

FERTILITY IN THE GENUS *BRASSICA*.

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(With One Plate and Seven Text-figures.)

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INTRODUCTION.

THE cross- and self-compatibility of most natural groups of plants have always excited considerable interest, principally, however, because of their bearing on phylogenetic relationships. The present study deals with the question of fertility in the genus *Brassica* from the point of view of economic plant breeding and seed production.

The genus is of considerable importance commercially and possesses great potentialities for the practical plant breeder. In planning any extended scheme of constructive plant breeding it is helpful to know what is crossable and what is not. In commercial seed production, especially in a country such as this, where the industry is extremely localised, it is essential to know the degree of crossing which may take place in the field, because this ultimately controls the spacial isolation of crops.



Within the genus *Brassica* (including *Sinapis*) there is a large number of cultivated species, each embracing many highly specialised varieties. These varieties have to be grown, flowered and harvested in a high state of genetic purity for certain definite significant characters. To the grower who would produce "pure" seed of as many *Brassica* types as possible on a limited area, and to the plant breeder working on the genus, the questions of "crossability" and "self-fertility" are therefore of prime importance.

The amount of crossing which takes place in the field in a given time equals PC , where P is the foreign pollen incident on the aggregate stigmatic surface of the crop in question, and C a constant applicable to any two crops involved.

It is difficult to determine a value for P , though not impossible. It depends on a large number of variables, such as the size of the crops involved, the incidence of a significant insect population, the general direction of the wind in relation to the crops at the time of flowering, etc. Clearly, C can never be greater than one, and, when it attains unity, the amount of rogues produced will be subject only to the factor P . In cases when the value of C has been found to be at the maximum the most important step is to decide the minimal spacial relationship which will render P equal to zero, and so allow genetically pure seed to be produced. The step of greatest practical importance, however, is to arrive at a value for C , because, obviously, where this is definitely zero, practical difficulties regarding spacial isolation of the crops vanish.

It may be noted here that the importance of self-sterility lies in the fact that pollen from a source external to the plant must be brought in. Thus, in the event of out-varietal pollen being incident on any plant, the chances of cross-fertilisation are controlled by the degree of compatibility of the cross. In wheat, which, normally, in this country, only very rarely crosses, Watkins (30), found that certain more or less self-sterile hybrids crossed freely in the field. In self-compatible plants there may be a bias against crossing due simply to the home pollen being completely effective. It is seen, then, that C , for any one variety in relation to another, is not simply the degree of cross-compatibility which may exist between the two, but is the resultant of their cross-compatibility with the self-compatibility of the one in question.

The most obvious method of estimating crossing would appear to be to grow plants of the various forms in various spacial relationships and get a result by counting the aberrant types in the progeny. This method suffers from a number of disadvantages. In the first place, all the

variables included under P are operative. Secondly, results from the precise study of the heredity of *Brassica* have only lately begun to appear, and, as much of the available commercial material seems to be somewhat unstable, and probably not of high genetic purity apart from the significant commercial characters of the variety, the variations observed might give quite misleading results. In the producing areas under the local conditions to which the results must apply the promiscuous planting of Brassicas is not desirable. The methods reported here are much more laborious, but it is hoped will eventually give precise results, and when coupled with studies of natural pollination factors will yield accurate data for field isolation.

SELFING.

For the selfing and all other work requiring isolation, "Glassene" paper blossom bags made under the personal supervision of the writer were employed. They were thus always of ample size and suitable shape. It is noteworthy that the self-sterile types which did not set a single seed when selfed under one of these bags set ample seed under an exactly similar bag when impregnated with pollen from a compatible fellow, the two lots of flowers blooming simultaneously.

A number of questions all more or less related to each other and to the evaluation of the constant C were involved in the selfing work. Firstly, it was required to know how far the plant's own pollen was effective when a sufficiency was available to the stigma. Secondly, there is a current belief that all the pollen available on the plant at a given time is not equally effective for fertilisation. That is to say, pollen brought from one flower to another on the same plant is supposed to be more effective than pollen simply transferred from the flower's stamens to its own stigma. Darwin (8), however, showed that in *Ipomoea purpurea*, in one sense at least, the converse is true, strict self-fertilisation (flower to itself) resulting in more vigorous progeny than by the mating of flowers on the same plant. Darwin did not note the fertilisation itself: he noted the vigour of the resulting progeny, though, as will be indicated later, there seems to be some relationship between vigour of fertility and the vigour of the resulting progeny. Price (24), when discussing a cabbage hybrid, says, "Attempts to self-pollinise individual flowers resulted in failure. It was also found practically impossible to secure seed by crossing different flowers on the same plant."

A comparison of the two degrees of pollination from the point of view of seed production was embarked upon. This is not so much a study of

pollination as a study of pollen conditions and relationship to the stigma. Through all these selfing experiments "Method 1" refers to the hand selfing of the individual flowers of a whole spike under a bag, no attempt being made to protect the flowers one from the other, though, of course, all natural aids to pollination were ruled out. "Method 2" refers to the hand transference of pollen from one flower to the stigma of another on the same spike under a bag¹, no effort being made to prevent the flowers selfing provided they could. The hand transference of pollen in practise takes a considerable amount of time, and in routine work introduces the possibility of error due to contamination. To find out if this could be eliminated a third method was introduced. "Method 3" refers to a whole spike being simply enclosed in a bag, securely fastened, and never removed until all the flowers had fallen. Every plant was noted by all three methods, the three tests on each plant running concurrently.

Method 1, ensured to each flower on a protected spike a supply of its own pollen. Method 2 ensured to every flower on a protected spike a supply of pollen from at least one other flower on the same spike, while Method 3 left the flowers on a bagged spike without aid from any pollinating agent, natural or artificial, apart from the shaking of the plant as a whole in the wind.

In Table I are given the results of selfing the parental types. The number of flowers protected is the denominator, and the number of pods produced the numerator of a "fraction," while the number of these pods containing seed and the average amount of seed per pod are given in separate columns.

TABLE I.

Results of selfing parental types.

Kind and year	Method*	Pods set	Pods with seed	No. of seed per pod	Remarks
		flowers bagged			
Cabbage 1924.	1	$\frac{70}{73}$	No seeds	—	Another plant of
var. Early	2	$\frac{68}{70}$	"		same var. gave a
Enfield Market	3	$\frac{53}{75}$	"		similar result
Cabbage 1925.	2	$\frac{176}{176}$	No seeds		
Scotch York					
Cabbage 1925.	2	$\frac{160}{165}$	12	1-2	The seeds were all
Drumhead					at the distal end
					of the pods

* See text.

¹ Pollen was transferred with sterile forceps, a whole burst stamen being grasped and used to touch the desired stigma. Forceps were wiped when changing from method to method and sterilised with spirit when passing from plant to plant.

TABLE I (continued).

Kind and year	Method*	Pods set	Pods with seed	No. of seed per pod	Remarks
		flowers bagged			
Cabbage 1926. Daniels' Defiance	2	See special note			
Borecole 1924	1	64	No seeds		
	2	73			
	3	66 66 22 82	"		
Savoy 1924	1	45	No seeds		
	2	47			
	3	62 70 158 169	"		
Savoy 1925	1	30	No seeds	—	Clone from the 1924 plant
	2	38	"		
	3	16 33 25 58	"		
Brussels sprout 1924. var. Solidity	1	30	No seeds		
	2	33			
	3	34 40 149 154	"		
Kohl rabi 1924. Green-top	1	62	All	22	Under Method 3 the fertile pods were situate on the lower portion of the spike
	2	74	"		
	3	80 82 35 82	22	22	
Kohl rabi 1925	1	88	20	22	Clones from the 1924 plant, i.e. 3rd year
	2	163	30	22	
	3	111 152 152	10	6-12	
Broccoli 1924. White heading	1	Every pod set	No seed	—	Accurate counts not made
	2	"	"		
	3	"	"		
Broccoli 1925. White sprouting	1	42	32	5	An unprotected spike set 35 pods from 98 flowers
	2	114	36	5	
	3	47 107 29 33	22	5	
Broccoli 1924. Purple sprouting	1	30	30	22	—
	2	84	45	22	
	3	45 153 80 140	80	22	
Swede 1924. "Mervue"	1	52	52	18	Plant grown as annual
	2	60	41	18	
	3	41 49 58 92	58	Variable	
Turnip 1924. Greystone	1	25	24	16	Plant grown as annual
	2	67	28	16	
	3	35 50 0 123	—	—	
Turnip 1925	1	36	33	17	Plants grown as annuals from the selfed seed saved in 1924
	2	48	4	17	
	3	9 18 18 24	2	3	
Rape 1925	1	36	33	7-8	Plants grown as biennials
	2	66	19	7-8	
	3	24 46 31 60	20	5-6	
Mustard. Brown and white	—	Both the mustards proved to be fully fertile by all three methods			

* See text.

All the "cole" types (forms of *Brassica oleracea*) were grown in the familiar way—as biennials; the turnip, swede and mustards as annuals. An exception to this rule was a certain number of cabbages which flowered in 1926 and are, later, specially mentioned. On systematic grounds at least, there may be taken to be three broad groups within the genus.

Firstly, there is the cole group which includes the cabbages, savoys, brussels sprouts, broccolis, kohlrabi, etc.; secondly, the turnip, swede, rape group; and thirdly, the mustards.

From the point of view of compatibility simply, the cole group would seem to comprise two sections, the first of these, including cabbage, savoy, borecole, brussels sprouts, and white heading broccoli, being totally self-sterile. The second section, containing kohlrabi and the sprouting broccolis, is more or less self-fertile. These data apply to plants grown as biennials, the case of cabbage plants grown as annuals being dealt with later.

A distinction drawn by Kraus and Kraybill (21), and East and Park (11), must be referred to here; that is, between fruitfulness and fertility. Plants producing fruit but no viable seeds are fruitful but sterile; only when seeds are produced are the plants regarded as fertile. Many of the self-sterile plants examined in these studies were highly fruitful, the fruits being here referred to as "false pods." Those pods are quite as large as the normal fully fertile pod, only that they are not plumped out with seed. Emasculated protected flowers produce only very small shrunken pods or none. Focke (13), and Herbert (16), both stress the multiple and distinct functions of pollen, fertilisation of the ovum and stimulation of the fruit.

The members of the second section of the cole group comprising kohlrabi and the sprouting broccolis are self-fertile, though their fertility may be very low. That heading broccoli is sterile while sprouting broccoli is fertile is worthy of note. In the case of kohlrabi, "crossing" two flowers on the one spike would appear to have been rather more effective than simply selfing the individual flowers. This is probably due to differences in the relative maturity of pollen and stigmas; many varieties in the general cole group are known to be protogynous. In the case of the broccolis no definite difference is apparent between the different methods, the highest number of seeds being produced by the untouched bagged spike of purple sprouting broccoli, while the lowest figure is shown by the spike of white sprouting broccoli left unprotected and open to the action of all the natural pollinating agents! This plant

was fairly well isolated from the other *Brassica* plants by intervening rows of sweet peas. The case of the cabbage investigated in 1926 requires somewhat extended description. The plants used were members of an ordinary crop grown for seed—var. “Daniels’ Defiance.” Sown in April, 1925, and planted out during the following July, flowering commenced in May of 1926, *i.e.* some thirteen months after sowing. The whole area was planted from the same stock seed and all the plants were treated alike. In the field two groups of plants were used. The first group, made up of eight plants, was situated on well-drained soil at the crest of a small knoll. The second group, of five plants, was on the lower portion of the slope. Another plant with white flowers growing in close proximity to the second group was, like all the plants in both groups, selfed by Method 2. The season generally was rather wet, and a common complaint amongst growers was, that seed crops “kept growing” and seemed loth to “pod up.” It is probable that Group 2 received rather more moisture than Group 1. It was noticed that a larger proportion of plants round Group 2 failed to shoot than was observed round Group 1. As a general rule a variable number of plants in all annual grown crops of cabbage fail to shoot. This in itself might be regarded as a form of sterility, or, at least, retardation of the reproductive phase. After selfing (Method 2) the following results were obtained:

Plant no.	Pods set flowers bagged	Pods with seed	No. of seed per pod	
Group 1. Dry area				
1	$\frac{29}{31}$	10	1-6	
2	$\frac{27}{30}$	22	2-22	
3	$\frac{29}{30}$	20	2-22	
4	$\frac{30}{32}$	11	2-4	
5	$\frac{20}{40}$	12	1-22	
6	$\frac{14}{24}$	4	1-3	
7	$\frac{17}{19}$	15	2-22	
8	$\frac{25}{30}$	5	1-2	
Group 2. Wet area				
9	$\frac{17}{28}$	4	1-4	
10	$\frac{24}{29}$	1	5	
11	$\frac{26}{40}$	1	4	
12	$\frac{40}{29}$	3	1-2	
13	$\frac{27}{39}$	1	4	
14	$\frac{66}{73}$	6	1-2	White flowered “rogue”

Consideration of the results shows that as regards fruitfulness both groups are practically equal, but as regards fertility the Group 2 (wetter area) is very much lower than Group 1 (drier area). This is in accordance

with Kraus and Kraybill who found that abundant moisture induced sterility. Further, the results support the general practise of seed growers who, as a much applied rule, grow all plants for seed production under rather reduced cultural conditions. Thus, crops when grown in pots are invariably somewhat pot-bound and kept rather drier than the ordinary gardener would like¹. Also, indoor fruit growers, as, for example, tomato growers, in many cases tend to keep the plants reduced until fruit sets (*i.e.* until after fertilisation), after which they feed the plants liberally in order to produce large juicy fruits. Again, the general practise of growing seed crops of many of the biennial vegetables (mangold, swede, turnip, cabbage, etc.) as annuals would seem to have more than a purely economic aspect², in that this too is only another method of reducing the vigour of the "vegetative phase" with, probably, increased fertility. It is to be noticed that functioning gametes per plant is not the interest of the seedsman so much as functioning gametes per unit of area, and therefore though the "annual" plants may be smaller, their increased fertility and greater number per unit of area compensates for their reduced size. Annual habit may involve reduction of the flower number per plant, a point which requires further research. The important aspect from the point of view of these studies, however, is that the value of the constant *C* is considerably altered by comparatively simple variation of the environmental conditions such as are commonly adopted in practice.

Turning now to the results given by the turnip, swede, rape group, a rather different state of affairs is found. Swede is practically completely self-fertile when a sufficiency of pollen is definitely applied to the stigma. Turnip proved to be rather less fruitful and therefore rather less fertile than swede³. Rape behaved in much the same way as turnip. The question of the low results from Method 3 in this group being evidently one of pollination, will be discussed separately. The mustards on all occasions by all methods proved to be fully self-fertile.

¹ Stout (26) has stated that with *Brassica pekinensis* self-compatibility of a plant as a whole or a family of plants may be decidedly changed by a cultural treatment which reduced vegetative vigour.

² By growing the main bulk of these biennials as annuals a year is saved; thus land and capital are earlier set free. Stock seed, *i.e.* seed used to produce the commercial crop, is usually borne on specially selected parents fully developed in the usual biennial manner.

³ Drummond (10), referring to plants at Corstorphine (near Edinburgh), in 1923, says, "All the swedes produced plenty of selfed seed, the turnips on the other hand proved to be comparatively self-sterile."

CROSS-COMPATIBILITY.

The question of the cross-compatibility of the *Brassicae* has received much attention in the past. In the earlier experiments the forms were simply planted together and natural pollinating agents allowed to operate, data regarding the crossability of the types being deduced from the character of the resulting progeny. Little or nothing was known, however, regarding the genetics of the parents. The value of this type of evidence is doubtful, but may be used when the facts are positive.

Concerning first the cole group. Darwin⁽⁸⁾, planted a white kohlrabi, a purple kohlrabi, a Portsmouth broccoli, a brussels sprout and a sugar-loaf cabbage near together and left them uncovered. Seeds from each kind were sown in five separate beds. The majority of the seedlings in all the beds were mongrelised in the most complicated manner, some taking after one variety and some after another. The effects of the kohlrabi were particularly plain in the enlarged stems of many of the seedlings.

The same authority planted together two varieties of cabbage with purple-green and white-green lacinated leaves. "Of the 325 seedlings raised from the purple-green variety, 165 had white-green and 160 purple-green leaves. Of the 466 seedlings raised from the white-green variety, 220 had purple-green and 246 white-green leaves." The former of these two cases cited is not altogether precise, but the second seems positive. If the two parent plants were totally self-sterile, as might reasonably be expected, and one heterozygous for purple colour, then the half and half numbers in each case are explained¹.

Focke⁽¹³⁾, quotes various authors who indicate some considerable degree of crossing between the members of the genus. Price⁽²⁴⁾, under strictly controlled conditions, made reciprocal crosses involving heading and non-heading cabbage, savoy, cauliflower, brussels sprout and kohlrabi. No difficulty seems to have been met with in making the crosses. Kristofferson⁽²²⁾, also made many crosses involving the *Brassica oleracea* (cole) group. Sutton⁽²⁸⁾, arranged the *Brassicae* in three groups according to their fertility when crossed. His third group comprising all the coles, Sutton concluded, was completely cross-fertile. Herbert⁽¹⁶⁾, crossed turnip with swede, using the flower colour of the progeny as an indication of what had happened. An anonymous writer in the *Gardener's Chronicle* for 1885, p. 730, reports on a case where contiguous beds of rape and

¹ Kristofferson⁽²²⁾, and Pease⁽²³⁾, have shown that purple colour in the leaf is based on a single Mendelian factor pair and its presence is dominant.

turnip flowered at the same time. The seed produced by the turnip, when sown, developed into a lot of mongrels with forked roots, double crowns and some rape-like plants. Ashby⁽¹⁾, reports a case of crossing between crops of swede and rape under field conditions, the damage to the swede stock being assessed at £400. Sutton⁽²⁸⁾, crossed swede with turnip reciprocally under controlled conditions and obtained seed. The two aspects of the cross were, however, not the same. When the swede was fertilised by the turnip, that is to say, when the swede was used as the seed-bearing parent, abundant, plump, black-coated seed typical of the swede was obtained. When, however, the turnip was fertilised by the swede, *i.e.* when the turnip was made the seed parent, the seed produced was small, shrivelled, and difficult to germinate.

