SCOTTISH PLANT BREEDING STATION
PENTLANDFIELD, ROSLIN, MIDLOTHIAN

# REPORT

## 1957

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## DIRECTOR'S REPORT

**Cereals.**—As in the past the work of the Cereal Section during the year has been confined almost entirely to oats. The work falls into two distinct categories, first, breeding and selection related to performance in three distinct environments, both fixed and unfixed material being grown at selection centres in Argyll and Inverness-shire as well as at Pentlandfield, and second, work which is at present confined entirely to Pentlandfield. Harvesting operations at Pentlandfield and the Inverness centre were severely hampered by wet weather and the seed from these areas is of poor quality. In contrast to this, harvest conditions at the Argyll centre were good and the quality and appearances of the seed are excellent.

The station is greatly indebted to the Staffs of the three Agricultural Colleges of Scotland for their co-operation in the provision of sites for the multiplication of elite stocks of the station's oat varieties and for the obtaining of suitable sites for the selection centres. We are also indebted to the farmers on whose land those centres were located, for their interest and help throughout the season.

The beginning of a new cycle at the selection centres started in 1956, when unfixed material in the $F_3$ generation was sown at these centres for the first time, twenty-five hybrids being included in replicated trials. In addition to the trial of unfixed material twenty-seven fixed strains, selected from a number of different hybrids, were included in a replicated trial at each centre together with controls appropriate to each environment. From the figures available to date there is a strong suggestion that there is less difference in yield between related strains than exists between unrelated strains. This impression is strengthened by comparison of yields from the trials of $F_3$ populations in which those of identical or similar parentage have very similar performances. Should this impression be confirmed in subsequent trials it means that whole hybrid progenies can be discarded in an early generation on a family performance basis and only those progenies which are themselves high yielding need be retained for further selection work.

The main work which has been carried on exclusively at Pentlandfield has been concerned with a search for resistance to stem eelworm of oats, *Ditylenchus dipsaci*. The procedure adopted has been the injection, by means of a hypodermic syringe, of approximately three hundred eelworm larvæ into oat seedlings 2-3 days after germination. Preliminary results suggest that more than one type of resistance or tolerance to eelworm may be present. The variety Milford, which is known to possess a high degree of resistance in the field, responded to injection by very severe stunting, but subsequently recovered with practically no further external symptoms. Early Miller, on the other hand, which again is reported to be resistant under field conditions, is little affected by injection, the plants being only slightly less vigorous than the control plants of the same variety which received no eelworm. It does, however, exhibit the characteristic crinkling and puffiness of the stem which in susceptible varieties such as Sun II is associated with severe stunting and ultimate death.

The year 1956 was not favourable to attack by stem eelworm in the field and considerable difficulty was had in obtaining infested plants as a source of eelworm for injection. Material collected from known infested areas on the mainland had only small numbers of eelworm in the tissues and these were generally very young larvæ. We were fortunate in obtaining through the kindness of Mr W. H. Campbell, Agricultural Adviser in Orkney, a supply of stubble which contained large numbers of well-grown eelworm larvæ.

It was the original intention when embarking on this work to carry out all the initial tests with eelworm from a single source to avoid confusion due to the possible existence of different races of eelworm, but the scarcity of infested material in 1956 has made it necessary to depart from this intention. In order that this difficulty may be overcome in future and to reduce the dependence on natural infestations, attempts have been made to inject eelworm into suitable alternative hosts in which populations can be built up and the races maintained under glasshouse conditions. The two most promising hosts for this purpose are Fodder Beet and Shallot and present work is aimed at developing this possibility.

**Herbage Plants and Genecology.**—In modern farm practice, the time of highest production is of greater importance than the actual total yield for the season and it is for this reason that the tendency of late years has been to concentrate more particularly upon the production of special maturity types. Again, under different sets of conditions distinctive growth-habits may also have their agricultural significance. In this connection a very erect type of late ryegrass originating from Danish wild material has been raised with a view to its use as a silage crop and has now reached trial standard. However, in an attempt to increase the vigour and at the same time retain the extreme erectness of this strain, further combinations of parental material were crossed last summer.

Recent trials have drawn attention to the fact that the actual increase in total seasonal production in the present bred strains of pasture grasses is disappointingly little greater than that of old established " commercial " strains when they are compared under uniform conditions of growth. It may be that some novel technique would yield a more worth-while result and, therefore, it was decided to experiment with a modified form of the customary polycross method of breeding synthetic strains. In this investigation, instead of building strains from a number of individual plants of good combining ability, commercially-available bred strains of a given maturity type from different environments and of different geographical origins are being tested for their ability to produce useful combinations. The trials which are being conducted at the Station involve seven early ryegrass strains and ten of late cocksfoot.

The genecological studies now in progress are directly concerned with the structural details and potentialities of plant communities and thus indirectly with the complex problem of hill land improvement. The primary need at the moment is to acquire fundamental information about the significance of ecotypic variation in community studies. A major difficulty in this kind of investigation is that of defining the effects of individual environmental factors. As mentioned in last year's Report, the tolerance of certain grasses to lead apparently afforded an example of an ecotypic response to the selective action of a single environmental factor. The study of lead tolerance has, therefore, been continued and soil samples from the waste tips of the lead mines in Lanarkshire and Dumfriesshire were collected and analysed for lead and zinc. Two different methods were used. The *total* amount of the metals present was determined after extraction with boiling concentrated nitric acid, and an attempt was made to determine the amount *available* to the plant by extraction with half-normal acetic acid. The figures for *available* lead are usually correlated with those for the *total*, but the former results seem to agree rather better with the recorded vegetation of individual tips, and this suggests that the acetic acid extraction method gives an estimate of *available* lead which may be of real value.

The testing of four hundred plants of *Festuca ovina* for resistance to lead has begun in the small controlled environment chamber. The rates of root growth in water and in a solution of lead nitrate containing 25 ppm. of lead are being compared, and the first few results show a definite relationship between growth under these experimental conditions and the amount of lead which can be extracted by the acetic acid method from the soil in which the plant was growing in the wild. It is not yet clear whether there are two types of fescue—tolerant and intolerant, suggesting a simple genetic mechanism—or a whole range showing every degree of tolerance. In the event of a continuous range of tolerance being found then it should be possible to relate it fairly closely to the amounts of lead in the soil. So far chromosome counts have only been made on a few fescue plants from the lead tips and they were all tetraploid.

*Deschampsia flexuosa* was also collected from the lead tips, and this is to be studied in a similar way. It is less easy to handle than *F. ovina*, as it does not root so readily under the experimental conditions so far tried.

A visit to some of the lead mines in Wales with Dr Bradshaw of Bangor showed them to be rather different from the Scottish ones, particularly in that *F. ovina* was almost absent, while *Agrostis tenuis* was very common, facts already reported by Bradshaw for the mine at Goginan. It is hoped to collect this year from lead mines in other parts of Britain, and those on the limestone in particular should make an interesting comparison with those on the acid rocks of Scotland and Wales. A garden trial has been prepared for planting out this year in which all the available material is included to see if the resistant forms can be distinguished by any morphological characters.

The experiments with *Euphrasia* have now been concluded because of the difficulties of large-scale cultivation, and the results are being analysed. A preliminary survey of the trial data shows that most of the characters of the parasite which were chosen for measurement were affected in some way by the choice of host species, and by the date of establishment on that host. From 1954 onwards attention was concentrated on the shape of the flowers, as this could be easily studied in both wild and cultivated material and the detailed measurements afforded a number of characters which differed from one population to another. Wild collections from the Pentland Hills in 1955-56 suggested that flower shape varied geographically from one river valley to the next, the valleys being separated by heather moorland in which *Euphrasia* did not grow. The comparison of the same populations sampled in two successive years, however, made it clear that differences due to changes of environment were much more serious than had previously been suspected, and in the absence of a garden trial the picture of local geographical differences derived solely from wild material must be regarded as very tentative.

Evidence is accumulating that the chance of isolating a genotype of a perennial species more than once in a population sample is much greater than had previously been supposed. Chance reduplication of genotypes leads to a low standard error and hence a spuriously high significance of difference between populations. This situation must be avoided and if it proves to be a serious source of error some of the methods of studying genecological phenomena may have to be changed.

In *Festuca rubra* strikingly similar plants (suggesting identical genotypes and vegetative origin from a single seedling) have been isolated from points 250 yards apart on the hills. Up to 70 per cent of the isolates from intermediate stations are of the same type, but it has not been isolated from areas beyond this boundary. The patch is not continuous, but divided by strips of a *Nardus* vegetation in which *F. rubra* apparently does not occur. However, to reach such a size a single genotype would have to be of great age, and historical vegetational changes may provide a reasonable explanation. Similar, but less striking examples have been found in *Holcus*. In *Festuca ovina* the vegetative spread of a single genotype to give a patch of four or five yards across seems to be common. In such a tufted species this too indicates great age of the clone.

Genecological investigation must of necessity relate genetical with ecological phenomena. However, neither ecology itself, nor genecology has a universally acceptable system for recording and classifying data. The parallel investigation, genecological and ecological, of vegetations is likely to be fruitful, and may lead to a fusion of the two approaches. The thirteen most abundant taxa in a series of eighty sites are receiving attention with this end in view. Data are being recorded in a manner suitable for statistical analysis and the programme is nearly complete for the ecological side. Chi square and multivariate techniques suggest a highly significant grouping of sites similar to that favoured by the continental plant sociologists.

A somewhat different picture is presented by the results obtained from data provided by *Agrostis* samples from communities which, in the language of the British school of ecologists, are known as *Agrostis*-fescue. Two species *A. tenuis* and *A. canina* were both present in samples which came from communities occurring under different habitat conditions though from one very heavily rabbit-grazed area, *A. tenuis* types only were obtained. On the basis of a detailed examination of floral characters, true *A. tenuis* and *A. canina* plants were taken from each community sample and a replicated trial of tillers was measured this year. As far as the work has proceeded, it has been found that though there is no statistical significance between different habitat populations in respect of the date of first ear emergence, length of the flowering stem or habit of growth in *A. canina*, the amount of variation between genotypes within each population for these characters is significant. On the other hand, whilst the significant difference between genotypes of *A. tenuis* within a population is high, the difference between populations from different habitats is also high. The presence in the original samples of apparently intermediate types between the two species required a programme of crossing and selfing under controlled conditions in order to obtain hybrids for examination.

The results to date of a large-scale international trial of *Poa* material organised by Dr Clausen of the Carnegie Institution of Washington in California are proving to be of very considerable interest. There are, however, still a number of points regarding which Dr Clausen requires more information and he has asked that the Station undertake the examination of a further series of hybrids. Seed of this material was duly received and the trial has been planted in the experimental garden.

**Potatoes.**—During the past three years the investigations on resistance to blight have changed in emphasis from field immunity to field resistance. Field immunity, which implies a hypersensitive response to infection by the parasite, was first found in *Solanum demissum*. It appeared to offer a ready means of combating the disease since the character was controlled by major genes which were inherited in dominant fashion. But eventually new races of the parasite, capable of overcoming hypersensitivity, were found. From the evidence collected, these races are now so widely distributed that the hypersensitive form of resistance must be regarded as unreliable, especially where climatic conditions favour the fungus. In consequence, greater attention has been directed towards field resistance which, as far as it is known, is not affected by parasitic specialisation. It is inherited in polygenic fashion and, with a favourable combination of factors, it provides a high degree of protection against the disease. Resistance is manifested in such types by an inhibitory effect on the growth and reproductive capacity of all known races of the fungus. A useful degree of field resistance is present in some commercial varieties of *S. tuberosum*, but a much higher degree has been found in *S. demissum* and several other wild species.

In some of the commercial varieties bred from *S. demissum* in the past, a relatively low degree of field resistance has been found to be present. Apparently, during the course of breeding for hypersensitivity, the method of repeated backcrossing to varieties of *S. tuberosum* tended to dissipate the field resistance of the original wild parent. Such varieties are liable to suffer severely if attacked by specialised races to which they are not hypersensitive.

A laboratory test for assessing the relative degree of field resistance in varieties and seedlings has been developed. Race 1,2,3,4, which was found in Canada in 1953, was employed, since it neutralised the hypersensitivity induced by the four known major genes, $R_1$, $R_2$, $R_3$ and $R_4$, thereby allowing the inherent field resistance to be expressed. By this method, plants, irrespective of their origin, were classified into five reaction groups according to the amount of damage incurred in a specified time. Although the classification was arbitrary, consistent results were obtained when test conditions were uniform. The results showed that a moderate degree of field resistance may be obtained from many different species including *S. tuberosum*, but that *S. demissum*, *S. stoloniferum* and other recognised blight resistant species provide a much higher degree of protection. Field resistant selections of high yielding capacity, bred from *S. demissum* and *S. simplicifolium*, are now in comparative trials.

The above test was applied to a number of seedling progenies bred from parents in which the level of field resistance had previously been ascertained. The classification of the seedlings into five groups was made as before in order to determine the relationship between the resistance of the parents and the distribution of the different reaction groups in the progenies. The results showed that transgressive segregation took place, but that it was much more pronounced at the lower than at the upper extreme of the parental range of field resistance.

In 1956, samples of 53 resistant seedlings were tested for blight resistance under natural conditions in Mexico through the kind co-operation of Dr J. S. Niederhauser of the Rockefeller Foundation in Mexico City. The test centre, in the Toluca Valley, probably provides the most severe blight conditions in the world for no variety or species was reported as free from the disease. Although the seedlings supplied from Pentlandfield were all blighted, they differed in the amount of damage suffered. These differences were found to correspond in most cases with the differences observed in the laboratory test. The severity of the blight attacks in Mexico appears to be due to favourable temperatures and persistent high humidity, together with a unique range of variation in the parasite. It has recently been reported by M. E. Gallegly and others at West Virginia University that two sexually compatible groups of races exist in Mexico and that oospores may be found in abundance both in nature and in laboratory cultures. No such compatibility between races of the fungus has been found in isolates obtained elsewhere. In these circumstances it is probable that maximum variability of the fungus exists in Mexico and that any potato varieties showing resistance in that environment will remain free from the disease in the main potato growing regions of Europe. Field resistance of that order, however, may be difficult to attain in economic varieties and, if so, a less extreme level of field resistance supported by major genes may prove adequate outside Mexico.

As indicated in the 1956 Report, breeding for resistance to

*Heterodera rostochiensis* has been complicated by the discovery of eelworm populations which break down the resistance which characterised the clone C.P.C. 1673 of *S. tuberosum* subsp. *andigena*. Such populations are, therefore, distinguished by their "aggressiveness" when compared with the eelworm populations previously used in tests of resistance. In order to obtain some information on the distribution of "aggressive" populations 113 soil samples were collected from eelworm infested land in fifteen Scottish counties and in East Anglia. These samples were obtained through the co-operation of the Department of Agriculture for Scotland and the National Agricultural Advisory Service. From the tests carried out, "aggressive" populations were detected in samples from South-East Scotland, South-West Scotland and East Anglia. This survey indicated that eelworm resistance, such as is derived from the resistant clones of *S. tuberosum* subsp. *andigena* which are at present available, could not be employed successfully in about 10 per cent of the infested fields which have been sampled to date.

The discovery of "aggressiveness" in *H. rostochiensis* presents new problems in the development of resistant potato varieties. The first essential is a source of resistance to both the original and the "aggressive" populations and some progress has already been made in this respect. Six eelworm resistant clones of *S. vernei*, which is a diploid wild potato, were tested against an "aggressive" population and remained free from cysts. More material will be tested in the coming season including some 350 clones of South American origin kindly supplied by Dr Toxopeus of the Netherlands.

Meanwhile the work with the existing breeding material will continue with the object of producing varieties which will contribute to the control of the potato root eelworm in the foreseeable future without, however, offering a complete solution to the problem. The "aggressive" strains are limited in distribution and it may be possible to contain them by control measures similar to those applied to wart disease. If so, the resistance of *S. tuberosum* subsp. *andigena* which has been extensively exploited, will have a valuable contribution to make.

