SCOTTISH PLANT BREEDING STATION

PENTLANDFIELD, ROSLIN, MIDLOTHIAN

REPORT

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DIRECTOR'S REPORT

Brassica Crops.—A range of brassicas has been obtained from various parts of the world and grown in order to select material suitable for use as parents in inter-specific combinations. In particular the wide range of variation found in *Brassica oleracea* and *B. campestris* (*sensu lato*) was investigated. Forty forms of *B. oleracea*, both wild and cultivated, and thirty-three forms of *B. campestris* (including sub-species *rapa*, ssp. *pekinensis*, ssp. *chinensis* and ssp. *nipposinica*) were observed for such characters as growth habit, leafiness and time of flowering. In *B. oleracea* wild-type kales were generally low in growth and branched from near the base producing shoots bearing smallish leaves with long petioles. Most of these flowered early and were killed off by winter frosts. A variety known as "Shetland Cabbage" formed heads late in the season and produced numerous large outer leaves which might be suitable for fodder during the winter months. "Shetland Cabbage" on superficial observation compares favourably with the well-known "January King" both for late heading and for frost resistance. *B. oleracea* var. *gongylodes* "Flammingers' Futterkohlrabi" appeared superior to three other kohl-rabi varieties for size of "bulb" and for leafiness.

In the *B. campestris* group the oil-seed forms, such as the Indian cultivars *sarson* and *toria*, flowered early and set abundant seed. These varieties were erect and branching, most of the leaves were cauline and general leafiness was poor. *B. campestris* ssp. *pekinensis* produced numerous large, broad leaves arising from the base but flowered early and showed very little tendency to form hearts. Ssp. *chinensis* (the Chinese cabbage) with entire, ovate leaves and thickened mid-ribs and petioles also flowered early and did not form hearts. Japanese cultivars of *B. campestris* were fairly vigorous and leafy but mostly early-flowering. Four of these ("Gujoyairai," "Mieyairai," "Isobeyairai" and "Hatanasyu") produced lyrate leaves typical of the turnip-rape whilst two ("Kosynewase" and "Hisagova") possessed large ovate leaves with smooth margins and thickened petioles resembling ssp. *chinensis*. Cultivars of *B. campestris* ssp. *nipposinica* produced very numerous leaves arising from a basal rosette. One form, "Mibuna," had narrow entire leaves whilst "Kyona" had finely dissected laciniate or pinnatifid leaves. These forms flowered late, some plants showing no signs of flowering and behaving as biennials. They were later severely affected by frost.

Plants of *B. campestris* ssp. *nipposinica* were found in 1959 to have a rosette of finely divided leaves which might be suitable for grazing. They were seeded as annuals and some experiments were carried out on the progeny. In a small catch-crop trial sown on 21st July, broadcast sowings were compared with those of dwarf rape, white mustard and buckwheat. The *nipposinica* crops looked like a sward of grass, but its leaves were very soft and had only 7 per cent of dry matter. It developed more quickly than dwarf rape, but was not so rapid as white mustard which had started to flower by 15th August and was setting seed by 8th September. On the latter date it still presented a grass-like appearance, thickened now by the development of numerous buds on its sessile crown ; but some plants had shot to seed. The yields of ssp. *nipposinica* were relatively heavy, but the plant stands were denser than those of the other crops. A clubroot test was carried out on several hundred seedlings grown in boxes of infected soil, and all were pronouncedly susceptible.

B. tournefortii, the so-called " wild-turnip," formed low bushy plants with small hispid, lyrate leaves and flowered early, the flowers being small and inconspicuous. This species is of interest because of its alleged immunity to *Plasmodiophora*. It has 20 chromosomes but does not appear to cross readily with any of the *B. campestris* group.

When assessing kales it has been customary to qualify the gross yields by stating the proportions of leaf and stem. While it may be supposed that all but a few dying leaves will be edible, the amount of stem that can be consumed must vary greatly with the age of the plant, the class of stock eating it, weather conditions and the method of presentation, *e.g.* cut whole or chaffed or left standing on its roots. Any of these factors may affect the consumption of stem more than the form of *Brassica* used. Limiting the enquiry to the feeding of sheep with whole plants of various kales and hybrids, some information has been gathered as to the extent to which the stems can be devoured. A short run was carried out with thousand-headed kale at the beginning of 1960, in which year-old lambs after several days' conditioning and when snow covered the grass consumed three-quarters of the gross plant weight, leaving about 40 per cent of the fully grown stems. When thin-stemmed plants from the unthinned plots were fed the consumption was higher and some stems were completely eaten. Experiments were recommenced in November in the hope of comparing different Brassicas, and particularly *B. nipposinica* var. *laciniata*, but this crop was badly damaged by a severe frost, and a foot-and-mouth standstill order closed the experiment before the lambs learned to strip the bark from the stems. Arrangements have been made to feed some tup lambs daily with kale or other brassicas, and they have learned to deal efficiently with different types of stems.

Crosses made between *B. napus* ($2n = 38$) and *B. campestris* ($2n = 20$) were successful, in some cases a high seed yield being obtained. Fodder rape varieties (New Zealand Club-root Resisting rape and Broad-leaved Essex rape) were used as *B. napus* female parents with *B. campestris* " Svalöf Duro " turnip-rape, *B. campestris* ssp. *nipposinica* var. *laciniata*, *B. campestris*, ssp. *chinensis*, *B. campestris* ssp. *rapa* " Aberdeen Greentop " and " Gelria " pollen parents. F_1 hybrids ($2n = 29$) were highly sterile when bud selfed, pollen fertility was approximately 40 per cent, the pollen being of variable size. Hybrids were treated with 0.5 per cent colchicine applied to the stem apex of seedlings at the cotyledon stage in order to obtain *B. napo-campestris* ($2n = 58$). A few *B. napo-campestris* plants so far examined appeared to form mostly bivalents at meiotic metaphase I with regular 29 : 29 segregation in some cells. Pollen fertility was about 95 per cent. *B. napo-campestris* may be regarded as a distinct synthetic species containing two chromosome complements of *B. campestris* and one derived from *B. oleracea*. *B. napus* × *B. oleracea* crosses were less successful. Forms of thousand-headed kale selected for low growth, good side-shoot development and general leafiness were used as *B. oleracea* parents in the inter-specific hybridisations.

Crosses within the *B. campestris* group were all successful. In most cases F_1 hybrids showed some degree of heterosis. F_1 hybrids have been selfed in order to study segregation and fertility in the F_2 generation. Crosses between *B. oleracea* and *B. campestris* at the diploid level were entirely unsuccessful. Two maternal plants were obtained. *B. oleracea* and *B. campestris* failed to produce hybrids with *B. hirta* (the white mustard) and there was no stimulation of ovary development.

The effects of different conditions of storage on the viability of pollen are being investigated. Pollen of *B. campestris* and *B. oleracea* appeared viable after several weeks dry storage in a deep-freeze incubator. Viability was assessed by germination *in vitro* using a modification of the hanging drop technique. Pollen stored at laboratory temperature (60-65°F) and at 40°F did not remain viable for more than a few days. Successful storage of pollen should facilitate crossing between species or varieties flowering at different times. Pollen germination and pollen-tube growth following inter-specific pollination and the possible advantages of injecting pollen directly into the region of the ovary are being examined.

Further varieties of *B. campestris* and *B. oleracea* have been treated with colchicine with a view to making inter-specific crosses at the tetraploid level. Chromosome pairing in newly produced *B. oleracea* auto-tetraploids was rather erratic, 0-5 quadrivalents per cell were observed at metaphase I (mean quadrivalent frequency per cell was 1.68). Some cells showed complete bivalent formation whilst segregation of chromosomes at anaphase was generally either 18 : 18 or 19 : 17. Pollen fertility was approximately 90 per cent. Seed set following artificial self-pollination in the bud stage was considerably lower than in diploids.

Chromosome behaviour in 4 × *B. oleracea* was less regular than in 4 × *B. campestris* and 4 × *B. hirta* previously examined. In these latter species pairing was comparatively uniform, 0-2 quadrivalents being usually found whilst regular segregation of chromosomes at anaphase was fairly frequent. An octoploid *B. oleracea* plant derived by colchicine treatment of diploid material showed 36 : 36 segregation at anaphase I (one cell) as well as 37 : 35 (four cells) and 38 : 34 (four cells). Pollen fertility of this plant was 60 per cent. No seed was set following artificial self-pollination in the bud stage.

Pollen grain size appeared to be a reliable criterion on which to judge polyploidy and this character, together with the usual gigas features such as thicker stems and leaves, larger and more deeply pigmented petals, etc., may be useful in the initial isolation of auto-tetraploids from treated material.

Auto-tetraploids of *B. oleracea* varieties, *B. campestris* (including oriental forms) and *B. hirta* are being multiplied both by hand crossing and by controlled insect pollination using a small nucleus colony of bees and a " Tygan screencloth " cage.

Selection within the thousand-headed kale form of *B. oleracea* was continued. Comparisons were made between the progenies of plants chosen from commercial crops in 1958 on account of their leafiness and relatively low growth. One set of trials, wherein seed was sown in short strips in mid-April, and left unthinned so that there were about fifty plants in 100 inches of drill, was tested in late summer and autumn by measuring each stem and assessing the yield of stem and leaf in each strip. A trial sown on the ridge and thinned to nine-inch intervals, was also observed by cutting a few plants from each plot in the autumn. February observations in conjunction with yield results were of value in reaching an order of merit for the plants whose progenies were under test in 1959-60, and it has been noted that a repetition of the polycross progeny of TH-54, which was then placed first, is again showing a good crop this year. Several lines of the type of thousand-headed kale known as T1 grew slowly, being relatively deficient in leaf in the autumn trials but appearing somewhat better in January when they have many leafy side-shoots.

The autumn of 1960 favoured branching, and some of the progenies of early branching plants were much too precocious in this respect. As a result a number of very long bare stems was obtained with leaves only at the tips. The best type appeared to be one in which buds throughout the length of the stem developed into short shoots by January; the worst type had a bare main-stem and nothing to replace the old leaves when they died down. New selections were taken from commercial crops in 1960, and some French cultivars were observed, but these were either marrow-stem, or types in which branching was very late. The plants selected in 1959 were propagated from cuttings in the greenhouse, though not all of these could be induced to flower, and also by seeding groups of plants in field observation plots.

The examination of derivatives from intra-specific hybridisations between thousand-headed kale and other cultivated forms of the cabbage family was continued. A few lines from kohlrabi crosses were tested in an unthinned-row trial and some new broccoli crosses were observed, but the bulk of the work was concerned with cabbage hybrids. It has been difficult to get cabbages to flower in the greenhouse simultaneously with the kale, and hitherto only the hybrids of spring cabbages, which have a tendency to bolt, were available. Now by sowing seed collected over the last few years, it has been possible to compare hybrids from cultivars such as "Large York," "Drumhead," "January King," "Flat-poll" cattle cabbage and "Shetland Cabbage." It was noticed that there were differences in the appearance of F_1-plants in regard to hearting, which was usually shallow and saucerlike, but sometimes more pronounced. There was slight segregation in leaf-pattern which might be petiolate or winged to the base, and also in the development of side-shoots. Segregating generations of "Flat-poll" and "Shetland" cabbage hybrids were not yet available, but those of the other cultivars were planted out in large plots. Strongly frilled individuals occurred infrequently in some segregations, as also did a few strongly hearted plants. Some frilling was general in the derivatives of some "January King" plants, which have a tendency in this direction; there was also considerable side-branch development in one of these.

Immunity, or even a high degree of resistance, to *Plasmodiophora brassicae* (clubroot) has not been encountered in any of the stocks so far examined, though some show evidence of being relatively less susceptible than others. But in order to recognise degrees of resistance a test procedure rather more reliable than the method of growing seedlings in boxes of infected soil is required, and for this reason the following technique is being tried. Clubroot spores were isolated by macerating infected roots and extracting the spores by filtration through muslin followed by centrifugation. Spore concentration of isolates was determined using a haemocytometer. Seeds were pre-germinated, spaced out into boxes and seedlings treated at the cotyledon stage, constant numbers of spores being applied by pipette. Seedlings examined six days after treatment contained plasmodia in the root hairs, showing that primary infection had taken place. Plants were later removed and scored according to the severity of clubroot galling. Sterilised soil used in these experiments was a mixture of 7 parts loam : 3 parts sand : 2 parts peat. Soil pH was 5.8 and a high moisture content maintained. This method gave almost 100 per cent infection. Variation in spore concentration appeared to have little effect over the range used. There were a few slightly affected plants in untreated control boxes suggesting that the fungus may be seed borne. Both *B. napus* (New Zealand club root resisting rape) and *B. tournefortii* were affected by the treatments, although in the latter signs of infection were absent from the lateral roots. A local strain of *Plasmodiophora* was used in these tests.

Herbage Plants and Genecology.—In the field of grass breeding, attention is being concentrated on breeding for earliness in two distinct groups of material. The first group consists of Italian ryegrass where there is a demand for earlier leafier types with increased ability to respond to heavy nitrogenous manuring. The second group consists of those hill grasses which show some evidence of being capable of making early growth. In both groups the first problems concern methods of selection.

The Italian ryegrass experiments are being conducted to compare the performance of plants under different spacings and at present this is confined to a comparison between small sown field swards and "artificial" swards consisting of seedlings at two-inch spacing in boxes, but material is also being vegetatively multiplied to enable comparisons to be made between the same genotype at different plant spacings including single clone "swards."

Preliminary observations have been made on plants of thirty existing cultivars (including tetraploids) of Italian ryegrass, grown as spaced plants with particular reference to winter hardiness and time of ear emergence. Some tetraploid varieties show promising early growth but some are much inferior to diploids. All tetraploids so far examined have low seed yields and poor germination although seeds which do germinate give rise to vigorous seedlings. During late 1960 about 2,000 seedlings of Italian ryegrass were treated with colchicine and of these 190 have been retained for cytological examination during 1961.

In the case of the hill grasses it is felt that low soil temperatures may have a delaying effect upon the onset of spring growth and equipment is under construction which will enable the temperature of soil in pots to be controlled, this equipment will be installed in the existing controlled environment room so that soil and air temperatures can be varied independently.

The work on perennial ryegrass and cocksfoot using intervarietal crosses obtained by open pollination has been discontinued ; an account of this work appears as an Occasional Paper in this Report.

The 1960 trial to assess the losses in ryegrass caused by infection with ryegrass mosaic virus included seven strains of ryegrass each represented by a number of clones. The trial was planted on 16th May and a single cut taken on 27th July when all strains were flowering. Yield reductions varied widely, even between different clones of the same cultivar and were greatest in those of early maturity. Table 1 illustrates the correlation between yield reduction and earliness of maturity.

TABLE 1

Cultivars in order of maturity	Number of clones	% reduction in yield (average of clones)
Western Wolths .	6	47
E.F.486 Italian .	9	47
Hybrid Italian, N.Z. certified mother H.1	10	45
Presto III perennial	10	25
S.24	10	21
Perennial, N.Z. certified mother . .	10	11
S.23	10	9

As in 1959, all control plants in the trial were infected by the end of the season. There were few infected plants in nearby ryegrass plantings and it seems that spread is limited over greater distances.

Much time has been spent during the past year in analysing the data obtained from the genecological investigation of the species components of certain hill communities. This particular study was designed to supply information regarding the patterns of intra-specific population differentiation and the ecological relationships of these patterns. Complementary to these strains at the population level investigations are in progress which have a bearing upon the within population ecological distribution of individual genotypes. For this purpose perennial plants capable of vegetative spread are particularly suitable, for not only is it possible from an examination of clonal patterns to arrive at an estimate of the age of population constituents but also to assess the ecological tolerances of the genotypes concerned.