Sutton surmised that many other crosses involving swede, turnip and rape would behave in a similar way. Kajanus⁽¹⁷⁾, crossed swede and turnip reciprocally.

No case of crossing between the two mustards commonly grown in this country, or between them and the other *Brassicæ*, occurs in the literature.

Focke⁽¹³⁾, quotes Sageret, who reported a successful cross between turnip ♀ and cabbage ♂ (*Brassica napus* L. ♀ × *B. oleracea* L. ♂), and also between rape ♀ and cabbage ♂ (*B. rapa* L. ♀ × *B. oleracea* L. ♂). Focke does not seem to be convinced. Baur⁽³⁾ states that in this way crossing radish with cabbage is easy, but that the crossing of cabbage with turnip and also the reciprocal has never succeeded in spite of many experiments. Karpetchenko⁽²⁰⁾, found the mating *Raphanus sativus* L. ♂ × *Brassica oleracea* L. ♀ to be sterile, while the reciprocal yielded a variable F_1 which was always sterile. The present writer made all the crosses shown in Table II with the attached results. The examples given from the cole group support completely the general conclusions of Sutton⁽²⁸⁾ and others, that the members of this whole group are inter-fertile. Some indication, however, is made here that there is a variation in the degree of fertility between them.

This variability all centres round what has always been looked upon as the stem line of the group—the cabbage itself. Thus the savoy is not so fertile with cabbage pollen as with foreign savoy pollen, while the cabbage reacts to savoy equally well as to pollen from another cabbage. There seems to be some indication of a difference in the reciprocal crosses. (Stout⁽²⁵⁾ has noted that reciprocal crosses between pairs of plants may give opposite results.) While purple sprouting broccoli is totally fertile with white heading broccoli either way; it is

TABLE II.
Results of crossing parental types.

Pollen parent	Seed parent	Result	Remarks
Savoy	× Cabbage	Practically complete fertility	Cabbage is as fertile with savoy pollen as strange cabbage pollen
Cabbage	× Savoy	„	
Purple sprouting broccoli	× Cabbage	50 % of seeds in pod. All pods set	—
Cabbage	× Purple sprouting broccoli	Rather less fertile	—
Brussels sprout	× Cabbage	Set about 70 % of seed in pods	—
Cabbage	× Brussels sprout	Practically complete fertility	—
Borecole	× Cabbage	Complete fertility	—
Cabbage	× Borecole	„	—
Brussels sprout	× Kohl rabi	„	—
Kohl rabi	× Brussels sprout	„	—
Purple sprouting broccoli	× Kohl rabi	„	—
Kohl rabi	× Purple sprouting broccoli	„	—
White heading broccoli	× Purple sprouting broccoli	„	—
Purple sprouting broccoli	× White heading broccoli	„	—
Swede	× Turnip	„	Seeds shrivelled
Turnip	× Swede	„	Seeds plump
Rape	× Swede or turnip	„	—
Swede or turnip	× Rape	„	—
Brown mustard	× White mustard	No seeds, small pods	The flowers fell early
White mustard	× Brown mustard	Neither seeds nor pods	„
Brown mustard	× Borecole	No seeds, small pods	„
Borecole	× Brown mustard	Neither seeds nor pods	No effect
White mustard	× Turnip	No seeds, small pods	Pods ripened quickly
Turnip	× White mustard	Neither seeds nor pods	—
White mustard	× Swede	No seeds, small pods	Pods ripened quickly
Swede	× White mustard	Neither seeds nor pods	No effect
White mustard	× Charlock	Neither seeds nor pods	—
Charlock	× White mustard	No seeds, small pods	—
Brown or white mustard	× Swede × turnip F_1	No effect	—

only 50 per cent. fertile in either direction when crossed with cabbage. Again, brussels sprout is completely fertile with kohlrabi, but only 75 per cent. fertile with cabbage.

Turning to the turnip, swede, rape group much the same state of affairs occurs: differential fertility between different crosses involving the same types is found, and the turnip-swede case cited by Sutton is noted. The two mustards (brown and white) did not cross with each other nor with any other *Brassica* included in these studies. The physiological result of pollination with mustard pollen on various *Brassic*as such as turnip, will be discussed later.

THE WORK WITH PARENTAL TYPES.

This part of the work, principally concerned with the chances of "rogue" production apart from questions of pollination, has shown that in the cole group of the genus there is a section comprising forms which, if not always, are nearly always, completely self-sterile when grown in the ordinary way as biennials, even though the gametes be perfectly viable in compatible relationships. In these types, then, every seed must be of "crossed" origin. Thus, the character of the progeny depends in large part on the character of a pollen supply produced *external* to the plant, the chance or ability to self-pollenise which may exist being of no account. A plant completely surrounded by plants genetically similar to itself and therefore unlikely to receive out-varietal but compatible pollen will reproduce its like, but the slightest influx of dissimilar pollen must ultimately show in the progeny. The proportion and nature of the rogues will of course depend entirely on the amount and nature of the foreign pollen incident on the stigma. The example of the leaf character in two cabbages already cited from Darwin is peculiarly apt in this connection. In the other section of the cole group which is more or less self-fertile, though still largely cross-compatible, there are greatly reduced chances of natural crossing, because here the fertilisation is not wholly dependent on an externally produced pollen supply. The relative "fertilising value" of various types of compatible pollen as compared with "home" pollen will require some attention, because, as Herbert⁽¹⁶⁾ observed with *Rhododendron* and *Azalea*, two compatible pollens may not act with equal rapidity on the same stigma.

Looking, then, at the genus as a whole it may be said that the constant *C* is highest in relationships involving the completely self-sterile, highly cross-compatible section of the cole group, and zero in the highly self-fertile, completely cross-incompatible mustards, those

forms showing partial self- or cross-compatibility taking an intermediate position.

RESULTS OF THE VARIOUS CROSSES.

The next step taken was to test the compatibility of the hybrids resulting from the crossing experiments just reported; also to try crosses back to parental types, and out to other types in various relationships. The simplest procedure will be to discuss briefly each hybrid in turn, referring to its self- and cross-compatibility, etc. The estimates of cross-fertility are necessarily arbitrary, but probably have a useful degree of accuracy. All the lots of hybrid seed were sown in early August of the year of harvest, and the plants, as soon as fit, planted out in the field. During the winter 1924/25 there was a very small death rate, and some of the lines flowered as "annuals" in the spring of 1925. All the plants were left in the ground, and during the winter of 1925/26 there was a rather heavy death rate. All the lines, however, which did not flower in 1925 survived and flowered in 1926 with only one exception. Hence there is some record either as "annual," "biennial," or both for every hybrid noted in Table II, with one exception. Selfing was done in the manner already described for the parental types.

Cabbage × savoy. Both aspects of this cross were alike in appearance, being "weakly" savoy as reported by Price (24). The F_1 which had cabbage as the seed parent flowered in its first year (annual) and was selfed with the following results:

Method	Pods set. Flowers protected	Pods con- taining seed	No. of seeds in the fertile pods
1	$\frac{52}{56}$	4	2-8
2	$\frac{44}{52}$	2	2
3	$\frac{19}{53}$	0	—

The increased pod production following on deliberate pollination similar to that found in the parental types is again to be noted along with the practical sterility of the plant. The reverse of this cross did not flower as an annual and both lines died out in the second winter.

Cabbage × purple sprouting broccoli. Both aspects of this cross were similar in appearance and had broccoli leafage. There was no sign of a "curd," a normal cole inflorescence being produced in the usual way. In the F_1 , which did not flower until its second year, the leaves during the first summer turned over and inwards as if to afford protection to a "curd." This gave a semblance of "heading." The sepals of the flower were deep purple like those of the broccoli parent. The F_1 plants which

had the broccoli as seed parent flowered in the first year, persisted, and flowered again in the second summer. Those with cabbage as the seed parent flowered only in the second year. The results of selfing are as follows:

Method	Pods set. Flowers protected	Pods con- taining seed	No. of seeds in the fertile pods
Cabbage ♂ × purple sprouting broccoli ♀, 1st summer (annual)			
1	$\frac{50}{116}$	No seed	
2	$\frac{46}{106}$	"	
3	$\frac{51}{109}$	"	
Same plant, 2nd summer (biennial)			
1	$\frac{39}{90}$	5	1-2
2	$\frac{60}{70}$	4	1-2
3	$\frac{32}{74}$	9	0
Purple sprouting broccoli ♂ × cabbage ♀, 2nd summer (biennial)			
1	$\frac{28}{38}$	No seed	
2	$\frac{30}{33}$	"	
3	$\frac{35}{40}$	"	

The interesting feature is that this is the F_1 of the mating of a completely self-sterile form with the form which gave the highest figure for self-fertility in the parental tests. Crossed with broad-leaved rape the hybrid ex cabbage ♀ produced aborted shrivelled seed when used as the seed parent, but was sterile when used as the pollen parent.

Brussels sprout × *cabbage*. Reciprocals were alike in appearance, and when mature produced an open loose head and open loose sprouts. The leafage of the plant was carried up some way on a bare "leggy" stem. Neither F_1 bloomed in the first year, and neither produced a single seed when selfed by the three methods in the second year, though every flower protected produced a pod by Method 1, not so many by Method 2, and still less by Method 3.

Crossed with rape this hybrid was quite ineffective as the pollen parent, but as a seed parent it produced weak, shrivelled, non-viable seed.

Cabbage × *borecole*. This hybrid was weakly "heading," and had typical kale leaves. It was the most winter-hardy of the hybrids. Both aspects of the cross flowered in their second summer only, and gave results very similar to those described for the last cross. They developed 11 seeds from 315 flowers protected by all methods. Crossed with rape it produced aborted, shrivelled seed when used as the seed parent, but proved quite sterile when used as the pollen parent. Crossed with the four hybrids involving matings of turnip with rape and swede with

rape it was sterile every way. The pods produced by the pollen of these four hybrids were very similar in size and appearance to those produced from protected, emasculated flowers, and flowers from which the stigma had been cut off in the bud. These pods are small and very often blue-coloured, seldom having the false septum completed, it being usually present as two little membranous frills down the inside edge of the pod. Thus it may be inferred that these swede (or turnip) \times rape hybrids are quite without effect on cole types, the pollen not even exerting the stimulative effect on the fruit so commonly observed within the genus. That this lack of effect is not due to lack of viability of the various gametes is evidenced by the wonderful fertility of both pollen and ovules in compatible relationships.

Brussels sprout \times *kohl rabi*. This hybrid produced much thickened stems, and at their apex a large number of buds similar to rather loose brussels sprouts. The line with brussels sprout as the pollen parent flowered both as an annual and as a biennial: the reciprocal flowered only in its first summer. The selfing results were as follows:

Method	Pods set. Flowers protected	Pods con- taining seed	No. of seeds in the fertile pods
Brussels sprout δ \times kohl rabi η , 1st summer (annual)			
1	$\frac{22}{32}$	All	10
2	$\frac{25}{33}$	20	8
3	$\frac{30}{30}$	13	2
Same plant, 2nd year (biennial)			
1	$\frac{22}{31}$	0	—
2	$\frac{43}{50}$	19	1-12
3	$\frac{46}{60}$	0	—
Kohl rabi δ \times brussels sprout η , 1st summer (annual)			
1	$\frac{23}{23}$	12	8
2	$\frac{15}{15}$	8	9
3	$\frac{15}{37}$	15	3-4

This again is a cross of self-sterile with a self-fertile parent, and two points of interest emerge from the results. In their first year both aspects of the cross are self-fertile. The plant, which persisted and flowered in its second year, was scarcely fully fertile and the fact that Method 1 produced no seed may be due to some disturbing factor which entered into the result, though none could be accounted for.

Purple sprouting broccoli \times *white heading broccoli*. This cross is of peculiar interest as it involves what may be looked upon as two distinct types of sterility in one parent and a certain degree of fertility in the

other. White heading broccoli normally produces many more flower primordia than ever develop; a very large number abort, and are seen, when the inflorescence which develops from the edible head extends, as small brown withered knobs. Aborted primordia were not observed in the purple sprouting parent. Further, the white heading broccoli proved to be completely sterile in those flowers which did develop, but produced false pods as shown in Table I. Purple sprouting broccoli had been found to be comparatively fertile. The hybrid plants were

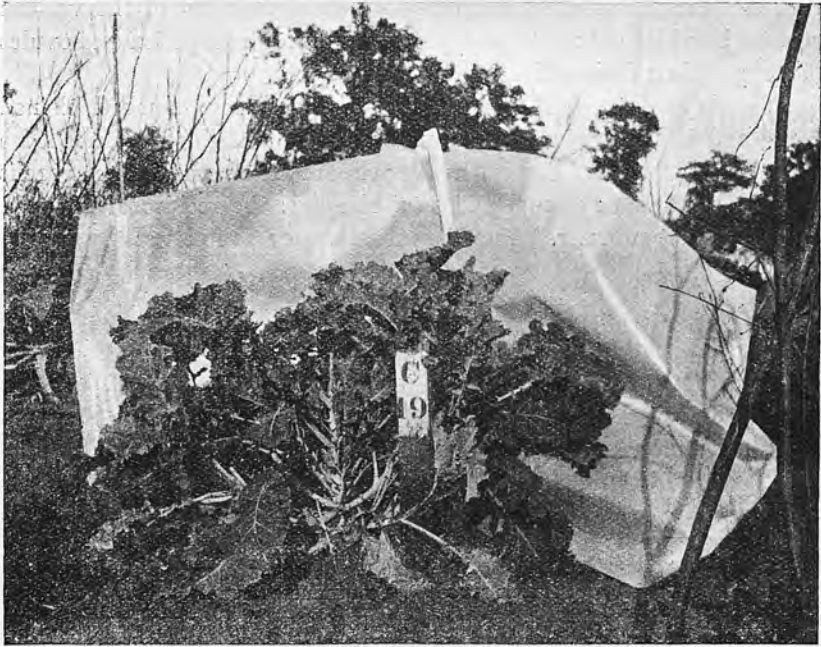


Fig. 1. F_1 plant of Purple sprouting broccoli \times White heading broccoli.

extremely vigorous, vegetatively, throwing up a large number of side shoots and forming a bushy leafy plant as seen in Fig. 1¹. Both aspects of the cross were identical in appearance. They did not flower in their first year, but produced a large number of purple broccoli heads in their second summer. A very large number of the flower primordia forming these heads aborted in the same way as the white heading parent did.

¹ The production of many side shoots in greater or lesser degree was characteristic of all those cole hybrids.



Not only were primordia shed, but buds in practically all stages of development were cut off. For those buds which developed the following results were obtained:

Method	Pods set. Flowers protected	Pods con- taining seed	No. of seeds in the fertile pods
Purple sprouting broccoli ♂ × white heading broccoli ♀, 2nd summer			
1	$\frac{48}{129}$	4	1-4
2	$\frac{113}{113}$	14	1-4
3	$\frac{0}{120}$	—	—
White heading broccoli ♂ × purple sprouting broccoli ♀, 2nd summer			
1	$\frac{0}{94}$	—	—
2	$\frac{0}{81}$	—	—
3	$\frac{0}{152}$	—	—

This hybrid seems to have received both forms of sterility with unimpaired intensity.

The turnip-swede-rape group. All the hybrids of this group sown in the autumn flowered during the following spring and summer. Hybrids involving turnip and swede, as has been mentioned, differ according to the way the cross is made. When turnip is used as the seed parent the resulting seed is weak, shrivelled and difficult to germinate. When swede is used as the seed parent the seed is plump and germinates strongly. Sutton⁽²⁸⁾, who reported this previously, found, however, that there was little or no difference in the hybrid plants once they became established. With the present writer, however, the hybrids which had had the swede for their seed parent were always rather stronger and more vigorous. They, too, produced more root buds¹. Both aspects were affected by "finger and toe," the vigorous line producing larger "warts" but, when later on towards the end of the flowering period the plants were affected by mildew, the weak line was more affected than the aspect of the cross which had swede for seed parent (Fig. 2 shows typical plants). The plants, apart from vigour, were quite similar, and might briefly be described as white fleshed swedes with the white swedes' light-yellow-coloured flower, though the typical swede "neck" was very slightly developed. When selfed, neither aspect of the cross developed a single pod. Left to open pollination, to some extent isolated from other *Brassicæ*, a large amount of seed was produced; this has been already noticed by Kajanus⁽¹⁸⁾. It was observed in these studies that the line derived from the swede seed parent, though, if anything, farther removed from other compatible types, set rather more seed than its reciprocal, and it is assumed that some of this seed resulted

¹ Kajanus (17), has discussed these malformations very fully.

from plant to plant pollination amongst the hybrids themselves. Various back and out crosses were attempted, and, as these later become somewhat involved, they are graphically represented in Figs. 3 to 7. In the figures the connecting lines join the forms crossed; the arrows indicate the direction the pollen was carried in; and the plus signs are estimates of the degree of fertility which obtained. The observations, from their very nature, could not be precise, and the difference between + + + and + + is not insisted on, but it is very probable that the difference

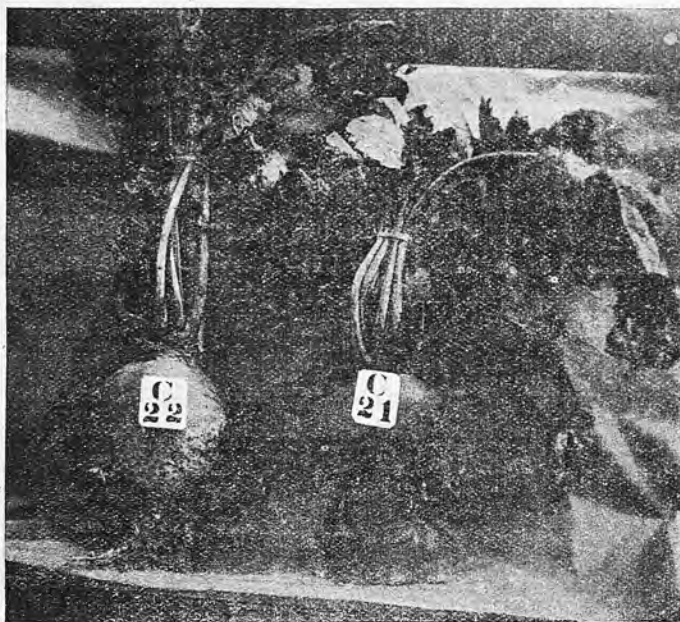


Fig. 2. Turnip swede hybrids. (C 21 had turnip as seed parent; C 22 had swede as seed parent.)

between + + + and + is quite significant. Plants of hybrid origin are shown as "fractions," the numerator always being the pollen parent. Thus $\frac{\text{swede}}{\text{turnip}}$ indicates a hybrid plant from the mating swede ♂ × turnip ♀. These back and out crosses were made to turnip, swede, rape, cabbage, mustard and radish. All the back crosses to turnip, swede and rape were more or less successful both ways. The out crosses to mustard and cole did not succeed in any case.

