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STUDIES in ROOT CROPS

by

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STUDIES IN ROOT CROPS.

INTRODUCTION.

At the Scottish Plant Breeding Station, a scheme for the breeding of root crops of Brassica spp. in which an attempt is being made to produce "pure lines" of economic value, has been in operation since 1921. This paper consists of observations upon a number of problems undertaken by the writer who has been assistant in charge of root crops since 1926. The swede or swedish turnip has been chiefly employed, and the investigations have been confined to cultivated forms of the species Brassica Napus var. Napobrassica, Petrm.; B. Napus arvensis, Hegi; and B. Rapa L.

Since swedes and turnips have biennial life terms, it has so far only been possible to study two generations, except in a few cases where hybrid plants have been forced to seed in twelve months and small F_2 generations obtained from crosses made in the second year of the studies.

The writer was indebted to the previous assistant, Dr. F.W. SANSOME, for part of the living material, in the form of seed or seed parent plants, of L_2 pedigree lines, F_1 and F_2 constituents.

The/

The experimentation to be discussed has been made for genetical study and for agricultural application. The observations mainly related to the mode of inheritance of the bolting tendencies, and colour of skin and flesh, while quantitative dry matter analyses were made in an attempt to distinguish between the hereditary and environmental causes affecting yield and feeding composition. Research into analytical chemistry has never been contemplated, and the methods of analysis employed were those approved by competent authorities. A series of small experiments on methods of drawing samples was also undertaken, to estimate the variability of dry matter determinations and to meet the peculiar requirements of seed-parent selection.

NOMENCLATURE AND RELATIONSHIPS OF THE SWEDE-TURNIP-RAPE GROUP.

In order to comprehend the relationships of the swede with other members of the Cruciferae, it seems desirable briefly to describe the various groups of related plants. There are vast numbers of cultivated species grown in different parts of the World, belonging to that portion of the Cruciferae which has been classed as Sinapis or Brassica. Roughly there are two large groups of these, to which the names Mustards and Coles may be given; the latter term being extended to cover the various forms both of cabbage and turnip. (BAILEY 1922). The species of Mustards were placed by Linnaeus into the genus Sinapis and the Coles into the genus Brassica. When later workers came to define the species and genera it was found that characters of taxonomic value occurred in such random fashion that the generic distinctions broke down, and, influenced by DARWIN'S theories, HOOKER (1870) and others attempted to attain a more natural classification by merging the two genera into one under the title Brassica. This classification has been continued until the present day by some systematists, but there has been a tendency/

tendency on the part of others to redivide the group, employing fresh taxonomic features (e.g. folding of cotyledons). The species have therefore had to be reassorted, necessitating in some cases transference from the Linnaean Brassica to the new Sinapis genus and vice versa. Those members of the mustard group which grow in Britain are apparently sexually incompatible with the swede-turnip-rape group (NELSON 1927).

In the Cole group there are recognised, firstly, a large number of horticultural and agricultural forms akin to the wild cabbage and interfertile inter se., e.g. cabbage, kohl rabi, cauliflower, marrow stem kail, thousand-headed kail, savoy, broccoli etc. and secondly, there are a number of forms grown eitherfor the oil in their seed (rapes), for their foliage (swede-like rape), or for their succulent storage organs (swede, turnip). These latter also form an interfertile group.

All the cultivated Coles together with a few closely related wild types are attributed to four out of nine original species of Brassica proposed by LINNAEUS (1753). These four species were:-

B. campestris
B. Napus
B. Rapa, and
B. oleracea with a number of varieties.

LINNAEUS/

TABLE I. SYSTEMATIC NAMES COMMONLY EMPLOYED FOR SWEDE; TURNIP AND RAPE.

AUTHORITY	SWEDE	TURNIP	SWEDE-LIKE RAPE
LINNAEUS (1753)	B.oleracea v. Napobrassica	B. Rapa	B. Napus?
DE CANDOLLE (1821)	B. campestris, v. Napo Brassica	B. Rapa	B. campestris & B. Napus v. oleifera
DYER (1871)	ditto	B. Rapa v. rapifera	ditto ditto.
BABINGTON (1922)	B. campestris B. Rutabaga	B. campestris B. Rapa.	B. campestris & B. Napus (L?)
BAILEY (1922)	B. Napobrassica.	B. Rapa.	B. Napus.
HEGI. (1906)	B. Napus v. Napobrassica	B. Rapa v. Rapa	B. Napus v. arvensis
BENTHAM (1865)	B. campestris B. Rutabaga	B. campestris B. Napus	B. campestris B. Rapa.
BENTHAM & HOOKER (1920)	ditto	ditto	ditto

LINNAEUS seems also to have considered the advisability of including B. Napus and B. Rapa in the species B. campestris. There is considerable uncertainty as to the position that swede occupied in his classification, for it has been identified both as B. oleracea, var. Napobrassica L., and also as B. Napus L. The former name may have been intended to denote Kohl rabi, while some writers contend that the Linnaean B. Napus was meant for rape alone; the description "fusiform" referring to the spindle shaped root of the rape, and not to the enlarged "bulb" of the swede (BAILEY 1922). The variety Napobrassica was removed from B. oleracea at an early date, and since none of the remaining varieties of this species are sexually compatible with swede, they need not be discussed further.

It is not the purpose of this paper to trace the intricate regrouping to which the forms have been subjected, but since so many systematic names for swede, turnip and rape are in current use, it may not be out of place to quote a selection of the more important (TABLE I.)