The first essential in work of this kind is the identification of individual clones which is by no means an easy matter in a grass sward which under natural hill conditions is usually a closed community. In the case of *Festuca rubra* and *F. ovina*, for example, it was found that, on the basis of observation and the measurement of attributes, plants grown from tillers taken from field samples suggested very strongly that the majority fell naturally into groups. Both *F. rubra* and *F. ovina* are more or less self-incompatible and, therefore, in order to test further the hypothesis that each group was composed of ramets of a single genotype an extensive crossing programme was undertaken. While it is manifestly impossible to prove without any question that individual tillers taken from the wild are in fact identical in genotype, it was shown that the amount of cross incompatibility within a morphologically similar group was more akin to the amount of selfing shown by the individuals composing the group than to the degree of out crossing between groups. Further evidence of marked similarity between individuals within a group was obtained from a trial in which twelve morphologically alike, cross-incompatible plants were cloned ten times and randomised so that each ramet from a single clone occurred once in each block. Throughout two seasons the degree of similarity over the whole trial was most striking and the statistical analyses of the five characters measured did not yield a significance of even 5 per cent. This is the kind of result one would expect to obtain from a randomised trial composed of ramets from a single genotype.

Ramets of one *F. rubra* clone were isolated from samples taken from three slight valleys which are separated from each other by strips of *Nardus* vegetation containing practically no *F. rubra*. The distribution of several other clones of *F. rubra* also indicated a connection between spread and edaphic conditions and the existence of presumably impassible barriers between the present valleys in the case of the large clone are presumably due to slow vegetational changes over a long period. The length of time involved must be very considerable since a spread of 240 yards was measured, yet under favourable spaced-plant conditions in the garden, the radial spread of a *F. rubra* plant does not exceed 9 inches in a year. On the other hand, *F. ovina*, which has no obvious means of easy vegetative spread, can be isolated on the hill over a distance of at least 10 yards. In view of this evidence it might be thought that *Trifolium repens* would be an ideal species for investigation but so far no individual genotype has been traced for any notable distance. However, it would appear that genotypes of *T. repens* are highly ecologically specialised.

Holcus mollis is another species in which clonal spread is being investigated and since the cross incompatibility test is not reliable here, the cloned clone trial is the technique which has been adopted to check the accuracy of the groupings. This species is, however, peculiar in that it is not uncommon to find significance at two levels; a highly significant level between supposed clones and occasionally a much lower level within them. A probable interpretation of this behaviour is that differences within a clone attributable to small fortuitous differences of environmental treatment of the parent from which ramets were derived months earlier may still be detectable.

Most usually, material for a trial is prepared in the autumn and planted out the following spring. Apart from casual observations, recording does not start until the next spring, most characters being scored 18-24 months from the time the parent material was broken down. Compared with other grass species *H. mollis* is a very quick grower and has accordingly to be treated somewhat differently. In this species the material may be prepared in the autumn but the preparations have even been left over until late winter or early spring. Such plants are, nevertheless, fully grown by mid-summer and are flowering freely and, therefore, most measurements are taken in the first season as little as four months after the time of division. At this stage both inter- and intra-clonal significances can be found. In the second season, by contrast with its appearance in the first, the trial is stunted and though few scores have been obtained from trials in this condition, it is interesting to note that the intra-clonal significance has gone, but that between clones remains.

A trial was laid out in 1960 to test the effects of deliberately-induced differences due to environmental pre-treatment of ramets and the results to date have been most rewarding. Twelve plants of the thirty-five chromosome race of *Holcus mollis*, all believed to be of one clone, were divided in the spring into 20 ramets each. The ramets were of five types, each represented four times for each parent plant. The types were started from rhizomes, aerial shoots or by division of the old sod, and those from aerial shoots were kept for the first few weeks in either a heated house, an unheated house or out of doors. The trial was planted out in early May and characters were recorded from late July to early September. Very little significance was found for differences between the twelve parent plants—about as much as has come to be associated with this type of trial within a supposed clone of *Holcus*. But very highly significant differences were found between the ramet types. These persisted throughout the season and gave very little evidence of diminishing, though the trend with time was very erratic. At planting there were very obvious differences between the ramet types but these proved to be little guide to the ultimate performance in the trial. This must cause some concern since some poorly treated ramets have actually produced better plants in the trial than others which were given apparently more favourable conditions in the early stages.

A large number of plants of *Agrostis tenuis* and *A. canina* were bagged in pairs under greenhouse conditions in order to produce many hybrids for study. Seedling counts permitted a comparison to be made between the results of selfing and crossing and it was found that in the majority of cases the seed set could be attributed to selfing alone, the *A. tenuis* plants proving to be more self-fertile on the whole than the *A. canina*. A random sample was taken from each lot and it was later possible to isolate 0.8 per cent seedlings on the grounds of mixed characters. Many of these plants have now been found to have odd chromosome numbers.

Oats.—The selection and testing of material at the Midlothian, Argyll and Inverness-shire centres proceeded along the lines described in previous reports and a number of selections derived from earlier work at the centres have now been multiplied for regional trials in suitable environments.

The breeding of oats resistant to oat stem eelworm is progressing satisfactorily. As the result of the dry spring and early summer few crops of oats in Scotland showed symptoms of attack. Fortunately, however, a limited supply of infested stubble was available from a field adjacent to that from which the particularly virulent strain used in 1959 was collected, symptoms of a light attack having appeared in this field late in the season. Inoculation experiments have shown the latter strain to be as virulent as the one used in the 1959 experiments, and it has, therefore, been used throughout in the 1960-61 series of tests.

Because of the very dry spring and summer conditions tests for resistance in the field in 1960 were inconclusive, but inoculations during the winter months, October to February, have again given consistent results, and where comparisons with field tests were available, have indicated that material selected as resistant in the laboratory is also resistant to attacks in the field.

An eelworm infested plot has been established at Pentlandfield in which resistant selections emerging from the inoculation tests can be tested for resistance in their normal environment before being distributed for trials on a field scale. Confirmation of resistance is also obtained by co-operation with the Department of Zoology, The North of Scotland College of Agriculture, which conducts independent tests in eelworm infested micro-plots at Craibstone Farm.

Last season, stunted oat plants with partly red or orange leaves were more numerous than in previous years and aphids collected in the field from affected plants and provisionally identified as *Metapolophium dirhodum* (Walker) transmitted barley yellow-dwarf virus to oat test plants. Aphid colonies derived from the original collections continued to transmit the virus, but all attempts to transmit the virus with a stock culture of *Rhopalosiphum padi* (L.) used in previous years failed. It appears that this species is not a vector of the strains of barley yellow-dwarf virus found in Scotland and the failure in previous years to transmit barley yellow-dwarf virus from plants apparently infected can be attributed to the use of a non-vector in the transmission tests. Even in a year favourable for virus spread, the number of infected plants was very low—too few to cause significant loss.

Potatoes.—As a result of its performance in the Merit Trials conducted by the Department of Agriculture and Fisheries for Scotland the Seedling 2319(a)3 has received " Commendation." It has been named " Pentland Dell," a name that will be registered in compliance with the provisions of the International Code of Nomenclature by the Scottish Department in its capacity as the National Registration Authority.

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

Maturity .	Early Maincrop.
Tuber . .	Kidney (pear-shaped) ; skin white, fairly smooth ; flesh white, firm ; eyes shallow, mainly on the point ; sprouts pink.
Foliage Type	Majestic.
Foliage .	Haulm of medium height, erect, fairly bushy, vigorous ; stems fairly frequent, medium to thin, branched, tinged pink at tops ; wings medium to narrow, slightly waved and edges faintly coloured especially near tops of stems ; leaf of medium size, open, rigid ; leaflets medium to small, light-green, matt, slightly folded, petioles fairly long with faint pink colour at bases ; secondary leaflets fairly frequent, small, cordate and occasionally on leaflet petioles.
Flower .	White, faint purple on backs of petals, fairly numerous ; anthers orange, generally regular ; inflorescence stalks of medium length faintly bronzed, cork ring coloured red ; buds red-brown, ovoid ; sepals fairly long, green with red-brown mid-ribs ; berries small, occurring infrequently.
Remarks .	Cropping : very good ; cooking quality : good ; keeping quality : moderately good ; field-immune from viruses X, A, B and C ; average susceptibility to virus Y ; both foliage and tuber field-immune from the common strain of blight ; moderately susceptible to dry rot, gangrene and skin spot.

With the co-operation of Dr R. M. Nattrass of the Department of Agriculture in Kenya a number of the Station's seedlings have been tested in East Africa, and five of them are now grown there on a commercial scale. Dr Nattrass has requested that these five be named. Accordingly, the following names have been suggested and as soon as official descriptions of the cultivars concerned are available these names will be registered by the Scottish Registration Authority :—

K52 Ref. No. 1565(4)	.	Roslin	Sasamua
E52 ,, ,, 1664a(12)	.	,,	Elementeita
K52 ,, ,, 1812a(8)	.	,,	Mt. Kenya
B53 ,, ,, 1521c(3)	.	,,	Ebura
C53 ,, ,, 1521d(24)	.	,,	Chania

Healthy stocks of these varieties are being multiplied for transmission to Kenya as required.

The name " Roslin Riviera " has been accepted for registration by the Scottish Registration Authority in respect of another Station seedling that has completed the two-year Wart Immunity and Identity Tests conducted by the Department of Agriculture and Fisheries for Scotland. This cultivar has greater local than general significance and has proved to be of particular interest to Cornish growers. In addition a red variant has been selected from the cultivar " Pentland Beauty " and as a preliminary to giving it the name " Red Pentland Beauty " this variant has been entered for the Wart Immunity and Identity Tests.

During 1960, approximately 3,700 seedlings bred from blight resistant parents were screened for resistance to race 1,2,3,4 of *Phytophthora infestans* under laboratory conditions. The survivors were grown to maturity and 197 seedlings, selected on the basis of tuber and other morphological characters, were retained for further investigation in 1961.

Samples of the corresponding material raised and tested in 1959 were sent to Mexico for test in the Toluca Valley in co-operation with Dr John S. Niederhauser of the Rockefeller Foundation. The main purpose of this test was to distinguish between true field resistance and hypersensitivity controlled by major genes other than R_1, R_2, R_3 and R_4.

About 250 samples of the more advanced seedlings selected solely on the basis of morphological characters, were grown in pots and screened for resistance to race 1,2,3,4 under laboratory conditions. About half of these seedlings showed a degree of resistance better than the average commercial variety, some of them being highly resistant.

Although the differential host series employed in the past for the classification of races of blight was based on four R genes derived from *S. demissum*, it is now clear that additional R genes exist and that the fungus possesses correspondingly greater variability. In order to examine this problem further, two clones of *S. demissum* (C5 and C6) obtained from Dr K. M. Graham, Canada, and one clone of *S. stoloniferum* (S6) from Professor R. Schick, East Germany, were tested with 62 isolates of the fungus, mostly of overseas origin. The three clones had previously reacted with hypersensitivity to race 1,2,3,4 and consequently must possess at least one gene other than the four already known. The results are summarised in the following table :—

Clone(s)	*No. of isolates causing disease*
C5	10
C6	29
S6	15
C5 + C6	6
C5 + S6	5
C6 + S6	10
C5 + C6 + S6	2

Analysis of the reactions shows that the new genes present in the three clones are different from each other and that races of blight capable of overcoming them already exist. On this evidence the species *S. demissum* contains at least six different R genes while *S. stoloniferum* possesses one that differs from the six in *S. demissum*.

Factors involved in field resistance to blight were examined in laboratory studies, using detached leaves of one named and six seedling varieties of potato and race 1,2,3,4 of *Phytophthora infestans*. Spore suspensions were used as inoculum and standard quantities were applied in each test. Records were made of the number of lesions produced per leaf, the rate of spread of the fungus, the rate of sporulation and the quantity of spores produced. It was shown that the different factors were correlated ; in the more resistant plants the fungus caused few, slow spreading lesions in which sporulation was both slow and sparse.

A trial was carried out to determine the extent to which potatoes would become infected with common scab when grown under normal conditions in a greenhouse in soil inoculated with a pathogenic strain of *Streptomyces scabies* Waksm. and Henrici. Thirty-four cultivars and seedlings were grown in 9-in. pots standing on the greenhouse floor, and 511 seedlings, the progenies of 9 crosses, were grown in 4-in. pots embedded in inoculated soil in the same greenhouse. When harvested, the resistance of the tubers to the disease was assessed. Each tuber was classified according to the proportion of surface covered by scab (cover score), and to the amount of damage caused by it (damage score). The cover and damage were scored according to the system shown in the following table :—

Proportion of surface covered by scab	*Score*	*Assessment of Damage*	*Score*
0	0	None	0
0-$\frac{1}{16}$	$\frac{1}{4}$	Very slight	$\frac{1}{2}$
$\frac{1}{16}$-$\frac{1}{8}$	$\frac{1}{2}$	Slight	1
$\frac{1}{8}$-$\frac{1}{4}$	1	Moderate	2
$\frac{1}{4}$-$\frac{1}{2}$	2	Severe	4
$\frac{1}{2}$-1	4		

Infection appeared to be more evenly distributed when the plants were grown in embedded pots, and the order of susceptibility was more or less the same when the varieties were arranged according to the damage score or the cover score. The reaction of the cultivars to the disease was as expected, those known to be very susceptible being most severely affected, and those reputed to be resistant showing the least infection. Results, comparable to those for known resistant cultivars such as Record, Frühperle and Ontario, were obtained for Pentland Ace, Pentland Crown and two seedlings which are included in the Merit Trials of the Department of Agriculture and Fisheries for Scotland. Among all the varieties tested the most resistant was a seedling bred from Pentland Ace, Dr McIntosh and a seedling of German origin. In the seedling progenies a wide range of susceptibility was observed, but, in general, the incidence of scab in a progeny bore a direct relationship to the degree of resistance possessed by its parents. This test showed considerable promise as a routine method of screening progenies for resistance to common scab.

Two diseases, mildew (*Erysiphe polyphaga*) and the bacterial disease (*Bacillus subtilis*) which were observed in 1959 were noted again in 1960. The mildew was apparent in a greenhouse in seedling stocks which had not been affected in 1959. The bacterial disease was evident in the field, but was restricted to the progenies affected in the greenhouse the previous year.

Breeding for resistance to potato root eelworm is progressing along four main lines bred respectively from (1) *S. tuberosum* subsp. *andigena*, (2) *S. multidissectum*, (3) *S. vernei*, (4) *S. sanctae-rosae*.

The " *andigena* " line dates from 1952 and now involves only routine testing and selection. The resistance, due to a major gene H, is no protection against invasion of the plants but subsequently very few larvae survive to female maturity in the Boghall populations maintained at Pentlandfield. The resistance is ineffective against the Duddingston strain. A seedling of genotype H bred at Pentlandfield is undergoing official merit trials.

The " *multidissectum* " line, which is about four years behind the " *andigena* " line in breeding, again depends for resistance on a major gene giving in this case the desired or standard level of resistance to the Duddingston strain but not to the Boghall strain. The " *andigena* " and " *multidissectum* " lines are thus complementary and separately ineffective against populations consisting of a mixture of the Boghall and Duddingston strains.

Breeding work with *S. vernei* makes slower progress because the resistance is polygenic and falls below the standard level in the first cross with commercial varieties of *S. tuberosum*. The main value of the resistance of *S. vernei* is that its equal effectiveness against all eelworm strains has been demonstrated repeatedly by workers in this country and abroad.