Distinct differences in fertility between the back crosses were noted. There is good evidence for stating that turnip pollen on the swede ♂



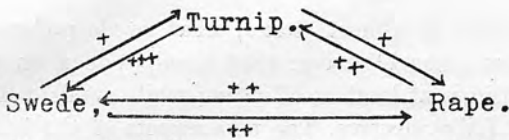


Fig. 3. Diagram to illustrate the fertility of inter-parental crosses.

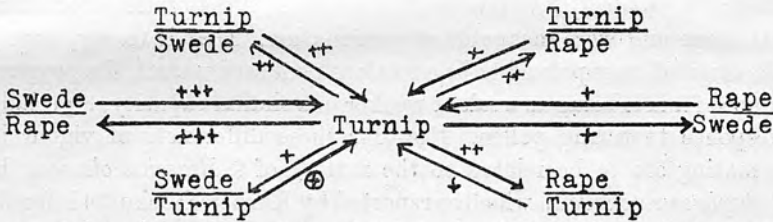


Fig. 4. Diagram to illustrate the fertility of crosses between hybrids and turnip.

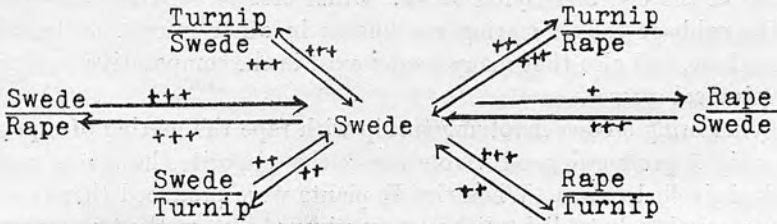


Fig. 5. Diagram to illustrate the fertility of crosses between hybrids and swede.

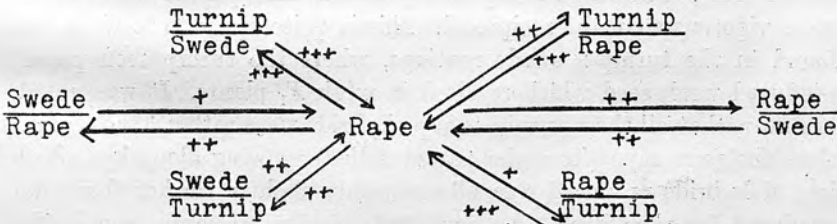


Fig. 6. Diagram to illustrate the fertility of crosses between hybrids and rape.

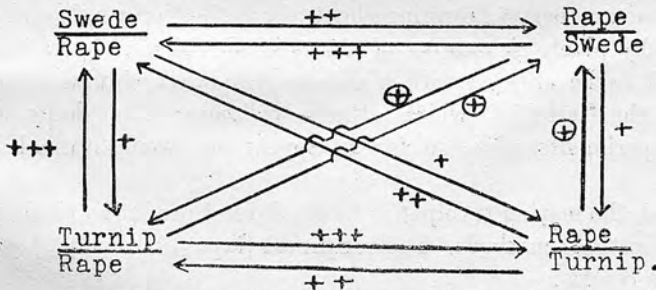


Fig. 7. Diagram to illustrate the crosses between hybrids.

× turnip ♀ hybrid is almost sterile; that swede pollen on the same hybrid is rather more effective; that turnip pollen on the turnip ♂ × swede ♀ hybrid is at least as effective; while swede pollen with this hybrid proved fully effective. The two aspects of the turnip × swede mating proved to be weakly fertile when crossed, but in the mating (turnip ♂ × swede ♀) ♂ × (swede ♂ × turnip ♀) ♀ the ovules aborted at a late stage and were incapable of germination. That is to say, turnip in the original cross proved to be a weak or poor seed parent, the progeny produced from it being as weak or weaker in a similar capacity, especially in response to turnip pollen. How far these differences of vigour in this mating are to be related to the mating of ♀ *Brassica oleracea* L. × ♂ *Raphanus sativus* L. which as reported by Karpetschenko⁽²⁰⁾ is fertile while its reciprocal is sterile, is difficult to determine. Are they both phases of the one underlying cause? Other crosses behaving similarly to the cabbage radish mating are known in other genera. Stout⁽²⁵⁾, notes these, and also that many grades exist in the comparative fertility of reciprocal crosses.

Considering crosses involving turnip with rape the mating of rape ♂ × turnip ♀ produced good viable seed; the opposite, however, gave weak shrivelled grains. When the F_1 plants were produced therefrom, there seemed to be a slight difference in vigour between the two aspects of the cross. The line having turnip as the seed parent was slightly more vigorous than the reciprocal. This is quite opposite to what was found in the turnip × swede matings, where the turnip seed parent produced weak seed which resulted in weak F_1 plants. It was noted, however, that all these turnip × rape hybrids were rather less vigorous than the pure rape (from the parent selfed) growing alongside. Both lots of hybrids produced a small root, only slightly thicker than that produced by rape itself. No root buds similar to those seen in the turnip × swede hybrids were observed. At flowering time they threw up a large number of flowering shoots from the "crown," producing a very bushy plant. A number of plants in all the rape hybrid cultures appeared to be affected with a disease somewhat similar in appearance to the "crinkle" which attacks potatoes. The plants used in these experiments were, so far as appearance went, normal in this respect.

Selfed, the mating turnip ♂ × rape ♀ did not produce a single pod by any of the three methods. The reciprocal (rape ♂ × turnip ♀) gave the following results:

Method	Pods set. Flowers protected	Pods con- taining seed	No. of seeds in the fertile pods
1	$\frac{17}{30}$	6	1-2
2	$\frac{48}{51}$	2	1-2
3	$\frac{0}{30}$	—	—

It is seen, then, that when the pollination was precise this aspect of the cross was to some extent fertile, and in its behaviour reminiscent of the turnip parent.

Back crossed to the parents and swede F_1 ex turnip $\delta \times$ rape φ proved to be more or less completely fertile. With rape and swede there was some indication that the hybrid was more effective as a polliniser than as a seed parent. With turnip the fertility was rather lower. F_1 ex rape $\delta \times$ turnip φ , when back crossed, gave similar results.

Crossing these turnip/rape hybrids with swede/rape hybrids gave in the main very poor results, except that the mating of (turnip $\delta \times$ rape φ) $\delta \times$ (swede $\delta \times$ rape φ) φ was highly successful, that is, when all the three "parental" types were involved and rape was the "common parent," being the *seed parent* of both of the plants. Further, it seemed clear in these matings of hybrids that turnip $\delta \times$ rape φ was rather more successful than its reciprocal.

In crosses involving swede with rape it was noticed that the first parental cross was completely successful either way, both aspects producing abundant, plump and easily germinated seed.

The hybrid F_1 plants were in many ways similar to the F_1 plants from turnip \times swede.

The roots were white fleshed and of fair size. No root buds were observed. A main flowering stem grew up and, though branched, there was no appearance of the many branches originating at the "crown," as was seen in the turnip \times rape hybrids. The flowers were lemon-yellow like the rape parent. The F_1 resulting from rape $\delta \times$ swede φ was somewhat weakly, due to heart rot. When selfed the two aspects gave the following results:

Methods	Pods set. Flowers protected	Pods con- taining seed	No. of seeds in the fertile pods
Swede $\delta \times$ rape φ			
1	$\frac{25}{25}$	23	28
2	$\frac{16}{19}$	16	28
3	$\frac{28}{32}$	23	28
Rape $\delta \times$ swede φ			
1	$\frac{35}{49}$	35	1-12
2	$\frac{28}{60}$	27	1-6
3	$\frac{28}{65}$	25	1-5

It may be mentioned in passing that Sutton's supposition that these hybrids would prove sterile is not well founded. The hybrid from swede ♂ × rape ♀ proved to be fully fertile with swede and turnip, but, curiously, rather less so with rape. The reciprocal (rape ♂ × swede ♀) was only fully fertile when used as the pollen parent on swede. With turnip it was only weakly fertile. The two aspects of the mating when crossed *inter se* were fully fertile. When crossed out to the turnip/rape hybrids the only mating which proved fully fertile was, as has been already shown, when the rape was the seed parent of both the hybrids mated.

DISCUSSION.

It is not proposed at this stage to develop any general discussion on fertility, but a few notes peculiar to the special point of view from which these studies are written will be offered.

Referring first to self-incompatibility, it seems clear that, in all the self-incompatible plants discussed, not of immediate hybrid origin, the cause of the incompatibility is the well known inability of the pollen tubes to proceed through the stylar tissue. That is to say, the gametes are in all probability quite capable of uniting successfully but they never meet; the last stage of the male gametes journey being interrupted. Whether this inability of the pollen to proceed through the stylar tissue is due to the production of an inhibiting substance, or to the non-production of some stimulating substance, was not decided by Correns (6), who discussed the phenomena in *Cardamine* and found evidence for the belief that they have a genetical basis involving a number of factor pairs which are transmitted according to a Mendelian scheme. Compton (5), who criticises the work of Correns, found evidence (4) in *Reseda odorata* for a simple scheme of Mendelian inheritance involving one factorial pair, self-fertility being dominant to sterility. Crane (7), working with plums and cherries, found no evidence to negative the view that self-sterility is a Mendelian recessive, but it appears that more than one factor is involved. East and Park (11) take the view that self-sterility is a condition determined by inheritance, but can be developed to its full perfection only in a suitable environment. The environment most suited to the development of self-sterility is stated by these workers to be one which promotes normal healthy vegetative growth during the active part of a flowering period. That self-sterile plants differ in their norms for self-sterility is also noted by East and Park. East and Mangelsdorf (12) working with species of *Nicotiana* give a genetical explanation involving three factor pairs for the self-sterility results they report.

In the results reported here it is interesting to note that when cabbage (totally self-sterile) was crossed with purple sprouting broccoli (self-fertile) the F_1 was practically completely self-sterile. When, however, brussels sprout (self-sterile) which produced a completely self-sterile F_1 with the cabbage just mentioned was crossed with kohlrabi (self-fertile), the F_1 showed practically complete fertility as an annual, and only slight fertility in its second summer. What degree of fertility would have obtained if the plants had not flowered until their second summer with consequent unimpairment of the vigour of the vegetative phase is an interesting question. If it be assumed, however, that self-sterility is dominant in these coles, that brussels sprout was heterozygous and the cabbage homozygous, then a simple Mendelian explanation could be offered. The view adopted here, however, is that though self-fertility may be conditioned by inheritance, sterility when it occurs, may, in practice, best be controlled by control of the environment rather than by the selection of self-fertile individuals.

The importance of "false podding" or fruitfulness accompanying sterility must not be overlooked. For the fruit grower this is obvious, but for the seedsman and plant breeder the question arises whether false podding may be looked upon as a promise of fertility when conditions are altered. Darwin⁽⁹⁾ regarded so slight an effect as accelerated flower-fall following on pollination as a case of "incipient fertilisation."

The foregoing discussion which applies, as far as this report goes, only to parental types and F_1 's within the cole group, does not apply to the crosses between species. It is practically certain that in the inter-specific crosses absence of complete fertility, or the appearance of total sterility, has a cytological basis. Karpetschenko⁽¹⁹⁾ has shown that all the forms examined by him belonging to the cole group (*Brassica oleracea* L.) have 18 chromosomes: the species to which the present writer believes his rape and, possibly, swede to belong (*Brassica napus* L.) has 36, while the species to which the turnip belongs (*Brassica rapa* L.) has 20. Brown mustard (*B. nigra* Koch.) has 16, while white mustard (*Sinapis alba* L.) has 24. The species of *Raphanus* have 18. All these numbers refer to the diploid phase. Regarding these results Karpetschenko concludes that the data of cytological investigation are also in conformity with the results of hybridisation: within the limits of separate genera plants having the same number of chromosomes are easily crossed, while the crossing of plants with different chromosome numbers is difficult. The further hybridisation results reported here agree, in the main, with this conclusion. All the coles are easy to cross and form a

natural group within a large species. The turnip-swede-rape group referred to here is not so homogeneous, for, viewed in the light of Karpetschenko's conclusion, and remembering Bailey's (2) opinion that swede has affinity with rape, the slight but clear differences between swede and rape in relation to turnip require some discussion. The swede and the rape probably do not occupy quite the same position phylogenetically; rather would it appear that rape in some way makes a slight approach towards turnip, or, possibly more correctly, the swede has diverged. The external appearance of the Essex Broad-leaved Rape used in all these studies is very much like a white-fleshed swede which has failed to develop a bulb; both have the lemon-yellow turnip-like flower instead of the swede buff-coloured flower. The fact that rape shows some approach to compatibility with cole might be taken to indicate that it is the true *Brassica napus* L., having 36 chromosomes as reported by Karpetschenko, rather than swede, because the mating of 18 with 36 may be possible, and swede shows no indication of compatibility with cole, though here a physiological bar may be operating in addition. The cytological position in regard to the swede \times turnip mating is unsatisfactory too, and it is likely that the fertility phenomena in connection with it reported here have a cytological basis. This supposition is supported by a parallel case in *Triticum*, reported by Watkins (29, 30) who crossed *Triticum turgidum* having 14 chromosomes with *T. vulgare*—21 chromosomes¹. He noted that all the grains resulting from the cross were shrunk and wrinkled, but those obtained when *vulgare* was the female parent were less so than the grains from the reciprocal cross. To note that in these *Triticum* and *Brassica* crosses, when the parent with the largest chromosome number was the female, the resulting seed was larger and more plump, is interesting and may be significant. It is to be remembered, of course, that the structure involved is a fruit in *Triticum* and a seed in *Brassica*.

While the vegetative weakness following on hybridisation in the turnip/swede cross, when the turnip was the female parent, may have the same cytological basis, the point requires confirmation. This reduction of vegetative vigour following on reduced fertility vigour and *vice versa* can hardly be related to the decrease in fertility vigour following on decrease of vegetative vigour seen in so many other cases. What is implied here by "reduced vegetative vigour" is illustrated in Pl. IX, figs. 1 and 2. The differences between the lots are striking in view of the fact that all the plants were sown on the same day and

¹ Haploid numbers.

every possible precaution taken that they should all receive the same treatment.

The results of selfing by Method 3 (isolation of the spike from every type of pollinating agent) may be briefly mentioned. They are offered here simply as an indication of the necessity for deliberate pollination in order to obtain selfed seed of certain plants. The low yield of pods and, in the case of self-compatible plants, of seeds may be ascribed entirely to an insufficiency of pollen reaching the stigma. This inability to self-pollinate, which in many cases, undoubtedly results from spacial and time relationships of flowers and flower parts, will be discussed elsewhere.

SUMMARY.

1. The paper deals with the cross- and self-fertility of certain forms of the genus *Brassica*.

2. It is shown that "rogue" production between two commercial crops depends on the amount of pollen of one incident on the aggregate stigmatic area of the other and a "constant" applicable to the relationship under consideration.

3. The "constant" is shown to be the resultant of the self-compatibility of the one crop and the cross-compatibility which exists between the two.

4. The value of the two components of the "constant" is shown to depend upon, and largely to be controlled by, the environment.

5. Relationships involving various *Brassicaceae* which might lead to valuable recombinations are discussed.

6. Weakened vegetative vigour following on weak fertility vigour and *vice versa* are noted and discussed.

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EXPLANATION OF PLATE IX.

- Fig. 1. On the right are shown two rows of turnip ♂ × (swede ♂ × turnip ♀) ♀ and next to them on the left two rows of rape ♂ × (swede ♂ × turnip ♀) ♀.
- Fig. 2. Reading from right to left are shown:—(turnip ♂ × swede ♀) ♂ × rape ♀ turnip ♂ × (turnip ♂ × swede ♀) ♀ (C 47); (swede ♂ × turnip ♀) ♂ × turnip ♀ (C 48); swede ♂ × (swede ♂ × turnip ♀) ♀ (C 49); (swede ♂ × turnip ♀) ♂ × swede ♀ (C 50).



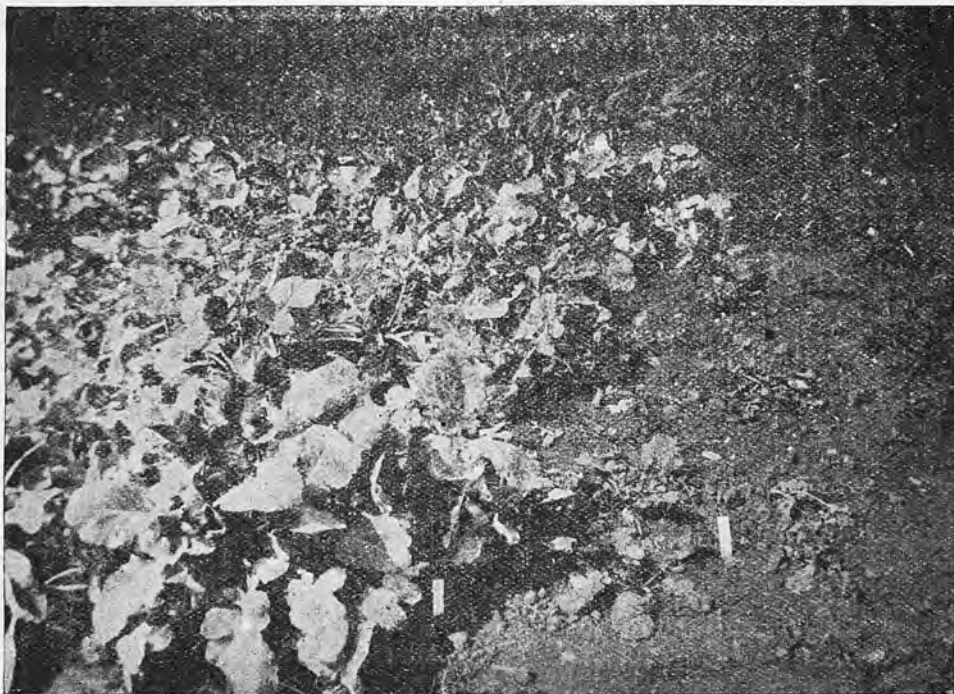


Fig. 1.

