, Gladstone, Great Scot, Irish Chieftain, Majestic, Parnassia, Redskin, and Ulster Emblem. Symptoms of systemic infection varied from none in Arran Peak, Di Vernon, Redskin and Ulster Emblem, to mild mosaic in the other varieties and to a moderately severe mosaic in Irish Chieftain, which was carrying virus A. Two varieties within the group, Arran Consul and Dunbar Cavalier, were unobtainable in an X-free condition. Both showed symptoms of a mild mosaic and these symptoms appeared to be unaffected by the introduction of X^D. There was, indeed, no evidence that X^D had entered those plants which were inoculated by sap transfers. From plants inoculated by graft transfers, however, the virus was recovered on Craigs Alliance, in two cases, both from Dunbar Cavalier, with the expression of typical foliar necrosis. More usually the Craigs Alliance plants showed a modified form of foliar necrosis in which necrotic areas were small and dispersed among the general mosaic pattern which developed as the major symptom of infection. An explanation of this behaviour is to be found in the protection against X^D afforded by the strain of virus X originally present in the Arran Consul and Dunbar Cavalier plants. This protection was apparently complete when the challenging X^D was introduced by sap inoculation, but it was not proof against X^D introduced by graft. Competition between the two strains continued when transfers were made to Craigs Alliance and only in the two cases noted above was X^D able to gain control and produce its full effects.

It is emphasised that all the above mentioned varieties were tolerant of the virus and none responded with top necrosis although Arran Consul, Dunbar Cavalier, Majestic and Up-to-Date were reported to react in the latter way to virus D (Bawden, 1934, 1936). The responses of Arran Banner, Di Vernon, Eclipse and Great Scot to X^D were similar to those recorded for virus D (Bawden, 1934, 1936).

Varieties carrying the gene Nb only, that is, type nx : Nb, are susceptible to and tolerant of strains of virus X in Groups 3 and 4 of the general classification. Towards strains of Groups 1 and 2, on the other hand, they are hypersensitive and when systemically infected with any of these strains they respond with a lethal top-necrosis. Thirty-three varieties of this type were tested with X^D and 31 of them responded by manifesting symptoms of foliar necrosis, as described earlier by Bawden (Bawden, 1934). Following sap-inoculation, 25 varieties, Ackersegen, Aquila, Arran Pilot, Arran Victory, Bintje, Craigs Defiance, Dr McIntosh, Dunbar Standard, Dunbar Yeoman, Erdgold, Frühmolle, Golden Wonder, Home Guard, Kerr's Pink, May Queen, Monika, Ostbote, Panther, President, Robusta, Sharpe's Express, Sickingen, Ulster Chieftain, Ulster Supreme and Urtica, showed local symptoms which varied from discrete local lesions to large watery necrotic blotches. Subsequent symptoms varied within the general pattern of foliar necrosis, each variety showing firstly a necrosis of the middle leaves followed by leaf drop and the development on the upper leaves of a necrotic mosaic pattern interrupted by interveinal necrotic areas. The intensity of the mosaic, the number of necrotic spots, streaks and blotches and the amount of deformity they caused all varied between varieties, but the diseases were generally similar and differed only in degrees of severity. The varieties Immune Ashleaf, Katahdin, Record and Ulster Prince showed no symptoms on inoculated leaflets but subsequently they developed full foliar necrosis. Bona and British Queen responded to sap inoculation by producing local lesions on the inoculated leaves but no further symptoms developed and the virus was not recovered from either the upper foliage of the inoculated plants or from plants grown from their tubers. Both varieties showed typical foliar necrosis when infected by graft inoculation. Tubers from infected plants of all 31 varieties were sound and they gave rise to plants which again showed the general characteristics of necrotic mosaic diseases ranging from mosaic with slight necrosis (Record) to severe mosaic with necrosis (Dunbar Yeoman) or severe necrosis with mosaic (Erdgold and Ostbote).

The two exceptional varieties of the nx : Nb type were Abundance and Catriona. In the case of Abundance only plants infected with virus X were available for test. Inoculation of this variety by the leaf-rubbing method failed to induce any sign of infection with X^D and no recovery of the latter strain was recorded after transfers were made from the inoculated plants to the indicator varieties Arran Victory and Craigs Alliance. Inoculation by grafting was followed by the appearance of small necrotic areas in the leaves of the Abundance plants but there was no general necrosis with leaf drop as shown by other varieties of the nx : Nb type. Scions taken from the graft-inoculated Abundance plants induced symptoms on Arran Victory and Craigs Alliance which were similar to those of the scion sources and also similar to those caused on these varieties by the mixed infections in Arran Consul and Dunbar Cavalier to which reference has already been made. As in the previous cases, it seems probable that the original virus X in Abundance prevented the entry of X^D when introduced by sap inoculation but not by graft inoculation. In the latter case, however, the challenging virus was unable to multiply freely in the presence of the X-virus already present and hence its effects were reduced. It seems probable that Abundance free from virus X would react to X^D by expressing foliar necrosis.

The variety Catriona reacted to X^D introduced by either method of inoculation with severe, but typical, symptoms of the early stages of foliar necrosis followed by complete necrosis of the stem apices and ultimately by the death of the infected shoots. In some cases death occurred before tubers were formed but when tubers were obtained they remained sound and in the following year they produced small plants which were severely distorted with necrosis. These plants died early but invariably they continued to produce sound tubers, and an affected stock has been maintained in the greenhouse since 1952. Inoculation from these plants to Arran Victory and Craigs Alliance has always induced typical foliar necrosis.