The Registration Trials conducted by the Department of Agriculture for Scotland in 1956 contained seven seedlings from Pentlandfield. Four of these have been recommended for further trial in 1957. A further group of eight seedlings has been submitted for inclusion in the 1st Year Registration Trials in 1957. Among the characters represented in these seedlings are field immunity from virus X, resistance to virus Y, resistance to leaf roll, field resistance to blight and resistance to the original population of the potato root eelworm.

The bulk stock of Pentland Beauty, amounting to half an acre, was grown in 1956 by the agents, Messrs Benjamin Main & Son, Ltd., Perth. The crop was inspected by the Department of Agriculture for Scotland and granted a Foundation Seed Certificate. A small virus-tested stock was also multiplied at the isolation centre in accordance with the conditions of the virus-tested scheme of the Department of Agriculture for Scotland.

Virus-tested potato stocks of twenty-nine commercial varieties and thirty-three advanced seedlings in various stages of multiplication were grown at Cauldhall. Initial serological tests made on this material revealed the presence of virus S in a few plants but when these were removed no further infections were detected during the rest of the season. It is still too early to claim that virus S has been completely eradicated from these stocks but it is considered possible that this objective may be achieved in 1957.

In continuance of experimental work on virus S the following additional species were examined for their reactions towards different strains of the virus :—

> *Atropa belladonna, Chenopodium amaranticolor, Datura metel, Hyoscyamus aureus, Nicotiana alata, N. debneyi, N. rustica, Scopolia lurida, Solanum aviculare, S. capsicastrum, S. dulcamara.*

Only *D. metel* and *N. debneyi* gave reactions of interest and their value as diagnostic host plants is being investigated.

The search for immunity or resistance to virus S in potatoes was continued in the examination of several clones of various tetraploid species of the Commonwealth Potato Collection. None of these clones showed any marked resistance but recent grafts of S-infected scions to the United States variety Saco failed to infect, thus confirming a report that this variety may be resistant to the virus.

From a small field trial laid down in 1955 and evaluated in 1956, indication was obtained of a range in susceptibility towards virus S among commercial potato varieties. Six varieties were used in the trial and the amount of infection incurred naturally ranged from 10/10 in Arran Pilot to 3/10 in Craigs Defiance as shown below.

TABLE A

| Variety | No. plants | No. infections |
|---|---|---|
| Arran Pilot . . . . | 10 | 10 |
| Craigs Defiance . . . | 10 | 3 |
| Dunbar Rover . . . | 10 | 8 |
| Majestic . . . . | 10 | 7 |
| Pentland Ace . . . | 10 | 6 |
| Up to Date . . . . | 10 | 5 |

The effects of virus S on plants of the varieties Craigs Alliance, Majestic and Kerr's Pink were assessed in a field trial of Latin Square design. Differences between growing plants of the S-infected and healthy series were less marked than in 1955 but S-infected plants of all three varieties matured slightly earlier than their healthy counterparts. On comparing yields, there was a general tendency in all three varieties towards the production of slightly smaller tubers by the S-infected plants but it was only in the case of Craigs Alliance that yield was affected to a statistically significant extent. In this variety S-infected plants produced 92·4 per cent in total and 88·5 per cent in ware of the yields of the corresponding healthy controls.

TABLE B

| Yield in lbs. | Craigs Alliance | | Majestic | | Kerr's Pink | |
|---|---|---|---|---|---|---|
| | Healthy | S | Healthy | S | Healthy | S |
| Total . | 384·25 | 355·25 | 392·75 | 400·75 | 418·00 | 402·25 |
| Ware . | 306·00 | 270·75 | 335·50 | 340·00 | 348·25 | 320·50 |

It will be noted that the S-infected Majestic plants yielded slightly better than the healthy control plants of this variety. This result might well have been due to clonal differences in yield, *vide* Cockerham and Macarthur, Rept. S.P.B.S. 1955, as two different stocks were used in this trial. The S-infected Craigs Alliance and Kerr's Pink, on the other hand, were derived from the same clonal stocks as those used for healthy controls.

The results of a field trial, laid down in 1955 to assess the resistance of the variety McIntyre and five seedlings to leaf roll and virus Y, are given below.

TABLE C

| Variety | Origin | No. of plants infected with— | |
|---|---|---|---|
| | | Virus Y | Leaf Roll |
| Arran Banner . | Scotland | 8 | 2 |
| Craigs Royal . | ,, | 15 | 2 |
| Gladstone . . | ,, | 0 | 2 |
| 2168d (1) . . | ,, | 0 | 1 |
| McIntyre . . | Canada | 18 | 24 |
| B24/76 . . | U.S.A. | 2 | 0 |
| B24/58 . . | ,, | 30 | 0 |
| F53 . . . | Germany | 33 | 11 |
| D151 . . . | ,, | 15 | 2 |

The trial was in the form of a random block with twenty-five replicates of 2-tuber plots of each variety. By making comparisons with the control varieties Arran Banner, Craigs Royal and Gladstone, it may be judged that McIntyre, B24/58, F53 and D151 are highly susceptible to virus Y and that 2168d(1), bred for hypersensitive response to the virus, is in fact resistant. With regard to leaf roll, it is evident that McIntyre and F53 are highly susceptible to the virus. The overall low infections with this virus make it impossible to assess the other seedlings although it may be that B24/76 and B24/58 show some resistance to leaf roll.

Studies on virus Y have brought to light two viruses of particular interest in that they possess characteristics which appear to link them to both the Y and the A groups of viruses. The two viruses, designated Y2 and NS, respectively, each cause symptoms typical of virus Y on tobacco and other non-potato hosts and have thermal death points between 52° and 58°C. In addition, the strain Y2 flocculates anti-Y serum and activates the gene Ny in *Solanum demissum* and *S. simplicifolium*. It differs from other strains of virus Y, however, in activating the Na gene in *S. demissum*. The virus is transmissible by sap inoculation but it has not yet been transmitted by aphides. Each of twelve potato varieties infected by sap inoculation responded by producing local lesions but none was systemically invaded. Strain NS is transmissible by both sap and aphis inoculation. It activates the Na gene in *S. demissum* but it fails to react with anti-Y serum. All attempts to infect potato varieties with this strain have failed.

A third virus, isolated from the variety Catriona, has been shown to possess all the characteristics of the C strain of virus Y and to differ from the latter only in being readily transmitted by aphides.

Selected Y-resistant seedlings derived from the following hybridisations *S. phureja* 4*x* (= *S. rybinii* 4*x*) × *S. tuberosum*, (*S. phureja* × *S. simplicifolium*) 4*x* × *S. tuberosum* and *S. stoloniferum* × *S. tuberosum* were tested for their reactions to fourteen strains of virus Y. No strain overcame the resistance of the seedlings which, according to parentage, showed either a null response to infection or a hypersensitive response.

Genetical studies on Y-resistance were continued in the examination of progenies representative of the first and second backcross to *S. tuberosum* of the resistant parents *S. phureja* and *S. stoloniferum*. Genetical studies relating immunity and hypersensitivity to virus X were also continued in material derived from *S. acaule*, on the one hand, and U.S.41956 and domestic varieties on the other.

Studies on strains of virus X comprised enquiries into the anomalous reactions of certain potato varieties towards strain $X^D$ and into the serological affinities of strains which have been assigned into groups on the basis of their activation of the two genes Nx and Nb. The results of cross absorption tests made in the latter investigation are not sufficiently complete to justify generalisation but it appears that the strains which activate the Nb gene only form a circumscribed and relatively uniform serological group characterised by the presence of a specific antigenic fraction and the absence of several antigens found in other groups. In relation to this work, the rabbits used in serum preparation were pre-tested with bovine red cells to ascertain their potential as antibody producers and, on the basis of the results obtained, rabbit breeding has been directed towards obtaining a stock of uniformly high producers.

Towards the end of the growing season our attention was drawn to an unusual mosaic disease in a potato seedling of a private raiser. The virus concerned has been identified as a strain of cucumber mosaic virus.

**Root Crops—**

*Swedes.*—A stage of the investigation into possible uses of self-fertilisation in the breeding of swedes is drawing to a close. It may be recalled that this started with the selection and self-fertilisation of plants of all types of swede obtained from field crops of commercial varieties. Pedigree lines were bred by the selfing in pollen-proof bags of plants selected in each subsequent generation. Some of these lines are still in existence, though in general they proved insufficiently distinct from the parental varieties to be worth naming as new varieties. The second stage consisted of intercrossing plants of pedigree lines representing all the main types of swede, and of selecting hybrid lines from the descendants. The crossing of some types gave very poor recombinations, particularly in respect of details of colour and form which receive considerable attention in British varieties, but satisfactory yielders of dry matter were found among the hybrid lines. Strict self-fertilisation was employed here also, and many of the lines were found, after as few as four generations, to be so true-breeding that defects in appearance could not be eradicated by further selection.

The best of the hybrid and pedigree lines were used as parents for a new series of crosses, but now phenotypically similar though unrelated lines were mated; larger numbers of selections were made from the $F_2$ generations of a few crosses; and the lines were propagated in several ways. Some lines were propagated by enforcing self-fertilisation in each generation; some were harvested from mother-plants open to pollination, though not necessarily cross-pollinated, by related plants of similar type; others were bred by alternations of these methods and in a few cases recombinations of related lines were made by hand-crossing. Lines which showed promise were generally multiplied by bulking seed from a number of plants propagated in natural isolation. From the $F_3$-generation onwards, the lines were tested in yield trials whenever possible. Trials in three years are usually considered necessary for the assessment of a root crop strain, but this was seldom possible with seed harvested from single plants. Insufficient seed could exclude a line for a generation or more, and though multiplication of a line ensured the seed supply, there were also years lost by crop failures. The performance of the major groups of lines has now been fairly well assessed, but the relative merits of individual lines within a group is more uncertain.

The conclusion seems to be that the use of the potential self-fertility of the swede holds little if any advantage over the methods practised by the Seed Trade. The seeding in mass of a large number of plants which have been carefully chosen to conform to an ideal phenotype, is an effective method of accumulating genes for certain desired characters such as intense purple colour, though less efficient for the exclusion of recessive genes. It is only infrequently that a new variety of distinctive appearance is put on the British market, and such a variety has probably been derived by inter-varietal hybridisation. If the variety becomes popular, it is propagated by a number of seed-growers and in course of time strains may be selected from it which vary somewhat in detail, and may possibly acquire new names.

Self-fertilisation, on the other hand, tends to give greater uniformity and to fix a type rapidly, which might be an advantage if only a few characters had to be considered, but is less suitable than mass-breeding for the retention of polygenes, for such elaborations as the improvement of colour or shape, and above all for the utilisation of heterosis. The mass propagated strain seems to be a mixture of cross- and self-pollinated seeds, and its vigour, as shown by yield, lies somewhere between that of the inbred line and the enhanced value of the $F_1$-hybrid. At present there is no method of producing $F_1$-hybrid seed on a commercial scale, but though the great majority of swede plants seem fully self-compatible, occasional self-incompatibility may be found, and a stock of this kind is at present being examined.

Three yield trials were carried out with swedes in 1956. Bulk samples were sown in the largest of these, and thirteen lines bred from several crosses were compared with three control varieties. Controls were also included in the other two trials where twenty-eight lines were under examination, the main comparisons being between lines of a cross. Statistical analyses of the trial results have not yet been completed, but selections were made from reserve plots after a preliminary examination of the data. In order to concentrate on the few groups which have given most promise, numerous other lines of swedes, for which seed was available, had to be discontinued, but a number of old pedigree and hybrid-lines were sown in observation plots and selected for maintenance. Any suspiciously small seed samples from plants pollinated in bags were sown out and selected. Similar selections had been made from few-seeded progenies in 1955, and these plants were examined by isolation in bags and by hand-crossing, and all the plants of one line were found to exhibit low degrees of self-fertility. Other selected plants from the 1955 trials were propagated in the usual way.

*Leafy Brassicas.*—In different parts of Scotland there is much diversity in the kinds of *Brassica* crops grown for their leaves, and also in the manner in which these crops are cultivated and fed to stock. In arable districts a considerable acreage was formerly planted out with cattle cabbage after early potatoes. Dwarf and Giant rapes are much used as catch crops and as cover crops for grass, and the acreage sown each year fluctuates greatly, but has been very large since the war. Marrow stem and thousand-headed kales became popular during the 'thirties and are grown both as spaced plants for cutting and in unthinned drills for grazing. In some parts white turnips are broadcast and grazed. There is, therefore, no simple formula for what is required in a new fodder plant, and the behaviour of hybrid combinations has to be studied both for spaced and unthinned plants, and also for sowings made at different times in the year. If the full grown marrow stem kale is excepted, it seems generally agreed that there should be a minimum of stem and a maximum yield of leaf, and in some districts it is further required that the plants should be so low growing that electric fences could be erected over them. The shortened stem of a rosette form does not appear to be a suitable framework for carrying a large weight of broad-bladed leaves, though if grazed at the right time it may be highly efficient at producing a second crop of foliage. Dwarf rape and hungry-gap kale are rosette forms, and in both cases there is criticism of the yield ; in rape because of a comparatively short period of use in the early winter, and in hungry-gap for lack of leafage, though this can be made available for feeding during a period of scarcity in the spring. These forms belong to the amphidiploid species *Brassica napus*, and are, therefore, separated from the kales of the cabbage tribe, *B. oleracea*, by a fertility barrier which is difficult, though not impossible, to surmount. The kales carry heavier crops of leafage than the rapes and have longer periods of use, particularly thousand-headed kale, which holds a considerable amount of foliage throughout the winter. On the other hand, kales develop stems parts of which become woody and useless as the plants mature. Moreover, they are regarded as inferior to rape for certain feeding purposes.

Hybridisation between *thousand-headed kale* and *kohl rabi* was started in 1952 with a view to exploiting the short-stem character of the latter, and possibly obtaining a leafy form for use into the winter. The aim was to breed a number of unrelated hybrid lines which could be combined when desired to secure heterosis. The parent plants were drawn from commercial varieties and Station strains of thousand-headed kale and from a number of kohl rabi varieties, and these latter included some, like " Earliest Vienna " and " Early Prague " which had hybrid derivatives that tended to start flowering from September onwards when sown in April. Other hybrid lines did not reach the flowering stage before January, but the leafage was at its best after a relatively short period of growth, and deteriorated later. Some kohl rabi types reappeared in the $F_2$ generation, and the foliage of most plants was scanty, but there were a few leafy segregates to be found. The short stem character of the kohl rabi was the chief point of interest, and the hybrid derivatives were mostly low growing, but only so long as they remained vegetative. Some plants had short, single stems about 15 cm. in length, compared with 60-80 cm. in thousand-headed kale. Others had short horizontal side stems with many nodes, so that the foliage was borne as a multiple rosette. Such a framework might be useful for grazing, though like the kohl rabi it would be difficult to cut near ground level. Since genes causing thickening of the stem or stems were frequently present, many of the stem systems were monstrous. It seems probable that there is insufficient yield of leaf in the thousand-headed kale × kohl rabi hybrids to develop a useful type, though the short stem character might be useful in further hybridisations, and triple hybrids have been made with broccoli as the third ancestral form.