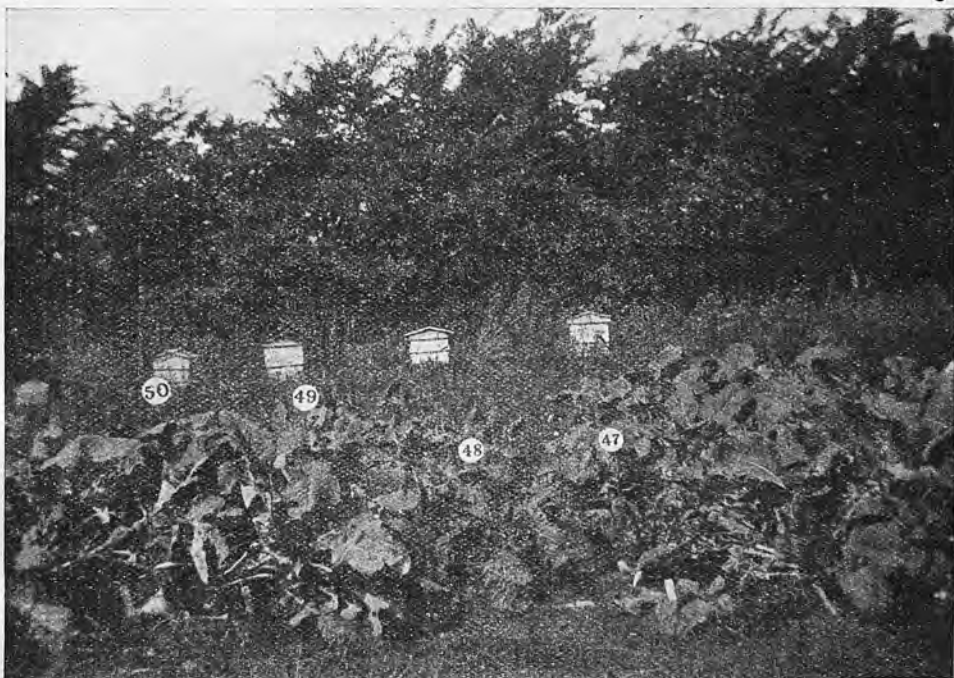


Fig. 2

THE GERMINATION OF *POA* SPP.

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(With 7 Graphs and 2 Text-figures.)

A LARGE proportion of the "seeds" used in agriculture is included in the Natural Order Gramineae and, arising out of the present day insistence on a viability test previous to sowing, the laboratory germination of this class is a problem of importance.

Regarded from the point of view of volume of trade, the genus *Poa* is not of prime importance. Regarded from the point of view of the seed analyst, however, the fickle nature of the species of the genus in germination gives them considerable interest.

The present study was planned, in the first place, to analyse the action of the various factors bearing on germination and correlate them one to the other. The action of various salts was studied, and later, the soil as a substrate was introduced.

Numerous workers have shown that alternation of temperature and exposure to light are aids to germinating "seeds" of the *Poas*. These two aids are part of the method standard in British laboratories (Saunders⁽²¹⁾). In American laboratories a 1 per cent. solution of potassium nitrate is commonly used in place of tap-water as a source of moisture. The nitrate increases the speed of germination and the total number of seeds germinating.

Material. Samples of "seed" of the four common species (*compressa*, *nemoralis*, *pratensis* and *trivialis*) crop 1924, were obtained and kept under room conditions until February, 1925, when tests were commenced. The purity of the samples to specific character was checked from Hellbo⁽⁷⁾. As each test was sown the "seed" to be used was drawn from the sample, care being taken that each individual was made up of a pair of "glumes" and a caryopsis.

Apparatus and Methods. Large, locally made, gas-heated tanks of the Jacobsen pattern, as shown in Fig. 1, were employed. Each 100 of "seeds" was sown on a circular blotting paper pad laid on two blotting

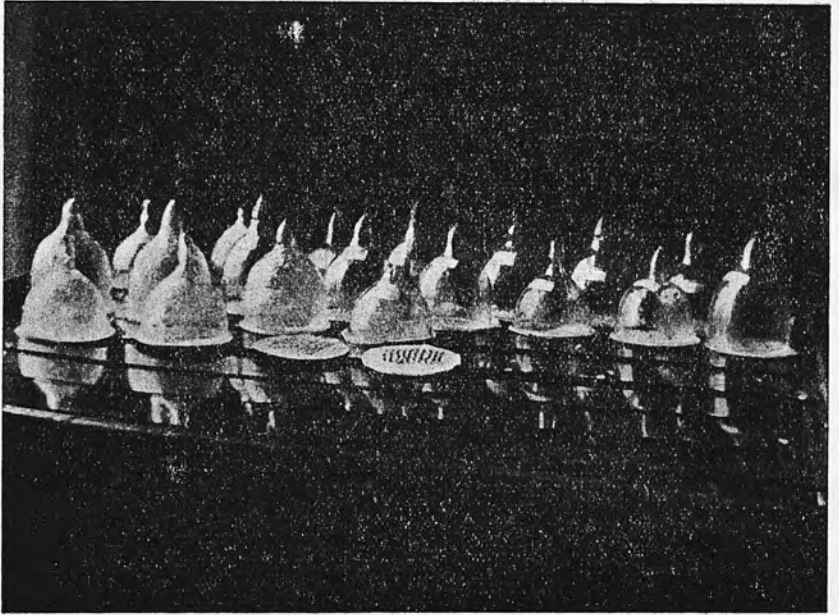


Fig. 1. Tests on germinating tank.

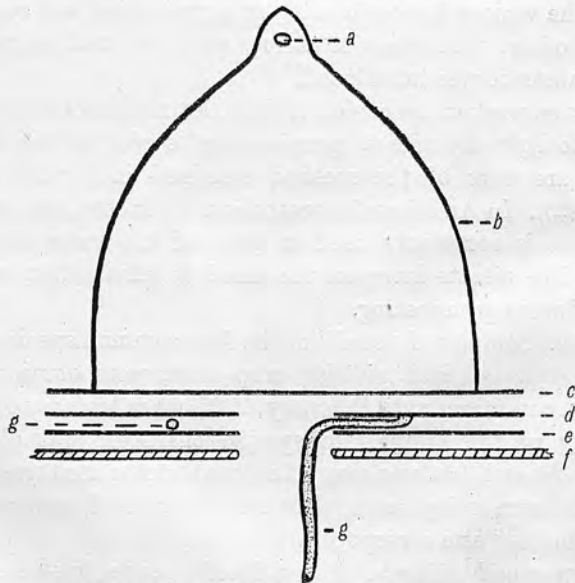
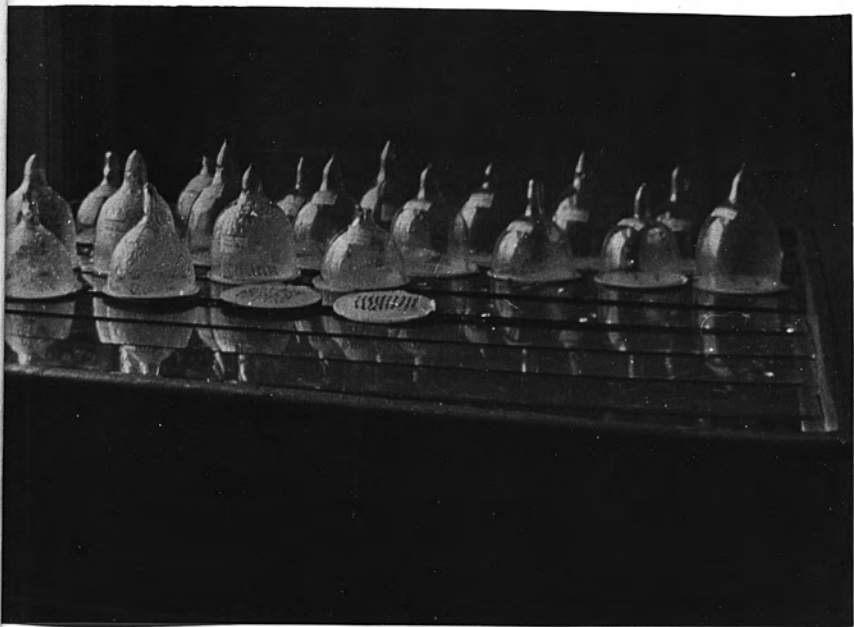


Fig. 2. Vertical section of germinating system.

a, Ventilating hole. *b*, Glass bell-jar. *c*, Blotting-paper "seed-bed" or pad. *d* and *e*, Blotting-paper rings. *f*, Glass bar supporting tests. *g*, Miners' wick.



paper rings. The pads were supported on glass bars running across the tank and kept moist by a length of miners' wick dipping into the tank water. Small clear-glass bell-jars covering the tests prevented excessive evaporation without excluding light (see Fig. 2).

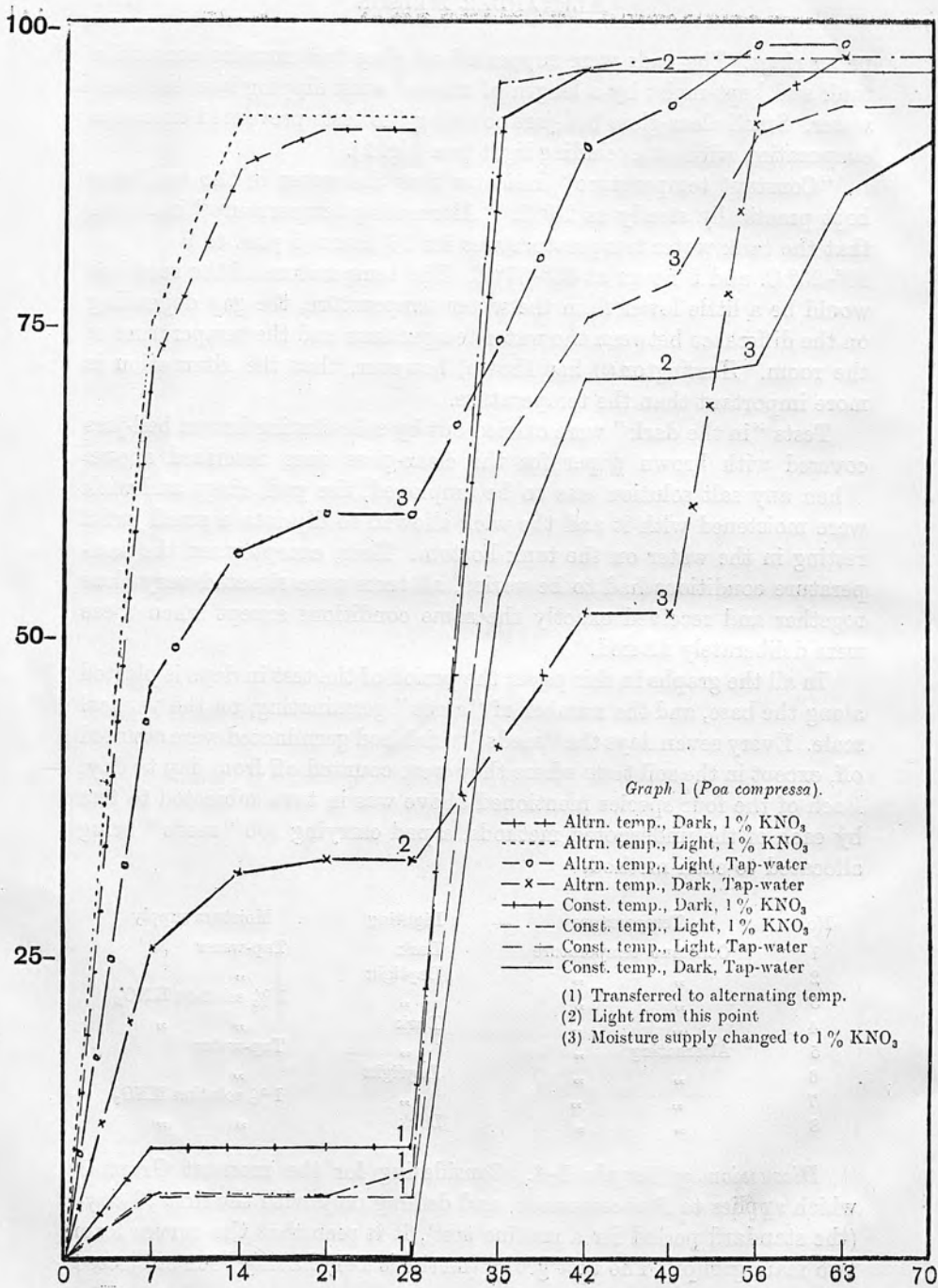
"Constant temperature" indicates that the water in the tank was kept practically steady at 25° C. "Alternating temperature" indicates that the tank water temperature was for 16 hours (5 p.m. to 9 a.m.) at 20°-23° C. and 8 hours at 35°-37° C. The temperature of the seed-bed would be a little lower than the water temperature, the gap depending on the difference between the water temperature and the temperature of the room. Harrington(6) has shown, however, that the alternation is more important than the temperature.

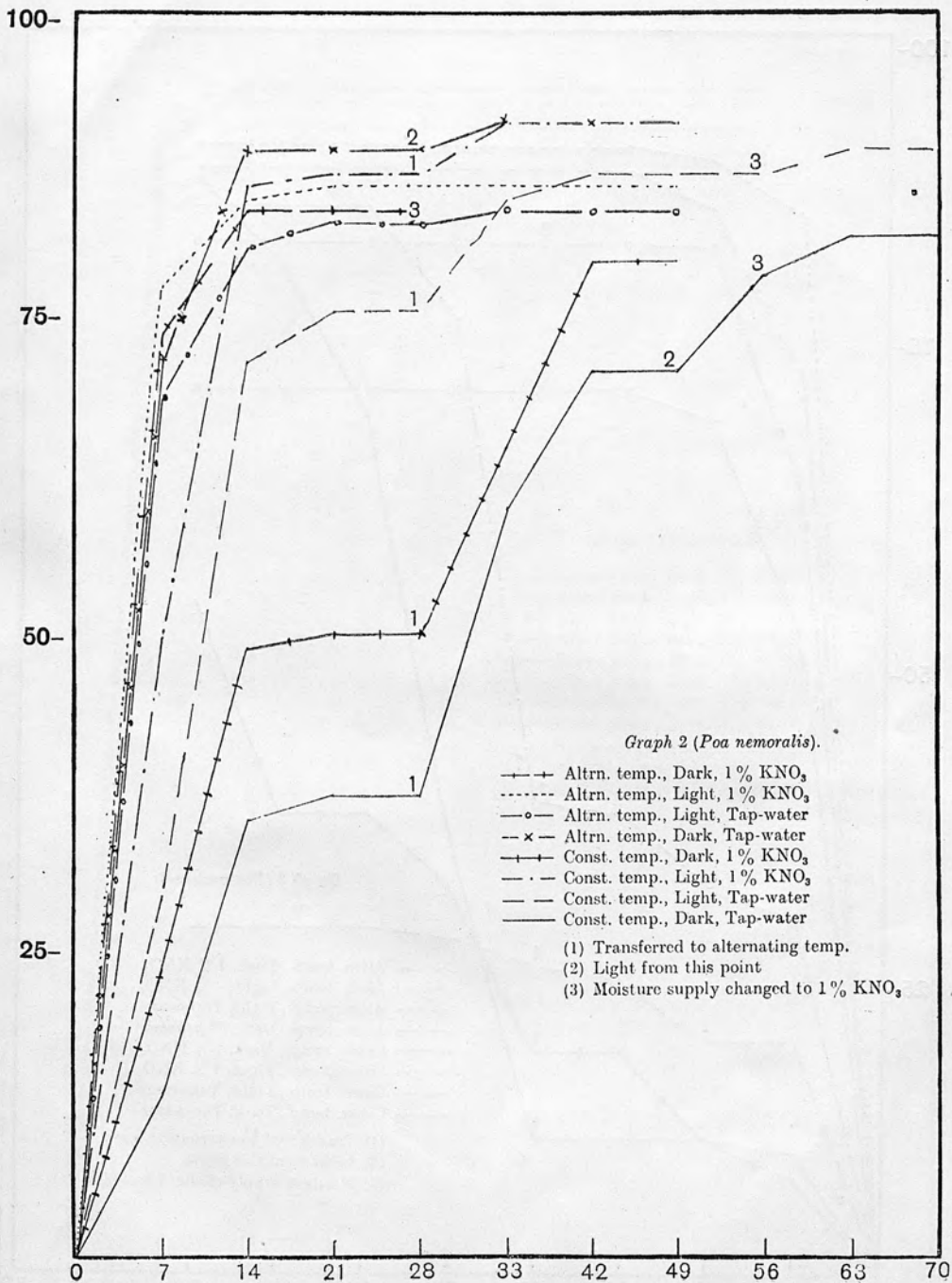
Tests "in the dark" were carried out by substituting brown bell-jars covered with brown paper for the clear-glass ones described above. When any salt solution was to be employed, the pad, rings and wick were moistened with it and the wick allowed to dip into a small jarful resting in the water on the tank bottom. Thus, except when the temperature conditions had to be varied, all tests were situated very close together and received exactly the same conditions except when these were deliberately altered.