Bawden (1934, 1936) examined sixteen varieties of the nx : Nb type for their reactions to virus D. Thirteen of them, Arran Cairn, Arran Chief, Arran Comrade, Arran Pilot, Arran Victory, British Queen, Edzell Blue, Katahdin, Kerr's Pink, May Queen, Rhoderick Dhu, President and Sharpe's Express, responded with foliar necrosis and three, Abundance, Catriona and Dunbar Yeoman with top necrosis. With the strain X^D coincident results were obtained with seven varieties but neither Abundance nor Dunbar Yeoman were killed with the virus, though both showed symptoms of foliar necrosis. Catriona was killed only occasionally and in special circumstances, though the disease manifested was always severe.

The extreme reaction of Catriona, and, indeed, the whole relationship between X^D and the gene Nb, was examined further by testing two seedling progenies with the virus strains X^B and X^D. In the first of these progenies, there were 64 seedlings of the parentage Catriona × Majestic and when infected with X^B by graft-inoculation 52 seedlings responded with top-necrosis, being thus similar to the parent Catriona, and 12 seedlings were anecrotic and tolerant as was the other parent, Majestic. Towards X^D, introduced by sap-inoculation, 11 plants showed severe, near-lethal necrosis like the parent Catriona, 41 plants showed the less severe forms of foliar necrosis and the 12 plants which were not necrotic to X^B were also not necrotic to X^D. These reactions with X^D were confirmed in the secondary symptoms of infection shown by plants grown from tubers of each seedling. Thus tubers from the

11 seedlings with severe necrosis produced small, necrotically-distorted plants similar to those produced from infected Catriona and there were 41 plants with necrotic mosaic diseases and 12 plants with anecrotic mild mosaic diseases. The above segregations approximate closely to a ratio of 5 : 1 for necrotic and anecrotic reactions to X^B and to a ratio of 1 : 4 : 1 for severe foliar necrosis, foliar necrosis and anecrosis in relation to X^D. They conform closely therefore, to the segregations expected from a cross between an autotetraploid parent having a dominant gene in the duplex condition and a parent carrying only the recessive counterpart of this gene. The indications are, therefore, that Catriona is duplex for a gene which controls not only a top-necrosis response to the strain X^B but also a foliar necrosis response to the strain X^D. Furthermore, it would seem that the reaction of foliar necrosis is intensified when the gene is duplicated as in the variety Catriona and, by implication, in the 11 seedlings which reacted in similar fashion.

The second progeny, Katahdin selfed, was examined to test this view and to corroborate the gene involved as that previously identified as Nb (Cockerham, 1943a, 1945). Katahdin reacts with top necrosis to X^B and with foliar necrosis to X^D. Earlier tests had shown that it was simplex for a gene Nb which conditioned its reaction to X^B. On selfing Katahdin, therefore, the expected ratio of genetic segregates in the progeny is 1 duplex : 2 simplex : 1 nulliplex with regard to the gene Nb. There were 48 seedlings in the progeny and duplicates of each were infected with X^B by graft-inoculation and with X^D by sap inoculation. The combined results of the two infections showed that 33 plants reacted with top-necrosis to X^B and that of these 11 were severely affected with near-lethal foliar necrosis and 22 with the less extreme foliar necrosis when infected with X^D. The remaining plants, 15 in number, were anecrotic and tolerant of both viruses. These data fit well with expectation and hence it is concluded that the necrotic effects of both X^B and X^D are due to the presence of the same gene, Nb, in the host plants and that the necrosis caused by X^D is intensified in plants in which the gene is duplicated.

Varieties carrying the gene Nx only, type Nx : nb, show local lesions or are systemically invaded with top-necrosis when infected with strains of virus X in Groups 1 and 3 but are tolerant of strains in Groups 2 and 4 and varieties carrying both the Nx and Nb genes, type Nx : Nb, show local lesions and/or top-necrosis towards strains of Group 1, 2 and 3 but are tolerant of strains in Group 4. Nineteen varieties of these two types were examined. They were Arran Crest, Cardinal, Craigs Royal, Early Market, Edgecote Purple, Epicure, International Kidney, Kepplestone Kidney, King Edward, Lymm Gray, Ninetyfold, Southesk, and Sutton's Early Regent of type Nx : nb ; and Craigs Defiance, Craigs Snow-White, Crusader, Harbinger, Mighty Atom and Pentland Ace of type Nx : Nb. All of them responded to infection with X^D by reacting with local lesions and/or top-necrosis according to the circumstances of inoculation.

Five varieties of the type Nx : nb were examined by Bawden for their reactions to virus D. He reported that Arran Crest, Epicure, King Edward and Ninetyfold responded to infection with top-necrosis and that International Kidney had an inconstant reaction but could act as a carrier of the virus (Bawden, 1934, 1936). As indicated above, International Kidney was found to respond with top-necrosis to the strain of X^D used in the present investigation.

The seedling U.S.D.A. 41956 is immune from virus X in general and it proved to be immune also from the strain X^D under examination. Additionally, 54 X-immune seedlings derived from X-immune *Solanum acaule* were also immune from infection with X^D.

Discussion

A general consideration of the results of infecting potato varieties with the virus strain X^D shows that it acts consistently in relation to the genes Nx and Nb. Varieties carrying neither gene are susceptible to and tolerant of the virus and they manifest either no symptoms of their infection or symptoms ranging from mild to moderately severe mosaic. Varieties carrying the gene Nb but not the gene Nx are also susceptible to X^D and they will support the virus even though the symptoms evoked are invariably necrotic. Exceptionally the necrosis may be lethal but only in varieties in which the gene Nb is duplicated and when infection becomes systemic before tubers are formed. Varieties carrying the gene Nx act in hypersensitive fashion towards the virus and it would be expected that under natural conditions they would be virtually immune from infection. These strain-gene relationships are completely in accord with those of a strain in Group 3 of the general classification of X viruses (Cockerham, 1955).