The " *sanctae-rosae* " line is the newest and appears to resist all strains, including Dutch and German strains, but the material has been less widely tested than that in the " *vernei* " line. No segregation of resistant seedlings was observed in the F_1 generation but appeared in the first backcross to *S. tuberosum*, suggesting fairly simple inheritance of much of the resistance.

Survivors of the collection of tuber-bearing *Solanum* species received from Dr Hawkes in 1958 were tested for their reactions to single strains of viruses X, Y and S. The great majority of clones were found to be susceptible to these viruses but there were a few which either escaped infection or were immune from infection with one or more viruses. In addition, there were a number of clones which reacted to the X or Y viruses in hypersensitive fashion. All this material may have value in resistance breeding and it will be studied further. For taxonomic purposes chromosome counts were made on four lines of *S. clarum* (all $2n = 24$), two lines of *S. michoacanum* (both $2n = 24$), two lines of *S. brachycarpum* (both $2n = 24$), five lines of *S. semi-demissum* (all $2n = 60$) and three lines of *S. vallis-mexici* (all $2n = 36$).

In the main line of breeding for resistance to viruses, over 6,000 seedlings were hand inoculated with X and/or Y viruses in the glasshouse. Susceptible seedlings were discarded and those apparently resistant were planted in the field for further selection on the basis of economic characters. About 500 seedlings were retained for extended trial.

The new cultivars Pentland Dell and Roslin Riviera were two of five unnamed seedlings to undergo evaluation for field resistance to leaf-roll and virus Y in 1959-60. The tests were carried out in field trials replicated at Pentlandfield and Cambridge. At both centres the spread of both viruses was greater than in 1958 but Pentland Dell with 4 per cent leaf-roll and 0 per cent virus Y was much more resistant than Majestic, 38 per cent leaf-roll and 6 per cent virus Y, at Pentlandfield and also at Cambridge where Pentland Dell contracted 84 per cent leaf-roll and 26 per cent virus Y as compared with 98 per cent leaf-roll and 65 per cent virus Y in Majestic. Roslin Riviera also showed moderate field resistance to the two viruses.

Genetical studies on reaction to infection and resistance to virus Y in wild species were continued. In the series *Demissa* attention was focused on the hexaploid species *S. spectabile* as a potential source of high level resistance to virus Y. Reactions to a single strain of virus Y varied within different lines of the species from an apparent immunity through various forms of necrosis indicative of hypersensitivity to susceptibility with varying degrees of tolerance. The general indication was one of similarity to the reactions already noticed in *S. stoloniferum* and *S. chacoense* where single genes have been found to differentiate resistance from susceptibility. Tests for allelomorphy of genes in *S. stoloniferum* failed and it would appear that within this species there are at least two independent genes concerned in determining reaction and resistance to Y viruses.

Seventeen potato cultivars were tested for their reaction to the beet ringspot strain of tomato black-ring virus, a virus found in sandy soils which infects potatoes grown on infective soil. Graft-inoculation caused severe systemic necrosis in some cultivars and only slight necrosis in others. In the following year no symptoms were visible in plants grown from the tuber progenies of graft-inoculated plants although the plants were shown to be infected by sap-inoculation to tobacco. In 1960, the tuber progenies from uninoculated and graft-inoculated plants were planted in a field trial to assess the yield loss caused by the virus in different cultivars. No virus symptoms were seen in any of the material. Yield reductions varied from 0-40 per cent, but the trial was small and the differences were barely significant. The produce of the 1960 trial will be used to plant a larger trial in 1961 when more reliable information should be obtained.

Sugar Beet.—The work is being carried out at the request of the Sugar Beet Research and Education Committee and though largely concerned with testing for bolting resistance material supplied by the Plant Breeding Institute, Cambridge, has this year also involved the testing of two experimental strains, Logie 5/F and KLT/Logie. The former resulted from the seeding together of the two best Plant Breeding Station selections while the latter was a mixture of these two families with three KLT non-bolting families bred by the Cambridge Institute. Klein E was used as the control and taking this cultivar as 100 the combination KLT/Logie gave 101 for yield of roots and 104 for sugar yield ; the corresponding values for Logie-5/F were 91 and 96. The relative merit of these two strains as determined last season at Pentlandfield closely resembles their average performance in the Scottish trial series conducted by the National Institute of Agricultural Botany.

Publications

Ciccarone, A., Black, W., and Bastos Cruz, B.P. (1959). " Preliminary observations on the races of *Phytophthora infestans* in the State of São Paulo, Brazil." (Trans. title.) *Arquivos do Instituto Biologico, Departmento de Defesa Sanitária da Agricultura*, Vol. **26**, 177-184.

A preliminary investigation was made of the races of *Phytophthora infestans* (Mont.) De By. present on potatoes and tomatoes, in the State of São Paulo, Brazil.

Races 4 and 1,4 were found to be prevalent on potatoes and races 3 and 3,4 on tomatoes. This indicates strong host preferences and suggests that epiphytotics in these crops may be partly independent of each other.

Races 0 ; 1,3,4 and 2,3,4 were also found but were very limited in distribution.

Blight populations in single localities often consisted of mixtures of races.

The composition of the populations was not influenced by the geographical position of the localities where collections were made, although some of these localities were distant and climatically very different from each other.

Brazilian blight isolates, tested in culture, were found to belong to a single compatibility group, viz. the group in which the European isolates tested against them were classified.

The origin of *P. infestans* in the State of São Paulo is briefly discussed. The racial composition of the blight populations appears to resemble that of North America and of Europe rather than that of Mexico or Peru.

SOME NOTES ON SHEEP FARMING IN THE CENTRAL HIGHLANDS

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These notes are on the economic and management aspects of the hill farm of Glenlochay, of which the writer has had experience during the last twenty years. It is stressed that any remarks apply only to Glenlochay, as hill sheep farming varied widely in different parts of Britain, due to terrain as well as local traditions. Conditions and accepted practices vary greatly between such general areas as the Welsh mountains, the Pennines in the North of England, the Cheviots in the Southern Scottish uplands, the Central Highlands, the West Highlands and the North-East, not to mention the crofting areas in North and West Scotland. Even within these areas local conditions can show marked differences. This point is stressed, as there is a tendency at large to regard all hill farming problems as the same over all Britain. This is very far from being the case.

The hill farm of Glenlochay, part of the enterprise run by Ben Challum, Ltd., may be taken as typical of a large part of hill farming in the Central and West Central Highlands. Since 1941 it has been under the same general direction and the very competent local management of Mr William Hunter. The ground lies some ten miles north-west of Killin and extends to about 16,000 acres. The Glen comprises the head-waters and catchment area of the River Lochay and is bounded to the west by the heights around Ben Challum itself, all of which rise to the four-thousand-foot mark. The floor of the Glen, which is narrow, is at about 800 ft., and the principal grazings rise steeply from the floor to a height of some two to three thousand feet. Above this the rolling tops are mostly suitable for deer and Alpine flora, but very valuable grazing is provided in late summer. The farm carries a regular breeding stock of black-faced ewes numbering some 4,000. A breeding herd of hardy cross Highland cows to the number of 120 is also carried throughout the year. The cow stock is maintained for the sake of fertility and to keep the herbage in a suitable state for sheep ;

it is doubtful if cattle would show a profit were it not for the hill cattle and calf subsidies.

Compared to other types of farming, there are several notable differences in the extreme hill type. Capital costs are low per unit of output, being restricted to houses, very simple buildings and fanks, and a certain amount of fencing. This last may be long in itself, but is nothing when compared to the fencing on an ordinary arable or stock-rearing farm. The costs of implements and other similar equipment are also negligible, when there is little or no in-bye or improvable land.

Labour costs too can be low compared to gross output when a favourable year is encountered. These costs, however, are extremely steady and in a bad year, as will be seen from the table, they can be heavy. The weather, too, plays, if possible, an even more important part than it does in any other type of farming, and there is even less that can be done about it. It is not only during the obvious spring months that the weather can help or harm, but at other times as in the early autumn, when the ewes are being got ready for the tup, during the tupping season toward the end of the year, and also during the summer spells of gathering.

The following table, based on figures per 100 breeding ewes, shows the differences that may be expected.

The results in column 1 are based on figures given by the Economics Branch of the Department of Agriculture for Scotland and published by them. In column 2 are figures for Glenlochay for the same year. It will be noted that the figures are sensibly the same. Those for Glenlochay are reassuring as the ground is tough, and some of the Department's sample farms must be kinder, as they show a small return of sales of crop and other stock than sheep or cattle. The year 1957 was the best financially that Glenlochay has had so far, and in column 3 are given figures for 1958-59, which are more nearly average. In column 4 are the figures for 1951, the last of the really bad years—for a long time, it is hoped!

Over the twenty years the average lambing has been 73 per cent, while in the two bad years of 1947 and 1951 it was as low as 40·8 per cent and 41·4 per cent respectively. These figures have been carefully kept and they represent the true percentage of lambs sold or taken into stock at the end of the year from ewes put to the tup. Against these low figures our present "high" was in 1959, 90·2 per cent—an excellent year, except

	Department of Agriculture 1956/57	Glenlochay 1956/57	Glenlochay 1958/59	Glenlochay 1950/51
Gross Output (per 100 Ewes)—	£	£	£	£
Cattle	66	86·9	108·1	68·0
Sheep and Wool	456	482·2	402·5	271·0
Other Livestock Income	9	..	..	..
Total Livestock Output	531	569·1	510·6	339·0
Other Income	28	2·4	2·8	..
Total Gross Output	559	571·5	513·4	339·0
Expenditure—				
Feeding Stuffs	64	49·5	54·2	56·0
Wintering	..	33·8	40·9	37·0
	64	83·3	95·1	93·0
Cultivations, Manures and Seeds	22	5·6	4·4	11·8
Labour	135	112·5	129·1	86·2
Power (Car and Tractor exp. Glenlochay)	35	22·0	27·2	16·3
Other Expenditure	61	54·1	60·7	83·0
Total Expenses	317	277·5	316·5	290·3
Profit	242	294·0	196·9	48·7
	559	571·5	513·4	339·0

for prices! Over these wide variations costs are similar and rising slowly. In fact, more and better labour is highly desirable when things are really bad. It is indeed lucky that the charges for capital are relatively very low.

The following table gives numbers of wether lambs sold, with average prices:—

Year	*No.*	*Average Price*	*Year*	*No.*	*Average Price*
1942	410	23/6¾	1951	719	60/7½
1943	640	30/10	1952	1175	67/1¾
1944	747	32/2¾	1953	1264	67/1¾
1945	726	34/10	1954	1193	61/11¼
1946	946	38/3¾	1955	1304	70/11¼
1947	461	54/8½	1956	1564	81/4¾
1948	1157	55/-½	1957	1645	93/4½
1949	1113	62/7	1958	1509	87/-
1950	1247	59/6½	1959	1844	78/5
			1960	1568	79/9

The above table is illuminating as it shows three things, first the steady build-up from 1942 till 1946, then the disaster in 1947. Recovery, however, was quick in the succeeding three years until the weather struck again in 1951. A further three years had to elapse before the build-up could proceed once again. It is also clear that the annual variation is in any case much greater than could be desired. If the sale of ewe lambs is also considered, the variations are even greater.

The great problem that faces the farmer in the extreme hill type of land is the difference between abundance in summer and dearth in late winter and early spring. He cannot fully use the summer abundance, which, if it is left unchecked, will lead to a deterioration of the whole hill. Burning off is no solution and usually makes things worse. This is where hill cattle have been proved so useful, as they not only tear away grazing during the summer, but even tackle it when it is half dead in the early winter. On the tougher type of hill it would be quite uneconomic to buy in store cattle in spring to do the same work and then sell them off in the autumn, although this practice may well be feasible on lower and grassier hills in more favourable situations. Resident hill cows also serve another useful purpose, as spreaders of bought-in fertility. During the past twenty years it is reckoned that some 4,000 tons of hay and good quality feeding straw have been bought in and the residues spread all over at least the lower faces of the Glen with no expense of further handling. It seems probable that this particular improvement by cattle has been of almost equal importance to that of their direct effect on growing vegetation.

Over the years cattle on the hill have undoubtedly improved the sward and certainly seem to have lengthened the grazing season for the sheep, both by encouraging an early bite in the spring and a later bite in the autumn.

Still the winter gap is by no means closed, and it is this gap, from late autumn well on into the spring, which is the limiting factor to the total carrying capacity and thus the productivity of the enterprise. Nobody seems fully aware what makes up the diet of sheep during the winter months. They probably live on a variety of small pickings and have to range widely for them. They may include small shoots of grass along paths and in sheltered places such as the edges of burns and small streams, shoots of heather and other plants. Later in the spring draw-moss is well known as a valuable food for ewes. Even so, it is an accepted fact that the hardy type of ewe can lose up to 10 per cent of her own body weight, including the lamb within her, and still produce a viable lamb at the end of winter. It is indeed only this capacity of the hardy hill sheep which enables the whole enterprise to go on. It is thus most important genetically to see that this characteristic is maintained or if possible improved. At the same time the liveweight loss at 10 per cent on 4,000 ewes is a harrowing thought. Some 20,000 lb. of mutton seems an expensive way of "bridging the gap"!

On some more favoured hills feeding ewes in the late winter has been practised with success, but when we have tried it on similar ground to Glenlochay it has not worked out very well in practice, apart from the additional expense. The essence of success seems to be to keep the ewes as well and sparsely spread out as possible during the critical months, and to let each ewe forage as best she may over her own ground. This makes feeding difficult, and a further disadvantage is that when the ewes are heavy in lamb, it is a mistake to expect them to traverse more rough, broken ground than is absolutely necessary.

Assuming a set winter stocking, and a figure of about 4,000 ewes for Glenlochay seems to be about the present limit, traditional methods certainly go some way toward coping with the disparity between summer plenty and winter dearth. During winter the ewe stock is limited to 4,000 along with 120 cattle, which are being fed hay on the lower slopes. During summer the ewe stock is increased by about 1,000 as the hoggs or gimmers are back on the hill from the wintering and the old ewes are not yet cast. In addition there are rather more than 3,000 lambs, and, say, 100 calves as well as the 120 breeding cows. Even so, the hill could probably carry yet more stock during the summer flush, but this can only be done economically by improving the winter carrying capacity.

To sum up, it seems both from our experience on the ground and from studying the figures that the limit of improvement with our present knowledge has very nearly been reached. The only way that a further advance might be made would be by mitigating, shortening, or even, if possible, entirely eliminating the winter gap. Any attempt to increase summer production would seem to be wasted and might indeed only aggravate the present position. For the winter, the animal geneticist might conceivably breed a sheep which could produce a viable lamb after losing even more than 10 per cent of its bodyweight. The animal nutritionist should certainly find out what hill ewes eat during the winter and early spring—how it is used and what is its nutritional value; the plant ecologist should have much rewarding work to the end of lengthening the times of available herbage supplies, both by extending them as far from the autumn into the winter as possible, and at the other end by the very earliest growth in the spring. The plant breeder too will surely be of help. The new techniques of surface treatment with coated seed may prove invaluable in changing plant populations in given environments, and cheaply at that. Following work on these lines practical men may be expected either to increase winter stocking, and thus the whole output from their hills, or at least to iron out the very violent fluctuations which now occur.