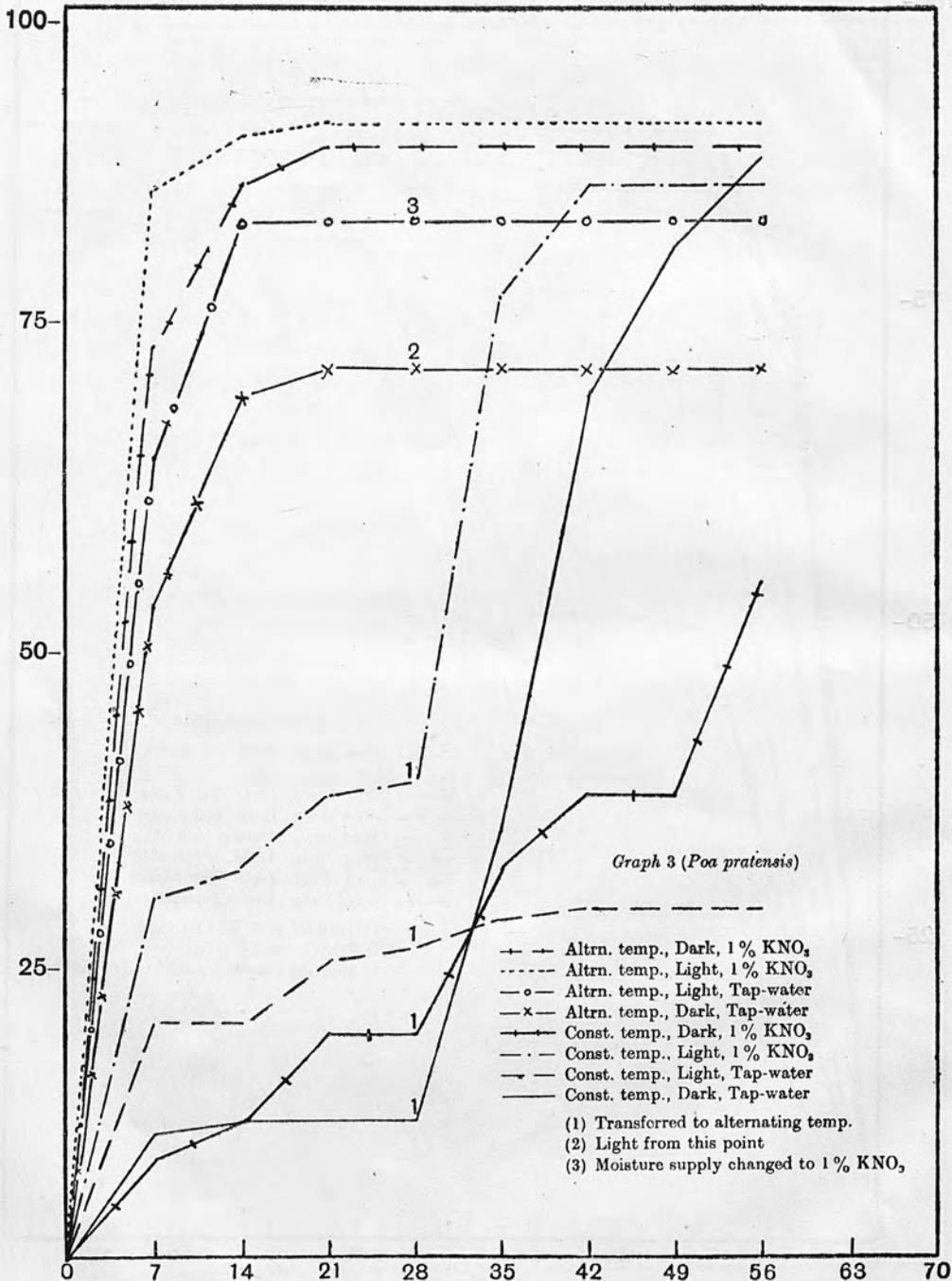
In all the graphs in this paper the period of the test in days is plotted along the base, and the number of "seeds" germinating, on the vertical scale. Every seven days the "seeds" which had germinated were counted off, except in the soil tests where they were counted off from day to day. Each of the four species mentioned above was in turn subjected to test by each of the undernoted methods, a pad carrying 100 "seeds" being allocated to each method.

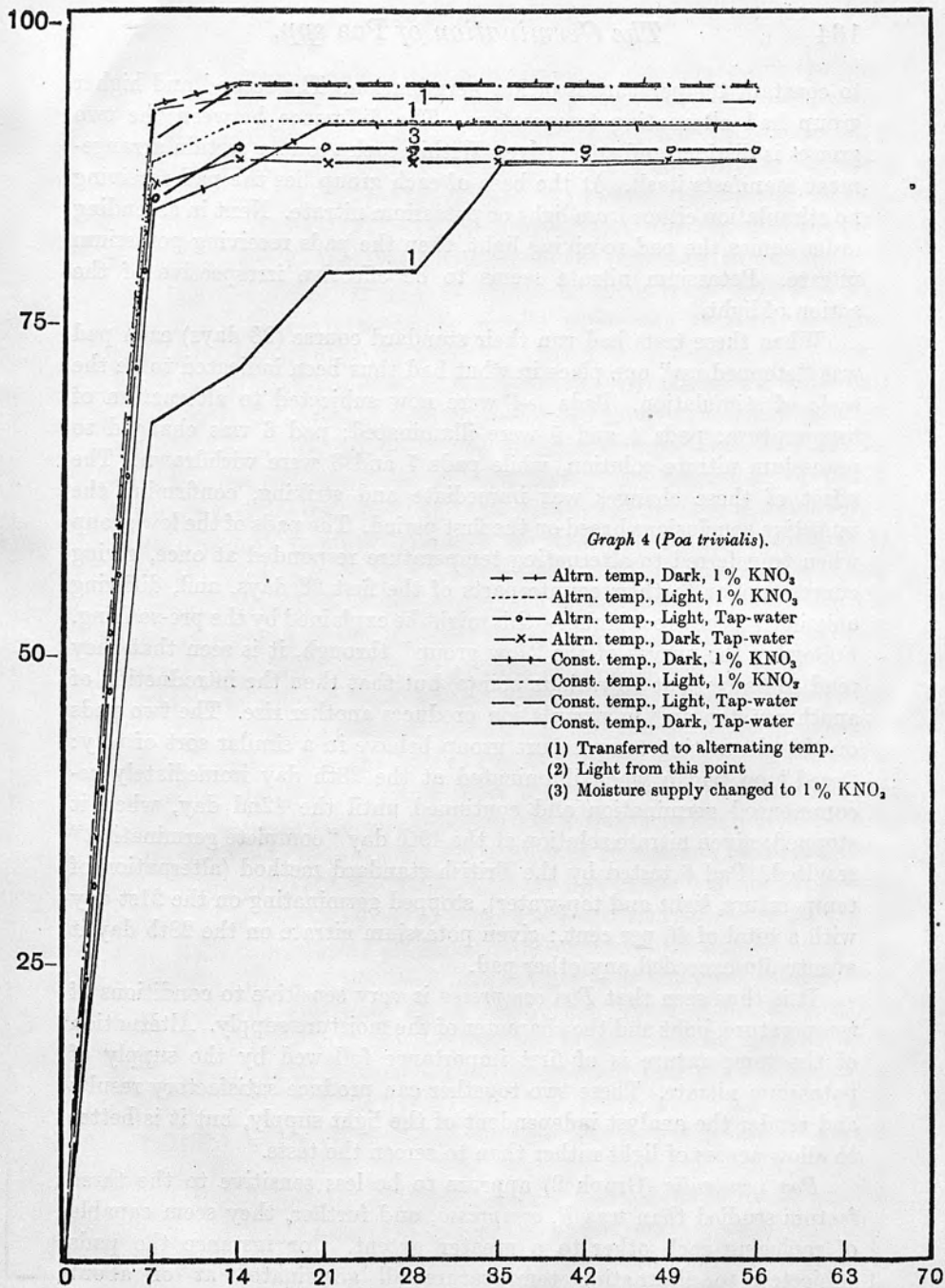
No.	Temperature	Lighting	Moisture supply
1	Constant temperature	Dark	Tap-water
2	" "	Daylight	"
3	" "	"	1 % solution KNO ₃
4	" "	Dark	" "
5	Alternating	"	Tap-water
6	" "	Daylight	"
7	" "	"	1 % solution KNO ₃
8	" "	Dark	" "

Discussion of Graphs 1-4. Considering for the moment Graph 1 which applies to *Poa compressa*, and dealing only with the first 28 days (the standard period for a routine test), it is seen that the curves form two main groups. The first group (methods 1-4) having been subjected









to constant temperature is of low germination. The second and higher group had alternating temperature. The difference between the two groups is distinct and conclusive. Within each group a certain arrangement manifests itself. At the base of each group lies the pad receiving no stimulation either from light or potassium nitrate. Next in ascending order comes the pad receiving light, then the pads receiving potassium nitrate. Potassium nitrate seems to be effective irrespective of the action of light.

When these tests had run their standard course (28 days) each pad was "stepped up" one place in what had thus been indicated to be the scale of stimulation. Pads 1-4 were now subjected to alternation of temperature: pads 4 and 5 were illuminated: pad 6 was changed to potassium nitrate solution, while pads 7 and 8 were withdrawn. The effect of these changes was immediate and striking, confirming the tentative conclusions based on the first period. The pads of the low group when transferred to alternating temperature responded at once, giving curves similar to their counterparts of the first 28 days, and, differing only in that they rose higher—this might be explained by the pre-soaking. Following the curves of the "low group" through, it is seen that they tend to flatten out at various points, but that then the introduction of another "step up" in stimulation produces another rise. The two pads on the alternating temperature group behave in a similar sort of way: "seed" on pad 5 when illuminated at the 28th day immediately recommenced germination and continued until the 42nd day, when it stopped: given nitrate solution at the 49th day "complete germination" resulted. Pad 6 tested by the British standard method (alternation of temperature, light and tap-water), stopped germinating on the 21st day with a total of 60 per cent.: given potassium nitrate on the 28th day it eventually exceeded any other pad.

It is thus seen that *Poa compressa* is very sensitive to conditions of temperature, light and the character of the moisture supply. Alternation of the temperature is of first importance followed by the supply of potassium nitrate. These two together can produce satisfactory results and render the analyst independent of the light supply, but it is better to allow access of light rather than to screen the tests.

Poa nemoralis (Graph 2) appears to be less sensitive to the three factors studied than was *P. compressa*, and further, they seem capable of replacing each other to a greater extent. For instance the pads subjected to alternating temperature all germinated at or about the maximum and the differences between them are not significant.

Therefore, it would appear that alternation of temperature is the only essential factor with this species, light being practically unnecessary and tap-water sufficient. In the "constant temperature group," however, a certain arrangement manifests itself, in that the two pads in the dark (1 and 4) are significantly lower than the two in the light (2 and 3). Further, in either pair the pad receiving KNO_3 is the higher of the two. "Stepping up" the pads produced significant responses, as was the case with *Poa compressa*. It may be concluded from these tests that *Poa nemoralis* will give satisfactory results when any two of the three stimulating factors are operative.

The results obtained with *Poa pratensis* (Graph 3) are somewhat similar to those obtained with *P. nemoralis*, though the effect of alternating temperature appears to be of greater importance and not replaceable by potassium nitrate and light. The behaviour of pad 2 (constant temperature, light and tap-water) is difficult to account for.

Poa trivialis is quite insensible to variations in the conditions as studied, except that the pad lowest in the "scale of stimulation" (constant temperature, dark and tap-water) is significantly lower than the others at the end of the standard period. Further, this deficit is made good by "stepping up," *i.e.* alternating the temperature.

The data offered here do not warrant any extended theoretical discussion of the processes underlying the various effects noted—especially apparent in the case of *Poa compressa*. Each factor evidently has a multiple effect, affecting more than one aspect of the life of the organism or, perhaps more accurately, the activities of the individual cell.

Harrington⁽⁶⁾ in reviewing the subject of alternation of temperature mentions a number of hypotheses advanced by earlier workers to account for somewhat similar effects in other species. Briefly these are:

- (i) That temperature alternation affects water intake.
- (ii) The reserve of materials made available at any given temperature is wholly or largely used up in respiration, but a slight surplus becoming soluble at a higher temperature is available for growth when the temperature is lowered with consequent reduction of intensity of respiration.
- (iii) The whole effect of temperature alternation is due to oxygen relationships.
- (iv) With alternation of temperature there is more lively gaseous interchange with consequent increase of respiration.

In discussing these with reference to the present study a number of lines of evidence taken from work covering the general flora may be

cited, though their application to germination must be guarded. Hoagland and Davis⁽⁸⁾ discussing the absorption of ions by plants from dilute solutions show that light exerts a considerable effect in the case of an alga (*Nitella*). These writers conclude that the absorption of ions by plants from dilute solutions involves energy exchanges, with light as the ultimate source of energy and they suggest that this absorption is intimately related to growth and metabolism. Jeffs⁽¹⁰⁾ suggested that the light-growth-effect reaction of multicellular organs is not due to increase in cell elongation simply, but to some other effect of light such as change in the rate of cell division. The periodic nature of cell division noted by Kellicott⁽¹²⁾ in *Allium cepa*, which probably holds good for many other plants, may be correlated in some way with the germination response to periodic alternation of external conditions and in this connection it is interesting to note that Reed⁽¹⁸⁾ has shown that *Spirogyra* can be stimulated to divide by keeping the filaments at a low temperature in the dark and then transferring to optimum conditions of light and temperature.

That germination in its initial stages, at least, is not growth simply, must be remembered; and, as is well known, conditions affecting growth do not necessarily affect germination with equivalent force but the possible energy effects of light and temperature and their effect on cell division are clearly indicated. Other effects such as increased permeability, quickened gaseous interchange and altered respiration likewise probably add their quota to the germination responses noted above.

In this discussion and also in what follows it is considered unnecessary to allow for any effect of the plant on the culture medium as reported by Hoagland⁽⁹⁾ because of the short period during which the plant is active: growth has proceeded only a short way when the seedlings are counted off.

Turning to consideration of the stimulation resulting from the use of potassium nitrate it would again appear that the effect is complex. Most of the published work connected with this aspect deals with tissues from the mature plant or at least with the plant long after germination.

Nobbe, Shröder and Erdman⁽¹⁶⁾ indicate that potassium has an effect on the translocation of starch. Copeland⁽²⁾ states that potassium is a direct factor in increasing the turgor of the cell. Purvis⁽¹⁷⁾ working with *Dactylis* concludes that potassium salts influence the physiological condition of the plant or its chemical composition. Macallum⁽¹³⁾ has shown that potassium is always found where new outgrowths are in

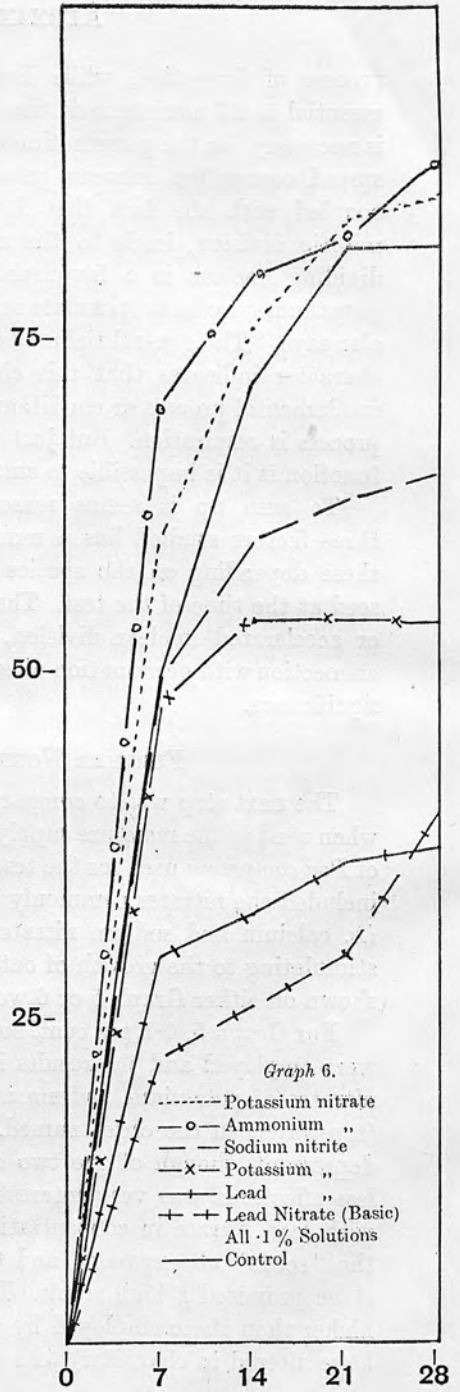
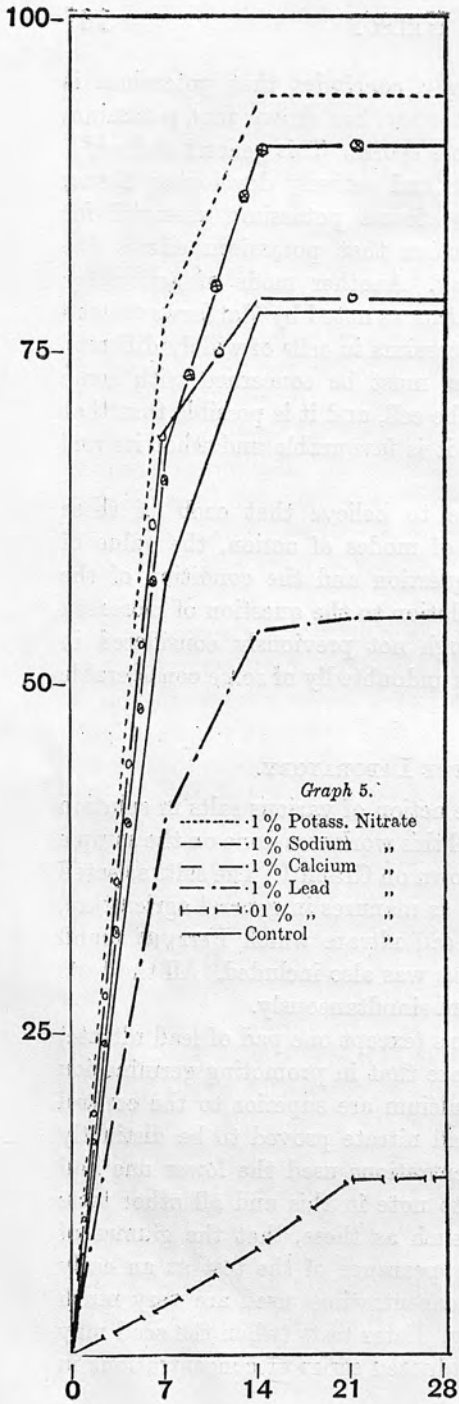
process of formation, while Dowding⁽⁴⁾ concludes that potassium is essential to all meristematic tissue. Reed⁽¹⁸⁾ has shown that potassium is necessary for the germination of moss spores. This general and widespread connection between potassium and actively developing tissue, coupled with the fact that Reed⁽¹⁸⁾ found potassium essential for mitotic division, leads to the conclusion that potassium effects the dividing nucleus in a favourable way. Another mode of action for potassium may be to stimulate respiration as noted by Matthews⁽¹⁴⁾ who also says, "The general richness of potassium in cells of widely different character indicates that this element must be concerned with some fundamental process or condition in the cell, and it is possible that that process is respiration. But just why it is favourable and what its real function is it is impossible to state."