The original virus D could not be placed in any of the four groups of strains chiefly because of its reported lethal effects on the nx : nb varieties Arran Consul, Dunbar Cavalier, Majestic and Up-to-Date. The present X^D does not have this lethal action but otherwise it resembles the original virus D from which it was derived, in its effects on potato varieties and, in particular, in its characteristic property of causing the distinctive disease, foliar necrosis, in the presence of the gene Nb.

The association of a single strain of virus X with both a non-lethal necrosis in the presence of the gene Nb and a lethal necrosis in the presence of the gene Nx may be a significant pointer to a step in virus evolution. This may be indicated by a consideration of the potential host ranges, within cultivated potato varieties, of the known strains of potato virus X. If genetic immunity be excluded as a newcomer to the range of potato varieties, then the host range of any strain of virus X is determined by the distribution of the two genes Nb and Nx since the lethal necrotic responses conditioned by these genes are protective against any strain which evokes them (Murphy, 1936 ; Cockerham, 1937, 1939, 1943a). Thus varieties carrying either of the genes Nx and Nb are not tolerant hosts for strains of virus X in Group 1 of the classification. These latter strains are consequently restricted in host range to varieties carrying neither gene, that is, varieties of the type nx : nb. With this limitation imposed upon them they would appear to be the most primitive strains of virus X yet disclosed. Strains in Group 2 and Group 3 have a wider host range in that they find suitable hosts in varieties which possess Nx and Nb respectively, whilst the only known strain in Group 4 has a host range which is unlimited by the two genes. Therefore, if evolutionary progress of a parasite is measurable by the extension of its host range, virus X would seem to have evolved, in relation to the cultivated potato, from Group 1 strains to Group 2 strains by overcoming the hypersensitive effects of Nx and to Group 3 strains by overcoming the hypersensitive effects of Nb, and from strains in Groups 2 and 3 to Group 4 by the complementary steps of overcoming the hypersensitive effects of Nb and Nx respectively. The relationships of the strain X^D

with the two genes appear to provide support for this argument for they may be interpreted to indicate that X^D had its origin in a virus which caused top-necrosis in the presence of either Nb or Nx, that is, in a strain of Group 1 viruses, but which has now crossed the threshold of Group 3 by overcoming the restrictive effects of the Nb gene without losing entirely its necrotic effects in the presence of this gene.

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Above—Symptoms of recent infection with X^D on seedlings of Catriona × Majestic.

Left to right—Mild mosaic ; foliar necrosis ; severe foliar necrosis.

Below—The effects of X^D on plants grown from tubers of infected plants. There are three genotypes with regard to the gene Nb.

Left to right—Majestic, nulliplex ; Katahdin, simplex ; Catriona, duplex.

THE REACTION OF SEVENTEEN POTATO VARIETIES TO TOMATO BLACK-RING VIRUS

D. A. GOVIER

Summary

Potatoes were infected systemically with tomato black-ring virus by graft inoculation more readily than by natural infection from the soil but even so some varieties were difficult to infect. Infected plants were necrotic in the year of infection but in subsequent years they were only slightly less vigorous than healthy plants. Infection reduced yield by nearly 50 per cent in some varieties but the yields of a few varieties were little affected. The virus was recovered from 96 per cent of plants grown from the tuber progenies of systemically infected plants.

Cadman (1956) and Harrison (1956) detected a virus of the ring-spot type in sugar beet and later Harrison (1957) reported more detailed studies with the virus and gave it the name beet ring-spot virus. Further experiments (Harrison, 1958a) showed that the virus was related to tomato black-ring virus, the cause of a disease originally described by Smith (1946), and it is now looked upon as a strain of that virus and referred to as the beet ring-spot strain of tomato black-ring virus. The virus is transmitted through the soil by a nematode vector *Longidorus elongatus* (Harrison, Mowat and Taylor, 1961).

Natural infections of potato with the beet ringspot strain of tomato black-ring virus have been described (Harrison, 1957, 1958c, 1959) and Harrison (1958a) has described the response of potato to manual inoculation with the virus, and has estimated the yield losses which are incurred as a result of infection (Harrison, 1958c, 1959).

Most of Harrison's experiments were done with Kerr's Pink potato and the aim of the present work was to test the reaction to the virus of a wider range of potato material.

Materials and Methods

Seventeen potato varieties were used : Arran Banner, Arran Peak, Arran Pilot, Craigs Defiance, Craigs Royal, Craigs Snow-White, Dr McIntosh, Dunbar Rover, Home Guard, Kerr's Pink, King Edward, Pentland Ace, Pentland Beauty, Redskin and Up-to-Date were from virus tested stocks, whilst Epicure and Golden Wonder were known to be infected with virus S and virus A respectively.

An isolate of the beet ringspot strain of tomato black-ring virus (TBRV) in Kerr's Pink potato was kindly supplied by Dr C. H. Cadman. The material was received as the tuber produce of two plants and a number of eyes cut from each tuber provided the scions used for my experiments.

All inoculations were done by graft in January, 1959 ; two plants of each variety tested were grafted with TBRV-infected scions and a third plant was left untreated as a control. The virus source material was grown as single plants and all the grafts, except those on Epicure, were made with scions derived from one of Cadman's original plants.