HILL GRAZINGS: IRRIGATION AS A POSSIBLE IMPROVEMENT TECHNIQUE

J. W. GREGOR

It has been estimated (Wibberley, 1959) that in Britain between 500,000 and 700,000 acres mainly on the better farm lands of the lowlands will be required before 1971 for "new urban developments and special uses." Moreover, at the same time as good land is being lost to agriculture the population of Britain is increasing by about 200,000 a year. In Scotland the acreage of crops and grass has declined since 1910 at an average rate of fully 10,000 acres a year (Symon, 1961). "What the annual loss of such land in Scotland is likely to be during the next twenty years is guess-work. But it may be the case that we will have lost an area of crops and grass not far short of the combined area of such crops in the three Lothians." At the present time crops and grass occupy only about one-third of Scotland's total 'agricultural' acreage, the remaining two-thirds being classified as the rough grazings of mountain and moorland. It therefore appears that if the agricultural output of Scotland is to be maintained despite this loss of good arable land the area now devoted to rough grazings will have a major part to play in restoring the balance.

Broadly speaking there are three ways of tackling this problem: by adding an area now in rough grazing to the arable acreage; by substituting an exotic pasture flora for the indigenous, or by extending the territory of the most valuable components of the indigenous flora. Obviously the first of these procedures means that the reclaimed area no longer forms part of the open hill grazing (and by open hill is meant that part of a hill grazing where a variety of different vegetations occur, all of which are subject to a common system of stock management). The same can be said of areas which have been re-seeded, for unless the activities of the grazing animals are suitably controlled, and for this fencing is essential, more or less rapid deterioration of exotic swards is virtually inevitable. But in Scotland these subtractions are never likely to be large relative to the area of open hill remaining. Although open grazings occupy land which, in the economic sense, is marginal, the very fact that they are relatively so extensive is alone sufficient justification for seriously considering their improvement, and it is with this particular aspect of hill land renovation that the present article is concerned.

Under the conditions obtaining and ignoring the deleterious effects of inappropriate stock management, one of the cogent arguments against introducing relatively high yielding cultivars—*e.g.*, of perennial ryegrass, cocksfoot and timothy—to the open hill is that these grazings already produce a greater bulk of *summer* herbage than can normally be utilised by stock whose numbers are perforce limited by the amount of winter keep available. Therefore, it would seem more realistic when contemplating the improvement of such areas to concentrate attention on raising the quality, rather than the quantity, of herbage, a point which receives added significance when it is remembered that the age of sheep using the open hill is falling as a result of the declining demand for mature wether mutton.

That the traditional system of managing hill sheep is not in itself inimical to the development and survival of native vegetations of well above average quality is evident from the reputations acquired by certain localised 'flushed' vegetations, and consequently the characteristics of such vegetations as well as possible ways of extending their territories merit consideration.

In this connection the investigations of Heddle and Ogg (1936) are particularly relevant, for by irrigating hill pastures with spring water they were able to study the influence of flushing upon the habitat and the effects of habitat changes upon the floristic composition of the vegetations involved. The method of irrigation which they adopted was "to cut a shallow ditch from the source of the spring, following, but with a slight fall, the contour of the slope. The water was allowed to flow freely down the slope from the end of the ditch. At convenient intervals of time the ditch was extended 1 or 2 yards so as to carry the water on to a fresh area of ground and in this way the flushed area was gradually extended along the slope". Soil samples were taken from five different areas where flushing experiments were being carried out, and in each case samples from the unflushed portions were taken from places immediately adjoining the flushed, and, at the same time, the soil profiles were examined to ensure as far as possible that there was no difference in soil type.

The results show a remarkable change in the soil acidity relationships brought about by flushing with water which came from an area of basic rocks. "In every case flushing has raised the pH and exchangeable calcium and lowered the amount of calcium required to bring the soil to a definite pH . . . the increase in pH due to flushing amounting to well over 1 unit in several cases, and the amount of exchangeable calcium being increased several-fold." These marked soil changes were accompanied by pronounced floristic changes: *Agrostis* spp., *Festuca rubra, Poa trivialis* and *Trifolium repens* were encouraged, while *Festuca ovina* and *Deschampsia flexuosa* were depressed.

Although Heddle and Ogg are convinced that flushing increased both the amount and palatability of the herbage no actual measurements of yield were made. However, some idea of the relative productive capacities of flushed and unflushed vegetations can be inferred from the data presented in respect of the total number of green shoots of all species considered collectively, recorded from each type of habitat. On averaging the counts given for six flushed and six unflushed floras the respective values are 6450 and 4560, or 141 : 100. With the exception of one area, the one from which, incidentally, the highest shoot count was obtained, all proved to have a very low phosphoric acid content, and this deficiency, as the authors point out, probably prevented improvement going even further than it did. Unfortunately, the fertilising effects of flush water cannot be separated from the effects of water as such. However, it is only reasonable to assume that irrigation during a spell of drought by compensating for the lack of rain would have a beneficial effect upon yield. Indeed irrigation at these times may actually cause herbage yields to surpass the level that they would normally have attained had there been no shortage of rain (Julén, 1951). Julén explains this phenomenon on the grounds that insolation during a period of drought is frequently more intense and that by supplying water then the plant is enabled to take advantage of the extra light. Presumably by adding plant nutrients to the water at these times this effect would be further accentuated.

Another interesting feature of the results of Heddle and Ogg is the closer resemblance between the herbage of grazed and ungrazed sections of the flushed ground than between that of the flushed and unflushed areas, which adds support to the statement made previously that traditional grazing practice is not an inevitable obstacle to the development of an improved vegetation.

A further ecological study and, in addition, a genecological analysis of indigenous plant communities occupying sites on the Pentland Hills near the scene of Heddle and Ogg's experiments has been made by Harberd (1961, *a* and *b*). This investigation involved the examination of the floras of 80 two-yard-square sites representing a range of conditions extending from leached to naturally flushed habitats. The data presented in the Table have reference only to the grass and clover records and summarise the frequencies in relation to differences in soil pH and moisture content. These frequencies are based on the presence or absence of species in $2\frac{3}{4}$ in. diameter cores, five of which were taken from each of the 80 sites, and although this method of assessing frequency differs radically from that employed by Heddle and Ogg the results of the two investigations have much in common.

Trifolium repens, *Festuca rubra* and *Poa trivialis* become more frequent towards the upper portion of the pH gradient, and *Festuca ovina* and *Deschampsia flexuosa* less common, results which are in agreement with the earlier findings. On the other hand, the *Agrostis tenuis* records present a novel picture for instead of exhibiting a similar pattern to that of *Festuca rubra* this species is now shown to occur with more or less equal frequency throughout the whole length of the pH gradient. But it is perhaps significant that in relation to the soil moisture gradient *A. tenuis* is recorded more often than *F. rubra* from the drier sites, a situation which is reversed at the moist end of the scale. It is, therefore, possible that the foregoing anomaly could be explained by changes in the relative competitive values of the two species at different moisture levels, for while the pH and moisture scales did parallel each other to a considerable extent the correspondence was not sufficiently close to exclude this possibility.

The ubiquitous distribution of *Agrostis tenuis* might, of course, reflect the occurrence of intra-specific ecotypic differentiation, but a genecological analysis of the data, which admittedly had reference almost exclusively to morphological attributes relating to plant size and shape, failed to reveal evidence of such differentiation. This, however, should not be taken to mean that *A. tenuis* is ecotypically unresponsive to

TABLE

Species frequencies in relation to soil pH and moisture content (Table compiled from Harberd's data)

pH	Percentage presence in sample cores								
	Trifolium repens	*Argostis tenuis*	*Agrostis canina*	*Agrostis stolonifera*	*Festuca rubra*	*Festuca ovina*	*Poa pratensis*	*Poa trivialis*	*Deschampsia flexuosa*
4·5	0	80	20	0	0	100	0	0	40
4·6	0	80	20	0	40	100	20	0	0
4·7	10	80	0	0	50	80	40	10	0
4·8	0	100	0	0	60	100	20	0	0
4·9	0	100	0	0	40	100	0	0	0
5·0	20	90	10	0	35	95	30	0	10
5·1	12	100	12	0	56	100	0	0	4
5·2	40	85	15	0	60	100	15	0	0
5·3									
5·4	40	100	0	0	90	70	10	10	0
5·5	60	96	0	0	100	56	20	16	0
5·6	77	97	3	0	90	50	30	7	0
5·7	75	93	0	0	98	55	43	25	0
5·8	60	90	0	0	90	60	35	20	0
5·9	100	90	0	0	100	50	50	20	0
6·0	87	87	0	7	93	40	20	17	0
6·1	51	89	0	0	100	71	6	0	0
6·2	76	96	0	0	96	48	4	28	0
6·3	88	70	0	13	100	48	38	48	0
6·4	90	70	0	30	100	5	30	65	0
6·5	85	80	0	15	100	20	35	60	0
Moisture scale									
1·2 (dry)	40	100	0	0	60	70	0	10	0
1·3	32	100	4	0	36	100	20	0	0
1·4	39	99	7	0	70	93	23	3	4
1·5	46	100	5	0	78	71	22	12	3
1·6	89	97	0	0	97	54	29	17	0
1·7	60	96	2	0	98	53	33	7	0
1·8	78	98	2	7	97	42	15	20	0
1·9	90	85	0	10	100	25	45	55	0
2·0 (wet)	100	70	0	10	100	40	75	35	0

flush conditions since it has been shown by Bradshaw (1959) that the average diameter and weight of plants in a population derived from a flush habitat in the Plynlymon Hills in Wales was greater than in a population from a Plynlymon ' nardetum ' habitat.

In contrast to *Agrostis tenuis*, Harberd did find evidence of genecological differentiation in *Poa pratensis* despite its more restricted ecological distribution : populations at the leached end of the gradient being earlier, longer leaved and vegetatively taller than those of flushed sites. It is, nevertheless, possible that these particular differences are not the direct result of the selective action of the soil factors, but are primarily selective responses to different grazing intensities associated with the edaphic changes. Be that as it may, the fact remains that flushing of certain soils with suitable water does bring about edaphic, floristic and perhaps also infra-specific changes that together raise the economic status of indigenous hill vegetations.

In the past the practice of extending flushed areas by cutting irrigation channels was by no means uncommon, and the decline of this practice is one of the factors " that accentuates the general downgrading of hill pastures " (Roberts, 1959). However, the former state of affairs is not necessarily irretrievable, for with the help of modern irrigation equipment it might well be an economic proposition to revive the practice and on a much more ambitious scale than hitherto.

It will be remembered that the outstanding result of the experiments conducted by Heddle and Ogg was that under flush irrigation the frequencies of *Agrostis* and *Festuca rubra* showed marked increases. But the unspectacular behaviour of *Poa pratensis,* which, though present in small amount, is also of interest just because this species proved so remarkably unresponsive to flushing. Yet *Poa pratensis* is by no means indifferent to manurial treatment, for in an experiment (Gregor and Watson, 1953) where nitrogen was liberally applied over a period of eight years to an *Agrostis*-fescue-*Nardus* community containing *Poa pratensis* the latter's annual contribution to the total dry weight of the herbage harvested rose from 1 per cent in the first year to 58 per cent in the eighth.

Since *Poa pratensis* is unquestionably one of the most desirable of indigenous hill species, its failure to respond to flushing while responding so readily to nitrogen only adds point to the suggestion made by Heddle and Ogg relative to the low phosphoric acid content of flushed areas, that changes for the better resulting from flushing do not exhaust the possibility of further improvement being made. It would seem, therefore, that in order to realise a vegetation's full improvement potential the nutrient content of irrigation water, even from the best natural sources, would require to be reinforced by appropriate additions. But even so, the success of irrigation as a means of improving the quality of hill pasture will obviously depend on the pre-existence of at least a minimum representation of the required species in the areas to which the water is taken.

By employing techniques which would make possible surface irrigation over greater distances than is normally practicable with ditch irrigation the chances are that the irrigation line will traverse areas lacking the requisite species. In these circumstances, in order to provide the essential basis for improvement, species such as *Agrostis tenuis*, *Festuca rubra*, *Poa pratensis* and *Trifolium repens* would have to be introduced, and it is in this connection that the practice of surface seeding described by Grant (1958) is of particular significance. Both he, and Copeman and Roberts (1960), stress that the success of surface seeding is largely dependent on adequate moisture following sowing as drought during that period can be fatal. Breaking of the soil surface to give a light cover to the seed will often help seedling establishment, but no cultivations on suitable sites are needed provided suitable weather conditions prevail.

Judging from the marked difference in performance of *Poa pratensis* under flushing and where nitrogen was made available, applied nitrogen may well have a far more vital part to play in hill land improvement than is generally imagined. Certainly Grant is of the opinion that in the case of surface seeding nitrogenous manuring is essential in order to facilitate establishment. However, in certain situations the problem of getting nitrogen, or for that matter other plant nutrients, or perhaps even rhizobia, to the chosen sites along with irrigation water might well present less practical difficulty than the employment of current methods of distribution.

It would obviously be premature to forecast the prospects of any developments along the lines indicated above becoming a practical proposition without more knowledge of the problems involved and of how best to solve them. But even so the ultimate pattern of improvement which might develop under a system of irrigation involving pipes can be envisaged as comprising a number of narrow permanently treated zones of relatively high quality vegetation scattered, wherever suitable sites and supplies of water happen to be available, throughout an extensive mosaic of differing types of plant community.

Since improvement in a floristic sense reflects the environmental pressures occasioned by the treatments employed it follows that to maintain an improvement these pressures must have a reasonable permanency. It is probably no exaggeration to say that the ephemeral nature of much hill land improvement is due to inadequate maintenance on account of cost. Any technique, therefore, which seems to offer some prospect of keeping maintenance expenditure within economic limits is worthy of serious consideration.

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INHERITANCE OF RESISTANCE TO POTATO ROOT EELWORM IN A BREEDING LINE STEMMING FROM *SOLANUM MULTIDISSECTUM* HAWKES

J. M. Dunnett

The usefulness of wild potatoes as parental sources of resistance to potato root eelworm varies with the level of resistance present, the scope of such resistance in relation to strains and its mode of inheritance. The first two aspects of the resistance of *S. multidissectum*, a diploid species indigenous to Peru and Bolivia, were dealt with in a previous paper discussing strains of potato root eelworm and a scheme for distinguishing between strains (Dunnett, 1960). It was found that certain clones of the progeny P.H. 1366, collected as seed in South America by Petersen and Hjerting and obtained at Pentlandfield through Dr J. G. Hawkes of Birmingham University, had the " standard " level of resistance to the Duddingston strain in that no cysts were seen on the root-balls of approximately 90 per cent of the plants grown in a sandy culture medium of 40 eggs/gm. infectivity. The resistance to the Boghall strain was considered " below standard " or too weak to be useful in practical breeding. This was the reverse of the relationship obtaining between resistant plants descended from *S. tuberosum* subsp. *andigena* C.P.C. 1673 and the same two Pentlandfield strains. The clone C.P.C. 1673 incorporated a dominant resistance gene H and was the starting point in breeding for resistance to potato root eelworm (Toxopeus and Huysman, 1953).

Crossing S. multidissectum and S. tuberosum.—One of the diploid clones of *S. multidissectum*, self-incompatible and grown under glass as a female parent, crossed surprisingly easily with a tetraploid breeding clone of *S. tuberosum*, yielding up to 39 seeds per berry and seedlings which were all highly self-fertile in the field. On cytological examination, eleven of these seedlings were tetraploid and the rest were presumed to be so. Evidently, they resulted from the union of unreduced female gametes of *S. multidissectum* with ordinary diploid gametes of *S. tuberosum*, a fact to be considered below in tracing the inheritance of resistance through three generations (F_1; B_1 and B_2 to *S. tuberosum*) of this breeding line.