To sum up it seems reasonable to believe that each of these three factors studied has a number of modes of action, the value of these depending on the species in question and the condition of the seed at the time of the test. Their relation to the question of increased or accelerated nuclear division, though not previously considered in connection with germination effects, is undoubtedly of some considerable significance.

FURTHER WORK IN THE LABORATORY.

The next step was to compare the action of various salts in solution when used as the moisture supply. All this work was done on the sample of *Poa compressa* used for the tests shown on Graph 1. The salts selected included the nitrates commonly used as manures in general agriculture, *i.e.* calcium and sodium nitrates. Lead nitrate which Berry⁽¹⁾ found stimulating to the growth of oat *plants* was also included. All the tests shown on either Graph 5 or 6 were run simultaneously.

For Graph 5, 0.1 per cent. solutions (except one pad of lead nitrate) were employed and the results indicate that in promoting germination nitrates of potassium, sodium and calcium are superior to the control (tap-water) in the order named. Lead nitrate proved to be distinctly depressant, though of the two concentrations used the lower one had less effect. It was very interesting to note in this and all other tests with lead nitrate in concentrations such as these, that the glumes of the "seeds" all expanded and the appearance of the test at an early stage promised a high result. The concentrations used are very much higher than those employed by Berry. Later tests (when the seed may have altered in character) with a graduated series of concentrations in



light and dark indicated that at no strength was a solution of lead nitrate stimulating to germination.

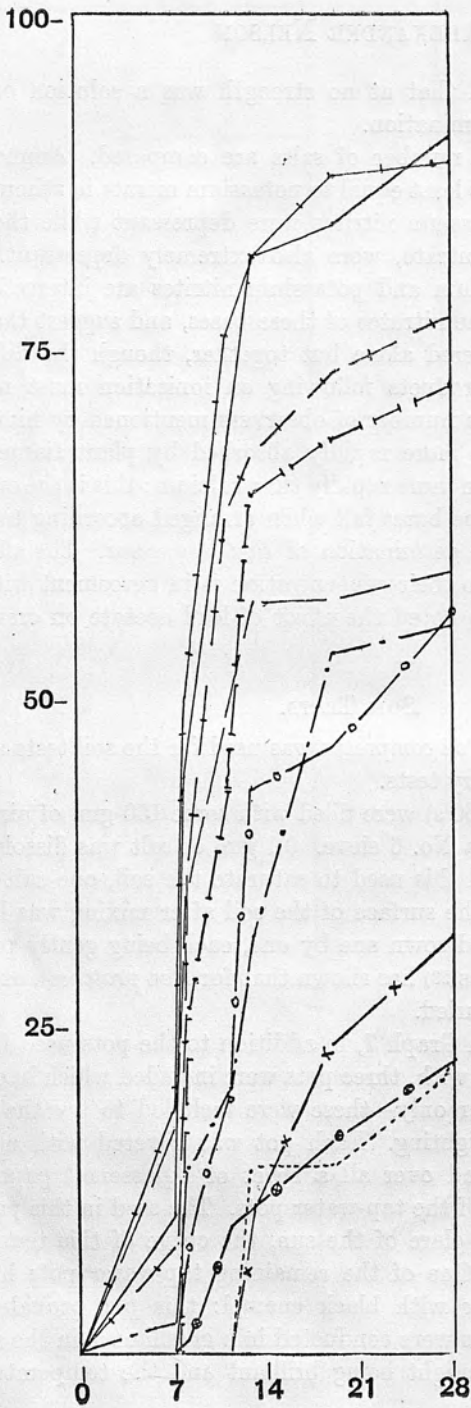
In Graph 6, again a number of salts are compared. Ammonium nitrate was found to be at least equal to potassium nitrate in stimulating effect. Sodium and potassium nitrites were depressant while the lead salts, nitrite and basic nitrate, were also extremely depressant. The relative positions of sodium and potassium nitrites are interesting as they are the reverse of the nitrates of these bases, and suggest that the ions must not be considered alone but together, though the different effect of the different products following on ionisation must not be forgotten. Stiles⁽²²⁾ and a number of observers mentioned by him have shown that potassium is more rapidly absorbed by plant tissue than sodium, and either of them more rapidly than calcium: this is the order in which the nitrates of these bases fall when arranged according to their stimulative effect on the germination of *Poa compressa*. The effect of lead salts in proportion to their concentration is in agreement with the findings of Dilling⁽³⁾ who noted the effect of lead acetate on cress and mustard seedlings.

SOIL TESTS.

The same sample of *Poa compressa* was used for the soil tests as was employed in the laboratory tests.

Method. Small pots (60 s) were filled with some 150 gm. of air-dried potting soil passed over a No. 6 sieve. 0.1 gm. of salt was dissolved in 100 c.c. of tap-water and this used to saturate the soil, one salt being allocated to each pot. The surface of the soil after mixing was lightly pressed level and the seed sown one by one, each being gently pressed into the surface. Williams⁽²³⁾ has shown that for *Poa pratensis*, at least, the seed should not be buried.

In the tests shown on Graph 7, in addition to the pots used for the seven salts experimented with, three pots were included which had been moistened with tap-water only—these were included to try the effect of different degrees of lighting. Each pot was covered with a small square of 21 oz. glass and over all a sheet of "glassene" paper was spread, except over one of the tap-water pots. The seed in this pot was thus exposed to the full glare of the sun, the curve of this test being designated "sunlight." One of the remaining tap-water pots had its glass cover painted over with black enamel: this pot provided the "dark" results. The tests were conducted in a greenhouse in the south-east of England, the sunlight being brilliant and the temperature as



Graph 7.
Soil tests.

- Sunlight
 - Shaded daylight
 - Dark
 - |·| Lead nitrate
 - +·+ Lead " (Basic)
 - Lead nitrite
 - Calcium nitrate
 - x- Ammonium "
 - Sodium "
 - Potassium "
- Nitrites of sodium
and potassium gave
no germination

read on the maximum-minimum thermometer very much like the alternation produced in the laboratory. "Seeds" germinating were counted off from day to day and the tests ran for 28 days. As the soil in the pots dried it was moistened with its appropriate solution by sub-irrigation. It is of interest to note that the "dark" pot and the pots moistened with nitrites (all bases) did not dry so quickly as the others, this difference between the pots being very striking.

Consideration of the results plotted in Graph 7 shows that of the three pots moistened with tap-water the one in shaded daylight is very significantly higher than those in "dark" or "sunlight." This indicates that the pots moistened with salt solutions were in the best light conditions.

Morada⁽¹⁵⁾ has shown that exposure to full sunlight for the whole period available per day has a depressing effect on the germination of *Carica papaya*, though exposure for a short time proved beneficial. Dark, he found, induced dormancy.

Considering the tests where salt solutions were employed, the very striking fact emerges that the salts found to be stimulating in laboratory water culture proved to be the most depressant in the soil, while the salt most depressant in water culture was the only one which equalled or exceeded the best control (tap-water). As has been noted, all the nitrite pots held the moisture much better than the others, but though the lead nitrite pot produced the largest number of plantlets the nitrites of sodium and potassium produced not one. Another point of interest was that the surface of the soil in all the pots excepting the "dark" and the "sunlight" pots and those moistened by sodium and potassium nitrite was covered in varying degree with a green alga. The lead nitrite pot had easily the heaviest growth of alga. Thus, while it may be that some of the stimulating effect of the lead nitrite on the seed was due to the better moisture conditions, it must be noted that the dark pot and the sodium and potassium nitrite pots provided equally good physical conditions but very much lower biological results.

Why there should be such a complete reversal of germination effect between the two groups of salts is difficult to explain, but the results certainly confirm the conclusion of Jensen⁽¹¹⁾ who worked with wheat seedlings. Discussing the toxic effect of salts, that writer concludes that it does not follow that because a salt is highly toxic in solution it is equally so in the soil, nor that one which holds a relatively high position in the toxic table of the soil should occupy the same relative position in solution cultures. It would appear too, from the results here

presented, that the same sort of conclusion is equally true of the stimulating effect.

Berry⁽¹⁾ noted in growth trials with oats that lead salts induced fleshier, broader and darker coloured leafage: this too was clearly seen in the tests reported here, the first leaves of the seeds which germinated on the lead pots being decidedly darker in colour, broader and more fleshy than those on the non-lead pots.

GENERAL DISCUSSION.

All the results reported here bear on several practical problems, more particularly on such questions as to how far laboratory tests are referable to soil conditions, and also in what way artificial manures may affect germination in the field. With regard to the first question it is interesting to note that the soil test in "shaded daylight" compares favourably with any laboratory test, though it must be remembered this pot would be under ideal conditions not likely to occur in the open field. With regard to the second question it is indicated that none of the manurial salts commonly employed in agriculture should be applied while grass "seed" is germinating. While the average concentration in the field would never be as high as those used in these tests, owing to the irregular distribution of the manure, certain areas would undoubtedly reach the concentrations here described and so, possibly, lead to a "patchy braid." These results obtained with *Poa compressa* may not apply absolutely to other grasses more commonly employed in agriculture.

The effect of lead salts on the growth of the alga and the physiological effect evidenced by the deep coloration accompanied by increased fleshiness of the grass leaf requires further study but of peculiar interest are the results obtained by Reznikoff⁽¹⁹⁾ working with *Amoeba*. This worker using $PbCl_2$ found two effects, one on the cell surface he ascribed to an effect of the acid formed following on ionisation of the salt. A second and more fundamental effect occurring within the protoplasm he ascribed to the cation. Only the first mentioned of these two effects was lethal. Reznikoff suggests that lead within the cell reacts with the phosphates and carbonates. This may be the mechanism resulting in the leaf effect described above.

SUMMARY.

The paper in its first part deals with the germination response, in the laboratory, of four species of *Poa* to variations of temperature, light and the nature of the moisture supply. The second portion deals with the same response of *P. compressa* to solutions of various salts used as moisture supply. The third part deals with the germination of *P. compressa* in the soil when all the above factors were varied. In the laboratory, alternation of temperature proved to be, generally, the most efficient stimulant followed by light and a solution of potassium nitrate as moisture supply. *P. compressa* proved to be more sensitive than any of the other species considered, *P. pratensis* and *P. nemoralis* rather less so, while *P. trivialis* was almost insensible to variations of the conditions. In the soil, excess of light (sunlight) proved to be depressant. Some salts, e.g. potassium nitrate, sodium nitrate, ammonium nitrate, etc., proved to be stimulating in solution culture, while salts of lead were depressant. As a general statement these salts, found to be stimulating in solution culture, proved to be more depressant in soil than those found depressant in the solution. Lead salts in the soil produced broader, deeper coloured leafage than the controls. Nitrites had a striking physical effect in preventing the drying up of the soil.

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(Received November 23rd, 1926.)

ADDENDUM.

(Being papers on cognate subjects offered
in support of the foregoing THESIS)

THE MEMBERS OF THE GENUS *AGROSTIS*
IMPORTANT IN THE SEED TRADE, WITH
SPECIAL REFERENCE TO THE NOMEN-
CLATURE

BY
ALEXANDER NELSON, B.Sc., N.D.A.

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THE MEMBERS OF THE GENUS *AGROSTIS* IMPORTANT IN THE SEED TRADE, WITH SPECIAL REFERENCE TO THE NOMENCLATURE

BY ALEXANDER NELSON, B.Sc., N.D.A.

WHILE none of the members of the genus *Agrostis* are at present important in agriculture in Great Britain, the fact that the trade in their seeds is largely international and, to a great extent, passes through this country, renders some knowledge of the international nomenclature of peculiar importance to seedsmen.

It may be stated at the outset that not only are the national literatures referring to the common names of the members of the genus in the different countries often vague and self-contradictory, but the botanical naming of the various species is in a chaotic state. All genera with cultivated members appear to be, more or less, in a similar state; the greater the number of species or varieties cultivated, the deeper the chaos. Such is the position that one doubts if the problem will yield to treatment along traditional lines and seems to call for co-ordinated effort, systematic and genetic, on the part of those dealing with cultivated types in the manner suggested by Drummond (6).

From the seed-trade point of view there may be taken to be three broad classes of *Agrostis*:

(i) Those seeds which are dealt in and sold for general purposes, mostly agricultural, *i.e.* for the production of hay and/or pasture.

(ii) Those for which there is a special use and for which a special provision is made, usually for the production of lawns.

(iii) Seeds which occur promiscuously as impurities, either in samples of seed of other genera or in samples of *Agrostis* sold under a definite name and where they can be recognised by the analyst.

Having noted these classes, it is necessary to enquire briefly what characters of a botanical nature would relegate any one plant to any class and render it, on the one hand, valuable to agriculture and/or horticulture, or, on the other hand, deleterious. In agriculture, all that is required is that the plant produce hay or pasture superior, or, at least, equal to any other plant which can be grown on the soil and

under the conditions in question. Also, that it persist but be easily eradicated by ordinary cultural methods when it has fulfilled the purpose for which it was sown and its removal is desired. Apart from those species which are grown purely for their ornamental value and which need not be further considered here, the horticulturist employs members of the genus in the formation of lawns. In this connection the character most insisted on is that the plant be a surface creeper and bind the other constituents of the lawn well together while producing fine, well-wearing verdure. Though the question of easy eradication does not arise prominently in connection with lawn formation, it is interesting to note that, though for different reasons, the horticulturist and the agriculturist both desire a surface creeper; the horticulturist, because a subsurface creeper does not bind the constituents of his lawn well; the agriculturist, because it is a difficult type to eradicate, and also because a subsurface creeper stores most of the surplus food below the soil, out of reach of grazing animals. It is clear, then, that in general agriculture or horticulture the desirable type cannot be a subsurface creeper. Thus are arrived at two apparently sharply divided classes founded on morphological features:

- (i) Surface creepers producing desirable leafage.
- (ii) Subsurface creeping types and those which do not produce desirable leafage.

From these criteria of what is good and what is bad, it is useful to enquire as to how far the seed trade can go in supplying seed likely to produce plants of a desirable type. Treating at the moment, only of the purity as defined by the seed analyst, it is generally admitted that few, if any, samples are pure to any one major type or species (Percival⁽¹²⁾, Armstrong⁽¹⁾, Stebler⁽¹⁸⁾). The important point, however, is, not the question of the analytical purity, but the question of purity as defined by the geneticist. The present writer has been unable to trace any work bearing directly on this aspect, but some writers have offered significant clues.

E. Bruce Levy⁽⁴⁾, states, "The cause of variation within and between the species" (*i.e.* of *Agrostis*) "is extremely difficult to account for, but it would appear that hybridisation played an important part, for it is in areas where the three species" (three aggregates, see below) "may be found together that one notes the greatest variation and often the most puzzling of forms. Again, where the habitat is such as to favour only the one species, the growth-form and character of that species become more constant. Also, there is affinity between the aggregate species. This

affinity asserts itself not so much by a general similarity in the plants, but rather by a manifestation of special features, such as the appearance of the long rhizomes in otherwise short root stock forms, or by the ready stolon development of otherwise non-stolon erect forms. These variations are distinct from habitat variations, which at times are extremely marked—so much so that to define the vegetative growth-form of the species botanically is almost impossible."

Ascherson and Graebner⁽²⁾ mention a number of hybrids and suggest that one recognised species (*Agrostis nigra*) is a hybrid arising out of *Agrostis alba* × *Agrostis vulgaris*. M'Alpine⁽¹⁰⁾, p. 77, states: "This genus" (*Agrostis*) "is extremely liable to variation and accordingly is very difficult to define." The same writer⁽¹¹⁾, writing of Common Bent, which he refers to *Agrostis vulgaris*, states: "In fact, Common Bent adapts its mode of growth to those circumstances in which it finds itself. If the water is on the surface, it is a surface creeper; if the water is deep underground, it becomes a deep underground creeper." Many other writers emphasise this variability of the members of the genus, but it is nowhere clear that more than observational evidence of plants in the wild is offered. Sinclair⁽¹⁶⁾, however, in a statement further discussed below, records that he found in controlled cultivated plants taken from the wild, certain types which were valuable *constant* surface creepers on ordinary loam and which, in one case at least, he refers to *Agrostis stolonifera* var. *latifolia*. From consideration of these citations, it would appear that some at least of the reputed species of *Agrostis* are inter-fertile and that many of the plants are of hybrid genetical constitution. Also, it would appear probable that many of them are capable of carrying factors for the production of certain major botanical characters, the expression of which may be suppressed by the environment. This possible alteration of such a character as stolon formation or alteration of the plane in which the stolons are produced, by environmental factors alone, opens up a very serious question for those workers who are attempting to breed up desirable strains of *Agrostis*, and indicates that before such strains are introduced into commerce they will require to be tested over a very large and varying range of situations. Despite all this variation, it is probable that the trade in seeds of members of the genus is likely to continue in the future along lines much as at present, and therefore it is of value to consider the various names, botanical and commercial, connected with the business, and equate them one to the other. In this connection the confusion in nomenclature which exists in most countries is, as has already been mentioned, further intensified

by the fact that the trade is largely international. There is a current of trade in one kind from Central and South Europe, sometimes via this country and sometimes direct to America. There is a current of trade from America to this country and Europe, while New Zealand is exporting to America and Europe generally. The procedure to be adopted here is to sift out each name in each country concerned and then, as far as possible, equate the results.