The produce of grafted and control plants was propagated in the greenhouse in the Autumn of 1959 and the leaves of grafted plants were tested for TBRV by sap inoculation to tobacco (*Nicotiana tabacum* cv. White Burley).

Infected plants and control plants provided material for a field trial in 1960 to assess the effect of TBRV-infection on yield. A total of 384 plants were fully randomised. During the growing period all grafted plants in the trial were tested for TBRV by sap inoculation from leaves to tobacco. When most varieties were mature the tuber produce was lifted and weighed.

The produce of the 1960 trial provided material for a further, larger trial in 1961. A random block arrangement with eight replications was used, with the size of plot varied according to the number of tubers available of each variety ; the healthy and infected plots of each variety contained the same number of plants. Before weighing, the produce was graded into ware-size and small tubers, using a $1\frac{5}{8}''$ riddle.

Results

Varieties varied in their reaction to grafting with TBRV-infected scions. In the more sensitive varieties (Home Guard, Arran Pilot, Dr McIntosh) necrotic spots developed in the lower leaves of the axillary shoots 14-18 days after grafting. Further necrosis developed acropetally, until systemic necrosis killed the shoot some twenty days later. Infection developed similarly in Kerr's Pink, Arran Peak and King Edward, except that death of the axillary shoots was delayed. In Up-to-Date, Dunbar Rover and Arran Banner, the axillary shoots developed many necrotic spots but were not killed before maturity. Necrosis appeared considerably later in Epicure, Golden Wonder, Craigs Snow-White, Craigs Defiance and Pentland Ace, and each expanding leaf developed only one or two necrotic spots. Craigs Royal, Pentland Beauty and Redskin showed no symptoms.

During subsequent propagation in the greenhouse, one or two plants of Kerr's Pink, King Edward, Dunbar Rover and Dr McIntosh developed slightly malformed leaves, but the malformation could not with certainty be attributed to virus infection. Sap inoculation of tobacco showed that all plants derived from grafted plants were infected except those noted below. One plant each of Pentland Ace, Pentland Beauty, Epicure and Golden Wonder produced only healthy progeny. Of the three tubers produced by the second Epicure plant, two gave rise to infected plants and the third to a healthy plant. Only one plant of Craigs Royal was grafted and its progeny produced one healthy plant and one infected plant. Each grafted Redskin plant produced two tubers and all four tubers produced plants from which no virus could be recovered on tobacco. The proportion of infected tubers of all varieties except Redskin was nearly 82 per cent. If mother plants producing only healthy tubers are excluded this figure rises to 96 per cent.

No differences between healthy and infected plants of the same variety were seen in the 1960 trial, but the complete randomisation made visual comparison difficult. Inoculum from five plants (two of Craigs Defiance and one each of Kerr's Pink, Epicure and King Edward) did not produce symptoms on tobacco, although their mother plants did so in the greenhouse test. Four Craigs Royal plants, five Golden Wonder and twenty Redskin plants derived originally from TBRV-grafted plants, but whose mother plants appeared to be healthy in the greenhouse test, also failed to produce symptoms in tobacco.

The proportion of infected tubers produced by infected mother plants was nearly 98 per cent. All plants giving no reaction on tobacco were excluded from the analysis of the yields. The results are presented together with those of the 1961 trial in Table 1.

Because of its apparent immunity, further tests were made with the Redskin variety. Six plants from the same Redskin stock were grafted in December 1960 with scions from TBRV-infected scions derived from Cadman's original Kerr's Pink plants. The leaves of all six plants developed a number of necrotic spots and when the tubers produced were grown, inoculation of tobacco showed that all plants were infected with TBRV. An interesting feature of the grafted plants was the development of aerial tubers at the apices of the shoots arising from below the graft union. The production of aerial tubers by the scion at the graft union is a common reaction when the stock is immune to a virus present in the scion (Raleigh, 1936; Webb and Schultz, 1957).

The grouping of plants in plots in the 1961 trial allowed a more accurate comparison of healthy and infected plants to be made. While the infected plants showed no symptoms in the form of necrosis or mottling, those of most varieties were lacking in vigour—this was noticed particularly in adjacent healthy and infected plots of Arran Banner, Home Guard, King Edward, Pentland Ace, Pentland Beauty and Up-to-Date.

For analysis of yields, varieties were grouped according to plot size. King Edward and Golden Wonder (24 plants and 18 plants respectively) formed one group while varieties with 6-12 plants per plot made up a second group. This expedient was justified by comparison of the error mean squares when the trial was analysed separately for each plot size. Craigs Royal, Dunbar Rover, Epicure and Home Guard were excluded from the analysis because of small plot size. The results of the analysis are presented in Table 1.

Yield reductions were surprisingly large in many varieties in view of the fact that the plants showed little in the way of symptoms. The yields of certain varieties—*e.g.*, Craigs Snow-White, Golden Wonder and King Edward were less affected by infection with TBRV than those of others—*e.g.*, Arran Banner and Craigs Defiance, and the variety x health interaction was significant in both trials.