The extreme short stem character was absent from the hybridisations of *thousand-headed kale* × *broccoli*, and though some of the derivatives were relatively low growing, others had stems quite as long as the thousand-headed kale. The main object here was to obtain the luxuriant foliage exhibited by the $F_1$ hybrid. An odd cross had been made during the war with "Royal Oak" as the broccoli parent, but the hybrid strain became feeble through inbreeding, and in 1952 when more crosses were made, one or two Royal Oak plants were used, but also plants of Veitch's Self Protecting broccoli, which was thought to have a larger leaf. Thirteen months elapses between sowing and curd formation in Royal Oak and its hybrids have shown no tendencies towards early flowering, but Veitch's Self Protecting broccoli with a vegetative season of less than seven months, gives hybrid derivatives many of which flower in the autumn. Evidently types with a long vegetative period should be chosen as parents, and plants of sprouting broccoli were used this year for new hybridisations. Some crosses between thousand-headed kale × cabbage have also been made.

The hybrid lines derived from thousand-headed kale × Royal Oak broccoli sown in April were still vegetative in January. Their leafage was good, but their stem system ranged between single rather long stems and the branched system of thousand-headed kale. In all these hybrid derivatives, the progenies of sib matings developed somewhat feebler plants than those in which the parents were unrelated. Both types were grown and compared, but because some of the crosses were rejected for one fault or another, there were few unrelated families left among the thousand-headed kale × broccoli derivatives to give good combinations.

Trials of widely spaced plants and of plants in unthinned rows were laid out in 1956. Hand-crossing in the greenhouse had provided ample seeds for the former, which were transplanted from seed-beds, but the row trials required rather more seed, about 1,200 per treatment, and this was obtained from isolations of pairs of plants, so that fewer samples were available from which to choose. The row trials were laid out as 6 × 6 Latin Squares having plots of two rows 244 cm. long and each sown with 100 viable seed. Seed-treatment kept the flea-beetle off, but the emerging seedlings were much reduced in number by sparrows which pulled them out of the ground. There were three trials of this kind, one containing lines of marrow stem kale types, one for thousand-headed kale lines, and the third for hybrids. Two Royal Oak broccoli crosses were best among the hybrids, a Veitch's Self Protecting broccoli cross ran to flower, and a line derived from a kohl rabi cross was also useless.

Weighings were made in August and November of the yields of leaf and stem in measured lengths of row. There was about the same amount of leaf on each date, but the weights of stem had greatly increased by November. When grown in crowded rows all types exhibited lengthened and generally unbranched stems. The thousand-headed kale control was tallest, measuring a metre to the highest point of leaf, and this also gave the heaviest yields of stem and leaf. One of the lines derived from kale × Royal Oak broccoli equalled the control for yield of leaf on both dates, though its stems were little more than half the weight of the kale stems. As the mother plant had been open-pollinated with sibs, this was an encouraging result. The height was about 70 cm.

Hybrid kales were also transplanted into plots of twenty in a five-plicate lattice trial. Nearly all the plants survived and grew well in the wet summer. There were sixteen treatments and it was possible in some cases to compare $F_1$ hybrids of the original crosses with a later generation. The weight of stem and leaf was noted individually for nine plants in each plot during November and December. By that time two lines of kale × Veitch's Self Protecting broccoli had shot to flower and were discarded as worthless. Two lines of a backcross on to kohl rabi closely resembled that form and had also shot to flower. The actual weights of so few plants have little value, but the leaf yield of thousand-headed kale plants was only exceeded by one hybrid, and this was an $F_1$-generation of which all four $P_2$ plants had been unrelated, viz., one broccoli, one kohl rabi and two kales. The Royal Oak broccoli hybrid lines were attractive and had somewhat higher ratios of leaf : stem than the kale control, but the kohl rabi hybrids had somewhat lower ratios.

The trials discussed above refer to sowings made in the middle of April, but other possible sowing dates have also to be considered, especially catch-cropping after early potatoes. There was not sufficient seed of any of the hybrid lines to sow an elaborate trial of unthinned rows, so ten treatments were sown in unreplicated blocks on different dates during the summer. The behaviour of marrow stem and thousand-headed kales, dwarf and giant rapes and hungry-gap kale were observed, together with five hybrid lines representing the various combinations of kale, broccoli and kohl rabi. Unfortunately, the sowings made after June were failures, and all that could be said of them was that the rape forms made better growth than the rest. The rapes and hungry-gap grew faster than the kales for the first month or two in all the sowings, but they then slowed down and were overtaken by the kales. None of the hybrids was outstanding, the Royal Oak broccoli hybrid-line having the best appearance. On different dates measured lengths of row were cut, and the yields of leaf and stem ascertained. The leaf was further divided into midrib and lamina, and the dry matter of each was estimated. The lamina contains 3-6 per cent more dry matter than the petiole, and as the proportions of lamina and petiole fluctuate greatly on leaves of the same plant and at different stages of growth, the difficulties of sampling are formidable.

The trials of marrow stem and thousand-headed kale lines are also being examined and yields of leaf and stem have been determined.

**Sugar Beet.**—The sugar beet research programme is mainly concerned with problems of obtaining and maintaining a strain which can withstand tendencies to bolt when sown early, or under unfavourable conditions in the northern parts of the beet growing areas. The work is undertaken at the request of the Sugar Beet Research and Education Committee of Great Britain, and is co-ordinated with that of the Plant Breeding Institute, Cambridge.

The change of date for the compilation of this Report entails a difficulty which affects all the root crop and brassica work, but the sugar beet particularly. Though the field work may have finished, the results have not yet been statistically analysed. The notes on sugar beet work given in previous Reports were based on detailed reports prepared for the Sugar Beet Research and Education Committee for the year ending 31st March, and in order to avoid erroneous assumptions it is proposed to defer discussion of the current programme until next year. In another part of this publication, some work on a particular problem of the Sugar Beet investigation is presented as an occasional paper.

## Publications

GOVIER, D. A. (1957). The properties of tomato aspermy virus and its relationship with cucumber mosaic virus. *Ann. appl. Biol.* **45** : 62-73.

*Chrysanthemum* plants infected with tomato aspermy virus (TAV) produce severely distorted and discoloured flowers but show only slight leaf mottle.

TAV infected twenty-five of forty-five species (belonging to seventeen genera) tested and was transmitted by the aphid species *Aulacorthum solani*, *Macrosiphoniella sanborni* and *Myzus persicae*.

Sap from infected tobacco leaves lost infectivity when diluted more than 1 in 10,000, when heated for 10 min. at above 65°C. and when stored for more than 42 hr. at 16-18°C.

Partial protection was obtained between TAV and two strains of cucumber mosaic virus. Evidence was obtained that this was true protection between related viruses and serological tests confirmed the view that TAV is a strain of cucumber mosaic virus.

GREGOR, J. W. (1956). Adaptation and ecotypic components. *Proc. Roy. Soc. B.* **145** : 333-337.

Botanical ecotypic investigations are still largely concerned with defining the patterns of ecotypically differentiated populations. Those patterns suggest that in the cross-fertilising plants ecotypic differentiation only becomes appreciable with the aid of at least a modicum of extrinsic isolation, except occasionally where, for instance, very strongly contrasting habitats happen to adjoin. The maintenance of a high intra-population variance in the face of what appears to be rather strong selection suggests that a broad ecological tolerance on the part of genotypes, attained by phenotypic adjustment, is ecologically an attribute of importance. Yet despite possessing a relatively high part of the species variation different habitat populations often exhibit striking individualities, but it is surprising how little of the variation contributing to these individualities has actually been shown to be ecoclinally distributed, and thus demonstrable as ecotypic.

GREGOR, J. W. (1956). Genotypic-environmental interaction and its bearing on a practical problem of international interest. *7th Intern. Grassland Congr. Paper No.* 18.

If the principle is accepted that the main object of herbage-plant strain trials must inevitably be to provide an estimate of potential usefulness, then it is not a very revolutionary step to accept the idea of conducting trials under conditions that have no exact replica in agriculture yet have a reasonable prospect of revealing a strain's probable place in agricultural practice. From the stand-point of the international exchange of strain information it becomes most desirable that the difference between a strain's actual performance in a given agricultural environment and its potential usefulness should be clearly understood. Thus in seeking a broader utilisation of trial results to meet the needs of international trade strains will not only have to be described in terms of those attributes which are indicative of potential worth, but the techniques employed in the assessment of such attributes will need to be standardised to provide an internationally equivalent scale of values. The position would be further improved if each country were to maintain a national register of the names of its native strains together with descriptions compiled from the results of standardised *potentiality* trials. However, a register loses much of its value unless at the same time steps are taken to ensure that *authentic* stocks of the named strains are in fact available.

HARBERD, D. J. (1956). Correlated Characters in Population Studies. *New Phytol.* **55** : 154-163.

For any pair of correlated characters there are an infinite number of pairs of independent derived ones. The different pairs of derived characters have slightly different properties. Among them one pair is likely to be of more biological interest than the rest; another, having the most extreme statistical significance, is the discriminant function.

A method is given for resolving correlated characters into independent ones, together with the appropriate means of analysis.

WATSON, P. J., and GREGOR, J. W. (1956). Reflections on hill-land improvement. *Herbage Abstracts* **26** : 137-145.

The extensive literature relating to the subject of hill-land improvement shows that the problem has been tackled from different angles in many countries though the most universally applied treatments have been ploughing-up, manuring and reseeding. Difficult terrain often makes these methods impossible to carry out economically. There have been many instances of the natural vegetation having been changed by the introduction of sown seed and also by manuring alone but the altered balance induced by such methods may not necessarily be beneficial since so little is yet known concerning the value of individual communities or even of the attributes of the species which compose them. Some chemical analyses of the components of plant communities have been carried out and the results are helpful as a guide to their usefulness. An interesting development has been the direct observation of grazing animals and assessment of the seasonal utilisation of different communities. The availability at a critical period of certain elements in the vegetation may be of greater importance to the grazing animal than their total productivity. The integration of land when improved, into the economy of the hill-land farm must be considered and the question of winter keep requires due attention. The use of complementary grazing involving the use of sown pastures or natural vegetation or a combination of both is discussed.

# THE PASTORAL UTILISATION OF NATURAL HILL VEGETATION

Patricia J. Watson

Hill land has always presented a problem to a community intent upon making the best use of its agricultural potentialities and in times of economic stress this problem inevitably becomes acute. The more fertile and easily cultivated lands of the lowlands have presented their own difficulties but with the help of increasing knowledge and technical skill, the breeding of new crop varieties and the availability of fertilisers, the productivity of the lowland arable acreage can now attain a very high level. The natural features of hill land are, however, a serious obstacle to the improvement of the many acres within Great Britain alone and one which cannot be overcome with both ease and economy. It is, nevertheless, obvious that any improvement which could be carried out would be of very great value to the country since even with the hill grazings in their present state, the economist authors of the recently published *Agricultural Significance of the Hills*, have come to the somewhat unexpected conclusion that the subsidies paid to hill farmers give a better return to the taxpayer than do those granted to lowland farmers. Indeed they say that if the object is to pay a subsidy according to the amount and value of farm production, then the hills and uplands have been rather under-subsidised. There is scope for much improvement and such heartening statements should act as an incentive to those interested in hill land to find the best methods of bringing about this desirable state of affairs.

There are upland areas where the problem is not so much that of hill land proper as of the marginal land type and in such, efficient amelioration can be effected by draining, liming and manuring and in some cases, where the soil cover is not too thin, ploughing-up and re-seeding may be economically worth while. Steep rocky slopes, boulder-strewn moorlands and poor pasture growing on thinly covered rock surfaces do not permit of the use of such direct methods.

The difficulty of transporting labour and materials to many of the relatively inaccessible hill areas provides another obstacle to their improvement and though the use of the aeroplane has been suggested, few attempts have been made to discover the potentialities of this promising method in Britain. It is interesting, therefore, to learn of the great importance of aircraft in the agriculture of New Zealand. In that country one of the chief obstacles in the way of the economic operation of a system of aerial distribution of fertilisers has been largely overcome by the construction of air strips close to the hill areas which require attention and in 1956 nearly four million acres were top-dressed from the air. It must be remembered, however, that the chief need under New Zealand conditions is for phosphate and a relatively small amount can effect a marked improvement. In Britain where large amounts of lime are frequently necessary before any other fertilisers can be usefully applied, it is possible that the economic return would be small, at any rate in the initial stages. It is unlikely that many individual cultivators of farms including hill land would be in a position to finance the cost of improvement of their relatively small acreages by means of the aerial sowing of fertilisers plus the initial heavy dressings of lime and unless a co-operative, grant-aided scheme were evolved, the use of aircraft seems to be impracticable.

The aeroplane is also being used for sowing seed in the hill areas of New Zealand, nearly 51,000 acres being treated in this way. It is, however, interesting to note that a slower but cheap method is being investigated. It is known from the work of various authors (Harmon and Kein, 1934; Dore and Raymond, 1942) that the seeds of at least some valuable fodder plants remain viable through the processes of mastication and digestion in the grazing animal. Herding of sheep which had grazed on a pasture containing seeding clover on to a clover-deficient hill area could result in the dissemination and establishment of a useful number of clover plants (Suckling, 1952). In New Zealand hill areas are very closely grazed immediately before the sowing of seed thus ensuring a quick contact with the surface.

The problem of the short period during which the natural hill vegetation is actively growing is common to most countries, however different their climatic conditions may be. It is interesting to note however that in different localities the application of artificial fertilisers to natural pastures and to sown swards alike does not necessarily give similar results. Hafenrichter (1956) found a rise in total protein content but no increase in the earliness of fertilised natural pastures on the sub-humid foothills of Western Oregon and Washington as compared with untreated, although under the conditions prevailing in the foothills of California, dressings of fertiliser rendered the natural pastures ready for grazing at least a month earlier than usual. In this latter area swards sown with specially selected strains of grasses and legumes and fertilised were at least a further month in advance of the untreated natural swards and, moreover, remained green for about six weeks after the annual strains had become mature and desiccated. Love and Williams (1956) came to similar conclusions concerning the application of fertilisers to range lands in California and consider that the earlier availability of grazing is the most important result of such treatment though they also stress the increase of total yields and the useful possibility of reducing the effects of the normal yearly fluctuations due to climatic changes. The growing period from late March to early July at the best, is of extreme shortness in the sagebrush-grass type of range land in the Western United States yet this type is said to be of great importance for grazing most of the year (Pechanec, 1956). The relatively low nutrient content of the forage by autumn is offset to a certain extent by the somewhat higher content of the widespread shrub growth. Nevertheless, under conditions of necessity, cattle and sheep feed on these areas from spring till autumn when they have to be moved to lower ground although the more usual practice is to herd them to grazings at high altitudes during the summer where such are available. Efforts to improve this type of range land have so far been directed to the removal of undesirable species by spraying and a policy of careful re-seeding and good grazing management.

The general floristic composition of the hill grazings in Britain is a matter of common knowledge and several workers have examined the most obvious components of the vegetation in an endeavour to determine the valuable nutritional elements which they contain. Chemical analyses of plants such as drawmoss and heather were carried out by Thomas and Trinder (1947) who came to the conclusion that the rich mineral resources of the drawmoss could be complementary to those of heather. Further, heather provides some of the minor elements which are absent from the grass component of hill pastures. In a series of experiments with sheep under natural conditions, Peart (1951) showed that heather provided a most valuable constituent in the spring diet and Armstrong and Thomas (1953) found that even in winter heather can compare favourably with hay of moderate to poor quality. The habit of growth of heather incidentally adds a further point in its favour since under moderate snow cover, the plants are shaken free of snow by the movement of the sheep themselves and are thus made available for grazing. Such results point to the efficiency within the hill economy of at least one floristic element in the natural vegetation and experiments have been commenced by Hunter which approach the question from a different angle. He hopes to assess by means of continuous detailed observations over a long period the relative values of different types of hill grazing for sheep. He has come to the conclusion from observations already carried out (1954) that it is less a matter of the productivity of a given vegetational type which determines its value to the sheep and rather a question of its availability at different seasons of the year.

In a recent paper by Thomas and Fairbairn (1956) attention is drawn to the fact that even the poorly regarded *Nardus* may not be entirely undesirable since in June the crude protein content may be as high as 16 per cent and it has a digestibility of nearly 60 per cent.