The first trade name which calls for attention is that of the genus itself: quite a number of samples change hands, described simply as *Agrostis*. There is little or no difficulty here, because, obviously, anyone purchasing under this description must be satisfied if the seeds (within the declared analysis) produce forms of *Agrostis*, no matter how mixed the types. "Bent Grass" (unqualified) may be taken to be synonymous with *Agrostis* in this connection.

Perhaps the most widely used and most ambiguous term is "Fiorin." In general commerce now, particularly in the home trade, this too, is taken to mean an indeterminate mixture of species of *Agrostis*. Trouble soon arises, however, when, as often happens, samples are described as "True" or "Genuine" Fiorin. What is implied by "true" or "genuine"?

Dr William Richardson, of Moy, Ireland, first introduced the name "Fiorin" about the year 1807 and applied it to a very luxuriant stoloniferous grass admirably suited to agricultural uses. It is probable that the type was not too well defined, being propagated mostly by vegetative means, though it seems clear that it was included under *Agrostis stolonifera*. Great confusion has arisen from the use of this name: the type is difficult to define and the name has arisen on more than one occasion. Sinclair(16), states: "That our *Agrostis stolonifera* is the *Agrostis alba* of Linnaeus is clearly proved by Sir James Edward Smith in his 'English Flora.' The error seems to have originated in Withering."

Percival(12) describes Fiorin under *Agrostis alba* L., and notes that the structure and habit are liable to vary. Armstrong(1) describes it under *Agrostis alba* L. var. *stolonifera* and emphasises the fact that it throws out *creeping surface stems*: later he describes Black Bent Grass, *Agrostis alba* var. *repens* = *Agrostis nigra* Withering, as having *stout underground rhizomes*. The important point here is the recognition of the two forms or varieties, and the splitting of the species. It is noteworthy that, of the two varieties, one is outstandingly valuable and the other the reverse. The same writer later describes another species, *Agrostis vulgaris* Withering, and suggests that it is simply a small variety of *Agrostis alba* L. Marshall Ward(9) describes Fiorin under *Agrostis*

stolonifera, but suggests that it, along with *Agrostis vulgaris* Withering, and possibly *Agrostis canina*, are mere varieties of *Agrostis alba* L. Notwithstanding this confusion, interfertility and variability between the species it seems clear that the *stolonifera* variety of *Agrostis alba* L. described by Armstrong actually exists in a constant state, being synonymous with Sinclair's *Agrostis stolonifera* var. *latifolia*, and is, moreover, the "ideal" Fiorin.

Somewhat the same sort of position is found on consideration of the main European literature. Hein⁽⁸⁾ notes that most of the trade samples are mixtures, the resulting plants being difficult to differentiate, and he says: "There is the stolon pushing variety of *Agrostis alba*, also the creeping variety of *Agrostis vulgaris*, and the more common variety of stem grass, which is a combination of these." Later he expresses the opinion that only the wet land forms, especially the stoloniferous variety of *Agrostis alba* L. can be called "*Agrostis stolonifera*" "Fiorin." (Nach meiner Ansicht kann indess nur die auf nassem Boden besonders vorkommende Abart von *A. alba* L., die species β^1 mit Recht "*Agrostis stolonifera*" und "Fioringras" genannt werden.) Hein quotes Courtin (Kulturgräser und Futterkräuter), who refers Fiorin grass to *Agrostis alba* var. *stolonifera*.

Stebler⁽¹⁸⁾ describes Fiorin or stoloniferous Bent Grass as *Agrostis stolonifera* L. or *Agrostis alba* Schrad. and mentions that the grass throws out long stolons which may lie either above or beneath the ground. He differentiates the grass from *Agrostis vulgaris* Withering. Ascherson and Graebner⁽²⁾ show quite clearly that from the start the specific name *stolonifera* has been a vague one to which many types have been referred. These authors, under the name *Agrostis stolonifera*, form a composite species which includes *Agrostis alba*, *Agrostis nigra* and *Agrostis verticillata*. Under *Agrostis alba* the common name "Fiorin" is given and the statement is made that this grass is almost exclusively surface creeping, very rarely having creepers below ground. *Agrostis verticillata* is described as being almost exclusively a subsurface creeper. Under *Agrostis nigra* no indication is given as to the plane of the creeping shoots and the authors state that the systematic significance of this species seems doubtful and suggest that it represents a fertile hybrid from *Agrostis alba* \times *Agrostis vulgaris*.

Owing to the importance given to species of *Agrostis* in America, where they are largely used in the formation of golf-course greens, etc., the literature is extensive, and it is found that writers have ceased to

¹ Species β = *Agrostis alba* L. β *stolonifera*. E. Meyer, English Fiorin, Bent Grass.

use the Linnaean names and have adopted those of other authorities. Piper and Hillman⁽¹⁴⁾ refer Fiorin to *Agrostis maritima* Lamark; *Agrostis stolonifera* var. *latifolia* Sinclair, and note that this is Richardson's grass referred to *Agrostis stolonifera* by many writers.

Hitchcock⁽⁷⁾ examined the specimens in the Linnaean collection, particularly those marked in the handwriting of Linnaeus himself, and from his description it seems clear that it is the stoloniferous form of *Agrostis alba* L. which is desirable in agriculture and horticulture.

Beale⁽³⁾ under *Agrostis alba* L. mentions Creeping or Marsh Bent, Fiorin, White Bent or White Top, thought by some to be *Agrostis stolonifera* L. Beale suggests that this is a variety of "Red-top" or *vice versa* (see "Redtop" below).

Clarke and Malte⁽⁵⁾ adopt the view that Fiorin and Redtop are synonymous, because under Redtop = *Agrostis stolonifera* they mention such other names as *Agrostis alba* L. Fiorin, Creeping Bent, etc.

The only other country at present handling Bent grasses in the International market is New Zealand. E. Bruce Levy⁽⁴⁾ deals with the New Zealand forms and reduces them to three large aggregates, the first of which he designates Redtop, *Agrostis palustris*, *Agrostis alba* of most botanists, Fiorin of the seed trade, *Agrostis stolonifera* of some seedsman's catalogues, "twitch." In his third aggregate, the same writer includes Creeping Bent (*Agrostis stolonifera*), Carpet Bent of American greenkeepers, *Agrostis depressa* and *Agrostis maritima* of some American botanists. He states that this is the grass commercialised by Richardson under the name Fiorin. The outstanding feature of the grass described under this third aggregate by Bruce Levy is its long overground stems (stolons).

Regarding all these citations referring to Fiorin, the following facts emerge: "Fiorin" is a luxuriant surface creeping grass which, in the earlier days of its history, was referred, along with many other types, to *Agrostis stolonifera* L. The type of *Agrostis stolonifera* has been from the beginning only vaguely defined and its general use might be discontinued, as it has led and is leading to confusion. Not only has this association with a vague though seeming specific name directly confused matters, but it has led in large part to a progressive debasement of the name Fiorin. In the beginning, the then *true* Fiorin was justifiably ranked as an excellent pasture grass, yielding as it does good grazing at a time of the year when other grasses are dormant. Either from the fact that useless and injurious types (underground creepers, etc.) were classified along with it in *Agrostis stolonifera* L. or from deliberate or

ignorant substitution, the specificity of the name Fiorin was lost and the grass quickly fell into disfavour. When, however, the true surface creeping type was clearly recognised and its constancy established, the position became clearer and the possibility of a genuine Fiorin emerged. The only known commercial source of such a grass is South Germany, from whence come samples which undoubtedly do contain some genuine Fiorin (about 1 per cent. according to Bruce Levy). In course of time these samples became better known, commanded a higher price and were named Genuine South German *Agrostis*, or latterly and more briefly, Genuine Fiorin. Hence the appellation Genuine has ceased to have any real significance. It is perhaps worthy of note that samples of this type received direct from Germany usually bear, alone or in addition, the name *Agrostis stolonifera*. This term, if used, as by Ascherson and Graebner, and to some extent by other botanists, to indicate a mixture of stoloniferous forms including True Fiorin, then the term would appear to be, in some degree, justified. It emerges, however, that there is at present in commerce no such thing as pure or semi-pure Genuine Fiorin, though its isolation and introduction should be welcomed and would probably prove profitable to the introducers. Any precise statement as to which botanical species Genuine Fiorin is to be referred does not come within the scope of this paper, but it seems abundantly clear that the grasses described by Sinclair under *Agrostis stolonifera* var. 1 *latifolia* and by Armstrong as *Agrostis alba* L. var. *stolonifera*, are very near, if not the ideal type. However, for practical purposes the filing of botanical specimens and description along with the naming may safely be left to the introducer of a non-varying, permanent strain.

The next trade name which falls to be considered is one not commonly known or used in British Agriculture, but widely used in the seed trade and is of American origin: this is "Redtop."

Hitchcock⁽⁷⁾, Piper⁽¹³⁾, Spillman⁽¹⁷⁾ and others refer this grass to *Agrostis alba* L. According to Hillman who, along with Piper⁽¹⁴⁾, refers it to *Agrostis palustris* Huds. (*Agrostis alba* of most botanists), it includes relatively few types. Bruce Levy names one of his aggregates "Redtop" and agrees with Piper and Hillman in referring the grass to *Agrostis palustris* Huds. Redtop would appear to be nearly synonymous with the commercial Fiorin of the British seed trade, differing perhaps in that it is comprised of fewer types.

"Rhode Island Bent Grass" another American trade name becoming known in this country refers, according to Piper and Hillman, to *Agrostis*

tenuis Sibth., and is identical with *Agrostis vulgaris* Withering. This grass is recommended for lawn formation by Hillman, who notes that samples are likely to contain "Redtop" amongst other types.

Bruce Levy names his second aggregate "Brown top" or Colonial Bent referred to *Agrostis tenuis*, the *Agrostis vulgaris* of most botanists. He agrees with Piper and Hillman that the New Zealand samples passing as Colonial Bent are identical with American Rhode Island Bent. A number of samples have been offered on the British market under the name "Waipu Brown Top." This is a name used only by Auckland seed merchants and growers and refers to Colonial Bent as noted above.

Confusion between Brown Top, as defined above, and the Brown Bent of British literature must be guarded against. Brown Bent is referred by British and American writers to *Agrostis canina* L. It is sometimes called Velvet Bent in America and strongly recommended for lawn production.

There are various other names current in the British seed trade such as Kentish Bent and so on, but these are all more or less mixtures of species of *Agrostis*. The Carpet Bent so much prized by American greenkeepers seems to be "Genuine Fiorin" as defined in this paper.

SUMMARY.

1. The paper deals with the members of the genus *Agrostis* occurring in the international seed trade; current names are enumerated and, as far as possible, related to each other.

2. The following relationships are established:

Trade Designation	Botanical Equivalent
Bent Grass (unqualified) <i>Agrostis</i> (unqualified) Fiorin (unqualified)	Indeterminate mixtures of species and/or forms of <i>Agrostis</i>
Redtop or Red Top	
"True" Fiorin "Genuine" Fiorin ? Carpet Bent	Do., but probably comprising fewer types Should be the "Fiorin" of Richardson, <i>i.e.</i> <i>Agrostis stolonifera</i> var. <i>l. latifolia</i> of Sinclair or <i>Agrostis alba</i> L. var. <i>stolonifera</i> of Armstrong. No pure strains in commerce though certain samples may contain a small percentage
Rhode Island Bent Brown Top Colonial Bent Waipu Brown Top	<i>Agrostis vulgaris</i> With.
Brown Bent	
Velvet Bent	
	<i>Agrostis canina</i> L.

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“HARD SEEDS” AND BROKEN SEEDLINGS IN RED CLOVER.
By ALEXANDER NELSON, B.Sc., N.D.A.

(Read 20th March 1924.)

While testing the germination of the seed of most cultivated species of Leguminosae there commonly occur seeds which do not absorb moisture, and in consequence these fail to swell up and germinate within the period of the test. These are known as “hard seeds.” This inability to absorb moisture is due to some peculiarity of the seed-coat, and in order to reduce the number of “hard seeds” in a consignment it is the usual practice in commerce to pass it through certain machines which scratch or abrade the surface of the seeds, thus permitting water to be taken up. It is believed that in time and in the soil untreated “hard seeds” will germinate and produce a plant. Many clovers, however, particularly red, occupy the land for a relatively short period, and so the hard type of seed may not be allowed enough time to germinate and assist in producing a crop. The germinating percentage of any given sample, for the purposes of a declaration under the seed-testing regulations, is reduced by the percentage of “hard seeds” which occur. The percentage of germinating seeds in Clover, Trefoil, etc., is usually further reduced by the occurrence of what are called broken seedlings. A broken seedling is one which during the germination test breaks into two or more portions, each of which is incapable of producing a plant: the break is usually in the region of the hypocotyl. A high percentage of either of these “impurities” lowers the market value of a sample considerably. It was noticed in certain cases in the course of the ordinary routine testing of seeds that the machining of a sample of red clover, though it had reduced the number of “hard seeds,” had not increased the percentage of seeds germinating, simply because the percentage of broken seedlings had been considerably increased. In the case of samples of Alsike or white clover the “hard seeds” were almost completely eliminated with no increase of broken seedlings. Critical tests of red clover seed were then commenced and the results noted, these being shown in Table I.

TABLE I.

Consign- ment number.	Absolute weight, 1000 seeds.	Treatment.	Per- centage of germinat- ing seeds.	Per- centage of hard seeds.	Per- centage of broken seedlings.	Per- centage of dead seeds.
404	2.22 grams	Unmachined	90.25	7.75	2.0	0.0
"	" "	Over A	86.75	7.75	5.0	0.5
"	" "	Over B	82.25	4.25	12.75	0.75
420	2.15 grams	Unmachined	82.5	13.25	3.5	0.75
"	" "	Over A	88.75	7.25	4.0	0.0
"	" "	Over B	86.0	4.0	9.25	0.75
656	2.15 grams	Unmachined	90.5	7.0	1.75	0.75
"	" "	Over A	87.5	5.0	6.75	0.75
"	" "	Over B	85.75	3.75	10.0	0.5
545	1.99 grams	Unmachined	91.5	8.25	0.25	0.0
"	" "	Over A	92.5	5.0	1.25	1.25
"	" "	Over B	93.75	4.25	1.75	0.25

Four consignments of unmachined seed were selected, and each divided into three portions. The first portion of each consignment was left unmachined; the second portion was passed through a machine designated A; while the third was passed through machine B. Thus were obtained twelve samples in all, three from each of the four consignments selected. The machines A and B are of the latest type and in general use by the seed trade. The action of machine B is more drastic than that of A.

The four consignments included two distinct types: those numbered 404, 420, and 656 were large, bright, and of Chilean origin, while the fourth (545) was a smaller-seeded type of English origin. As a fairly accurate guide to the relative sizes of the seed the absolute weight is given, this being the average weight of at least five lots each of 1000 seeds.

The twelve samples were then tested for germination in the usual way—two pads of blotting paper each carrying 200 seeds and marked X and Y respectively, moistened and put in a germinator run steadily at 22° C. The complete results after ten days are given in the table. All pads were under exactly the same conditions during the whole course of the test. A duplicate germination test was carried out some time later, which fully confirmed the figures given. The control

samples ordinarily used in the routine working of the station behaved in a normal manner during the period of these tests.

CONCLUSIONS.—From these tests it would appear that the use of abrasive machinery on large, well-developed red clover seed gives negative results. The “hard seed” percentage is undoubtedly reduced, but the percentage of broken seedlings is raised by an equal or even greater amount, leaving the declarable “germinating percentage,” which it was desired to raise, as low as or lower than before treatment.

In the case of a smaller type of seed, such as sample 545 in these tests, machining does reduce the number of “hard seeds” without materially increasing the number of broken seedlings.

It is suggested that the increase in the number of broken seedlings in large red clover seed noted after the use of abrasive machinery may be due either to the thinning down of the seed coat in certain regions, thus upsetting the normal action of the stresses which occur in the germinating seed, or to actual damage to the embryo. It is also suggested that determination of the absolute weight of a sample provides a guide to seed merchants as to whether it will be profitable to subject any consignment to an abrading process.

The writer desires to acknowledge the courtesy of Messrs. David Bell, Ltd., in whose station these tests were made, for permission to publish the results.

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HARD SEEDS AND BROKEN SEEDLINGS IN RED CLOVER
(*Trifolium pratense*). II. STORAGE PROBLEMS.

By ALEXANDER NELSON, B.Sc., N.D.A.

(Read 20th May 1926.)

As is well known, there commonly occur seeds which, when offered ideal conditions for germination, fail to absorb moisture and therefore remain dormant and hard. These so-called hard seeds are typical of the *Leguminosae*, and usually germinate promptly if the testa be scratched or abraded. In practice, when a consignment is known to contain a high percentage of hard seeds, it is passed through various machines specially designed to cause abrasion in varying degree.

Many seeds in samples of clover, particularly Red Clover, produce, during a germination test, plantlets which break, usually in the region of the hypocotyl. Increased severity of abrasion has been found to result in an increased percentage of these broken seedlings. In practice it is desired to reduce the hard seed content to the minimum while causing no increase in the broken seedlings: thus increasing the percentage of seed which may be declared viable under the regulations (5). Only this percentage is of primary value in commerce, and the short term "valuable seed" will be used for it hereunder.