TABLE I

YIELDS OF TBRV-INFECTED POTATOES (EXPRESSED AS PERCENTAGES OF HEALTHY YIELDS)

Variety	*1961*			*1960*
	Ware	Small	Total	Total
King Edward . .	*100·0*	**72.2**	*95·5*	*86·8*
Golden Wonder .	*103·7*	**72·6**	*96·6*	*83·2*
Arran Banner .	80·6	**49·5**	**79·2**	**51·8**
Arran Peak . .	82·0	*96·4*	82·8	62·7
Arran Pilot . .	*102·8*	*77·7*	*98·3*	**56.4**
Craigs Defiance .	**73·4**	*72·1*	**73·3**	59·4
Craigs Snow-White .	*108·2*	*103·8*	*107·9*	*125·0*
Dr McIntosh . .	**72·3**	**51·9**	**69·6**	*83·5*
Kerr's Pink . .	*93·9*	*82·3*	*92·3*	**63·6**
Pentland Ace. .	**73·6**	*110·1*	79·2	*84·0*
Pentland Beauty .	*91·8*	*75·3*	*90·2*	72·4
Up-to-Date . .	*90·7*	*75·5*	*89·3*	*79·4*
Mean . .	**89·4**	**78·3**	**87·8**	**75·7**

Heavy type = significantly different from healthy, P = 0·01.
Ordinary type = significantly different from healthy, P = 0·05.
Italics = not significant.

Yield losses were usually greater in 1960 than in 1961. A lower overall yield in 1961 (about $\frac{2}{3}$ of the 1960 yield) would tend to reduce differences between the yields of healthy and infected plants. This lower overall yield could be attributed to reduced spacing between plants in the drill ($1\frac{1}{2}$ feet instead of 3 feet) and to leaf-roll infection contracted in the 1960 trial and expressed in 1961.

In most varieties losses of small tubers were greater than those of ware-size but this trend was markedly reversed in Arran Peak and Pentland Ace.

Three varieties, Dr McIntosh, Arran Pilot and Kerr's Pink gave sharply differing results in the two trials. These differences cannot be explained, but emphasise the need to conduct potato trials over a number of years before drawing conclusions.

The outstanding yield of TBRV-infected Craigs Snow-White is apparent in both trials. Virus infection can cause an increase in yield when the crop is lifted comparatively early and the virus-infected plants mature earlier than their healthy counterparts but this could not explain the figures for the 1960 trial when all Craigs Snow-White plants were mature at lifting.

Discussion

With naturally infected Kerr's Pink potato, Harrison (1959) describes three stages of infection: (1) Virus confined to roots (usually throughout first year); (2) Necrotic spotting symptoms in second year; (3) Most plants without symptoms, some stunted and distorted and a few with necrotic spotting symptoms in the third year. My results show that these stages are not obvious following graft infection and that few varieties fail to show necrotic spotting within a few weeks of grafting. In subsequent years symptoms were slight and never of the necrotic type.

Harrison's figure of 6 per cent for incidence of virus in the progeny plants (Harrison, 1957) is misleading, as it is based on figures including 31 mother plants which produced all healthy progeny, and were probably never systemically infected. His later figures (Harrison, 1959) for transmission through the tuber show 20-55 per cent for the year following infection, 50-80 per cent for the third year, and the figure rises in the next generation, as he points out, to nearly 100 per cent, which is in close agreement with my own results. I found few grafted mother plants which produced all healthy progeny indicating that systemic infection is initiated more readily by graft-inoculation than by natural infection through the roots. It is possible though, that natural infection through the roots could result in more systemic infections in varieties other than Kerr's Pink used by Harrison.

Harrison (1958b) has reported that although some varieties of raspberry are susceptible to the beet ringspot strain of tomato black-ring virus, many others are resistant or immune. Although I found that some potato varieties were less readily infected by graft-inoculation than others, no variety tested was immune when this method of inoculation was used. It would be interesting to find out whether any of these less readily infected varieties are not invaded systemically by the virus when planted in infected soil.

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THE INTERNATIONAL CODE OF NOMENCLATURE FOR CULTIVATED PLANTS

(Third edition, published 1961: available in Britain from the ROYAL HORTICULTURAL SOCIETY, VINCENT SQUARE, LONDON, S.W.1., price 2s. 6d.)

The inconvenience of alterations to the Code can be readily appreciated. However, since the 1958 edition was published a number of useful suggestions for the improvement of the Code have been made, and because of their importance it was felt that they ought to be incorporated in a revised text: hence the reason for the issue of a new edition so soon after the last. It is to be hoped that the Code in its present revised form will remain current for a considerable number of years.

The purpose of the Code is to promote uniformity, accuracy and fixity in naming cultivated plants: its provisions are presented in a total of 56 Articles, but its more important features can be summarised briefly as those which relate to (1) the cultivar; (2) the registration of cultivar names; (3) the description of cultivars; and (4) the establishment of registration authorities.

The term 'cultivar' is an international one for the category known in different languages by different names — *e.g.*, "variety" in English, and denotes an assemblage of cultivated individuals which is distinguished by any characters significant for the purposes of agriculture, forestry or horticulture. Thus any selection showing sufficient differences from existing cultivars to render it worthy of a name is to be regarded as a distinct cultivar. The Code makes it quite clear that the cultivar is the ultimate crop unit — *i.e.*, there are no sub-cultivar categories.

The value of registration as a way of stabilising names is emphasised. Registration means the acceptance of a cultivar name by a recognised Registration Authority and the recording of that name in its register. Equally important is the stipulation that a named cultivar must be described, and that "the description should, when possible, contain particulars to distinguish the cultivar or, when this cannot be done, to place the cultivar in an accepted classification." Since the Code definitely states that registration of a name does not necessarily imply judgement on the merit of the relevant cultivar it follows that the relative agronomic merits of cultivars cannot be directly deduced from their descriptions which, for obvious reasons, will be to a large extent founded on botanical rather than agronomic criteria. Nevertheless, even a strictly botanical description has its agricultural significance in as much as it can provide the basic information required to form an intelligent forecast of the potential suitability of a particular cultivar for a particular economic purpose.