Investigations of this nature are most interesting since they suggest methods of improvement which may appear to be unorthodox. Following this line of thought, it may be more important to adjust the proportions of the plant communities rather than to attempt a general improvement over a wide area. How such an adjustment could be achieved is suggested by the work of Scott (1956) in South Africa and Mitchell (1956) in New Zealand. Both workers are concerned with the effect of defoliation, whether by cutting or by grazing, upon the growing plant and both emphasise the serious result upon all species. Scott has carried out further investigations into the growth rhythms of different species and concludes that "if the periods of elongation (of the internodes) and times of differentiation of the inflorescence are different in the most important species, it would be possible to rest the veld for a certain period to encourage the flowering of a desirable species and to mow or practise heavy grazing at a stage when an undesirable species is particularly vulnerable to defoliation."

It is of interest to note that Scott places the emphasis on when to rest rather than when to graze a sward, perhaps a small point but one which stresses the importance of developmental studies. It is as well to bear in mind that detailed work on individual species has already revealed, for example, the existence of different chromosome races within species as in *Agrostis* (Davies, 1953; Jones, 1956), *Festuca ovina* (Jenkin, 1933, and Watson, unpublished), *Holcus* (Beddows and Jones, 1953), *Molinia* (Guinochet and Lemée, 1950). Even within a single chromosome type ecotypic races may occur as in the altitudinal races in the diploid sexual and tetraploid viviparous fescues (Watson, unpublished). Such differences indistinguishable as they may be to the general observer, are likely to be reflected in the agricultural values of apparently comparable vegetations and will almost certainly become obvious in a varying response to any uniform method of improvement. The British school of ecologists have been accustomed to summarise the most obvious features of a community without enquiring into the detailed variation which undoubtedly exists. It has been customary for example to talk of a heather-dominant vegetation as *Callunetum vulgaris* though the different communities to which this term is applicable may vary considerably in detail and therefore have quite different agricultural values. Until, therefore, more work has been carried out on these detailed problems and at least an idea of the geographical distribution of the variants has been acquired, it could be a somewhat uncertain matter to suggest a broad scheme of improvement for the natural hill vegetation.

In Britain it is common to advocate the keeping of more cattle particularly in view of the benefits derived from their less selective grazing habits and the damage which they cause to the bracken which certainly constitutes one of the most serious problems of the hill land. The cutting, which must be constantly repeated in order to be effective, even when the fern appears to be practically eliminated, is an expensive item with present-day labour costs. However desirable it is to have cattle on the hill grazings, they must be in sufficiently large numbers to effect a noticeable improvement and it is at this point that the most serious limiting factor becomes apparent. It would be quite possible for the present hill grazings to carry some more stock during the summer months but that increase would put an impossible strain upon the already small amount of winter feed. It is imperative, therefore, that any scheme to increase the number of grazing animals upon the hills, with the laudable aim of improving the grazing conditions, must first attack the problem of making provision for those months when there is little or no natural growth.

In Scotland the period during which the hill vegetation can supply a diet of reasonable protein content is relatively short lasting from early June until September and no change in the composition of the vegetation due to manuring is likely to extend the period materially although the yield of protein may be considerably increased. In fact, in areas where it is possible to re-seed hill pastures, little difference in earliness can be detected under usual conditions of management since the sown grasses are equally subject to the prevailing climate. During the major part of the year, therefore, the natural hill vegetation provides a fair quantity of dry matter but of low protein content and this must be supplemented if the stock-carrying capacity is to be increased. Gordon and Sampson (1939) remark upon a similar deficiency of protein for beef cows grazed on the natural pastures of the San Joaquim Range, California. They experimented with feeding a protein supplement to one group and found that the cattle in that group not only thrived better but also consumed more of the low-protein herbage than did those which did not receive any addition to the natural diet. Under Scottish conditions the purchase of supplementary protein-rich feed is not customary and the hay or silage normally produced by a hill farm is frequently not sufficient in quantity. Some help could be obtained, however, from an application of the complementary principle.

In this country hill farms consist of an acreage of arable land together with a large area of hill land or the right to share in the grazing provided by these upland areas. As a general rule the return in cereals and roots from the arable acreage is small under the high rainfall conditions prevailing in hill country and it does not seem likely that changes in cultivation methods would make a sufficient difference. It would, therefore, seem quite feasible to restrict the rotational crops to the best land and utilise the poorer areas adjacent to the hill grazings for sown grass, a crop which is known to thrive under the climatic conditions and which can be treated intensively with profitable results. In this way the maximum yields for such districts could be realised from the rotational crops whilst providing the means for maintaining an increased number of grazing animals on the hill and in better condition. Such sown swards, which have been described as "successional" (Gregor, 1942), can be used as the complements of natural vegetation. Swards of this type treated with heavy dressings of nitrogenous fertilisers together with adequate amounts of basic dressings from mid-March will provide a high protein diet from mid-April. This high quality production can be maintained until the natural growth commences on the hill by the combined use of manures and grass strains of different maturity. As soon as the native grasses are growing satisfactorily, the arable fields may be shut to stock and silage or hay crops taken to supplement the winter feed. A further period of grazing is possible in the autumn provided it is not prolonged too late in the season. A series of experiments along these lines was carried out (Gregor, 1947; Gregor and Connell, 1948) with satisfactory results. The lavish application of nitrogenous fertiliser up to two tons per acre during the growing season, seems rather extravagant under general conditions but is necessary to realise the full potentialities of the cultivated grass in such a complementary system. The arable swards are scarcely trampled or fouled since the animals are able to obtain (in a matter of little more than twenty minutes) sufficient high quality feed to enable them to thrive and utilise the roughage provided on the hill grazings. It is obvious that under such a system a slow improvement in the adjacent hill pastures is likely to take place and that this improvement will spread further as the policy is continued. However slow it may be, this improvement will be of very great value to the hill farmer and will gradually increase his stocking capacity with relatively little outlay or effort.

A good example of an application of the principle involving a number of swards is given by Hafenrichter (1956). On the Californian foothills the productive period can be considerably extended by using seeded perennial pasture, fertilised annual pasture, untreated annual pasture and seeded perennial pasture in that order. The principle may also be applied to provide part-time protein rich grazing as a supplement to the low-quality natural pastures at particular seasons of the year.

It may be that there is no arable land both suitable for re-seeding and sufficiently close to the hill grazings to be of use under a complementary system. It does happen that the nearest land is unploughable because of the number of boulders, the thinness of the soil cover or where the light sandy soil of some coastal districts makes seed establishment a matter of difficulty. In many such cases the natural sward of these areas is of a higher quality than that of the upland grazings and since they are accessible, it is possible as an alternative to ploughing to give the existing vegetation intensive manurial treatment. A further series of experiments (Gregor, Watson and Connell, 1949, 1950) showed that such treatments can have so beneficial an effect that after a period of four years the natural swards could compare favourably with re-seeded in everything but the length of growing period since they did not commence growth much earlier than untreated hill areas. As far as the dry matter and crude protein yields during the summer months were concerned, however, the treated natural swards were quite equal to the re-seeded. The effect of the manurial treatment upon the floristic composition of the sward was very marked. In the case of *Agrostis/Festuca* swards there was a widespread replacement of the less nutritious fescue by smooth-stalked meadow grass, *Poa pratensis*, which is evidently more capable of utilising the large amount of nitrogen efficiently. The change was very striking in one instance where *Poa pratensis* had been a very minor element in the sward (2 per cent) but under the manurial system increased to 58 per cent (Gregor and Watson, 1953). The importance of this change can be appreciated when it is added that the yield from this intensively treated sward was 270 per cent greater than that from a similar one treated over the same period with phosphate only. Such intensively treated natural swards do not contribute much to the difficult spring period but they can provide material for conservation and would be invaluable for stepping up summer milk production.

It can be readily appreciated that the utilisation of hill land is a subject which has many aspects and much research remains to be pursued in what may appear to be unrelated fields of study. It is obvious that a great deal can be achieved by the use of manures, sown swards of different maturities, the complementary use of artificial and natural plant communities and even the use of differential herbicides, but it would seem that the grazing animal itself must to a large extent be regarded as the principal improving agent under most conditions. Yet before it can be used with maximum efficiency, much more must be known about the responses of the constituents of hill vegetation to animal activity so that changes can be controlled with a view to realising the potentialities of these extensive areas.

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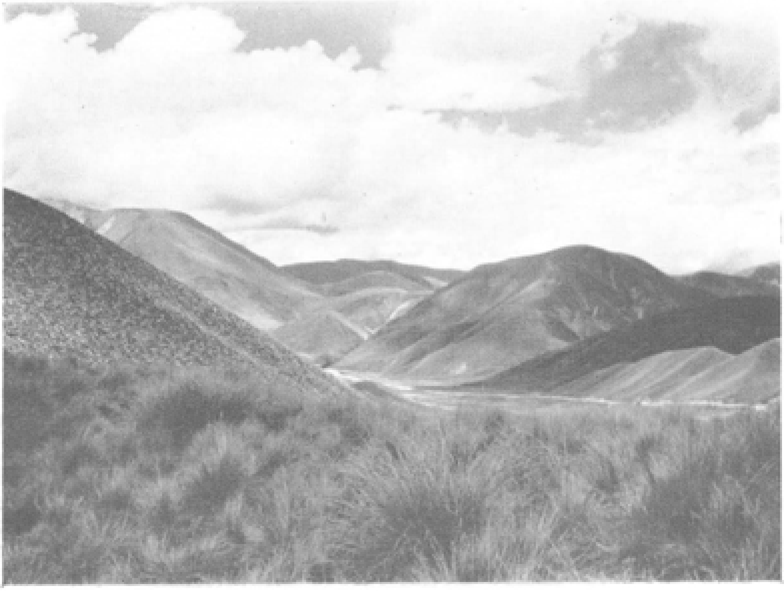

Mixed Tussock at 3,400 feet with Tall Tussock beyond (January).

Exotic Legumes among Hard Tussock at 2,200 feet (November).

# THE PASTORAL UTILISATION OF NATURAL HILL VEGETATION: NOTE ON THE TUSSOCK GRASSLANDS OF NEW ZEALAND

J. W. Gregor

A point that will immediately strike the visitor to New Zealand is the remarkable success achieved by alien species in the pastoral economy of the country, and on first impressions one is inclined to imagine that it is only a matter of time before the remaining natural vegetation will be replaced by exotic introductions. It is certainly true that in North Island in particular, where pastoral development of hill land has involved the conversion of forest, or secondary scrub, alien species are very much in evidence. In marked contrast to these very recently developed North Island hill pastures are the extensive indigenous tussock grasslands of South Island. These grasslands fall roughly into three altitudinal categories dominated by different tussock species, and the respective techniques devised for their improvement vary very considerably. Where the total destruction of tussock and its replacement by cultivated pasture happens to be practicable, and free from the risk of dire consequences, then improvement follows orthodox lines. The grasslands dominated by the large Red Tussock (*Danthonia rigida*, Raoul) are a case in point for though *D. rigida* does occur at relatively high altitudes, it is essentially an inhabitant of sour but, in the main, potential arable land at low elevations. As a rule the conversion of Red Tussock to productive pasture presents no peculiar problem and for that reason these communities receive no further comment here. On the other hand, an entirely different and novel set of problems is presented by the sub-alpine tall- and montane low-tussock grasslands for here the destruction of the tussock species may actually make pasture improvement extremely difficult, if not impossible. These indigenous species have evolved in the absence of grazing animals and their continued survival since the introduction of sheep is probably a reflection of their unpalatability even after burning.

From the time of settlement (1840-1860) burning of both tall- and low-tussock country has been extensively practised, partly to destroy unwanted plants and partly to induce a more palatable herbage. The disastrous effect of such treatment is now apparent in many localities where interference with the tussock has resulted in serious soil erosion. On the basis of the available evidence, Zotov has reached the conclusion that in the past the climax vegetation at elevations between about 1,800 ft. and 3,500 ft. was forest. Within the area of low precipitation below the old forest line, grass associations appear to have been a feature of the original vegetation. The same is almost certainly true of the area extending from the 3,500 ft. forest limit up to somewhere in the region of 6,000 ft. Thus the intervening tussock grassland that replaced the destroyed forest, and which, incidentally, was already present at the time of European settlement, must be regarded as being of comparatively recent origin, and on that account has been called the *induced steppe* formation by Zotov.

The pastoral potentialities and floristic differences which separate the sub-alpine tall- and montane low-tussock communities make it necessary when considering the improvement of these grasslands to treat them as distinctive pastoral entities despite the fact that in nature the line of demarcation is not always clear.

**Tall Tussock.**—The tall-tussock grasslands are dominated by large Snow Tussock (*Danthonia flavescens*, Hook. f.) and occur over an area of about five million acres on the mountains of South Island at altitudes between approximately 2,500 ft. and 6,000 ft. There is some evidence to suggest that much of the present day *D. flavescens* is a relict population which is now out of tune with the prevailing climatic environment. Apparently seedlings are seldom seen and as the individual plants are reputed to be very long lived the chances are that generations replace each other at very long intervals, and it may even be that the majority of individuals comprising the present population date back to a previous climate. If this is a correct appreciation of the situation then unless the species can respond selectively to the current climate, its ultimate disappearance can be foreseen. Be that as it may, one thing is certain and that is that much of the original high-altitude tussock is either in the process of disintegration or has already deteriorated to such an extent that scree has taken its place.

A flourishing *Danthonia flavescens* community is, practically speaking, of negligible pastoral value, and if in the interests of stock it is opened up by fire the danger of initiating soil erosion becomes very real. Indeed the Tussock Grassland Committee are convinced that damage done by fire and the grazing animal is the major factor responsible for the lamentable expansion of the eroded areas, and have even gone so far as to say that there is no justification for retaining high-altitude snow-tussock grassland in pastoral use *until some method of re-vegetation is found*. On the face of it there would seem to be no compromise possible between soil conservation and pastoral interests, though the rehabilitation of a healthy tall tussock would by preventing erosion confer an indirect benefit upon farming in general. In the meantime, therefore, it is only reasonable to take all practicable steps to protect the surviving Snow Tussock from the hurtful agents that are known to lead to its destruction.

**Low Tussock.**—The principal Tussock grasses belonging to this category are Hard Tussock (*Festuca novae zealandiae* Ckn.), Silver Tussock (*Poa caespitosa* Spreng.) and Blue Tussock (*Poa colensoi* Hook. f.) the first being most generally abundant, gives character to much of the low-tussock grazings, especially those in localities of low precipitation and strong insolation. Although Blue Tussock is evidently the least abundant of the three it has the reputation of being relatively palatable, and for that reason it may well have its own particular contribution to make to the pastoral development of tussock grassland.

Within the last hundred years or so certain alien pasture elements have succeeded in gaining a footing in the low-tussock country and this has encouraged attempts to bring about improvement by the intentional sowing of exotic plants of recognised pasture value. For instance, Sewell (1950) reports how the introduction of cocksfoot into some 1,800 acres of mixed Hard and Silver Tussock rendered the sward more valuable. The use of leguminous plants is a feature of current improvement experimentation. It so happens that unpalatable *Carmichaelia* spp. are the only indigenous legumes in this tussock country and their influence upon the nutrition of associated vegetation is certainly not obvious and is probably very slight. Hence the exclusive use in these improvement studies of exotic species. Yet raising the nitrogen fertility of the soil by the introduction of these exotics to a level sufficiently high to enable the pasture components of the vegetation to flourish may well have unforeseen and even dire consequences. For instance, if the indigenous tussock species were to be rendered more palatable, and, therefore, more vulnerable to animal attack, their extinction might be the ultimate result. That a rise in soil fertility can occasion an uncongenial environment for tussock was observed in a small, sheltered area where stock had been receiving supplementary feeding. At the centre of this patch where fertility was obviously highest, the alien grass *Poa pratensis* had formed a dense and vigorous sward in which only remnants of Hard Tussock were visible, whereas at the periphery, where less fertile conditions obtained, the *Poa*, much reduced in vigour, occurred only as a minor element in a normal stand of tussock. This example shows that it is possible under certain conditions to establish an exotic sward, and it may even be that in the more favoured localities of low-tussock land, especially where irrigation is practicable, the tussock species will ultimately be regarded as superfluous and swards composed solely of pasture plants established and maintained. But taking into account the probability that over the greater part of the territory climate will remain a major limiting factor to improvement, especially in so far as the use of exotic introductions is concerned, the application of any large-scale treatment that is likely to lead to the extinction of tussock might easily be calamitous because it has still to be established that a permanent improvement can be attained without the aid of the protective tussock. Before risking taking a step that may have irretrievable consequences it is perhaps well to ponder the history of hill-land improvement which has so often revealed that it is one thing to achieve initial success, but quite another to maintain it indefinitely.