Numerous observers have reported on the behaviour of seed and grain under storage, paying particular attention to the percentage of living seed, its decrease with age, and the point where the last of the seed becomes non-viable. In the case of the agricultural seeds, at least, this information is valuable only with regard to the second item, and then only for the first few years, because rarely is a consignment carried over for longer than eighteen months after harvest. Further, though information regarding the percentage of seed capable of germination is of prime importance, the behaviour of the other constituents may be only slightly less so. In the tests reported here full details will be given.

Materials and Methods.—A consignment of new Red Clover seed of crop 1924 was selected in December of that year and a sample reserved from the delivery; two further samples were obtained from two portions which were slightly and severely

abraded respectively. Each of these three samples was divided into four portions, giving twelve lots in all, and one from each group stored in each of the four following ways:—

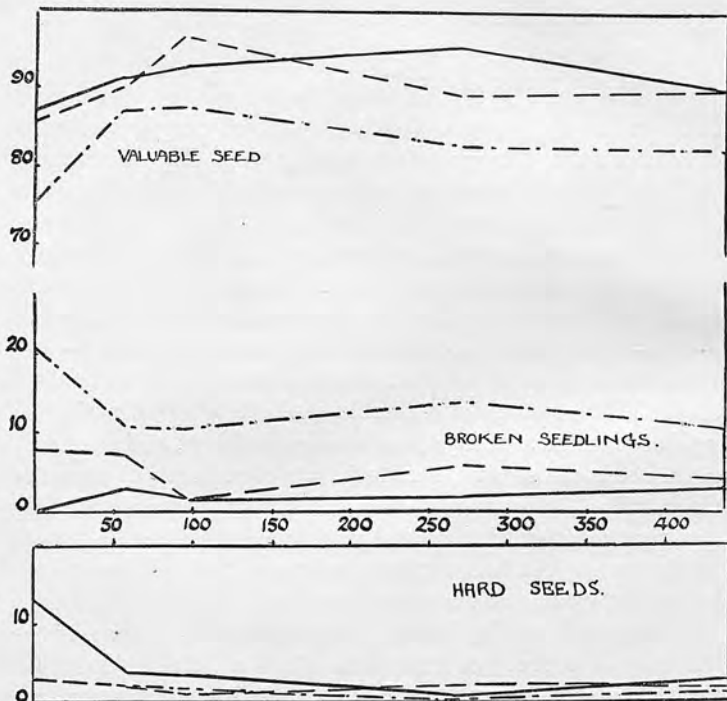
- (a) Over CaCl_2 in a desiccator (excessively dry conditions).
- (b) Over a solution of NaOH (moist conditions).
- (c) In glass tubes tightly packed with seed, the corks being sealed in and capped with beeswax (poorly ventilated conditions).
- (d) In glass tubes stoppered with cotton-wool (approximately normal conditions).

The aim in (a), (b), and (c) was to produce exaggerated conditions which might operate in practice with less intensity.

Both of the lots subjected to abrasion were machined on the same day, and forthwith all three samples were put to test, divided, and set to store; the results of this first test provides the starting-point of the graphs. In all cases in the figures the solid line — refers to the non-abraded seed, the broken line - - - - - to the mildly abraded lot, while the chain line — · — · — · refers to the severely abraded sample. The main figures (1-4) show the percentage of valuable seed (those germinating to produce normal seedlings), the broken seedlings, and the dead. Hard seeds are shown separately. As a measure of economy the vertical scale in some cases has been broken and only the significant portion of the graph shown. Time in days is plotted along the base; the percentage of the different constituents found, on the vertical scale.

Discussion and Conclusions.—A general examination of the graphs shows that the immediate effect of abrasion has been to increase the percentage of broken seedlings at the expense of the hard seeds and, what is very undesirable, at the expense of the valuable seed, thus reducing the commercial value of the consignment to below the pre-machining point. After storage under excessively dry and approximately dry conditions, the broken seedling curve dwindles away, the percentage being added to the valuable seed so that the commercial value of the consignment rises much above that of the unmachined seed. This would indicate that for best results the merchant should store seed for some fifty to one hundred days after abrasion. This, however, is not always convenient. Excluding the graph of moist storage, fig. 4, further examination shows that after

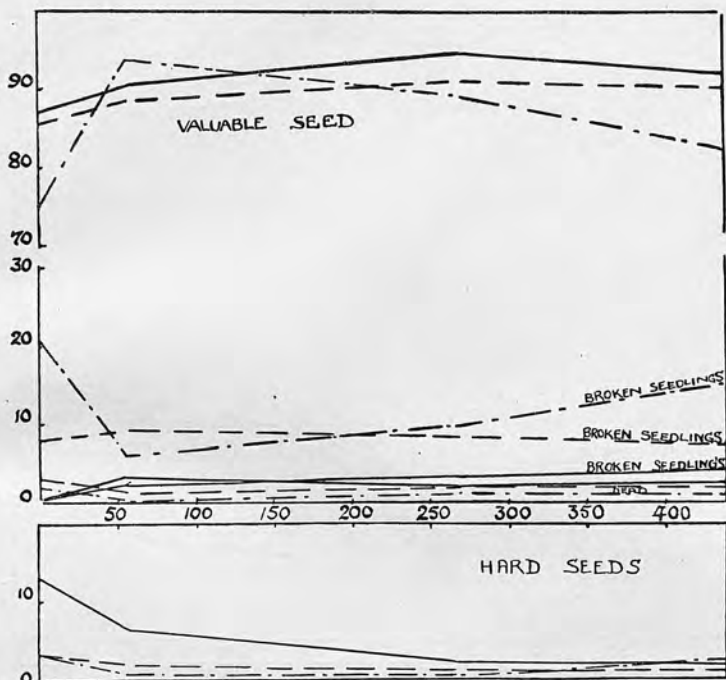
reaching a high point the curve of valuable seed commences to fall; the rapid decline being particularly noticeable in the case of the excessively dry stored lots. This loss is not due to a return of the broken seedlings, but to the seeds becoming dead. This is brought out clearly by the form taken by the curves of the total seed germinating (valuable seed plus broken seedlings), fig. 5.



FIGS. 1 and 1A.—Seed stored normally. (The dead negligible in every case and not shown.)

It is commonly believed that in a dry atmosphere the hard seed content increases; this is not clearly indicated in these tests, but it is interesting to note that in the case of the un-abraded seed under excessively dry conditions, the hard seed curve tends to rise towards the end of the period reviewed. Dorph-Petersen (2) records a case of a sample of Red Clover which, stored under slightly drier than normal conditions, dropped from 6 per cent. hard in its harvest year to 1 per cent.

in the fourth year, rising to 11 per cent. in the sixth year, this figure remaining constant until all the non-hard seeds had died ten years later. It is noteworthy that in the tests here recorded the least fall in hard seed content is found in the unabraded seed stored under very moist conditions. It is possible that these tests have not continued long enough for any reappearance of hard seeds to develop, but it probably is significant

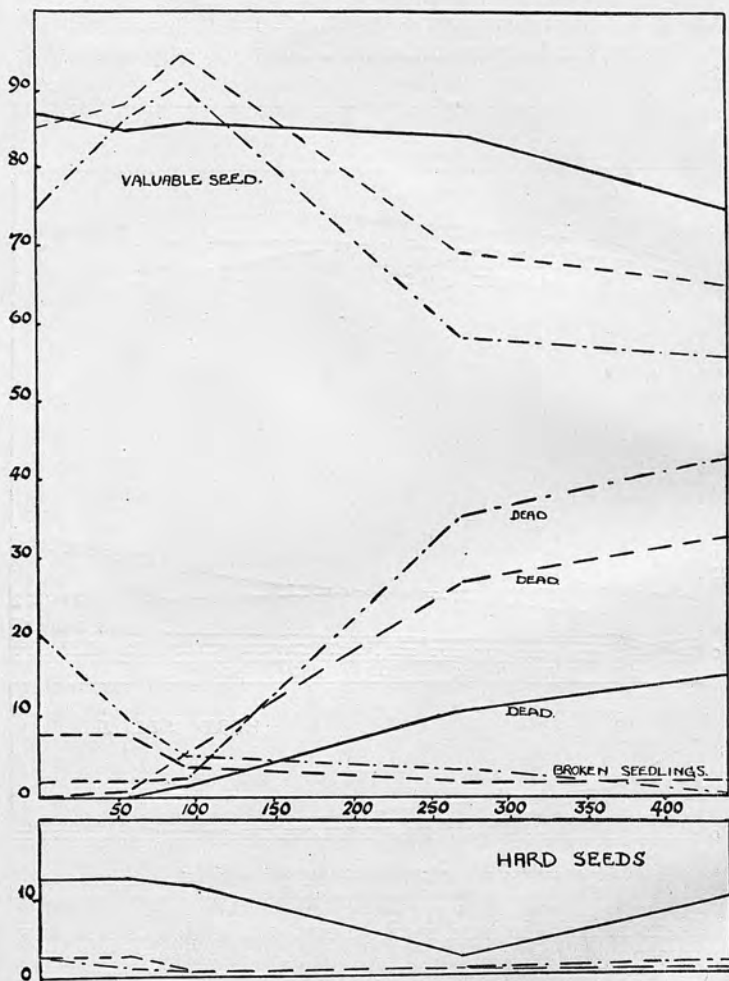


Figs. 2 and 2A.—Storage in sealed tubes.

that no increase in hard seed content can be detected in any abraded lot.

Considering for the moment only figures 4 and 4a, which represent the results of storage under very moist conditions, it is to be noted that in the case of all three lots there is a sharp and immediate rise in the dead seed curve. This rise in dead seed, coupled with a slight rise in broken seedlings in the case of the non- and slightly abraded lots, results in a fall of the valuable seed curves. At a comparatively early date this rise

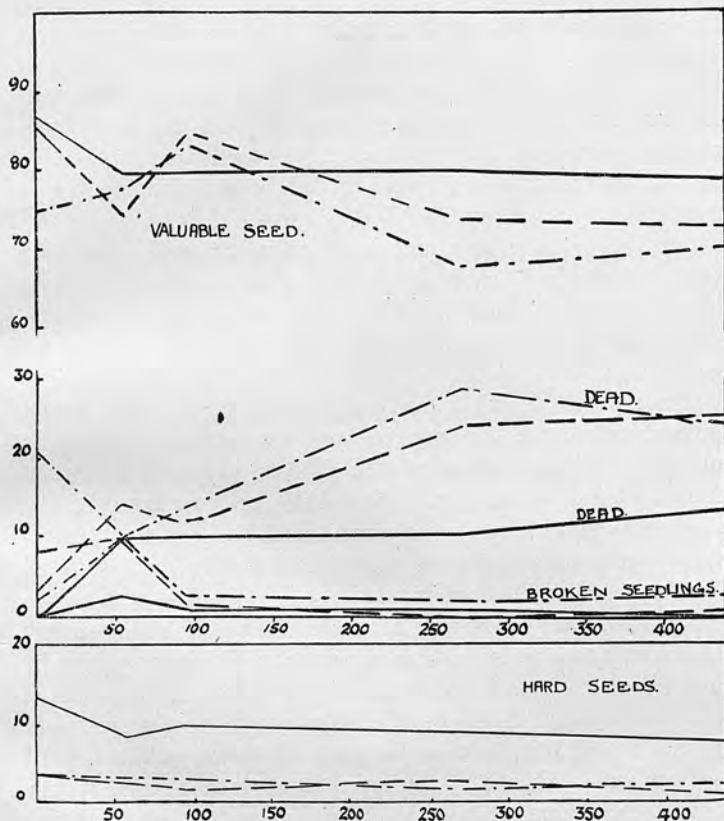
in dead seed ceases and the valuable seed curve flattens out, while a continued death-rate in the abraded lots brings all



FIGS. 3 and 3A.—Storage under excessively dry conditions. (Broken seedling of unabraded seed negligible and not shown.)

three curves into relative positions similar to that found for the other types of storage. Dealing still with moist storage only, fig. 5, which represents the total seed germinating, shows that the death-rate in the first fifty days or so for each

of the lots has been similar, irrespective of the machine treatment, the three curves being practically parallel. It would seem clear that there is some proportion of the seed in the sample peculiarly sensitive to the lethal effects of moist storage, and that these are not specially related (as with the lethal



Figs. 4 and 4A.—Storage under moist conditions.

effects of dry storage) to the class producing broken seedlings. In this connection it is to be noted that Pearl and Allen (4) found that when samples of seed were steeped in solutions of ethyl alcohol for three hours the germination was depressed. This depression of germination was not proportional to the strength of the alcoholic solution, but was constant at 8 per cent. for all strengths of solution up to 8 per cent. of alcohol.

The subsequent growth of the seedlings from seed which had been steeped in the alcoholic solutions was very much more vigorous than that of seedlings from seeds steeped in water only. The authors conclude that the alcohol killed off the weak members of the sample, leaving only the strong and vigorous. It is suggested that the moist storage described here acted in a somewhat similar way, selecting out and killing those embryos deficient in vigour. This would seem to be the essential difference between moist and dry storage. Excessively dry storage acts particularly on the seeds with thinned coats, probably through more rapid denaturation of the embryo proteins—a cause of loss of germinating power suggested by Crocker (1). Wet storage, while allowing denaturation of the embryo proteins to go on, attacks particularly seeds containing embryos of low vitality—possibly those harvested in an immature state—and this by simple rotting. The samples in moist storage showed mould attack at an early date.

The reason why those seedlings which break when tested immediately after abrasion become normal after storage is obscure. It has been suggested [Nelson (3)] that a broken seedling results from a thinning down or weakening of the seed coat (as by excessive abrasion), with consequent derangement of the normal stresses and resistances to pressure offered by the testa to the swelling embryo. If storage resulted in either the repair of the seed coat or a weakening of the energy of the enclosed embryo, then a return to normality might be looked for. If the whole of the initial rise in the percentage of valuable seed in the abraded lots be due to the return to normality of the testa, then the later continuous fall is difficult to explain. When the thinned coats reach normality, the curve of valuable seed should flatten out and run parallel with that of the machined seed. If, however, it be accepted that the storage results in a progressive reduction in vigour of the embryos, the initial rise in the valuable seed curve is explained by the seeds which had produced broken seedlings reaching a point where internal pressure following loss of vigour becomes reduced to a value suited to the reduced strength of the testa. This would also explain the later continuous falling off in the valuable seed curve due to increase in the dead: a continuous process is postulated. Further, this view would explain the

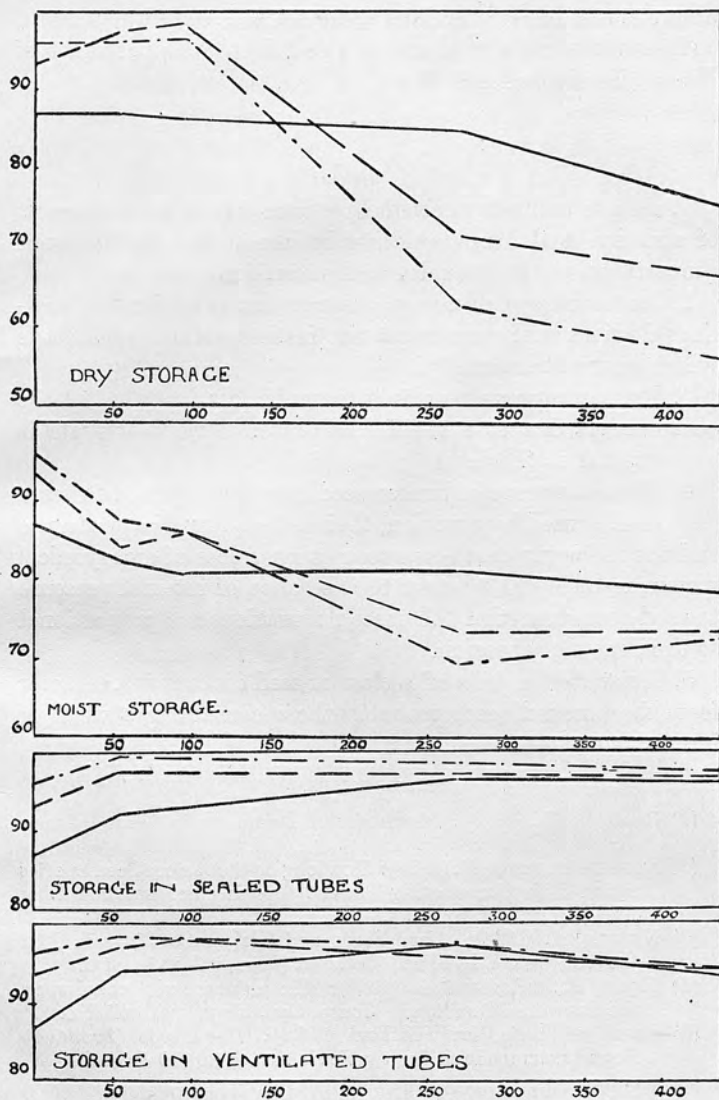


FIG. 5.—Total seed germinating. (Valuable seed plus broken seedlings.)

proportionality which obviously exists between the degree of abrasion and the fluctuations of the various constituents.

The tests were carried out in the Scientific Department of Messrs. David Bell Ltd., Leith.

SUMMARY.

1. As has been shown in the previous paper, a direct result of abrasion is the production of broken seedlings in amount proportional to the intensity of the abrasion.

2. Immediately on storage the percentage of broken seedlings declines with concurrent rise in the percentage of seeds which germinate normally.

3. Further storage results in a rapid loss in value of the abraded lots due to a rapid death-rate. This death-rate is proportional to the degree of abrasion.

4. The occurrence of broken seedlings is attributed to testa weakness, caused by abrasion, their subsequent disappearance and the following death-rate to continued loss of embryonal vigour, resulting in a return to a balance of internal pressure to seed-coat strength. All these fluctuations are proportional to the degree of abrasion.

5. Moist storage kills off a class of seed distinct in character from the abraded seed, probably those containing a weak or immature embryo.

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