In order to implement the purpose of the Code the establishment of Registration Authorities is a primary essential. Indeed the International Commission responsible for the Code believe that such authorities, both national and/or international are of vital importance, and has taken steps, with the co-operation of the Food and Agricultural Organisation of the United Nations, to promote the formation of authorities to encompass as many crop plant groups as possible.

In this country the Department of Agriculture and Fisheries for Scotland has already appointed its Scientific Services Station at Edinburgh, as the National Registration Authority covering cultivars of native origin within all agricultural and horticultural plant groups. Pending official notification in the press, any Scottish breeder, or other interested person, should make enquiries of the Director, Scientific Services, East Craigs, Edinburgh 12.

J. W. G.

A NOTE ON SEGREGATION RATIOS IN TETRAPLOID GRASSES

D. J. Harberd and P. J. Watson

In the course of our routine work it has frequently been necessary to check that individual grass plants of normally self sterile species are in fact self sterile, since occasionally self fertile individuals are recorded. Our check involves the germination—or attempted germination—of the products of self fertilisation and some of the progenies from self fertile parents produced crops of seedlings containing albinos in addition to the normal green seedlings. It has been our practice in these cases to record the numbers of normal and albino seedlings since, while the figures are of no importance to the problems we have had in hand, the records in themselves are of some interest. We are aware, of course, that we are probably dealing with more than one type of chlorophyll deficiency.

Among diploid species like ryegrass the most frequent proportion of albinos when present is one-quarter, clearly suggesting that the parent plant was heterozygous for the condition and segregating in the well-known 3 : 1 Mendelian ratio.

Among naturally tetraploid species we have not yet recorded a 3 : 1 segregation for albino seedlings, though it is known that this ratio can be found. The use of the segregation ratios of green : albino seedlings for elucidating the nature of polyploidy has been discussed by Nordenskiöld (1953, 1960). The interest in this approach is that the genetical investigation can be conducted independently of a cytological examination : one would assume that where both methods could be satisfactorily applied the results should reinforce one another. However, polyploids need not be either allo- or auto-polyploid, they could, for instance, be allopolyploid for some part of the nuclear material and autopolyploid for the rest. The gene segregation ratios would then depend on which part of the chromosome complement carried that locus.

The results we have obtained for albino segregations on selfing natural tetraploids of *Agrostis* are listed in Table 1.

Only one plant of *Agrostis tenuis* (D32t) has yielded albinos on selfing. It was a big progeny, and the ratio obtained was an almost perfect fit with the 35 : 1 ratio of tetrasomic inheritance with random chromosome assortment (2·8 per cent). Our cytological observations are in agreement with those of Jones

TABLE 1

Species	*Ref. No.*	*Normals*	*Albinos*	*Total*	*% Albino*
A. tenuis	D32t	4,374	125	4,499	2·8
A. canina	H110c	6,488	189	6,677	2·8
A. canina	A6c	57	3	60	5·0
A. canina	B85c	663	10	673	1·5

(1956) in that the species is almost entirely bivalent forming. Jones also obtained evidence that the species, though a segmental allopolyploid, is near autotetraploid. In interpreting our result we would go further and suggest that at this locus the species is autotetraploid, the case being closely analagous with that of *Lotus* described by Dawson (1941), who also obtained tetrasomic inheritance in a bivalent forming tetraploid.

For *Agrostis canina* there are segration ratios for three plants. Again our cytological work confirms that of Jones ; the species is quadrivalent forming. Only one of the three plants (H110c) has yielded a big progeny on selfing and again the ratio is an almost perfect fit to the 35 : 1 ratio. The two smaller progenies are more difficult to interpret. The result from A6c is actually a close fit with random chromatid assortment in tetrasomic inheritance (4·6 per cent) but the numbers are too small to draw any conclusions. The segregation ratio for B85c is significantly different at the 5 per cent level from 35 : 1 but does not give a better fit with any ratio that is intelligible to us. (We note the close fit with the 63 : 1 ratio of disomic triplicate factor but are reluctant to conclude anything from it.) It is perhaps worth noting that B85c was atypical for *A. canina* in its high pollen fertility.

Apart from B85c the *Agrostis* segregation figures show a good agreement with the cytological constitution.

TABLE 2

Species	*Ref. No.*	*Normals*	*Albinos*	*Total*	*% Albino*
F. ovina	P2	96	7	103	6·8
F. ovina	P21	481	37	518	7·1
F. ovina	P21/4	78	6	84	7·1
F. ovina	110/4	35	2	37	5·4
F. ovina	Total	690	52	742	6·9

The results for four tetraploid plants of *Festuca ovina* (Table 2) all correspond closely to the 15 : 1 ratio (6·25) of duplicate factor inheritance and this implies that the loci are functionally diploid and hence that the material is allotetraploid. In this species the conclusions to be drawn from the segregation ratios are at variance with those obtained from cytological examination. We know from our own work and from that of others that the tetraploid *F. ovina* is quadrivalent forming and there is also further cytological evidence suggesting that the species is autotetraploid (Jenkins and Thomas, 1949). Furthermore, the diploid and tetraploid forms are so similar morphologically that an autotetraploid condition seems to be the more likely. But in each family we have only found evidence of allotetraploidy in the genetical ratios. It should be noted that there is no reason to suppose that the loci concerned in the separate plants of *F. ovina* were the same. In fact it is most unlikely that they were, except in the cases of P21 and P21/4, where the latter plant was a daughter of the former. While our figures do not show that the tetraploid *F. ovina* is allotetraploid, they do show unequivocally that it is not simply an autotetraploid.