The B_1 crosses were made in the midst of a crop of the pollen-sterile variety Craigs Defiance, which was the female parent, and the resistant parents of the B_2 crosses were selected mainly on tuber conformation from among 183 first-year seedlings which had been emasculated and pollinated in the field earlier in the season. Bagging of the pollinated flowers was omitted in the interests of good seed set, since it was known from experience that there was only a small risk of effective cross pollination by insects.

Inheritance of resistance.—The tests of resistance were done in a heated sand plunge under glass by growing transplanted seedlings in 3-inch pots containing a sandy culture medium of 40 eggs/gm. infectivity. The B_1 and B_2 progenies comprised from 46 to 54 seedlings excepting progeny 4081 with only 36 seedlings. The number of seedlings which grew too poorly for scoring seldom exceeded four in a progeny.

Scoring was based primarily on presence or absence of cysts on root-balls, although 9·4 and 8·9 per cent of the resistant segregates in B_1 and B_2 generations, respectively, were seen to support up to 5 cysts (" occasional cysts "). On this basis, the resistant class as a whole could be said to possess the standard level of resistance, although strictly speaking the definition of standard resistance (Dunnett, 1960) stipulated 4-inch pots. The susceptible class comprised 50·0 per cent (B_1) and 53·3 per cent (B_2) seedlings that were considered to be less than fully susceptible but distinct from seedlings with " occasional cysts ".

Table 1 records segregations in the 31 progenies tested during the first three years of breeding. The probability of deviation from expectation is given in cases of doubtful agreement and for aggregate segregations. Yates's correction for continuity was included in the calculations when there were 10 seedlings or fewer in a class.

None of the 19 segregations in the B_2 generation differed significantly from resistant/susceptible ratios of either 5 : 1 or 1 : 1. These ratios could be expected in *duplex* × *nulliplex* and *simplex* × *nulliplex* crosses assuming resistance due to a dominant gene, but not necessarily due to the same dominant gene in every progeny.

Considering first the hypothesis of resistance conferred by the same dominant gene in every progeny, the parental clone of *S. multidissectum* (S. 14/5) was evidently heterozygous since

TABLE 1

SEGREGATIONS OF SEEDLINGS RESISTANT AND SUSCEPTIBLE TO THE DUDDINGSTON STRAIN IN A BREEDING LINE STEMMING FROM *S. MULTIDISSECTUM*

Generation	*Progeny reference*	*Resistant parent*	*Segregations resistant : susceptible*	*Hypothetical ratio* *	*Chi-square for difference from expectation*	*P*
F_1	3246	*S. multidissectum* 14/5	11 : 1	1 : 1		
	3479		38 : 10	1 : 1		
B_1	3486	3246/2	8 : 35	All susceptible		
	3487	3246/3	38 : 9	5 : 1		
	3488	3246/4	35 : 7	5 : 1		
	3490	3246/5	45 : 3	5 : 1	3·04	0·05–0·1
	3491	3246/6	37 : 7	5 : 1		
	3492	3246/7	31 : 14	5 : 1	5·76	0·01–0·02†
	3495	3246/9	35 : 5	5 : 1		
	3497	3246/11	32 : 13	5 : 1	4·00	0·02–0·05†
	3498	3246/12	40 : 6	5 : 1		
	3499	3246/13	40 : 8	5 : 1		
	Sum of presumed 5 : 1 segregations		333 : 72	5 : 1	0·36	0·50–0·70
B_2	4067	3487/19	23 : 28	1 : 1		
	4069	3487/40	29 : 25	1 : 1		
	4070	3488/10	33 : 20	1 : 1		
	4071	3488/18	33 : 19	1 : 1	3·25	0·05–0·10
	4073	3488/35	34 : 10	5 : 1	0·79	0·30–0·50
	4078	3490/40	27 : 27	1 : 1		
	4079	3490/41	43 : 7	5 : 1		
	4081	3490/46	20 : 15	1 : 1		
	4082	3491/5	25 : 29	1 : 1		
	4083	3491/43	35 : 4	5 : 1		
	4084	3492/44	25 : 29	1 : 1		
	4085	3495/12	45 : 9	5 : 1		
	4086	3495/18	24 : 28	1 : 1		
	4089	3497/5	45 : 9	5 : 1		
	4090	3497/24	26 : 24	1 : 1		
	4091	3498/1	24 : 28	1 : 1		
	4095	3498/19	16 : 17	1 : 1		
	4098	3499/24	27 : 26	1 : 1		
	4101	3499/47	50 : 4	5 : 1		
	Sum of presumed 5 : 1 segregations		252 : 43	5 : 1	0·23	0·50–0·70
	Sum of presumed 1 : 1 segregations		332 : 315	1 : 1	0·44	0·50–0·70

* = monofactorial inheritance
† = significant deviation

susceptible segregates occurred in the hybrid progenies 3246 and 3479. These progenies had the same parentage, but 3246 was raised a year earlier and eleven of the twelve hybrids comprising it were backcrossed. Nine of them gave segregating progenies and the only susceptible hybrid (3246/8) gave a fully susceptible progeny. The remaining backcrossed hybrid (3246/2) remained cyst-free in a repeat test of resistance, but gave a B_1 progeny (3486) showing a more or less continuous range of resistance and including very few seedlings with less than five cysts. It was concluded that 3246/2 was not a true resistant segregate, but had a high level of some supplementary form of resistance in the absence of the major resistance gene. Such supplementary resistance was confirmed on investigation and is discussed under a separate heading. Thus the poor agreement between the aggregate F_1 segregation (49 : 11) and the expected 1 : 1 ratio could be partly explained by the masking effect of supplementary resistance.

In the segregating B_1 progenies only 5 : 1 segregations could be expected since their different resistant parents had each received a doubled genome from the heterozygous diploid S. 14/5. The aggregate segregation agreed closely with this expectation, although the susceptible class was significantly in excess in two of the progenies. One of these (3497) included a resistant seedling (3497/5) which gave an exact 5 : 1 segregation (4089) in the B_2 generation and was evidently duplex, thus helping to establish that the parent of 3497 was duplex too. In view of this, a small amount of foreign pollination would account for the excess of the susceptible class in 3497 and 3492.

Looking more closely at the B_2 generation, the number of approximate 5 : 1 segregations (6) and approximate 1 : 1 segregations (13) was reasonably close to 4 : 15, this being the nearest possible approach to the ratio of 1 duplex : 4 simplex resistant parents expected, if, as already inferred, these parents were all selected from *duplex* $\times$ *nulliplex* B_1 crosses.

At this point, it is necessary to compare agreement with the above hypothesis and a second hypothesis that S. 14/5 was heterozygous for two different dominant genes independently conferring the standard level of resistance to the Duddingston strain. This immediately solves the former difficulty in the F_1 generation because now a 3 : 1 ratio would be expected, making it unnecessary to stress the masking effect of supplementary resistance and agreeing exactly with the finding that at least nine of the twelve hybrids in the progeny 3246 had a major gene for resistance. Three of these would be expected duplex for one gene, three duplex for the other gene and three duplex for both genes, giving the expectation of six 5 : 1 segregations and three 35 : 1 segregations in the B_1 generation. There are now two possibilities to consider: (*a*) the expected 35 : 1 segregations did not materialise because the number of progenies investigated (9) was too small to ensure this; (*b*) one or more 35 : 1 segregations were mistakenly interpreted as 5 : 1 in outlining the first hypothesis. In the first case the two genes would be no longer in combination in the breeding line; therefore, neglecting any difference in the locus of the resistance gene in different progenies, only one gene would appear to be present in B_2 and further backcrosses. In the second case, 35 : 1, 11 : 1 and 3 : 1 ratios could occur in the B_2 generation. Although none of the B_2 segregation differed significantly from either 5 : 1 or 1 : 1, at least two agreed better with 11 : 1 (4101) or 3 : 1 (4073).

Therefore, although the data as a whole justified the assumption of major gene resistance, owing to factors (*a*) and (*b*) it is impossible to decide whether one or two resistance genes were present in the breeding line originally. It is worth noting that two genes appear to control resistance to potato root eelworm in both *S. kurtzianum* and *S. famatinae*, two diploid species of potato investigated respectively by Huysman (1959) and by Dr H. Ross of the Max Planck Institute, Cologne (personal communication).

Meanwhile, it is proposed to bypass this problem in *S. multidissectum* because (i) if two genes are present in the breeding material they are indistinguishable in effect and inheritance in backcrosses and can be treated as one and the same in the current phase of the practical breeding; (ii) in the work of classifying strains in relation to host genotypes, it can be ensured that all workers use the same gene, as present in all the resistant descendants of a particular simplex parent. Such a system of classification is under consideration at present and it is not proposed to label the S. *multidissectum* gene that will be used in it, pending agreement on nomenclature between workers in Britain, Germany and the Netherlands.

Supplementary resistance.—The progenies 3486, 3490 and 3492 were re-grown from tubers and one plant of each clone was tested against each of the Boghall and Duddingston strains

TABLE 2

CYST INDICES IN PROGENIES DESCENDED FROM *S. MULTIDISSECTUM*

Progeny	Boghall strain			Duddingston strain		
	No. of seedlings	Range of cyst index	Mean	No. of seedlings	Range of cyst index	Mean
3486	26 r	35-259	125	32 r	0-89	25
3490	1 r		212	1 r		13
	37 R	5-150	62	44 R	all cyst-free or " occasional cysts "	0
3492	10 r	57-189	121	11 r	6-68	28
	16 R	4-134	45	21 R	all cyst-free or " occasional cysts "	0
71/17, control cone	6 r	145-252	190	10 r	91-195	134

R = segregates resistant to Duddingston strain, r = susceptible segregates in two series of 4-inch pots containing culture medium of 40 eggs/gm. infectivity. Table 2 records the mean cyst indices (number of cysts per 100 windows showing roots) obtained by the perforated can method (Dunnett, 1957). In the discussion following, the term "segregate" is always used with reference to the Duddingston strain.

Only one resistant and one susceptible segregate were found to have been wrongly classified a year earlier when the progenies were first scored for resistance to the Duddingston strain. The segregations already given for 3490 and 3492 in Table 1 were the amended segregations. These progenies were selected for re-test because they contained the highest and lowest proportions of resistant segregates in the B_1 generation.

The progeny 3486, lacking a major resistance gene, had a mean cyst index with the Duddingston strain which was less than a quarter of that for the susceptible control clone 71/17 infected by the same strain, and the two ranges of cyst index did not overlap. All the susceptible segregates in 3490 and 3492 had cyst indices with the Duddingston strain within the range recorded for 3486. This established the presence of supplementary resistance to the Duddingston strain in all three progenies. Since the level of this supplementary resistance appeared to vary within progenies and all but one of the clones of 3486 were clearly less resistant than their cyst-free parent (3246/2) a polygenic basis is suggested at present for the supplementary resistance to the Duddingston strain. This polygenic resistance was almost completely ineffective against the Boghall strain, because now the plants lacking a major resistance gene and the control 71/17 had very similar cyst indices.

The resistant segregates varied very widely in cyst index with the Boghall strain. Some were clearly as susceptible as 71/17, indicating that the simplex major gene(s) alone conferred practically no resistance to the Boghall strain. Other segregates appeared to have a degree of resistance comparable to the average level of supplementary resistance to the Duddingston strain, possibly due to dosage or complementary effects involving the major gene(s).

Summary

It was known that S. *multidissectum* possessed an adequate level of resistance to the Duddingston strain, but not to the Boghall strain, both maintained at Pentlandfield, and that the reverse was true of S. *tuberosum* subsp. *andigena* C.P.C. 1673. Like C.P.C. 1673, S. *multidissectum* appears to possess major gene resistance but whether one or two dominant and independently acting resistance genes were present originally in the breeding line remains an open question. However, it is possible to ensure that all workers use the same S. *multidissectum* gene in classifying strains in relation to host genotypes. S. *multidissectum* also possesses supplementary and probably polygenic resistance to the Duddingston strain. This, like that conferred by the major resistance factor(s), is ineffective against the Boghall strain. Dosage or complementary effects involving the major resistance factor(s) seem occasionally to give a moderate degree of resistance to the Boghall strain.

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NOTE ON CHOKE DISEASE IN *FESTUCA RUBRA*

D. J. Harberd

Choke disease of grasses is caused by the systemic fungus *Epichloe typhina*. The mycelium perennates within the vegetative organs of the plants and only appears on the surface during the summer months when it partially or completely suppresses flowering. The fungus has been reported from many different grass species (Sampson and Western, 1954), some being much more seriously affected than others. *Festuca rubra* is one of the least affected species, infected plants producing in some cases a full seed crop. Nearly thirty years ago Sampson (1933) established that a very high proportion of the seed produced by infected plants of this species gave rise to infected plants. By contrast seed production is seriously reduced in *Dactylis glomerata* but the seed from an infected crop does not carry the disease. Indeed until recently (Western and Cavett, 1959) the mechanism of disease transmission in species other than *Festuca rubra* was unknown. These authors have examined the problem exhaustively in *Dactylis glomerata* and despite many ingenious treatments they have failed to achieve seed transmission: even seeds infested with the mycelium of the pathogen give rise to healthy plants. Nor were they successful in transmitting the disease to undamaged healthy plants. But under favourable conditions, notably a lengthy period of high humidity, the pathogen did invade new host plants through the cut ends of flowering shoots, and by this means alone established new infection. The authors point out that many of the peculiarities of the disease in *Dactylis* seed crops can be understood in the light of their results. Thus first harvest year crops are normally healthy because the pathogen has not had the opportunity to invade; but precocious flowering in the seed year can, if cut, lead to disease in the first true harvest year. Failure of the disease to spread among spaced plants, as distinct from row material, is interpreted as a direct result of the lower humidity associated with the former method of culture.

Turning now to the spread of the disease under natural conditions it is feasible that damage of the flowering stem by stock grazing can give potential sources of infection, and

Western and Cavett cite an example in *Dactylis* where grazing of seed year flowering preceded a diseased crop in the first harvest year. It seems likely then that this method of disease spread could apply to other species of grass. But we have already seen that a highly effective means of transfer in *Festuca rubra* (via the seed) is not effective in *Dactylis glomerata* so we should be cautious of assuming too much until proper tests have been completed. In the meantime some casual observations of the disease in *Festuca rubra* may be of interest to pathologists and others.

During the course of genecological work with *Festuca rubra* many hundreds of wild plants have been dug up and grown in the experimental garden for a few seasons. Some of these have been infected with *Epichloe* and for the most part our observations merely confirm those of earlier workers. *Festuca rubra* is not seriously affected: many diseased plants flower freely, the only evidence of infection being the production of a few stromata that are easily missed by the casual observer. Some of the particularly lush plants are found to be infected so that it seems possible that sometimes infected plants may be more vigorous than healthy ones. Within the limits of recording error, plants scored healthy or diseased one season are similarly classified in another: the disease does not seem to spread among spaced plants. Again within the limits of error the ramets of a cloned plant are either all healthy or all diseased according to the status of the mother plant.

It was observed that among the cultured plants often times two or more could be matched together and found to have such extreme resemblance in morphological and physiological characteristics that it seemed very likely that they were members of the same natural clone, derived by vegetative reproduction from a single seedling. A considerable body of observational and experimental evidence was collected to support this contention (Harberd, 1961) and in summary it can be said that though the matter cannot be proved no other plausible interpretation of the data is known. Accepting it for the time being it appears that natural clones of *Festuca rubra* are in existence with ages to be measured in centuries and with spatial spreads of furlongs. It should be stressed that there is no evidence of organic connection now between isolated portions of one clone.