For economic if for no other reason it is fairly certain that sheep must remain the principal users of these tussock grasslands, and it may be that even at the higher levels of soil fertility a desirable balance between pasture elements and tussock could be maintained provided appropriate grazing techniques could be found. Whether cattle can be employed more successfully than sheep in holding this balance has still to be proved. There are, however, those who believe that it would be easier to do so, and at the same time keep a better ground cover, by adopting a narrow cattle/sheep ratio since cattle graze less severely than sheep. On the other hand, cattle being less selective in their choice of food plants are not so likely to discriminate between tussock and the associated pasture species. One suggestion which has gained considerable support is that regardless of whether cattle or sheep are employed, a system of rotational " mob " stocking is preferable to the customary set stocking. However, no matter what system of controlled grazing is ultimately adopted, and there would seem to be little doubt that some form of control is urgently needed, fencing will have to play a part, but in view of the expense it would be unrealistic to imagine that more than just a fraction of the tussock acreage would warrant sub-division to any great extent. Yet, if it were possible to bring about improvement by this means even on a limited scale the effects might in time influence grazing management far beyond these more intensively treated areas.

However, experiments relating to grazing techniques must perforce take into account the long term ecological consequences of animal activity, which in turn require a detailed knowledge of the floristics of the region concerned. With the New Zealand situation in mind it is now some years since Cockayne, aware of deficiencies in this respect, emphasised the hopelessness of understanding the ecology of a community until the taxonomic status of its components is understood. While the taxonomic situation has materially improved since then it is, nevertheless, interesting to note that in the programme of research recommended by the Tussock Grassland Research Committee in 1954 with reference to the snow-tussock grasslands of South Island, the taxonomic study of *Danthonia flavescens* heads the list of proposals. In New Zealand at the present time the work of the taxonomist is being supplemented by experimental taxonomic investigations, and Connor's study of the four native species of *Agropyron* affords an example of the usefulness of this bio-systematic approach. The ecologist, it is true, cannot be expected to make field identifications below the rank of ecospecies for at the ecotypic level such identifications are virtually out of the question. But that is no reason why infra-ecospecific variation should be disregarded for the chances are that ecospecies of high ecological tolerance are ecotypically fractionated and that not all the fractions will respond similarly to a given treatment. Moreover, a detailed knowledge of the life histories, breeding systems, seed setting, germination and seedling survival of sward components will be of real practical significance when contemplating the improvement of natural grassland

and especially such difficult subjects as the mountain tussock lands of New Zealand where pastoral problems are so intimately linked with those of soil erosion.

To what extent exotic introductions can be successfully employed to increase the productivity of these upland grazings it would be unwise to predict. The possibility that they will not play any appreciable part much beyond the more environmentally favoured areas cannot, however, be ignored, and on this account, if on no other, the exploration of the structure and pastoral potentialities of the native species is a worth while task.

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I am most grateful to Mr Harry M. Sievwright of the New Zealand Department of Agriculture for giving me the benefit of his wide experience of tussock-grassland farming and its problems, and also interesting days in the field.

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# INCIDENCE OF PHYSIOLOGICAL RACES OF *PHYTOPHTHORA INFESTANS* IN VARIOUS COUNTRIES

W. Black

Pathogenic variation in *Phytophthora infestans* was noted by Gidding and Berg (1919) when an isolate of the fungus taken from potato caused no disease on tomato, whereas an isolate from tomato was pathogenic to both potato and tomato. Other noteworthy records of differences in pathogenicity were made in 1932 when hybrid potato seedlings that had hitherto behaved as immune, succumbed to the disease (Schick, 1932; O'Connor, 1933). Since that time physiological races of the parasite have been found in many countries, sometimes associated with hybrid seedlings bred from blight resistant species, sometimes only with commercial varieties of *S. tuberosum*. Investigations on pathogenic variation carried out independently in different countries resulted in the establishment of several collections of differential host plants and of cultures of the fungus. How far these collections corresponded with one another was not known until the differential host plants employed in Holland, U.S.A. and Scotland were exchanged for test purposes and an international system of classification was formulated (Black *et al.*, 1953). The adoption of this scheme has made possible the comparison of races occurring in different countries and the assessment of their distribution over wide areas.

Since 1947, when the fourth R gene controlling hypersensitivity was recognised, many isolates of the blight fungus from various countries have been received for identification at the Scottish Plant Breeding Station. The different races distinguished in these tests and the countries from which they came are shown in Table I together with races reported by others as indicated by the references given. This combined Table provides an indication of the distribution of biotypes in widely separated parts of the world. It shows that 15 of the 16 races identifiable by the existing host series have been found, including the race with the widest host range, viz. 1,2,3,4. Race 2,3 is the only one not so far recorded. The Table also indicates that the most widely distributed races during the past five years were 4, 0, 1,4 and 1 in that order.

The relatively wide distribution of races, 1,4 and 1 may be attributed to the increase in the cultivation of varieties possessing the gene $R_1$ during the past decade.

## TABLE I

### DISTRIBUTION OF RACES OF *PHYTOPHTHORA INFESTANS* OBSERVED OR REPORTED IN LITERATURE

| Country of Origin | Ref. | Physiological races | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 0 | 1 | 2 | 3 | 4 | 1, 2 | 1, 3 | 1, 4 | 2, 3 | 2, 4 | 3, 4 | 1, 2, 3 | 1, 2, 4 | 1, 3, 4 | 2, 3, 4 | 1, 2, 3, 4 |
| Scotland | .. | + | + | .. | + | + | .. | .. | + | .. | + | + | .. | .. | +[a] | .. | .. |
| England | .. | .. | + | .. | + | + | .. | .. | + | .. | .. | + | .. | .. | .. | .. | .. |
| ,, | 1, 2 | + | + | .. | .. | + | .. | .. | + | .. | + | .. | .. | .. | .. | .. | .. |
| N. Ireland | .. | .. | + | + | .. | + | + | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| ,, | 6 | + | + | + | .. | + | + | .. | + | .. | .. | .. | .. | + | .. | .. | .. |
| Eire | .. | .. | .. | .. | .. | + | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Holland | 4 | + | + | + | .. | + | .. | .. | + | .. | + | .. | .. | + | .. | + | +[b] |
| Belgium | .. | .. | + | .. | .. | .. | .. | .. | + | .. | .. | .. | .. | .. | .. | .. | .. |
| Germany | 8, 20 | + | + | .. | .. | + | + | + | + | .. | .. | .. | .. | .. | + | .. | .. |
| Denmark | 14 | .. | .. | .. | .. | + | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Sweden | 5 | .. | + | .. | .. | + | .. | .. | + | .. | .. | .. | .. | .. | .. | .. | .. |
| Switzerland | 14 | .. | .. | .. | .. | + | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Portugal | 14 | .. | .. | .. | .. | + | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Cyprus | .. | .. | .. | .. | .. | + | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Jordan | .. | + | .. | .. | .. | + | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Kenya | .. | + | .. | + | .. | + | + | .. | .. | .. | + | + | .. | .. | .. | .. | .. |
| Tanganyika | .. | .. | .. | + | .. | .. | .. | + | .. | .. | + | + | .. | .. | .. | .. | .. |
| S. Rhodesia | .. | + | .. | .. | .. | + | .. | .. | + | .. | .. | + | .. | .. | + | .. | .. |
| S. Africa | .. | .. | + | .. | + | .. | + | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Canada | .. | .. | .. | .. | .. | .. | + | .. | .. | .. | .. | .. | + | + | .. | .. | + |
| ,, | 11 | + | + | .. | .. | + | + | .. | + | .. | .. | .. | .. | + | .. | .. | .. |
| ,, | 12 | .. | .. | .. | .. | + | .. | .. | + | .. | .. | .. | .. | .. | .. | .. | + |
| U.S.A. | 4 | + | + | + | .. | + | .. | .. | + | .. | + | .. | .. | .. | .. | .. | .. |
| ,, | 17 | + | .. | .. | + | + | .. | .. | + | .. | .. | .. | .. | + | .. | .. | .. |
| ,, | 13 | + | + | .. | .. | + | .. | .. | + | .. | + | .. | .. | .. | .. | .. | .. |
| ,, | 24 | + | + | + | + | + | + | + | + | .. | + | + | .. | + | .. | .. | .. |
| Colombia | 18 | + | .. | .. | .. | + | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. | .. |
| Peru | .. | + | .. | .. | + | + | .. | .. | .. | .. | .. | + | .. | .. | .. | .. | .. |
| ,, | 21 | + | .. | .. | .. | + | .. | .. | .. | .. | + | .. | .. | .. | .. | .. | .. |

+[a] Occurred in laboratory. +[b] Privately communicated.

When the differential host series was established in 1947, race A, *i.e.*, race 0 in international terminology, was regarded as the common race since all seedlings possessing any of the R genes introduced from *Solanum demissum* were virtually immune from it. During the past few years, however, evidence has accumulated which shows that race 4 is now predominant in commercial varieties bred from *S. tuberosum*. Unfortunately, no direct evidence is available to determine how long race 4 has been in existence or when it became the most prevalent.

In Scotland race 4 was first recorded in 1947, its discovery being coincident with the identification of genotype $R_4$. Since this genotype was new, it is probable that race 4 had been in existence before that time. A survey of blight occurring in commercial crops in Scotland was made in 1946 (Black and Haigh, 1947) but the $R_4$ genotype was not then known and no means were available of distinguishing between race 0 and race 4 in these tests. During the next few years only occasional samples of blight were collected. The majority of these, however, proved to be race 4, suggesting that this race was widely distributed in commercial crops.

## TABLE II

RELATIVE FREQUENCY OF THE OCCURRENCE OF BLIGHT RACES 0 AND 4 IN DIFFERENT COUNTRIES

| Country | Reference | Year(s) | Frequency | |
|---|---|---|---|---|
| | | | Race 0 | Race 4 |
| Scotland | 7 | 1955 | 2 | 10 |
| ,, | .. | 1955-6 | 0 | 8 |
| England | 1 | 1954 | Infrequent | Predominant |
| ,, | 2 | 1955 | 0 | 8 |
| N. Ireland | 6 | 1954 | 3 | 70 |
| Holland | 14 | 1951 | 20 | 2 |
| ,, | 14 | 1952 | 22 | 59 |
| ,, | 14 | 1953 | 0 | 4 |
| ,, | 14 | 1954 | 0 | 15 |
| Germany | 8 | 1955 | 0 | 33 |
| Sweden | 5 | 1956 | .. | Predominant |
| S. Rhodesia | .. | 1952-3 | 2 | 13 |
| ,, | .. | 1954-6 | 0 | 16 |
| Canada | 11 | 1952-3 | 21 | 24 |
| ,, | 12 | 1954 | Rare | 178 |
| Colombia | 18 | Before 1953 | Predominant | 1 |

The findings of various investigators concerning the relative occurrence of race 0 and race 4 in a number of countries are summarised in Table II. In 12 samples collected in Scotland in 1955. Foister (1955) found two cases of race 0 and ten of race 4. In seasons 1955 and 1956 the writer tested 8 samples from different crops and found that all were race 4. Somewhat similar results were obtained in England in 1954 and 1955 and in Northern Ireland in 1954. In Holland, the work of Mastenbroek and de Bruin (1955) showed that race 0 was predominant in 1951, had declined to second place in 1952, and was not present in the samples taken in 1953 and 1954. Reports from Germany and Sweden showed that race 4 was predominant in 1955 and 1956 respectively.

In Canada races 0 and 4 occurred with approximately equal frequency in samples collected during the period 1952-53 but in 1954 race 0 was reported as " rare " while race 4 was registered 178 times. These figures indicate a relatively rapid decline of race 0 around 1953. A similar decline of race 0 about the same time occurred in Southern Rhodesia. Samples received in the period 1952-53 contained two isolates of race 0 and thirteen of race 4. Since then race 0 has not been found in potatoes while race 4 has been present in sixteen samples. Race 0, however, has not entirely disappeared from that country because two isolates taken from tomatoes in 1956 proved to be race 0.

Prior to 1953, race 0 was predominant in Colombia but the presence of race 4 was also established. Unfortunately, no information is available to determine whether race 0 had declined as in other countries during the intervening years.

The above evidence points to the gradual and simultaneous decline of race 0 in many potato growing countries during the past five years and its replacement by race 4 as the common biotype in commercial crops. The reason for this change is not clear. It cannot be attributed to the selective influence of genotype $R_4$ because none of the popular commercial varieties is so constituted.

Although few details are available, maximum variation in *P. infestans* is probably centred in Mexico. Niederhauser (1954) found that no species or variety in a wide range of blight resistant material remained free from the disease in the Toluca Valley, although certain clones exhibited a valuable degree of resistance. Conditions of temperature and humidity in this region were undoubtedly conducive to severe attack but, in addition, highly specialised biotypes of the fungus were presumably involved since many different clones of *S. demissum* and other recognised resistant species were blighted in the test plots. New light has, however, been thrown on the whole problem of variation in *Phytophthora* by the recent discovery of sexual compatibility between two groups of races existing in Mexico (Gallegly and Galindo, 1957). Oospores were produced abundantly both on infected leaves and in pure cultures when certain races were paired. Thus the intercrossing of compatible biotypes may occur freely in Mexico, resulting presumably in the production of an array of physiological races unequalled elsewhere. The investigations of Smoot, Gough and Gallegly (1957) suggest that blight races prevalent in the British Isles, Western Europe, Africa and North America all belong to the *same* group and are, therefore, sexually incompatible. In that event, the variation potential of the fungus is much greater in Mexico than in other parts of the world.

**Breeding for resistance.**—The wide distribution of most of the known races of *P. infestans* indicates that resistance through hypersensitivity will eventually break down, especially in regions noted for frequent and severe attacks of the disease. Thus the protection afforded by the R genes is unreliable as a safeguard against epidemics and must be supplemented by inherent field resistance. It cannot be assumed, however, that field resistance will remain unaffected by mutation or adaptation of the parasite. The old variety Champion was thought by observers to have lost much of its original resistance after a number of years in cultivation, but accurate details of the circumstances are not available. Evidence, however, has been presented by Toxopeus (1956) to show that the original degree of resistance exhibited by the variety Voran has not been maintained in the Netherlands, and he attributed this change to adaptation of the parasite. But such adaptation appears to be relatively slow and incomplete as compared with the sudden collapse of hypersensitivity when appropriate races of the fungus arise. For that reason, field resistance appears to be more enduring than hypersensitivity and should, therefore, provide a more reliable protection against crop failure.