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THE ECOTYPE CONCEPT IN RANGE MANAGEMENT

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The significance of the concept of ecotypic differentiation to range management is based on two major premises. First, that the ecotypic concept is a fundamental, if somewhat neglected, concept in ecology; and second, that the range scientist, like other managers of wild (uncultivated) lands, is primarily a practising ecologist.

The first premise is based on the fact that the ecotype concept has to do with the relationship between plant populations and environment, and thus falls into the area of interest of the ecologist. The pioneer investigations of Turesson (1922) clearly indicate that the ecotype concept was considered by him to be primarily an ecological one. This view is further shown by his designation of "genecology" as the name for this new field of study. The fact that the significance of ecotypic variation has to date been realised more fully by taxonomists and geneticists in no way negates the soundness of Turesson's view. As Constance (1953) has pointed out, the change of name from "genecology" to "experimental taxonomy" may be classed as an example of synonomy.

The important point is that ecologists as a group have failed to participate fully in this new and fruitful field of research. Most ecologists continue to operate on the assumption that plant species are uniform populations whose constituents are uniform morphologically, physiologically and genetically wherever they occur. As a result, the current fund of knowledge concerning the significance of ecotypic variation to ecological problems is limited. The failure of range managers and research workers to grasp the full implications of ecotypic variability in plants does not constitute a special case, but reflects the attitudes of ecologists generally.

The second premise, that of range management as a phase of applied ecology with economic motivation, needs little elaboration. The worker engaged in the management of native grazing lands is deeply involved with the relation of organisms to environment, with cause and effect relationships, and with the manipulation of plant and animal populations on a scientific basis. He is compelled to deal with whole ecosystems in all their complexities and often with an inadequate fund of available knowledge. Hence the range manager is vitally concerned with the subject matter of ecology and with advances in this field. Concepts such as plant succession, plant competition, and more recently that of the ecosystem as a basic working unit in land management have been widely and fruitfully applied in this field.

The nature and extent of the resource with which the range manager works are such as to render his ecological problems a matter of considerable importance. Native grazing lands constitute a major natural resource in virtually all parts of the world. In the United States alone, lands of this nature occupy some 728 million acres in the western part of the country and another 200 million in the southeastern states.

While range lands differ greatly in nature, they share one major characteristic, that of unsuitability for cultivated agriculture under present or immediately foreseeable economic and social conditions. This situation results from a variety of factors including deficiencies in precipitation, shortness of growing season, low productivity or instability of soils, and rough topography. As might be expected, lands of this nature encompass a great variety of habitats and of plant communities. The latter include many types of grassland, shrub, savanna, and forest. Most of these lands have other values including watershed, timber and outdoor recreation, but all have as a major use the grazing of domestic livestock and/or native herbivores.

Historically, the management of native grazing lands has been of a decidedly extensive nature. Economically speaking, both input and output have been low, and only limited efforts have been made to manipulate the various plant and animal populations for maximum sustained production. Low production per acre has been compensated by the vast extent of native ranges and, until recently, demands for increased production could usually be met by expansion into previously unexploited areas.

This situation is now changing under the impact of increased demand for animal products and lack of new lands for expansion. This change is most marked in the more highly developed countries, but represents a trend which will in time affect all native grazing lands. In many areas, such as the United States, increasing demand for the products of grazing lands is associated with a range area which is not only incapable of further expansion, but is actually shrinking due to increasing demands of other land uses.

A major result of the pressures described is a decided trend towards intensification of range management and development. Improvements in use and production are sought by means of controlled grazing practices, improved fencing, and stock water facilities, and the development of improved types of livestock. There is also a marked increase in the use of direct vegetational manipulation including reseeding of depleted ranges to adapted forage species, control of undesirable plants by herbicides or other means, and the use of commercial fertilizers. Naturally, the application of such measures must be geared to the potential of the habitat, and many range types are too limited by natural factors to warrant use of any but the simplest and cheapest application of the measures listed above. In spite of such natural limitations, it appears that most range types in North America are capable of significantly greater production than is now obtained, and the same is doubtless true in other parts of the world.

The need for more intensive development and use of range lands points up a corresponding need for fuller understanding of their ecology. At present, relatively little is known about the life history, requirements, and response to management of most native range plants, and understanding of the communities formed by these species is also limited. In particular, the potential of major species and communities to respond to specific methods of treatment is largely unknown. It is in this context of need for increased basic ecological knowledge that the significance of the ecotype concept for range management must be considered.

During the past two decades there has been increasing evidence of interest in the concept of ecotypic variation as applied to the management of ranges and other wild lands in North America. Much of the stimulus for this trend has come from the classic investigations of Clausen, Heisey and Keck, and their associates of the Carnegie Institution in California.

The impressive results obtained from study of duplicate plant materials grown in a series of transplant gardens and, more recently, in controlled growth chambers, have aided greatly in establishing the value of this type of research. Their work with species of *Potentilla, Achillea, Pentstemon,* and more recently *Poa,* has shown the great diversity to be found in native species of this continent, particularly in the highly diverse environments of the mountainous western states.

Another approach to studies of variation in native species has been from the agronomic and plant breeding viewpoint. The principal objective in this case has been to select superior strains of native species for use in range revegetation. Investigations of this nature, while confined largely to characteristics of economic importance, have yielded much information, especially for dominant grasses of the Great Plains region.