In the second of the two observational plots of *Festuca rubra* concerned, presence or absence of *Epichloe* in the plants was recorded. Several of the plants (both healthy and diseased) were not grouped into clones and the data in the Table refer only to the supposed clones present. All of the infected plants are found to belong to either of two clones, and all except two of the plants in these clones were recorded as infected. The two exceptional plants recorded healthy belonged to the W genotype and this is one where infection is very easily missed. All plants of W that have been grown on the station since have been found to be infected and the failure to record infection in these two cases is regarded as an error. It is concluded that the natural clones of *Festuca rubra* so far recorded are either completely healthy or fully infected.

TABLE

NATURAL CLONES OF *FESTUCA RUBRA*, TOGETHER WITH THE INCIDENCE OF *EPICHLOE TYPHINA*

Clone	*Number of ramets isolated*	*Number infected with* Epichloe
W	60	58
50	10	0
32	7	0
H	7	0
18	5	0
65h	5	0
64	5	0
C	4	0
8	4	4
G19	3	0
10	2	0
21h	2	0
G15	2	0
25	2	0

It is clear from what we already know of the disease that the whole clone derived from an infected seedling will be infected, and since the disease can be seed-borne in this species it is likely that the two diseased clones were infected at this stage. But there is strong circumstantial evidence that the disease was not transmitted in any other way. Had any infection taken place through cut stems we should expect that some clones would be represented by both healthy and infected isolates. There are several provisos to this statement, but none of them are regarded as being of any likely importance. Thus if infection took place through the first flower stem produced, and if at that time the plant was still one organic whole, then it might become infected throughout, but there have been hundreds of seasons since, infection during which would have given rise to the partial condition. Variability of an extreme kind in genotype susceptibility within *Festuca rubra* might give complete presence or absence of the disease; for instance, some genotypes successfully avoiding infection and others readily succumbing, and while some variability of this sort would not be surprising the extreme version postulated is unlikely. Similarly variation in host response might produce the situation, but it is unlikely to do so. For instance, newly infected plants might be so weakened that they would not survive competition in the field thus maintaining that clone in a healthy state, but this would be unlikely in view of the prevalence of the disease under field conditions. Alternatively, as has been suggested by Bradshaw (1959) for the association of the disease with *Agrostis tenuis*, infected plants might under some circumstances have an advantage over healthy ones. It is perhaps not without interest that the W genotype is apparently the most successful genotype of *Festuca rubra* yet encountered, about one-third of the tillers in an area of nine acres being of that type, and it is an infected one. Accordingly, the infected form of a clone might be able to exterminate its healthy counterpart by competition. But this is unlikely, and since in any case the process would be a slow one taking many years to complete we should expect to have an example of it at an intermediate stage.

One final observation should be recorded: *Festuca rubra* is not very freely flowering in the habitat from which the material was derived. Thus while the supply of cut flowering stems would be very low compared to, for instance, a seed crop, some stems are produced every season. On the other hand, no stroma of the disease has been observed in the natural habitat and maybe there is a shortage of natural infection near at hand: but against this we must remember that stromata are very easily missed in this species.

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INTER-CULTIVAR POLYCROSSES IN PERENNIAL RYEGRASS AND COCKSFOOT

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Introduction.—In 1954 an investigation was started into the possibility of increasing grass yields by the use of hybrid seed produced by open pollination between plants of existing cultivars, it being hoped that cultivars of different origin would be genetically sufficiently different to yield useful heterotic effects on crossing. It should be emphasised that the object was not to conduct a full breeding programme involving selection for combining ability but to see if it was possible to raise yields simply and rapidly by using polycross progeny from existing material, a procedure which would have the merit of enabling " F_1 " seed to be produced on a large scale.

Materials and methods.—It was decided to use two species, perennial ryegrass and cocksfoot, and two polycrosses were laid down in 1955. The ryegrass polycross consisted entirely of early flowering varieties and contained 96 plants of each of seven cultivars. These were raised from seed sown in pans, pricked into boxes and later planted in the field on 21st July 1955, the whole polycross area being divided into 96 plots each containing one plant of each cultivar, the position of each plant within a plot being at random. The cocksfoots were similarly treated except that 10 cultivars were used. The cultivars concerned are shown in Table 1. The seed from both polycrosses was harvested in 1956, the seed from each mother cultivar being kept separate, this seed being used to sow yield trials in 1957.

For each species two separate trials were laid down, one as single-spaced plants at 3 feet spacing, and one as a sward. Each trial contained, besides the polycross progeny, the original mother strains, so that in the case of the ryegrass there were fourteen treatments and in the case of the cocksfoot, twenty. The spaced plant trials each consisted of a random block with four replications each containing fourteen (perennial ryegrass) or twenty (cocksfoot) plots each of twenty plants. The sward trials were laid out in a split plot design where the main treatments were strain origins—*i.e.*, mother plus progeny and the subsidiary treatments were types of strain—*i.e.*, mother or progeny. Seed was sown broadcast at the rate of 30 lbs. per acre. The entire trial area received a dressing of 3 cwts. per acre of fertiliser of composition N 12 per cent, P_2O_5 8 per cent, K_2O 8 per cent. No further fertilizers were applied during the course of the experiment.

TABLE 1

RYEGRASS AND COCKSFOOT ; KEY TO CULTIVARS USED AS MOTHER VARIETIES

Ref. No.	Ryegrass	Cocksfoot
1	Northern Ireland	Late Roskilde
2	Ayrshire	Svalof Frode
3	Oregon Blue Tag	English Akaroa
4	Øtofte Early	Adefa
5	Devon Eaver	Brage
6	Pajberg Early	S 143
7	N.Z. Mother	S 26
8		Tardus II.
9		N.Z. Cert. Mother
10		N.Z. Grassland

The spaced plant trials were each scored for ear emergence and were harvested in the middle of June (perennial ryegrass) and the beginning of July (cocksfoot). See Table 2. The material from each spaced plant plot was bulked and weighed when cut and again after being air-dried for three weeks, final drying being carried out by warm air over a sack dryer: the spaced plant dry weight is referred to as the " hay " weight.

In the sward trial each sub-plot was 6 feet by 9 feet. At each harvest an area of 7 feet by 2 feet was harvested by Allen autoscythe followed by a cylinder type mower. All the clippings from a sub-plot were bagged in a polythene bag, and later tipped into wire mesh trays for oven drying. Cuts were taken as shown in Table 2.

Even in material of relatively uniform maturity type there is reason to expect a considerable range of variation in flowering time, and this will affect the extent to which two cultivars are

TABLE 2

RYEGRASS AND COCKSFOOT: SOWING OR PLANTING AND HARVEST DATES

	Spaced Plants			Swards			
	Planted	Harvested	Sown	Cuts			
				1	2	3	4
Ryegrass . .	4/VII/57	23/VI/58	6/VIII/57	4/V/58	2/VI/58	16/VII/58	18/VIII/58
Cocksfoot . .		9/VII/58	6/VIII/57	7/VII/58	8/VIII/58		

TABLE 3

RYEGRASS: PROPORTION OF PROGENY SEED OF VARIOUS ORIGINS ASSUMING EAR EMERGENCE AND FLOWERING DATES COMPLETELY CORRELATED (BASED ON DISTRIBUTION CLASSES IN FIG. 1)

♀ \ ♂	1	2	3	4	5	6	7
1	·026 18·2	·018 12·6	·020 14·0	·018 12·6	·021 14·7	·021 14·7	·018 12·6
2	·018 12·6	·022 15·4	·020 14·0	·022 15·4	·021 14·7	·019 13·3	·020 14·0
3	·019 13·3	·020 14·0	·020 14·0	·020 14·0	·018 12·6	·020 14·0	·022 15·4
4	·018 12·6	·022 15·4	·020 14·0	·024 16·8	·022 15·4	·019 13·3	·020 14·0
5	·021 14·7	·021 14·7	·018 12·6	·021 14·7	·027 18·9	·017 11·9	·014 9·8
6	·021 14·7	·019 13·3	·020 14·0	·019 13·3	·017 11·9	·022 15·4	·022 15·4
7	·018 12·6	·021 14·7	·022 15·4	·020 14·0	·015 10·5	·022 15·4	·026 18·2

Upper line in each square shows proportion as decimal of all seed produced.
Lower line shows proportion as percentage of all seed produced by the mother cultivar.

able to exchange pollen. Flowering time of the actual mother cultivars in 1956 was not scored in the present material and the only measure of it is the date of ear emergence scored in spaced plant material in 1958 (mother cultivars in Fig. 1 ryegrass; Fig. 2 cocksfoot). Ear emergence in the ryegrasses is spread over about five weeks and in the cocksfoots about four weeks. The largest difference for mean date of ear emergence per cultivar in the ryegrasses is eight days (between cultivars 5 and 7 in Table 4) and in the cocksfoots three days (between cultivars 2 and 10 in Table 5).

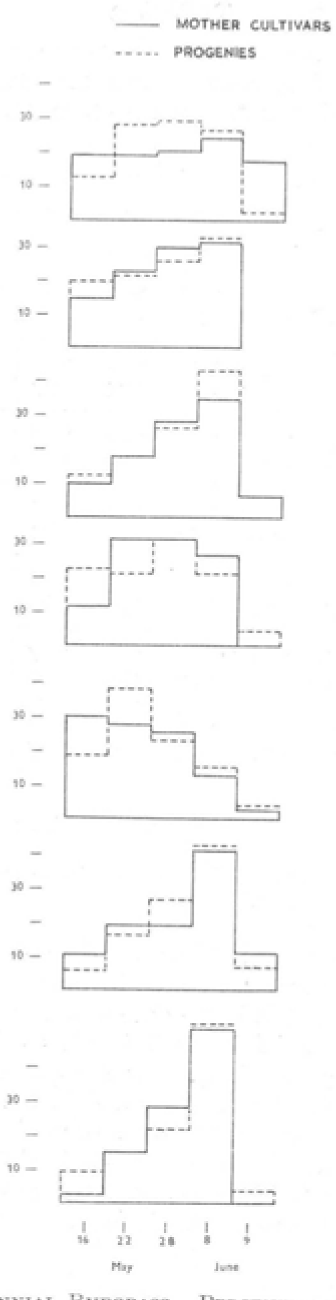

FIG. 1. PERENNIAL RYEGRASS. PERCENTAGE DISTRIBUTION OF DATE OF EAR EMERGENCE IN SPACED PLANTS, 1958.

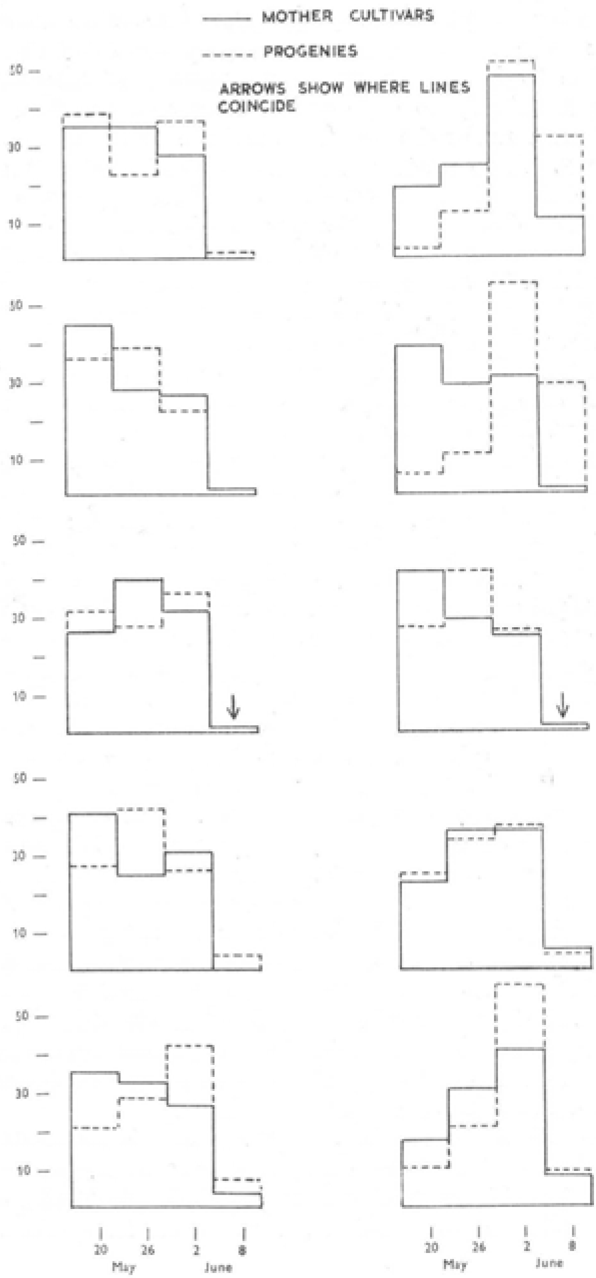

FIG. 2. COCKSFOOT. PERCENTAGE DISTRIBUTION OF DATE OF EAR EMERGENCE IN SPACED PLANTS, 1958.

If it is assumed for the moment that dates of ear emergence and maximum flowering are completely correlated then it is possible to form estimates of the amount of inter-cultivar pollination likely to have occurred between any two. This has been done for the ryegrasses and the results are shown in Table 3. A completely random distribution of pollen (*i.e.*, necessitating simultaneous flowering of all plants and equal quantities of pollen per cultivar) would give values of ·020 in the top line of each square of the Table and of 14·29 per cent in the second line. The actual values range from ·027 (18·9 per cent) to ·014 (9·8 per cent). These are probably the extreme limits since flowering of individual plants is spread over a period of about three weeks. In the cocksfoot the shorter range of date of ear emergence and hence of flowering time would give increased chances of inter-cultivar pollination.

Comparison of parent and progeny performances.—The trial results for perennial ryegrass are shown in Table 4 and for cocksfoot in Table 5. In the ryegrass spaced plant trial two of the progenies give significantly higher fresh weight yields than their parents, but the corresponding differences for air dry weight are not significant. In the swards the only significant superiority of progeny over parent occurs in progeny 1 in the second cut, at the time of peak yield, this progeny is inferior to its parent in terms of total yield. In the cocksfoot none of the progenies significantly exceeds its parent under spaced plant conditions, but two (progenies 2 and 6) show significantly higher yields in the first sward cut.

Parent-progeny correlation and regression coefficients for time of ear emergence, spaced plant " hay " yield and total sward yield are given in Table 6. Since cultivars having similar mean dates of ear emergence will have a greater chance of exchanging pollen it is to be expected that there will be a fairly high parent-progeny correlation for this character, in addition it is a character having a high heritability (Cooper, 1960) and it is interesting to note that the simple parent-progeny regression coefficient in the present experiment is similar to that found by Cooper in experiments crossing known pairs of plants in Kent and Irish ryegrass.