Field resistance is a complex character, the exact nature of which is not known, but its mode of inheritance shows that it is controlled by a number of different genetic factors. It is probable that some of these factors may be affected by parasitic specialisation while others are not. The field resistance present in certain commercial varieties of *S. tuberosum* appears to be closely linked with late maturity, all the early maturing varieties of economic importance being field susceptible. A corresponding linkage, however, does not necessarily exist in all species. Early maturing seedlings possessing a relatively high degree of field resistance have been obtained by interspecific hybridisation involving *S. simplicifolium*, *S. phureja*, *S. demissum* and *S. tuberosum*. In view of the complex hybrid origin of these seedlings, the exact source of their resistance is difficult to establish, but it is probable that both *S. demissum* and *S. simplicifolium* have contributed towards it. Whether such field resistance in early maturing varieties will be affected by adaptation of the fungus is not known. In any event, the best protection attainable is, no doubt, a combination of both hypersensitivity and field resistance in the highest possible degree. That should be the ultimate aim, but in the course of achieving it, greater emphasis should be placed on field resistance which has for so long been obscured by the presence of R genes in seedlings bred from *S. demissum*.

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# "EMBEDDED CYSTS" IN RELATION TO THE UTILISATION OF POTATO ROOT EELWORM RESISTANCE

J. M. Dunnett

The discovery (Anon., 1956; Dunnett, 1957) that Potato Root eelworm resistance derived from the clones C.P.C. 1673, 1685 and 1690 of *Solanum tuberosum* subsp. *andigena* is not proof against the multiplication of certain populations of the eelworm which occur in Britain, has two important consequences. Firstly, the initial usefulness of such resistance will vary between different eelworm infested fields. Secondly, when resistance is operative against a certain eelworm population, the rare development of cysts on the roots of the resistant plant may be readily interpreted as incipient variation of pathogenicity within that eelworm population. Toxopeus (1956) and Huijsman (1956) have already discussed the significance of the "occasional" cysts which arise on the roots of resistant plants. The purpose of this paper is to draw attention to the development of cysts also on the tubers of resistant plants. These latter cysts, which develop *in situ* on potato tubers, may be described as "embedded cysts," in contradistinction to the detached cysts which may be found in soil adhering to the tubers.

At Pentlandfield, the investigation of embedded cysts began with an initial observation that the roots of an eelworm resistant seedling were apparently cyst-free under test conditions, whereas a few embedded cysts were present on each of the small tubers of the same plant. Subsequently, on the completion of routine tests of eelworm resistance, the tubers of resistant seedlings were inspected closely and embedded cysts were recorded frequently. A controlled comparison was made under test conditions between the incidence of embedded cysts on (*a*) the tubers of susceptible, commercial varieties and (*b*) the tubers of resistant seedlings. Circumstances also favoured a study of the development of cysts on the tubers of a susceptible variety in the field.

## The incidence of embedded cysts under test conditions.

The problem of freeing tubers from adhering soil without removing embedded cysts was minimised by growing the plants in a prepared, infective soil which comprised four-fifths pure sand. The infectivity of this soil was 110 larvæ per gramme. Fourteen plants of the early maincrop variety Craigs Defiance and single plants of 16 resistant seedlings were grown under glass in four-inch pots containing this soil. In this way, the incidence of cysts on the tubers of a range of resistant seedlings of varying maturities could be checked against a good estimate obtained for tubers of Craigs Defiance. Single plants of Craigs Royal and Pentland Ace were also grown, and served to illustrate that the phenomenon of embedded cysts is not peculiar to Craigs Defiance among commercial varieties.

## TABLE I

THE INCIDENCE OF EMBEDDED CYSTS ON TUBERS OF COMMERCIAL VARIETIES AND EELWORM RESISTANT SEEDLINGS UNDER CONTROLLED CONDITIONS

| | Number of tubers | Tubers with cysts | |
|---|---|---|---|
| | | Number | Average cysts per tuber |
| *Commercial varieties* | | | |
| Craigs Defiance | 32 | 28 | 19·4 |
| Craigs Royal | 3 | 3 | 17·3 |
| Pentland Ace | 3 | 3 | 46·0 |
| Combined varieties | 38 | 34 | 21·6 |
| *Resistant seedlings* | | | |
| 2356 (12) | 4 | 3 | 3·3 |
| 2361b (23) | 4 | 3 | 1·4 |
| 2357b (22) | 4 | 2 | 2·0 |
| 2371b (1) | 3 | 3 | 2·9 |
| 2499b (1) | 3 | 3 | 3·0 |
| (3) | 4 | 3 | 3·0 |
| (17) | 3 | 2 | 6·0 |
| (43) | 3 | 1 | 5·0 |
| (45) | 4 | 3 | 4·0 |
| 2508 (2) | 3 | 0 | .. |
| (61) | 4 | 1 | 2·0 |
| (70) | 5 | 3 | 1·7 |
| 2527 (22) | 3 | 0 | .. |
| 2531 (17) | 3 | 0 | .. |
| (77) | 2 | 2 | 6·5 |
| (86) | 7 | 3 | 1·3 |
| Combined resistant seedlings | 59 | 32 | 3·1 |

At the end of the growing period, tubers were recovered by the gentle erosion of root-balls under a spray. During the subsequent examination for embedded cysts, tubers were impaled upon a mounted, triangular needle and rotated under a binocular microscope. Embedded cysts were detached and transferred to moist filter paper by means of a blunt needle.

The average diameter of 97 tubers which were examined was 2.2 cms. Eighty-nine per cent of all the tubers of commercial varieties had at least one embedded cyst. The corresponding figure for resistant seedlings was 54 per cent. The greatest number of embedded cysts recorded on one tuber from a susceptible plant is compared below with the greatest number of cysts recorded on one tuber from a resistant plant :—

susceptible variety : 70 cysts : av. diameter of tuber = 3 cms.
resistant seedling : 12 cysts : av. diameter of tuber = 1·6 cms.

From Table I it can be seen that the average number of embedded cysts per tuber of Craigs Defiance was about 6 times greater than the average number of cysts per tuber of resistant seedlings. No embedded cysts were observed on any of the tubers of three late maturing seedlings and some tubers of the remaining plants also remained free from cysts. These cyst-free tubers were not included in the calculation of average cysts per tuber for different seedlings or varieties, since there was no definite evidence that these particular tubers had been formed or infected over a period longer than that required for completion of the eelworm life cycle.

Estimations of the average egg content of embedded cysts were made by the method described by Goodey (1951). Cyst samples were taken which comprised the whole complement of embedded cysts from one or more tubers. Since embedded cysts are necessarily cysts of the current season, all were found to be viable, but very few appeared to be completely mature. As recorded in Table II, an average estimate of 91.2 eggs per cyst was obtained for three samples of cysts from tubers of Craigs Defiance and corresponding values of 67.2 and 87.2 were obtained for two smaller samples of cysts from tubers of resistant seedlings.

**The incidence of embedded cysts under field conditions.**

In part of an eelworm infested plot at Pentlandfield, a second early variety, Pentland Ace, was grown in order to maintain

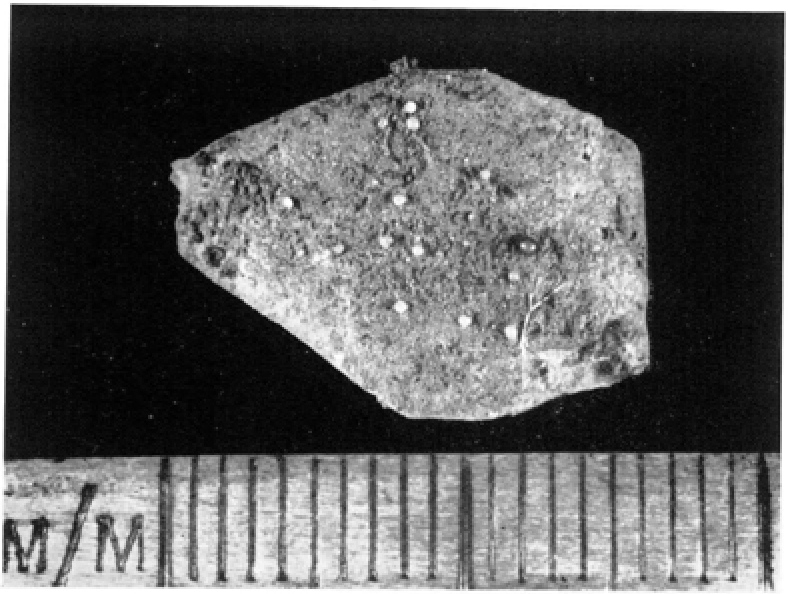


FIG. 1.—TUBER PIECE WITH CLUSTER OF EMBEDDED CYSTS. TUBER INFECTED UNDER FIELD CONDITIONS.

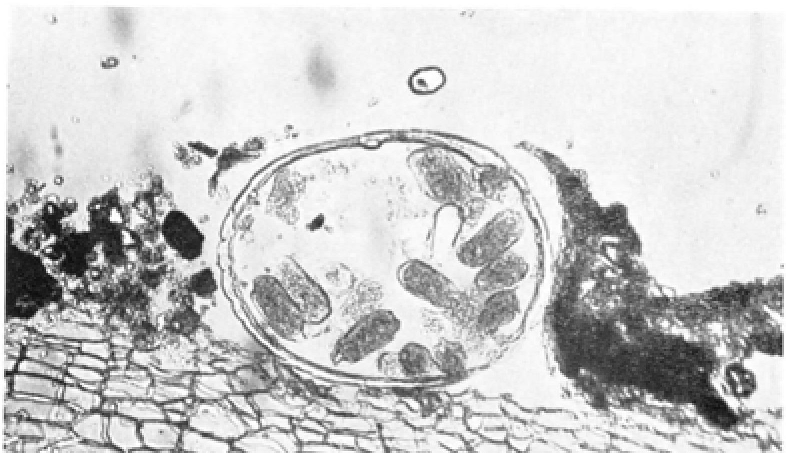

FIG. 2.—SECTION OF TUBER WITH EMBEDDED CYST CONTAINING EGGS.

## TABLE II

ESTIMATION OF EGGS OR LARVÆ CONTAINED IN EMBEDDED CYSTS

| Origin of cyst sample | No. of cysts | Average eggs or larvæ per cyst |
|---|---|---|
| 1 tuber of Craigs Defiance . | 64 | 97·1 |
| 4 tubers Craigs Defiance. . | 73 | 89·7 |
| 6 tubers Craigs Defiance . | 74 | 86·7 |
| Combined cysts from Craigs Defiance . . . . | 211 | 91·2 |
| Tubers from 4 eelworm resistant seedlings . . . | 40 | 69·2 |
| Tubers from various eelworm resistant seedlings . . | 36 | 87·8 |
| Combined cysts from resistant seedlings . . . . | 76 | 78·5 |

## TABLE III

THE INCIDENCE OF EMBEDDED CYSTS ON A SAMPLE OF PENTLAND ACE TUBERS FROM THE FIELD

| Size grouping | Number of tubers | Tubers with cysts | |
|---|---|---|---|
| | | Number | Average cysts per tuber |
| Chats under $1\frac{1}{4}$ in. . | 2 | 2 | 2·5 |
| Seed $1\frac{1}{4}$ in.-$2\frac{1}{4}$ in. . | 12 | 10 | 14·7 |
| Ware over $2\frac{1}{4}$ in. . | 9 | 9 | 28·3 |

the eelworm population at a level suitable for the testing of eelworm resistance. Planting took place in mid-April and a sample of tubers was carefully dug in late September, after the plants had matured. The tubers were soaked in water until adhering soil could be removed easily. Each tuber was then halved and the pieces were laid out and scanned for embedded cysts with the cut surface downwards, which helped to prevent the accidental removal of embedded cysts during examination.

Twenty-one of the 23 tubers which were examined had embedded cysts. As can be seen from Table III, the average number of cysts per tuber was greatest for ware sized tubers, and least for the small tubers under seed size. The greatest number of cysts recorded was 71 embedded cysts for one ware sized tuber. For all tubers, the percentages of cysts which were classed as white, yellow and brown were 24.3, 64.3 and 11.3 respectively. White cysts were usually deeply embedded and only partially visible above the tuber surface, but most brown cysts were lightly attached by the head only. Nearly all the brown cysts occurred on ware sized tubers. Embedded cysts were not associated with any external appearance of damage to the tuber and were distributed unevenly over the whole surface of individual tubers. Clusters of cysts were occasionally observed and on one tuber 20 cysts were counted within the 1.05 cm. field of a binocular microscope. Fig. 1 is an illustration of one such cluster on a tuber piece which was being prepared for sectioning. The close association between an embedded cyst and the underlying tuber tissue is illustrated in Fig. 2. Unfortunately, a good section through the neck of an embedded cyst was not obtained.

## Discussion

Under controlled conditions in pots under glass, the incidence of embedded cysts on the tubers of susceptible, commercial varieties was greater than the incidence of cysts on the tubers of resistant seedlings. This conclusion is based on the following facts: at least one embedded cyst occurred on 89 per cent of all the tubers of commercial varieties, as against 54 per cent for all the tubers of resistant seedlings: the greatest number of embedded cysts recorded on one tuber of a commercial variety was 70 cysts, as against a greatest number of 12 cysts recorded on one tuber of a resistant seedling: considering only the tubers which had cysts, the average number of cysts on tubers of Craigs Defiance was 6 times greater than the corresponding figure for the tubers of resistant seedlings. Therefore, since the tubers of susceptible varieties and resistant seedlings were formed in the same infective soil, there are good grounds for believing that seedlings with resistant root systems produce resistant tubers. Should this be so, then the egg-containing cysts which arise on resistant tubers are of special significance for two reasons. Firstly, the cyst itself may represent an eelworm biotype which has been subject to selection for ability to mature in resistant tissues and this character may be inherited to some extent by the larvæ which hatch from the parent cyst. Secondly, embedded cysts are more likely to be transported with seed stocks of future resistant varieties than are the cysts which arise infrequently on the roots of these varieties. A crop raised from a seed stock which was contaminated in this way could continue to exert a selective influence on the eelworm biotypes which hatched from embedded cysts. This danger appears to be real enough to warrant some investigation of the tubers of future resistant varieties, when these are exposed to eelworm attack in the field.

Embedded cysts, on the tubers of susceptible, commercial varieties at least, are frequently recorded under field conditions. Grainger (1951) reported that a sample of Ayrshire grown Epicure tubers had an average of 1.3 embedded cysts per tuber after washing. At Pentlandfield, after careful handling of a sample of Pentland Ace tubers from an eelworm infested plot, an average of 17.7 embedded cysts per tuber was recorded. Using this figure as a basis for calculation and assuming 600 tubers per cwt. sack, 10 tons of tubers per acre and 1,000 tons of top soil per acre, the incidence of embedded cysts alone was estimated to be equivalent to an eelworm infestation of 0.2 viable cysts per 100 gms. of soil. Most of these cysts were still immature at harvest time, for which one good reason is that infection of tubers must necessarily occur later in the season than infection of the greatest part of the root system, which is formed first.

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# THE SOWING DATE OF SUGAR BEET IN SCOTLAND

V. McM. Davey

In former times it was customary in the East of Scotland to delay sowing root crops till risks of damage by frost became negligible at about the beginning of May. This suited the swede and the turnip which required relatively short growing seasons, and the mangold was very little grown, but the sugar beet, when it was introduced, was unable to yield large enough crops if sown so late. Growers were persuaded to advance the sowing date to about the middle of April, but even so the development of the crop in a summer of long daylight, but lacking in sunshine, was not altogether satisfactory, and a further advance of the sowing date to the beginning of April has been advocated. The risks of bolting would be greatly increased thereby and strains of sugar beet less susceptible to bolting than those available seem desirable.

The long, cold Springs of the Scottish lowlands often include spells of dry weather in March, when the sowing of sugar beet seed would be possible if it were worth while. Some farmers indeed do use such opportunities, despite an almost certainty of heavy bolting, to spread their manual operations over a longer period. Towards the end of March or at the beginning of April the land may dry and become slightly warmer, and sowing might then be profitable, except for the risks of heavy bolting. In parts of the Lothians, a drought frequently follows, and a delay in sowing may result in the seed lying ungerminated in the soil till May. In general, however, growers aim at sowing about the middle of April, and this seems to be the modal date of sowing. From an analysis of sugar beet factory records, Murdoch (1949) concluded that "sowing beet after mid-April gives small and probably uneconomic yields." Considerable improvements have been made in methods of crop production since the period studied (1943-46) so this conclusion might not still apply.