Examples of this approach include the investigations of Anderson and Aldous (1938) and Cornelius (1947 on variation in *Andropogon scoparius* (little bluestem); of Riegel (1940) on *Bouteloua gracilis* (blue grama); and of Hopkins (1941) on *B. curtipendula* (side-oats grama). In all cases, significant differences were found in the progeny of seed or clones collected from areas of different latitude when these were grown together in test plots. Northern strains matured earlier and produced less forage than southern lots when both were grown at mid-latitude stations, while southern strains were highly productive but susceptible to winter killing.

Considerable research on ecotypic variation in grasses of the Great Plains region has been done by C. E. Olmsted and his students at the University of Chicago. These workers have emphasised the effects of photoperiod on the growth and reproduction of races of *B. curtipendula* (Olmsted, 1944) and *Andropogon scoparius* (Larsen, 1947). Marked differences in the response of northern and southern strains of both species to day length were demonstrated by these authors.

Recent studies of ecotypic variation in perennial range grasses include those of Bohmont and Lang (1957) and Landers (1955). The former authors have isolated some fifty " geographic strains " of *Oryzopsis hymenoides* (Indian ricegrass), a species of wide distribution in western North America. A detailed study of twelve of these strains revealed significant differences in their palatability to rabbits as well as in plant growth characteristics. Landers found significant differences in drought resistance among races of *Bouteloua hirsuta* (hairy grama) collected in Texas and Mexico.

One of the earliest studies of a native range grass by the methods of the Carnegie Institution group was made by Lawrence (1945) with *Deschampsia caespitosa* (tufted hair-grass). Material of this widespread species collected on a transect across California and from northwestern Europe was shown to include five climatic ecotypes. These races differed greatly in such characters as survival, phenology, height, amount of vivipary, growth and disease resistance when grown together in the Carnegie Institution gardens. Morphologically, these populations were similar in their native habitats, and all five were referred to the subspecies *genuina* of *D. caespitosa*. In *D. caespitosa*, which has three recognised subspecies, ecotypic (and ecological) differentiation has been independent of morphological variation. Lawrence's comment that " a species of such wide tolerance is not a good ecologic indicator, but its ecotypes are " is highly applicable to problems of range management.

Variability within another native grass of wide distribution, *Festuca idahoensis* (Idaho fescue) is under investigation by the author (Tisdale, 1961). Material of this species from a variety of habitats in the far western states and British Columbia showed great variability when grown in nurseries at Moscow, Idaho and Stanford, California. It is evident that great variability exists within populations of this species as well as among them. Characters showing marked variation include survival, phenology, height, growth, basal diameter of plants, relative culm and leaf production, seed production and disease resistance. Certain major groupings are evident among the eighteen collections studied. This is especially apparent in collections from (*a*) the Palouse grasslands of northern Idaho and adjacent areas, (*b*) mountain grasslands on the eastern slope of the Rocky Mountains in Montana and Wyoming, and (*c*) sagebrush-grass vegetation of southern Idaho and Oregon.

Ecotypic variation has been shown to exist in some of the introduced annual grasses which have become abundant on North American range lands. Hulbert (1955) found variations in height and phenology in collections of *Bromus tectorum* (downy brome or cheatgrass), from sites in the United States and Canada. In another annual brome, *B. mollis* (soft chess), a superior strain called Blando brome has been selected from several ecotypes of this species for range planting by the U.S. Soil Conservation Service. Recently, the presence of ecotypic variation in a weedy annual, *Elymus caput-medusae* (medusa-head), has been demonstrated by Robison, *et al.* (1960). Significant differences in rate of germination, rate of root growth, plant height and phenology, were found in material from the four western states in which this plant has become common.

Few studies have been made of ecotypic variation in the shrubs which are so important on many range areas. The investigations of Ward (1953) on *Artemisia* indicate that such varation exists in *A. tridentata* (big sagebrush), and that this is associated in part with the existence of diploid and tetraploid chromosome races. This species occupies a wide range of habitats in the Intermountain Region of western North America, but no comprehensive study of its intraspecific variability has been made as yet. *Purshia tridentata* (antelope bitterbrush) is another common and widespread shrub which appears to possess considerable ecotypic variation.

Collections under nursery study by Nord (1962) show marked differences in growth form and phenology. Blaisdell and Mueggler (1956) have shown that the ability of *P. tridentata* to sprout after fire is at least partially a racial characteristic.

Virtually all of the studies described above have been concerned with the variability within individual species. McMillan (1959) has studied groups of associated dominant grasses from a large number of plant communities on the Great Plains. The variation displayed by this clonal material in transplant garden and greenhouse indicates the existence of more or less parallel variation among these associated species. McMillan interprets this ecotypic variation as the mechanism which enables this group of grass species to occupy the great variety of habitats occurring in the Great Plains region.

In conclusion, it is apparent from the studies reviewed that ecotypic variation is well developed in many species of plants important on native grazing lands of North America. The fact that most of the variation described to date appears to be climatically induced does not exclude the importance of other types of racial differentiation. The presence of edaphic ecotypes is suggested by the findings of Kruckeberg (1951) on races adapted to serpentine soils. Biotic ecotypes produced under heavy grazing pressure are also a distinct possibility as yet unexplored. Results of ecotypic investigations in other areas, such as the hill pastures of Great Britain, lend support to these suppositions.

It is to be hoped that the present increase of interest in ecotypic variation in plants of range lands will continue and increase. Benefits to be expected from research of this nature include increased predictability of the reaction of species and communities on particular sites to management or improvement practices. Greater accuracy in the extrapolation of research results should be another benefit. On the side of plant improvement, the findings of Clausen and associates (Clausen, 1952) that the progeny from a cross of two ecotypes may excel either parent in desirable characteristics also holds much promise.

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