Comparison between spaced plant and sward yields.—A secondary object of the experiment was to compare yields under spaced plant and sward conditions. In Tables 6 and 7 the relative orders of merit for yields for ryegrass and

TABLE 4

RYEGRASS: EAR EMERGENCE (EE) AND YIELD DATA 1958
EAR EMERGENCE DATES: 3·0 = 20TH MAY, 4·0 = 23RD MAY
5·0 = 26TH MAY, 6·0 = 29TH MAY

	Spaced Plants			Swards Dry wts/cut/lbs/ac				
	EE	Yield fresh lbs/ac.	Hay yield lbs/ac.	1	2	3	4	Total
1 M 1 Px	5·5 4·9	7750 9970*	2120 2500	935 602	1230 1660*	693 485	468 258	3426 3005
2 M 2 Px	5·0 5·0	9580 9350	2430 2400	660 605	1730 1610	421 466	327 348	3138 3029
3 M 3 Px	5·6 5·6	8620 8840	2145 2285	815 807	1390 1320	543 471	488 392	3236 2990
4 M 4 Px	5·0 4·6	10080 9840	2580 2540	925 770	1610 1640	449 496	411 325	3395 3231
5 M 5 Px	3·9 4·3	8990 10340	2360 2600	640 568	1730 1440	404 392	325 320	3099 2720
6 M 6 Px	5·7 5·8	12100 10730	3070 2680	670 650	1680 1810	503 486	452 435	3305 3381
7 M 7 Px	6·4 5·9	8470 10220*	2070 2470	739 688	1280 1540	416 460	411 423	2846 3111
a	0·74	1588	435	NS	296	91	143	514
b	0·74	1588	435	NS	NS	102	159	696
c *d*		9370 9899	2396 2497	769 670	1521 1574	490 465	426 357	3155 3067

a Minimum significant difference (5%) between parent and progeny.
b ,, ,, ,, ,, between any other two treatments.
c Parental mean
d Progeny mean
Asterisks indicate progeny yields significantly (5%) greater than parent
In this and subsequent tables M = mother cultivar
Px = polycross progeny

TABLE 5

COCKSFOOT: EAR EMERGENCE AND YIELD DATES 1958
EAR EMERGENCE DATES:
3·0 = 24TH MAY, 4·0 = 27TH MAY, 5·0 = 30TH MAY

	Spaced Plants			Swards Dry wts/cut/lbs/ac.		
	EE	Yield fresh lbs/ac.	"Hay" yield lbs/ac.	1	2	Total
1 M	3·3	12499	4403	1741	336	2077
1 Px	3·5	11648	4202	1751	396	2147
2 M	3·1	11222	3988	1297	300	1597
2 Px	3·3	11850	4162	1518*	320	1838
3 M	3·8	12186	4269	1537	398	1935
3 Px	3·7	10371	3602	1576	372	1948
4 M	3·4	10819	3828	1451	339	1790
4 Px	3·6	11200	3936	1624	336	1960
5 M	3·6	12163	4416	1462	276	1738
5 Px	4·1	13350	4642	1319	252	1571
6 M	4·4	12163	4056	1093	403	1496
6 Px	5·9	12522	3868	1347*	413	1760
7 M	3·5	11715	4056	1400	398	1798
7 Px	5·7	12432	4109	1335	387	1722
8 M	3·3	11245	3909	1755	355	2110
8 Px	3·6	12074	4389	1623	358	1981
9 M	4·0	10797	3615	1566	384	1950
9 Px	4·0	9229	3108	1360	353	1713
10 M	4·3	10774	3708	1489	343	1832
10 Px	4·9	9565	3268	1381	307	1688
a	0·57	1425	523	210	NS	NS
b	0·57	1425	523	300	90	374
c		11553	4025	1479	353	1832
d		11424	3929	1483	349	1833

a Minimum significant difference (5%) between parent and progeny
b ,, ,, ,, between any other two treatments
c Parental mean
d Progeny mean
Asterisks indicate progeny yields significantly (5%) greater than parent

TABLE 6

RYEGRASS AND COCKSFOOT: "PARENT-PROGENY" CORRELATION AND REGRESSION COEFFICIENTS (BASED ON TREATMENT MEANS)

	Ryegrass		Cocksfoot	
	r	b	r	b
Spaced plant "Hay" yield	+0·7385 NS	+0·2443 NS ±·0983	+0·6586*	+1·1624* ±0·4695
Total sward yield	+0·2805 NS	+0·2911 NS ±·4455	+0·5323 NS	+0·4746 NS ±0·2668
Spaced plant Ear emergence	+0·8851**	+0·7098** ±·1670	+0·6489*	+1·3696* ±·5680

cocksfoot respectively under the two environments are given. The yield figures themselves have already been referred to in Tables 4 and 5. There is not, either in the ryegrass or cocksfoot material, any closer relationship between the orders of merit under the two sets of conditions than would be expected on a purely random basis. If, for example, in the cocksfoot one selects the ten highest yielding cultivars when grown as spaced plants then only five of these are in the first ten under sward conditions. Similarly in the ryegrasses only four of the seven best yielders as spaced plants are also in the first seven as swards. Clearly in this material performance measured as gross yield in spaced plants is no guide to behaviour under sward conditions. This is in conformity with the results of other work based on similar comparisons (Ahlgren, Smith and Nielsen, 1945; Kelly, 1958; Knight, 1960; Green and Eyles, 1960), although Lazenby (1957) obtained results suggesting that relative performances under spaced plant, sown row and sward environments were comparable.

TABLE 7

Ryegrass: relative orders of merit under spaced plant and sward conditions

	Sp. plant "Hay" yield	Total sward yield dry	Cut 1	Cut 2	Cut 3	Cut 4
1 M	13	1	1	14	1	1
Px	6	11	13	5	6	14
2 M	8	7	9	2	11	10
Px	9	10	12	7	8	9
3 M	12	5	3	11	2	2
Px	11	12	4	12	7	8
4 M	4	2	2	7	10	6
Px	5	6	5	6	4	11
5 M	10	9	11	2	13	11
Px	3	14	14	10	14	13
6 M	1	4	8	4	3	3
Px	2	3	10	1	5	4
7 M	14	13	6	13	12	6
Px	7	8	7	9	9	5

Conclusions

In the material used (early ryegrass and late flowering cocksfoot)

(1) there does not seem to be any indication that any useful advance in yield has been achieved by mass pollination between individual cultivars ;

(2) yielding ability under spaced plant conditions did not give any reliable indication of yielding ability under sward conditions.

TABLE 8

COCKSFOOT: RELATIVE ORDERS OF MERIT UNDER SPACED PLANT AND SWARD CONDITIONS

	Sp. plant "Hay" yield	Total sward yield dry	Cut 1	Cut 2
1 M	3	3	3	14
Px	6	1	2	5
2 M	11	18	19	18
Px	7	9	9	16
3 M	5	8	8	3
Px	18	7	6	8
4 M	15	12	12	13
Px	12	5	4	14
5 M	2	14	11	19
Px	1	19	18	20
6 M	9	20	20	2
Px	14	13	16	1
7 M	9	11	13	4
Px	8	15	17	6
8 M	13	2	1	10
Px	4	4	5	9
9 M	17	6	7	7
Px	20	16	15	11
10 M	16	10	10	12
Px	19	17	14	17

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PHENOTYPIC RESPONSES TO CONTRASTING ENVIRONMENTS IN THE GENUS *POA*

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The relationship of the genotype to its environment has been the subject of much thought and experiment particularly since the beginning of the present century and the investigations have largely followed two main complementary trends, the study of a genotype introduced from its own habitat into different communities and that of genotypes transplanted from various habitats into the uniform environment of a garden. The latter studies have provided most useful information concerning the major phenotypic differences between populations but the interaction of individual genotype and environment is much more difficult to investigate for a primary requirement is that the genotype itself should remain constant. The advantages of a plant which is capable of being cloned are obvious, but transport constitutes a problem where considerable distances between experimental areas are desired.

In the course of investigations into the genus *Poa* which has a very nearly world-wide distribution, Clausen and colleagues came to the conclusion that there was a valuable source of material in this genus for experimentation in widely separated geographical areas since it contains a large majority of species which are normally asexually reproducing, a fact which made possible the use of seed clones. Apomixis is facultative in this genus and several workers have reported that it is frequently possible to obtain some hybrid seed as a result of fertilisation [Müntzing (1933, 1940); Åkerberg (1942); Kiellander (1943)]. It was thought that widely separated geographical areas might well answer another requirement for the accurate assessment of genotype environment interaction, namely that " environmental changes should surpass seasonal and periodical annual fluctuations in the native environment to which the organism is evolutionally adjusted " (Clausen and Hiesey, 1958).

Clausen *et al.* (" Year Books," Nos. 42-57) have made full use of the possibility of obtaining hybrids and though the percentage may be small, they are usually readily picked out in the seedling stage after two to three months' growth. It rarely happens that a hybrid is already apomictic in the F_1 and as a general rule the progeny of a cross shows evident lack of internal balance. Ir later generations, however, the apomictic system can become re-established and the chances of thus obtaining a new line are good. Work on the *Poa* species has a special importance in agriculture as well as providing most interesting material for study, since where crosses result in a sexual F_1 and segregating F_2 " the genomes of distinct parent species may be added together unchanged, or broken up, recombined and established into new constant systems that behave much like new species which are balanced both internally and with respect to specific environments or even to large ranges of climatic differences " (Clausen, 1952). For example, *Poa pratensis* is the most important pasture grass in Sweden, but the indigenous species suffers from serious defects. Nygren and Åkerberg (1957) conducted trials at several different centres of various *Poa* species and hybrids from California in order to gain information concerning their useful range and characteristic phenotypic expression before embarking upon a breeding programme.

Some ten years earlier, Clausen and colleagues initiated a series of intercontinental trials with *Poa* clonal material and these trials have been conducted at centres in several European countries including Great Britain, some Scandinavian countries, as well as many centres in the U.S.A. A very considerable volume of data is now being prepared for publication. The present paper is concerned with a small trial which involved three centres, Edinburgh and two in U.S.A., namely Stanford and Pullman. Two species and several hybrid lines selected in these environments provided the experimental material.

The experimental garden at Stanford (38°N) is located between the outer and inner Coast Ranges and has a mild coastal climate. The altitude is about 100′ (30 m) and winter frosts do occur, but in general, conditions are favourable for a considerable amount of growth even during the winter since the average minimum temperature remains relatively high.

Winter conditions indeed are much less likely to hinder growth than the heat and drought of the summer. The Soil Conservation Service Nursery at Pullman (46°N) in Eastern Washington has very different conditions, with an altitude of 2,400′ and moderately severe winters including some very low temperatures. The Edinburgh station involved in the present trial was the experimental garden of the Scottish Plant Breeding Station at Pentlandfield (56°N). The altitude is 500′ and growth is favoured during spring, summer and autumn only, and though the winters are relatively mild the average minimum temperature is lower than at Stanford.

The parent species were *Poa ampla* and *P. pratensis*, species with very different characters. *Poa ampla* is a rather variable species with a somewhat restricted distribution and does not occur naturally in Britain, though it grows satisfactorily in spaced-plant plots. It is a very tall-growing, winter-active bunch grass which is most successful in the continental climate of the Pacific Northwest where it is native. The strain used in the present cross was collected near Kahlotus, Franklin Co., Washington, and grown at Pullman, Washington. The chromosome number is reported to be $2n = 64$. *Poa pratensis* has a very wide distribution in the Northern hemisphere and is indigenous in Britain : but the progeny from which the parent plant was selected was produced from a seed population grown at Stanford and originating from the " Delta " cultivar grown at the Central Experimental Farm, Ottawa. This cultivar had itself been derived from a single plant collected in the Athabaska region (*c.* 55°N) and is a highly rhizomatous, summer-active, winter-dormant type with a chromosome number of $2n = 70$.

Clausen (1954) stated that " facultative apomicts maintain a rudimentary, although still functioning, sexual process," and some aberrants may be produced by any apomictic genotypes. Plants which do not conform to a type in an apomictic line are referred to as aberrants and they are most frequently rather weakly and have deviating chromosome numbers. Details of an examination of aberrants provide some interesting information in " Year Book " No. 44 (p. 79). Aberrant offspring from a single plant of a normally asexually reproducing race of *P. ampla* from Albion, Washington ($2n = 63$), were cytologically examined and found to have different chromosome numbers varying from $2n = 56$ to 126. The important point is that in spite of these chromosomal abnormalities "all are characteristic of *ampla* and even of the Albion race." No cytological examinations were carried out on the material in the present trial.

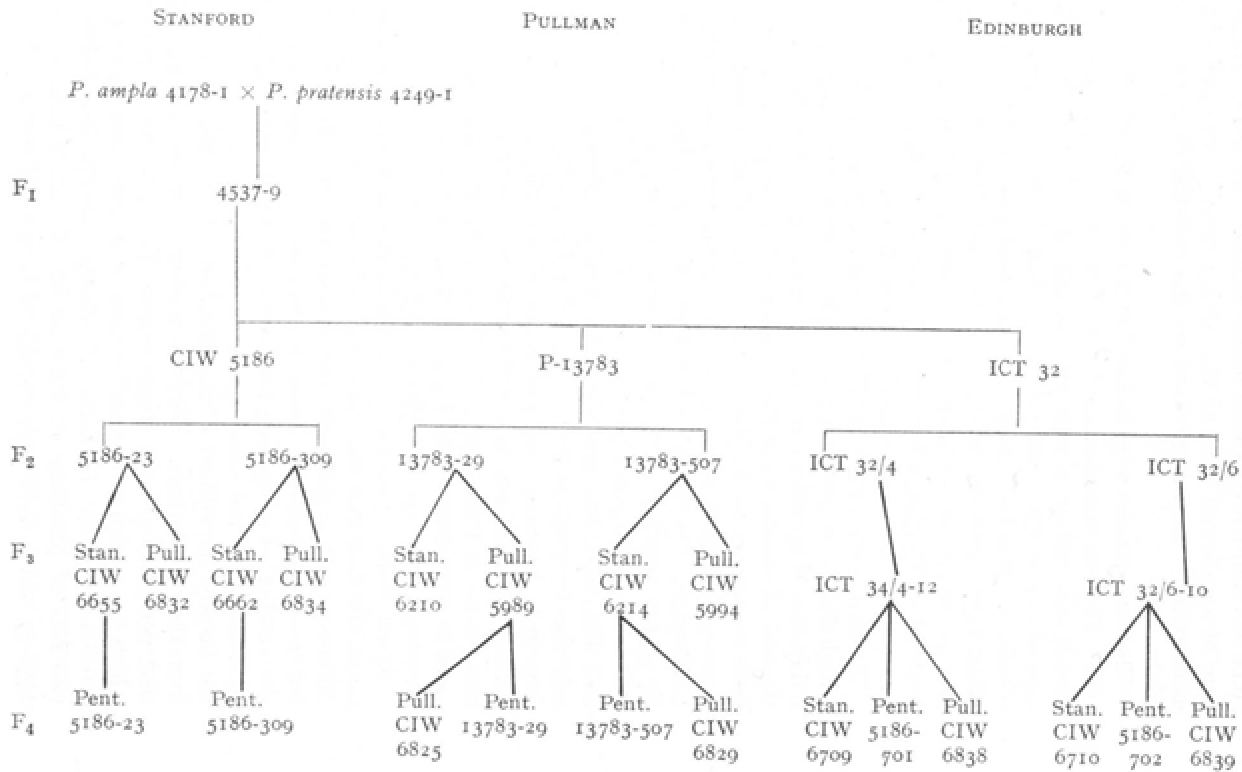
The two parents were isolated in a cage at Stanford and in spite of severe rust damage to the female parent, *Poa ampla*, twenty-one hybrid plants were obtained and it is from the seed of one of these plants, 4357-9, that the hybrid lines were obtained. Random samples of the seed produced by the F_1 plant 4357-9 growing at Stanford were distributed to the three centres, Stanford, Pullman and Edinburgh, where they were sown as an F_2 generation and, as is commonly the case, there was obvious segregation under all conditions.