The need for a variety of sugar beet which would resist bolting when sown early was obvious, but when cultivation of the crop started in the United Kingdom in the 'twenties, there was none adapted for this purpose. The varieties grown in Central Europe are sown after the hard winter has ended, in a warm and frostless spring. Such varieties threw the most bolters when grown in Scotland, while others bred in Germany, Holland and Scandinavia proved less susceptible. During the War, Dr G. D. H. Bell at the Cambridge Plant Breeding Institute commenced an investigation to see whether a strain of sugar beet could be produced which would withstand bolting under severe conditions, and yet give good yields of sugar (Bell and Bauer, 1942). In 1948 the Scottish Plant Breeding Station was asked by the Sugar Beet Research and Education Committee to join in the search for a non-bolting sugar beet, and in the first instance to assist in testing the Cambridge material under Scottish conditions.

It was apparent that when sown before the middle of March, a strain which showed a negligible amount of bolting could outyield a normal variety containing a large percentage of early bolters. It was by no means certain, however, that an early sown non-bolter would outyield a later sowing of the normal variety. The trials discussed in this paper were laid down in an attempt to clarify the interactions of sowing date and strain. Normal and non-bolting types of sugar beet were sown together on a succession of dates in three years, 1952-1954, at Corstorphine, near Edinburgh. The Station was then removed to Pentlandfield, and as there was no prospect of carrying out further trials at Corstorphine, it seems an appropriate time to examine the data obtained there.

## Sowing Dates

Four sowing dates were distinguished, the first representing an "opportunist" sowing made, when favourable conditions occurred, about the middle of March. In 1952, sowing was possible on the 11th, and in 1953 on the 9th of the month, but no dry spell occurred before the end of March in 1954, so sowing No. I was missed in that year. Sowing No. II was designed for the period of favourable weather which often occurs in the last few days of March or at the beginning of April, and it was made in 1952 on the 3rd, and in 1953 and 1954 on the 2nd of April. Sowing No. III was intended for the middle of April, the modal date for growers in Scotland, and it was carried out on the 16th both in 1952 and 1954, but was delayed by wet weather in 1953 until the 20th-21st.

Later sowing than this was not really within the scope of the enquiry, but since no mid-March sowing had been possible in 1954, and this year was evidently a "late season," a sowing No. IV was made on the 28th April to fill the vacant plots of the trial.

The sowings were made in randomised blocks, three date treatments being replicated six times in 1952 and eight times in the other two trials. Comparisons between strains, which will be discussed later, were made possible by use of split-plot designs. Each of the main plots for sowing dates was divided into two (in 1954 into three) equal parts, and the strains to be compared were allocated at random to these sub-plots. Singling was carried out when each sowing reached the optimal stage.

TABLE I

Effects of Sowing Date on the Yield of the Unbolted Plant

| Sowing Dates | | I mid-March | II early-April | III mid-April | IV late-April | s.e. | F |
|---|---|---|---|---|---|---|---|
| Number of plants per yard of row | 1952 | 3·59 | 3·65 | 3·05 | .. | 0·099 | † |
| | 1953 | 3·81 | 3·67 | 3·73 | .. | 0·041 | * |
| | 1954 | .. | 3·40 | 3·55 | 3·60 | 0·041 | * |
| Root weight in lb. | 1952 | 1·32 | 1·29 | 1·43 | .. | 0·047 | * |
| | 1953 | 1·52 | 1·59 | 1·45 | .. | 0·037 | † |
| | 1954 | .. | 1·10 | 0·96 | 0·90 | 0·049 | † |
| Sugar content percentage | 1952 | 17·84 | 18·13 | 18·02 | .. | 0·127 | NS |
| | 1953 | 16·10 | 16·36 | 16·44 | .. | 0·147 | NS |
| | 1954 | .. | 17·09 | 17·10 | 16·98 | 0·082 | NS |
| Sugar per root in lb. | 1952 | 0·235 | 0·233 | 0·258 | .. | 0·009 | * |
| | 1953 | 0·244 | 0·260 | 0·238 | .. | 0·007 | * |
| | 1954 | .. | 0·188 | 0·163 | 0·153 | 0·008 | † |

F. test probability ; † = 1 per cent level ; * = 5 per cent level ; NS = not significant.

As one object of the investigation is to assess the worth of a bolter-free strain, it is proposed first to consider the development of those plants in the several sowings which did not bolt ; then the incidence of bolting can be examined, and finally some attempt made to assess the actual yields of strains under the different conditions of sowing which occurred in the three trials. The figures in Table I refer to the mean unbolted plant of each sowing date, and are obtained from the values of the sub-unit strains which are not shown separately. As always when perfect stands are not obtainable, the density or blankness of the plant population must be suspected as a possible disturbing factor.

The number of plants per yard of row are set out at the top of Table I. Liberal amounts of seed were sown on the flat, and the seedlings were blocked with a hoe before hand singling to secure uniform spacing. There was no great disparity among sowings in 1953, when the average distance between plants was less than ten inches, nor in 1954 when it was slightly wider, yet in each of these years the small difference between greatest and least plant stands was significant at the 5 per cent level. A more serious discrepancy occurred in 1952, when the first two sowings had similar, good plant stands, but the third, made in mid-April, brairded thinly. The average spacing was about a foot, but many plants of this third sowing had ample room to develop large roots. Mishaps leading to thin plant stands are not peculiar to any sowing period, though the mid-April period may be more prone to damage by drought and the earlier periods to cold, wet soils and surface pans. The consequences of sowing date might be extended to include any damage due to adverse conditions when the plants are ready for singling. In fact, the plant density was affected by the treatment sowing date, and when the covariance effects of plant numbers on weight and sugar content were examined, it was found that there was nothing to be gained by adjusting the figures. The coefficient of correlation between plant numbers and root weight was −0.21 in 1952, −0.52 in 1953 and +0.24 in 1954, and similar correlations were found between numbers and sugar per root. The correlations with sugar percentage were all negative but only significant in 1954 with −0.75. Adjustment in most cases hardly affected the differences between sowings, and when applied to the root weights of the early and mid-April sowings of 1952, the standard error became very large. Consequently, the yields in Table I have not been adjusted for plant density which must be regarded as a consequence of the treatment.

**Root Weight.**—Comparisons can be drawn between sowings made in mid-March and early April in two years and in neither 1952 nor 1953 was the difference significant. The crop of the mid-March sowing might yield as well as that sown in early April, but there was nothing to suggest that it would outyield the latter. Comparing crops of the early and mid-April sowings, the root weight was significantly in favour of the earlier sowing in both 1953 and 1954. In 1952, however, the advantage is apparently with the mid-April sowing, and it must be left to a later section to show that the large roots did not fully compensate for lack of numbers. The late-April sowing of 1954 had a significantly lower root weight than the sowing made at the beginning of the month, but not significantly less than that of the mid-April sowing.

**Sugar.**—The percentages of sugar in the three sowings of any one year were not significantly different, and the yield of sugar per root followed the root weight for there were no significant differences between crops of the mid-March and early April sowings, and the early April outyielded the mid-April sown crop in 1953 and 1954. The mid-April sowing of 1952 was relatively high in yield of sugar per root, as might be expected on account of the large root size, and the late April sowing of 1954 yielded poorly.

**Top Weight.**—The conditions affecting the production of foliage, particularly the state of maturity and the effects of frost, are too complex to allow any comprehensive comparisons of top weight in these trials. Actually, the sub-plots were lifted by halves, some weeks elapsing between the two operations. In the first sampling of 1952 an accident invalidated the weighings, and the foliage had been frosted before the second sampling when the crops of the three sowings showed a ratio of top : root weight of about 0.74 : 1 with no significant differences. In 1953 the foliage of the mid-March sowing could be recognised as largest throughout the season, and in the first sampling it showed a ratio of 1.20 : 1, while the early April sowing had 1.04 : 1 and the mid-April 1.11 : 1, but this was the only suggestion of increasing top weight by early sowing, for the second sampling had been damaged by frost. There was no frost damage in 1954, and there was no significant difference between the three April sowings, whose ratio stood at about 1.2 : 1, which appears wide though the actual tops, like the roots, were small in 1954 and the leaves hardly met over the drills.

## Bolting Behaviour

At the time these trials were carried out, the Scottish Plant Breeding Station was testing the resistance to bolting of various samples of sugar beet bred by the Cambridge Plant Breeding Institute, and a stock of their family, KNB 178, was used in all three trials as the non-bolting type. In 1954 another sample, KLT/NF was also included, and it should be noted that both these non-bolters were experimental units and not strains prepared for the market. Sharpe's Klein E sugar beet variety was chosen as the normal type, because it is known to grow well in Scotland and to be relatively unaffected by bolting ; moreover it has a common ancestry with the Cambridge non-bolters.

All the plants of the plots, including those in rows adjacent to other plots, were used for the bolting counts, and these were made once a week from June to mid-September. In 1952 the total number of plants per strain for each sowing averaged 770, there were 1,200 in 1953 and about 850 plants in 1954. Final counts, made in mid-September are shown in Table II, and it will be seen that the mid-March sowings had a severe test in both 1952 and 1953, but more bolting was induced in the latter year when nearly half the Klein E plants bolted, and almost 8 per cent of the KNB 178.

April sowing caused little bolting in 1952, but in 1954 bolting was more serious, for Klein E showed 16 per cent for the early April sowing, 6 per cent for the mid-April sown crop, and even some bolters in the sowing made at the end of that month. Conditions in April 1953 were intermediate in severity, for the early April sowing of Klein E bolted 12 per cent, but the sowing made on 21st-22nd of that month escaped. Under all these conditions the " non-bolters " gave satisfactory resistance.

The incidence of bolting, once it had started, seemed regular, a similar percentage of the crop bolting within each weekly period throughout the season, and no spasmodic outbursts were observed. This is shown in Fig. 3, where the per-

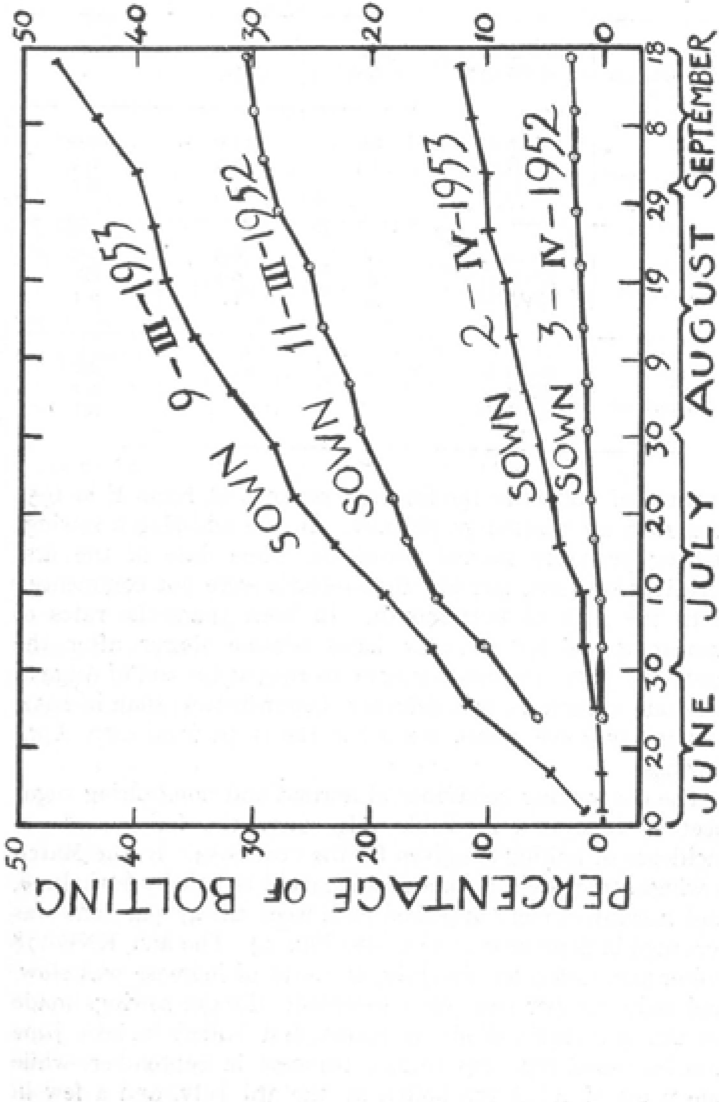


Fig. 3—Incidence of Bolting in Klein E.

## TABLE II

PERCENTAGE BOLTED BY MID-SEPTEMBER

| Sowing date | Strain | 1952 | 1953 | 1954 |
|---|---|---|---|---|
| I Mid-March | Klein E<br>KNB 178 | 30·6<br>2·3 | 47·0<br>7·7 | . .<br>. . |
| II Early-April | Klein E<br>KNB 178<br>KLT/NF | 2·6<br>0·3<br>. . | 11·9<br>0·6<br>. . | 16·0<br>1·2<br>0·2 |
| III Mid-April | Klein E<br>KNB 178<br>KLT/NF | 1·7<br>nil<br>. . | 0·9<br>0·1<br>. . | 5·9<br>nil<br>0·1 |
| IV Late-April | Klein E<br>KNB 178<br>KLT/NF | . .<br>. .<br>. . | . .<br>. .<br>. . | 2·0<br>0·1<br>nil |

centage of bolters in the first two sowings of Klein E in 1952 and 1953 are plotted graphically. In the mid-March sowings bolting probably started about the same date in the first fortnight of June, but the 1952 records were not commenced until the 24th of that month. In both years the rates of appearance of bolters may have become slower after the middle of June, accelerating again in 1953 at the end of August. The rate of increase was definitely faster in 1953 than in 1952, and this was even more marked in the crops from early April sowings.

The contrasting behaviour of normal and non-bolting sugar beet is illustrated in Table III, where the full records of incidence of bolting are given for the year 1953. In the March sowings some Klein E plants had started to bolt by 12th June, and thereafter more appeared each week till 47 per cent was recorded in September. (See also Fig. 3.) The first KNB 178 bolter was noted on 3rd July, the rate of increase was slow, and only 7.7 per cent were recorded. In the sowings made on the 2nd April, Klein E plants first bolted in late June and increased regularly to 11.9 per cent in September, while one plant of KNB 178 bolted by the 3rd July, and a few in

## TABLE III

### Percentage of plants bolted in 1953 Trial

| Date recorded | Sowing I 9th March | | Sowing II 2nd April | | Sowing III 20th-21st April | |
|---|---|---|---|---|---|---|
| | Klein | KNB | Klein | KNB | Klein | KNB |
| 12 June . . | 1·3 | .. | .. | .. | .. | .. |
| 17 ,, . . | 4·3 | .. | .. | .. | .. | .. |
| 26 ,, . . | 11·5 | .. | 0·3 | .. | .. | .. |
| 3 July . . | 14·7 | 0·1 | 1·5 | 0·1 | 0·1 | .. |
| 10 ,, . . | 18·8 | 0·1 | 1·7 | 0·1 | 0·1 | .. |
| 16 ,, . . | 23·1 | 0·3 | 3·6 | 0·1 | 0·2 | .. |
| 22 ,, . . | 26·4 | 0·5 | 4·3 | 0·1 | 0·2 | .. |
| 29 ,, . . | 28·2 | 0·9 | 5·2 | 0·1 | 0·3 | 0·1 |
| 5 August . . | 31·8 | 2·0 | 6·3 | 0·1 | 0·3 | 0·1 |
| 12 ,, . . | 34·9 | 3·0 | 7·6 | 0·3 | 0·5 | 0·1 |
| 19 ,, . . | 37·3 | 3·8 | 8·4 | 0·4 | 0·7 | 0·1 |
| 26 ,, . . | 38·7 | 4·3 | 9·3 | 0·4 | 0·7 | 0·1 |
| 2 September . | 40·1 | 5·1 | 9·8 | 0·4 | 0·7 | 0·1 |
| 9 ,, . | 43·3 | 6·3 | 11·0 | 0·5 | 0·8 | 0·1 |
| 16 ,, . | 47·0 | 7·7 | 11·9 | 0·6 | 0·9 | 0·1 |

August and September. In the sowings made on 20th-21st April less than 1 per cent of bolters was found in Klein E, again starting at the beginning of July, but only one plant bolted in KNB 178 and this had the appearance of a mangold and was probably a rogue.