At each centre, vigorous F_2 plants were open pollinated and a high degree of uniformity of the F_3 progeny was taken as an indication of apomictic reproduction in the F_2 generation. In the case of Stanford and Pullman a random sample of the seeds from the apomictic F_2 plants was mutually distributed to both centres, but the F_3 generations of these lines were not grown at Edinburgh. On the other hand, the F_3 generations of the six F_2 plants selected at Edinburgh were grown at that centre only. Four progenies proved to be highly variable in the F_3 and discarded, but two were sufficiently uniform to warrant selection for trials at Pullman and Stanford. The seeds for the Stanford, Pullman and Pentlandfield plantings of the two Edinburgh lines came out of the same two bags harvested from two plants at Edinburgh. All lines in the Pentlandfield trial sown in 1957 were of the F_4 generation from the original cross or second apomictic generation (Fig. 1).

Apart from a possible variation in the proportion of aberrants, the fact that the same generation of a line was sown in different years at different centres does not invalidate the data for cross comparisons. Some readers may raise doubts about the validity of comparing measurements taken upon different generations of the same apomictic biotype, but such doubts are largely unjustified if the aberrant plants are eliminated from the calculations. What does seem to be of importance is that comparisons at a single centre should be between lines which have been grown and measured in the same years and at the same sites. In Table 1. is shown a comparison between two sets of plantings at Pullman in the years 1951-52 and 1956-57 which show very considerable size differences. These

FIGURE 1

SOURCES OF MATERIAL



differences must be attributed to variations between years and between planting sites because 13783-507 is a highly apomictic line, and it is difficult to see how these differences could occur between generations for any other reason. All lines were taller in the 1956-57 plantings than in previous plantings.

TABLE 1

Generation	Years of scoring	Mean for two years for apomicts only: Basal Width	Stem Length	Stem Number	Vigour	% of Aberrants
13783-507						
F_3	1951-52	28·5	71·6	279·2	7·3	8
F_4	1956-57	34·2	104·1	369·1	8·2	9
13783-29						
F_3	1951-52	26·4	65·8	200·5	6·7	50
F_4	1956-57	24·8	82·8	121·5	6·0*	42

* Values calculated from one year's measurements.

Unlike 13783-507, 13782-29 is a sexual line and though the "apomictic" fraction looks phenotypically very uniform, there are upon closer examination minor variations which betray the sexual origin which no doubt accounts for the fact that in this line the differences are more erratic, but still sufficient to make years of scoring important when making comparisons.

The most significant trials were conducted at Pullman and Pentlandfield (Edinburgh), and while it was only to be expected that the lines would differ genotypically from each other, each line ultimately studied was judged, on the basis of its performance in the two gardens, to be of sufficient uniformity to be regarded as essentially of one genotype, in spite of the fact of the occurrence of a small proportion of aberrants. These aberrants have been excluded from the trial analyses. The

TABLE 2

COMPARISONS BETWEEN LINES AT THREE CENTRES (DATA FOR TWO YEARS AVERAGED)

Centres	Characters	Lines						Centre Average
		pa	pp	S-23	S-309	P-507	E-701	
Pentlandfield 1957/58	Stem Length	100·0	81·7	77·4	84·9	93·4	85·2	87·1
	Stem Number	115·4	107·7	93·7	100·3	50·9	116·4	97·4
	Basal Width	11·1	55·2	45·8	48·4	40·9	40·8	40·4
	Vigour	7·6	7·6	8·4	7·5	6·6	6·7	6·1
	Date of Flowering	12th June	23rd May	10th June	30th May	3rd June	21st June	7th June
Pullman 1956-57	Stem Length	83·7	86·7	75·0	83·3	104·1	73·7	84·4
	Stem Number *	153·3*	391·0*	207·0*	316·5†	369·1*	260·5*	289·9
	Basal Width	13·4	44·8	27·5	25·8	34·2	28·5	29·0
	Vigour	5·9	7·7	5·5	6·9	8·2	6·2	6·7
	Date of Flowering	31st May	6th May	1st June	26th May	20th May	28th May	18th May
Stanford	Years	1950-51	1950-51	1955-56	1955-56	1954-55	1957-58	
	Stem Length	69·2 ‡	76·8	58·8	81·9	82·8	38·8	
	Stem Number	59·2 ‡	132·1	53·3	61·5	99·0	30·0	
	Basal Width	12·1 †‡	34·3†	22·7†	23·6†	27·6	38·5	
	Vigour	4·2 ‡	5·2	5·3	6·8	6·9	4·9	
	Date of Flowering	23 May‡	13th Apr.	21st Apr.	15th Apr.	16th Apr.	12th Apr.	

* Values for a random sample (2 years).
† Values calculated from one year's measurement.
‡ Not many plants survived for measurement.

same parents and hybrids were also grown at Stanford, but not all in the same year.

The measurements taken at the three centres were in most cases recorded by different workers, but every effort was made to ensure that as far as possible they were taken in exactly the same way on spaced plants. The data relating to the Pullman and Pentlandfield comparisons are presented in Table 2 where the figures for 1st and 2nd years of growth have been averaged. Also in this Table are the similarly averaged Stanford observations and throughout the letters *E*, *P* and *S* refer to the place where the selections were made, Edinburgh, Pullman and Stanford, whereas the original *Poa ampla* and *Poa pratensis* parents are denoted by the letters *pa* and *pp* respectively.

Ear Emergence was scored at Pentlandfield instead of Date of Flowering as it was felt to be a more easily recognised point in the growth cycle at this centre, but the latter occurs with a good degree of regularity about three weeks after the panicles have grown beyond the enclosing leaf sheath and this calculated date is used in the Tables. All other measurements were made upon the mature plant. Two of the hybrid lines have been omitted from Table 2 because they were obviously still segregating in the F_3 and F_4 generations and mean values in such cases do not present a true picture of the lines. From a perusal of the Table it is possible to appreciate the relative performances of the " native " selections when transferred to different environments and their " success " relative to parental responses at the three centres, as well as the nature and extent of any changes in the phenotypic expressions of the same genotype.

While it is impossible to assess the " success " of lines in different environments, except from relative performance in a trial, it will be seen that the centre averages for height and basal width are greater at Pentlandfield than at Pullman, while it is difficult to draw general conclusions from the Stanford results. At the latter centre, however, from the present trial it seems that both parent lines are generally smaller and poorer at Stanford than at Pullman having shorter and fewer stems, narrower basal width, and poorer vigour, but it is interesting to find that *pa* attains its maximum height at Pentlandfield rather than at Pullman, which is very near to its native habitat.

In the environment at Pullman all lines produce a very much larger number of stems than at either Stanford or Pentlandfield. This may be due to the much lower average minimum temperatures in winter at Pullman than at either Pentlandfield or particularly Stanford, for Cooper (1959, p. 187) points out that winter cold and/or short day are necessary before most perennial ryegrasses can head and upon the degree of cold treatment depends the proportion of tillers which form heads in any one year. P-507 is obviously a very good line at Pullman, better in some characters than *pp* which it closely resembles, but is less " successful " at Pentlandfield. There is probably greater variability at Stanford than at Pullman and this seems particularly true of the incidence of flowering as well as the number of flowering heads. Stanford is the only centre where a considerable number of plants in some lines failed to head.

More information can be obtained from the Pentlandfield data for the whole trial which included more lines selected at Stanford and Pullman (Table 3). The Table shows that all the Stanford-selected lines have a shorter mean stem length in the Pentlandfield environment than those selected at Pullman and the E-701 selection is intermediate. Omitting the latter, the variances were worked out and, though showing a fair range, were found to be homogeneous, thus permitting an analysis of variance of the means. This analysis shows that the means for all the S-lines are significantly different from those for the P-lines. Table 3 also shows that in regard to the five characters the relative order of the parents and the twelve selected lines changes from character to character. This, of course, happens at the other two centres also. Date of flowering at Pentlandfield is of particular interest because nine of the twelve hybrid lines are later than the latest parent, *P. ampla*. No such transgression towards lateness was detected at either Stanford or Pullman where *pa* was consistently later flowering than any of the hybrid selections.

It has already been mentioned that aberrants may occur in the most apomictic line and it is interesting to compare the numbers occurring at the three centres (Table 4). It must be stressed here that the parent and apomictic lines were always obviously apomictic whereas those apomictic fractions which occurred in the sexual lines did not obscure the essentially segregating characters of these lines. As regards numbers of aberrants the apomictic lines show reasonably good correspondence between centres, years and generations.

TABLE 3

PARENTS AND ALL APOMICTIC HYBRID LINES GROWN AT PENTLANDFIELD, 1957-58

Line	Stem Length	Line	Stem Number	Line	Basal Width	Line	Vigour	Line	Ear Emergence
S-316	68·6	P-507	50·9	pa	11·1	S-316	3·6	pp	23rd May
S-323	75·9	S-323	51·3	S-311	35·8	S-20	4·5	S-309	30th May
S-23	77·4	S-316	66·1	S-20	37·5	S-323	5·3	P-507	3rd June
pp	81·7	S-20	67·0	S-316	38·1	P-33	6·0	S-23	10th June
S-20	81·9	P-33	72·5	S-323	39·5	S-311	6·5	pa	12th June
S-123	83·3	S-311	88·7	E-701	40·8	P-208		P-208	13th June
S-311	84·4	P-208	93·0	P-507	40·9	P-507	6·6	S-20	14th June
S-309	84·9	S-23	93·7	S-123	42·2	E-701	6·7	S-123	
E-701	85·2	S-309	100·3	P-208	42·3	S-123	7·0	S-311	16th June
P-33	86·5	pp	107·7	S-23	45·8	S-309	7·5	P-301	17th June
P-301	87·7	S-123	114·9	P-33	46·9	pa	7·6	S-323	20th June
P-507	93·4	pa	115·4	S-309	48·4	pp		P-33	
P-208	96·8	E-701	116·4	P-301	49·8	P-301	8·1	E-701	21st June
pa	100·0	P-301	131·2	pp	55·2	S-23	8·4	S-316	27th June

Nygren (1951) has suggested that from one generation to another the environment of the plant at the time of reproduction may alter materially the relative proportions of aposporous and sexual embryo sacs formed. In the present case it is impossible to say to what extent, if any, the observed differences are due to this cause. When, however, the seed sown at different centres comes from the same source, differences in the proportions of aberrants cannot be due to generation effects but must be due to differences in environment. It must be said that such differences may not only induce differing phenotypic expressions in a line but influence one fraction to such an extent that it appears to be absent under certain conditions. For example, some " twenty-four of the established apomictic hybrids were sown thickly in drilled rows in field plots " at three U.S.A. centres and " the significant discovery was made that the extent of elimination of sexual aberrants in such densely sown field rows may differ strikingly in the same apomictic strain when it is grown in different environments " (" Year Book," No. 52, p. 152). The example of a particular *P. ampla-pratensis* cross is given in which it was observed that in dense plantings in California of line 4535-6 the sexual aberrants were scarcely noticeable, but that at Pullman they were much stronger and highly observable; yet in contrast, a sister line, 4535-26 had very conspicuous aberrants in California and very weak, small ones at Pullman. Such situations are rather exceptional, but may account for some differences in the percentage of aberrants in the same apomictic line but in different environments. No such explanation can be used here where the seedlings were planted individually.

TABLE 4

PERCENTAGE OF ABERRANTS OCCURRING AT DIFFERENT STATIONS

Line		Stanford		Pullman		Pentlandfield	
	Generation	Year of observation	% aberrants	Year of observation	% aberrants	Year of observation	% aberrants
pa		1950	23*	1956	13	1957	7
pp		1950	0	1956	3	1957	8
S-23	F_3	1955	13	1956	6		
	F_4					1957	14
S-309	F_3	1955	6	1956	2		
	F_4					1957]	2
P-507	F_3	1954	14	1951	8		
	F_4			1956	9	1957	5
E-701	F_4	1957	3	1956	6	1957	14
			Sexual Lines				
E-702	F_4	1957	100	1956	100	1957	34
P-29	F_3	1954	53	1951	50		
	F_4			1956	42	1957	100

* Based on few individuals.

It is possible, however, that the rate of germination of apomictically- and sexually-produced seeds harvested on the same biotype differs in different environmental conditions. Difficulties in the early stages of a trial were recognised by Mather and Vines (1952) in an experiment with a cross of *Nicotiana rustica* when they say " there may still remain a tendency for slower germinating or very small seedlings to be overlooked, with consequent selection of phenotype and disturbance of gene ratios." In the present trials every attempt was made to take all seedlings irrespective of size, but should there have been any considerable time lag between the germination of one type and another, it could lead to an error in interpretation, though in the present case such an explanation is considered to be unlikely.

The difference between centres is far more striking in the behaviour of the two sexual lines P-29 and E-702 (Table 4, lower) than in that of the apomictic lines. P-29 was considered to be moderately apomictic at Pullman and even at Stanford where in general variability is greater. When the Pentlandfield results were available, however, it could be seen that this line is in fact sexual. In contrast E-702 was thought to be completely sexual at Stanford and Pullman, but at Pentlandfield 66 per cent appeared apomictic, though it is true that this fraction did show slight variations in some minor characters. Table 5 gives random examples of the behaviour of E-702 at Pentlandfield and at Stanford. P-29 behaved in a somewhat similar manner and undoubtedly each of the cryptically sexual lines had a higher percentage of apomictic types at its centre of origin. Clausen and Hiesey (1958) have discussed in detail instances of the influence of climate upon variability particularly in grass species and the results of this experiment add further information concerning the phenotypic expression of genotypic variability under contrasting environmental conditions.

TABLE 5

EXAMPLES OF RECOMBINATION BETWEEN WIDTH AT BASE, STEM LENGTH, ABILITY TO FLOWER, AND NUMBER OF FLOWERING STEMS (DATA FOR TWO YEARS AVERAGED) IN LINE E-702.

Plant No.	*Width at base cm.*	*Stem length cm.*	*First Flowers date*	*Number of stems*
		(a) PENTLANDFIELD		
1-3	50	69	12th June	107
1-7	51	69	12th June	113
2-1	35	80	8th June	181
2-3	36	86	6th June	286
2-5	34	80	12th June	136
3-1	37	72	12th June	145
3-2	35	84	12th June	245
3-4	31	80	12th June	223
3-5	37	61	12th June	72
3-7	36	86	3rd June	247
4-1	44	83	10th June	168
4-3	42	90	8th June	220
4-10	46	70	8th June	109
5-2	48	92	29th May	220
5-10	37	61	15th June	101
		(b) STANFORD		
1-1	5	..	no flowering	..
1-2	36	41	27th April	28
1-3	41	49	13th April	134
1-5	35	11	no flowering	..
1-6	20	28	6th May	8
1-9	31	..	no flowering	..
2-1	11	17	23rd April	1
2-2	22	..	no flowering	..
2-19	42	44	23rd April	39
2-22	8	..	no flowering	..
2-23	13	..	no flowering	..
3-15	26	37	23rd April	29
3-21	19	14	15th May	1
3-22	16	..	no flowering	..
3-23	12	15	15th May	1

Summary

1. The apomictic lines are interesting for they reveal the extent to which differences in the phenotypic expression were manifested at different centres.
2. An apomictic line selected on the basis of its successful performance at one centre may actually perform relatively better at another centre.
3. Sexually-produced plants still occurred in the third and fourth generations of essentially apomictic hybrid lines.
4. Where sexuals occur in apomictic hybrid lines they are most frequently weakly and verging on the semi-lethal.
5. In certain sexual lineages, genotypic differences which were phenotypically expressed at one centre remained undetectable under different environmental conditions.

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Leached and flushed grasslands in the Southern Uplands, January