### Estimates of Yield

Yields of small plots are liable to be enhanced by outside effects and although the outer rows of plots were discarded, the ends of rows used for yield determinations were not trimmed. This was done so that the data of plant stand and bolting would apply to the row sample, and also because the two rows of each sub-plot were lifted on different occasions, to allow for possible comparisons of lifting dates. The best treatments in the three years yielded 15.7 tons in 1952, 18.9 tons in 1953 and 12.3 tons per acre in 1954.

## TABLE IV

### Estimates of crop yields in 1952 Trial

| Sowing Date and Strain | Number of Plants per acre | | | Yield per acre in cwt. | |
|---|---|---|---|---|---|
| | Total | Bolted | Unbolted | Roots | Sugar |
| I. 11th March | | | | | |
| — Klein E . | 25,875 | 8,703 | 17,172 | 202 | 36.6 |
| — KNB 178 | 26,201 | 372 | 25,829 | 298 | 53.8 |
| II. 3rd April | | | | | |
| — Klein E . | 26,247 | 233 | 26,014 | 314 | 56.5 |
| — KNB 178 | 26,806 | 140 | 26,666 | 290 | 53.1 |
| III. 16th April | | | | | |
| — Klein E . | 22,385 | 372 | 22,013 | 290 | 51.7 |
| — KNB 178 | 21,966 | 0 | 21,966 | 270 | 48.7 |
| S.E. difference | | | | | |
| — for same date . | ........ | | | 7.8† | 1.24† |
| — for different dates . | ........ | | | 11.2 | 2.16 |

F. test significance: † = 1 per cent probability.

The yields of the 1952 trial are given in Table IV, but they are calculated on the unbolted stands. The early April sowing of Klein E gave the best yield of sugar, significantly greater than that of KNB 178 sown on the same day, but not significantly greater than the yield from the mid-March crop of KNB 178. Although as far as yield alone is concerned there was no advantage in sowing the non-bolter in mid-March, yet if such an early sowing was desired for other reasons, KNB 178 could give a satisfactory crop. Klein E, on the other hand, when sown in March had a third of the crop impaired by bolting, and even if the 8,703 bolted plants had given as much sugar per root as the non-bolted ones, the total yield would only have been 54.9 cwt. How many processible roots there may have been and how much sugar they contained were not accurately established, though a rough estimate suggested about 9 cwt. making 45.6 cwt. of sugar from the mid-March sowing of Klein E. In 1952 the bolters were not removed and they caused some shading and even smothering of adjacent plants; in subsequent years they were pruned back to avoid such effects. The sowings made on 16th April suffered from insufficient plant populations, and the enhanced values of the roots did not compensate for lack of numbers.

## TABLE V

ESTIMATES OF CROP YIELDS IN 1953 TRIAL

| Sowing Date and Strain | Yield of Roots in cwt. per acre | | | Yield of Sugar in cwt. per acre | | |
|---|---|---|---|---|---|---|
| | Unbolted | Bolted | Total | Unbolted | Bolted | Total |
| I. 9th March | | | | | | |
| — Klein E . | 173 | 164 | 337 | 27·6 | 23·3 | 50·9 |
| — KNB 178 . | 309 | 45 | 354 | 50·2 | 6·8 | 57·0 |
| II. 2nd April | | | | | | |
| — Klein E . | 330 | 49 | 379 | 53·2 | 7·4 | 60·6 |
| — KNB 178 . | 350 | 2 | 352 | 58·1 | 0·3 | 58·4 |
| III. 20th April | | | | | | |
| — Klein E . | 355 | 2 | 358 | 57·7 | 0·3 | 58·0 |
| — KNB 178 . | 341 | 0 | 341 | 56·7 | 0·0 | 56·7 |
| S.E. difference | | | | | | |
| — for same date . | 10·7† | .. | 8·3 NS | 16·0† | .. | .. |
| — for different dates . | 9·3† | .. | 8·1 | 15·7 | .. | .. |

F. test significance: † = 1 per cent probability; NS = not significant.

Bolting was more severe in 1953, and the yields of bolted roots included in Table V were calculated from weighings, but some of these roots would not have been accepted by the factory. There were sufficient roots of bolters in the March-sown Klein E to allow sugar determinations for each plot, and an average value of 14.2 per cent was obtained. There were insufficient roots of bolters for accurate tests in the other treatments, and as most of the bolting was late in the season, a round figure of 15 per cent has been used in calculating their yields. The early April sowing of Klein E is again the heaviest yielder, but only if a large proportion of its 49 cwt. of bolters can be sent to the factory. The early April sown crop of KNB 178 is good, and hardly affected by bolting. The March crop of KNB 178, with 45 cwt. of bolter roots yields as much root, but slightly less sugar than the second sowing. The early April sowing of each strain is insignificantly better than its mid-April counterpart, but here again this depends on the processibility of the bolter roots in Klein E.

TABLE VI

ESTIMATES OF YIELDS IN 1954 TRIAL

| Sowing Date and Strain | Number of plants per acre | | | Yield per acre in cwt. | |
|---|---|---|---|---|---|
| | Total | Bolted | Unbolted | Roots | Sugar |
| II. 2nd April | | | | | |
| — Klein E | 24,775 | 3,539 | 21,236 | 237 | 39·8 |
| — KNB 178 | 24,593 | 590 | 24,003 | 237 | 41·1 |
| — KLT/NF | 24,775 | 91 | 24,684 | 245 | 41·7 |
| III. 16th April | | | | | |
| — Klein E . | 25,773 | 1,634 | 24,140 | 228 | 38·3 |
| — KNB 178 | 25,818 | 0 | 25,818 | 212 | 36·8 |
| — KLT/NF | 25,864 | 45 | 25,818 | 219 | 37·3 |
| IV. 28th April | | | | | |
| — Klein E . | 25,410 | 590 | 24,820 | 219 | 36·7 |
| — KNB 178 | 26,363 | 0 | 26,363 | 202 | 35·0 |
| — KLT/NF | 26,590 | 0 | 26,590 | 206 | 34·6 |
| S.E. difference | | | | | |
| — for same date . | ........ | | | 7·5 NS | 1·2* |
| — for different date | ........ | | | 13·3 | 2·2 |

F. test significance : * = 5 per cent probability ; NS = not significant.

In 1954 the land was too wet to make a seed bed in March, and Klein E showed considerable bolting tendencies in all the April sowings. The plant stands were reasonably good but the yields were poor, and the foliage hardly met in the rows. In the other two trials the siting had been favourable, for there was relatively little variation within the block, but unfortunately, in this trial a narrow strip of infertile soil ran across four blocks, damaging sub-plots in each and thereby increasing the errors. The yields are shown in Table VI, and they represent the total crop because the roots of plants which bolted in 1954 continued to swell and nearly all of them could have been processed. The yield appears to diminish as the sowing date is delayed, and there is some significance between performances of strains in the early and late April sowings. The second experimental non-bolter, KLT/NF, was found to be nearer the " E " type than KNB 178 which tends to have higher sugar percentage and to lack yield.

## Discussion

It is desirable to secure freedom from bolting in sugar beet for several reasons. Losses in yield of sugar are caused not only by " early " bolters which have worthless roots, but to a lesser extent by " late " bolters whose roots may be small or low in sugar percentage. Interference with mechanical lifting may be caused by bolters with hard stems forcing the topping knife to ride high over the next few plants or otherwise obstructing the passage through the crop. Bolters are often centres of black aphis infestations, but the chief objection to them is perhaps the labour required for their removal.

There is little question that a non-bolting sugar beet strain would be popular in Scotland, and probably in parts of England too if it yielded as well as the good normal varieties. High degrees of resistance to bolting can be obtained by special methods of selection (Bell and Bauer, 1942) as has been demonstrated by the Cambridge Plant Breeding Institute material used in these trials and elsewhere. It is a matter of time for heavy yielding capacity to be combined with high resistance to bolting. Some of the families of the earlier selections, of which KNB 178 was an example, belonged to a type with higher sugar percentage than Klein E, and this seldom has the yielding capacity of the " E " type but more recently selected families such as KLT/NF appear to resemble the Klein E type while exhibiting high resistance to bolting. These families were used in the trials because no market strain with such a high degree of resistance to bolting was available.

With regard to bolting, it appears from these trials that a strain like KNB 178 would suit the requirements of a grower wishing to make a sowing in March ; but caution is required because environmental conditions in some districts may be much more rigorous than those experienced at Corstorphine, and the extent to which a resistant strain would bolt under extreme conditions is not yet known. The degree of resistance in such material as KNB 178 is probably sufficient for practical needs. Selection against bolting might be pushed further but if it went too far, seed production might be affected. There are genotypes in sugar beet which do not flower in their second year of growth. A line of this kind was obtained at this Station, but it would have been very expensive to propagate.

The three trials discussed in this paper at least illustrate the diversity of the Scottish climate. If sowing was possible in March, the Klein E crop suffered degrees of severe bolting, while the "non-bolter" stood up to these conditions well, having 2 per cent of late bolters one year and 8 per cent under the more severe conditions of another season (Table II). In sowings made on the 2nd or 3rd of April bolting varied from less than 3 per cent to 16 per cent in Klein E, but in KNB 178 only exceeded 1 per cent in the severest year, 1954. In that year also there was some bolting in the mid- and late-April sown crops of Klein E.

It would be misleading to leave the impression that the varieties of sugar beet on the market are necessarily static with respect to improvements such as resistance to bolting. In several at least tendencies to bolt seem to be diminishing (Thompson, 1956).

The terms "early" and "late" when applied to bolters distinguish plants with roots which are worthless or fit to be processed respectively, and certainly the earliest plants to bolt are most likely to be those with thin, wooden roots and tall, hard stems; while plants bolting late in the season have usually developed large storage organs, and their stems have little time to harden. Nevertheless, these trials show there is much variability and overlapping, and particularly that there was no discontinuity in date of incidence. (See Fig. 3.) Plants started to bolt at all stages of development, and showed individual idiosyncrasies, some passing rapidly into the flowering stage while others grew long stems but remained vegetative. On the crop as a whole some seasons seem to favour transit to the flowering condition while others such as 1954 are characterised by large rooted bolters, and this has an important bearing on the yield of sugar obtained from the crop.

So far as can be judged from a study of the behaviour of unbolted plants (Table I), date of sowing had no marked effect on sugar percentage, but advancing the date from mid-April to the beginning of the month increased the weight of the root and consequently of the sugar in it ; though no further gain was obtained by advancing sowing to the middle of March. This only applied when the plant populations were approximately of the same density, for the roots grow large when there is a sparse stand. Estimates of yield have been made for the three trials separately (Tables IV-VI), and if anything emerges it is the great diversity of climatic environment experienced in different years in the same field. Conclusions based on only three years are of limited value, but it may, nevertheless, be interesting to see how certain questions have been answered in these trials and, to facilitate this, Table VII has been prepared from data supplied in previous Tables and text.

TABLE VII

GAIN OR LOSS IN CWT. SUGAR PER ACRE DUE TO SOWING ON DATES OTHER THAN MID-APRIL

| Sowing . | Mid-March | | Early April | |
|---|---|---|---|---|
| Strain . | Klein E | KNB 178 | Klein E | KNB 178 |
| 1952 . | − 7·5 | + 5·1 | + 4·8 | + 4·4 |
| 1953 . | − 7·1 | + 0·3 | + 2·6 | + 1·7 |
| 1954 . | .. | .. | + 1·5 | + 4·3 |
| Mean . | − 7·3 | + 2·7 | + 3·0 | + 3·5 |

The plant breeder is told that non-bolting strains are needed to enjoy the benefits of early sowing, but how many cwt. of sugar per acre may these benefits confer? When Klein E was sown on 9th or 11th March in two years, its yield was reduced by about 7 cwt. of sugar judged by the yields of normal sowings made in the middle of April. When the non-bolter was sown on the early dates, it incurred no loss in 1953 and showed a gain of 5 cwt. of sugar in 1952, though this latter result may have been affected by a disparity in plant population. The sowing of beet before the last few days of March in Scotland (equivalent to about the 20th March in England), is not always possible as was found in 1954; nor is it a common practice, but it is one for which a non-bolter strain would obviously be suited. A more important economic consideration is the advancing of the sowing date by a fortnight or so to the beginning of April. When sown on the 2nd or 3rd of April, Klein E gained on an average 3 cwt. and KNB 178 gained 3.5 cwt. of sugar per acre. Klein E suffered to a varying extent from bolting, while KNB 178 had very few bolted plants. (See Table II.) Freedom from bolting is desirable but not sufficient in itself; a non-bolter must be an efficient yielder to compete successfully with Klein E at this sowing period. No account is taken in Table VII of the different yielding capacities of the strains used. It is apparent from the earlier Tables (IV-VI) that KNB 178 was not so efficient as Klein E, but it should be remembered that no market strain with such resistance to bolting was available.

In conclusion it should be stressed again that the above results were obtained from trials in only three years on a field at Corstorphine where the soil was good but somewhat heavier than that of typical beet growing land. Trials in different districts and for a number of years would be required to give an adequate picture of the effects of sowing date on sugar beet in Scotland.

## Summary

1. Studies of the effects of sowing on different dates in the Spring were made in three years. Normal and special "non-bolting" types of sugar beet were compared, and the incidence of bolting was noted each week during the summer.

2. The incidence of bolting was regular, nearly the same number of plants starting each week, but the rates of increase varied in different years and treatments, and the dates on which bolting was first noted also differed.

3. Sowings made on 9th or 11th March of normal sugar beet bolted 31 and 47 per cent in two years while a non-bolter had 2 and 8 per cent. Early April sowings of normal beet bolted from 3 to 16 per cent, mid-April sowings 1 to 6 per cent, while the non-bolter sown on these dates gave 1 per cent to nil.

4. When plant stands were approximately equal the date of sowing did not affect the sugar percentage of *unbolted* plants. Advancing date of sowing from mid- to early-April increased the mean root weight and the sugar per root. No further gain was obtained by advancing the sowing date from early April to the middle of March.

5. When sown on the 9th or 11th of March instead of the normal date in mid-April, normal beet was estimated to have been reduced by 7 cwt. of sugar per acre, due to bolting ; the non-bolter suffered no loss one year and gained 5 cwt. another. It was obviously the better adapted for such early sowing.

6. When sown on the 2nd or 3rd April instead of in the middle of the month, the non-bolter gained 3.5 cwt. of sugar per acre on the average of three years, while the normal beet gained 3 cwt. There was thus little margin, and a non-bolter would have to be an efficient yielder to compete with a normal variety at this sowing period.

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A large part of the field work, estimations and computations was carried out by Mr F. J. W. England, B.Sc., who was working with Root Crops and Sugar Beet during the years under discussion.

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*Printed by William Blackwood & Sons Ltd., Edinburgh*

Dr Jens Clausen at Pentlandfield examining the *Poa* trial which is part of an intercontinental transplant experiment organised by the Department of Plant Biology, Carnegie Institution of Washington.