DE CANDOLLE (1821) employed the varietal name Napobrassica for swede, and transferred it to the species B. campestris. He described three types of rape, one being a "bulbless" form of the turnip/

turnip, one grouped with the swede, while the third was classified as "B. Napus, v. oleifera, rape, navew or coleseed".

The terms "bulb" and "root" are both used in agriculture to denote the storage organ in the swede, but since this is composed of shoot, hypocotyl and root tissues, neither term is botanically correct. The words "bulb" and "bulbless" will be used in this paper in order that there may be no confusion between storage organ and the true root.

A controversy concerning one of the bulbless forms led to a reconsideration of the group by WATSON (1869 and 1870) and DYER (1871). DYER considered that the group consisted of three species, B. campestris, B. Rapa and B. Napus, each of which contained a bulbless, oil-bearing, annual form and a bulbed biennial type. The bulbed forms consisted of swede, turnip, and a vegetable grown in France under the name "navet", to which the term B. Napus L. esculenta, De Cand., was applied. This vegetable must since have dropped out of cultivation or have been identified with one of the other bulbed forms.

At the present time there is no general agreement in classifying the group; and three examples are quoted in TABLE I, from Britain, America, and Germany.

BABINGTON/

BABINGTON (1922) places the whole group in B. campestris (L), and gives two types of rape, B. campestris (L), —, and B. Napus (L?); he uses B. Rutabaga to denote the swede.

BAILEY (1922) raises Napobrassica to species rank to define the swede alone, and restricts the use of B. Rapa to the bulbed turnip.

The Continental authorities, who have to deal with many forms of oil-producing Brassicae little known in Britain or America, seem to follow a different hypothesis, probably based on the breeding experiments of LUND and KJAERSKOU (1886) and KAJANUS (1913 and 1917). G. HEGI (1906-30) has apparently entirely discarded the species B. campestris (L), grouping all the forms as either B. Napus or B. Rapa. His classification is given in detail in TABLE II, and will be used here because it appears to follow a more natural arrangement.

The last classification quoted in TABLE I, is that of the BENTHAM and HOOKER floras. It will be noted that the terms are interchanged and that B. Napus is used to denote turnip, and B. Rapa for rape. This is a source of great confusion in agricultural literature. The trouble is an ancient one, because the various European languages have adopted names for Brassica crops, based indiscriminately on the/

TABLE II. CLASSIFICATION OF HEGI (1906)

B. NAPUS L. (excluding Napus silvestris transferred to B. Rapa, as var. silvestris.)

I. var. arvensis.

f. annua	Summer swede-like rape
f. biennis	Winter swede-like rape

II. var. Napobrassica (L) Peterm.
(= B. oleracea var. Napobrassica L)
Swede.

B. RAPA L.

I. var. silvestris
1. — "Wilde Rübenkohl" Field Brassica.
2. f. annua, Summer turnip-like rape.
3. f. biennis, Winter-turnip-like rape.

II. var. Rapa
sub-var. oleronensis, Turnip, slender type
sub-var. pygmaea. Turnip, broader types
sub-var. communis, Turnip, white.

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the Latin word "rapa" and the Anglo-saxon "Neipa" (DE CANDOLLE 1889).

AGRICULTURAL RELATIONSHIPS OF THE SWEDE-TURNIP-RAPE GROUP:

Members of the swede-turnip-rape group are sexually compatible with one another; but judged by the fertility of their hybrids they fall into two natural sections corresponding to the species B.Rapa and B. Napus as above defined by HEGI. (TABLE II.) The hybrids of members of the same section are fertile, but those having parents from both sections behave irregularly. The common names of the wild and cultivated forms comprising the group are as follows:-

Section I.	Section II.
(1) Field Brassica	- - - - - - - - - -
(2) Summer turnip-like rape	(6) Summer swede-like rape
(3) Winter turnip-like rape	(7) Winter swede-like rape
- - -	(8) Ragged Jack Kale
- - -	(9) Asparagus Kale
(4) White-fleshed turnip	(10) White-fleshed swede
(5) Yellow-fleshed turnip	(11) Yellow-fleshed swede.

SECTION/

SECTION I.

Field Brassica (GERMAN ACKERKOHL) an annual, grows on borders of fields and waste places throughout Europe and Russian Asia, and is a frequent weed of cultivation in Britain (BENTHAM & HOOKER 1920). Although it is generally held that there is only the one wild type (KAJANUS 1913, BENTHAM & HOOKER 1920) other forms have been described as indigenous in Britain (e.g. WATSON 1869).

(2) Summer turnip-rape, (GERMAN - SOMMERRÜBSEN), annual, and (3) Winter turnip-rape, (GERMAN - WINTERRÜBSEN), biennial, are domesticated forms not grown as crops in this country. Crossing experiments carried out by LUND and KJAERSKOU (1886) and summarised in KAJANUS' paper (1913) indicate that these forms are closely related to the wild species, to the common turnip and to one another in sexual compatibility and that certain anatomical features in the hypocotyl region resemble characters strongly developed in the "bulb" of common turnip, but absent in field Brassica.

Common turnip is a cultivated biennial. This species includes two agricultural types, (4) white-fleshed and (5) yellow-fleshed turnips characterised by a single mendelian allelomorph governing flesh and/

and flower-colour, and by distinct physiological differences as indicated by the proportions of dry matter, and by the winter hardiness of the "bulb".

Both types exhibit a series of colours on the skin of the "bulb" dependent upon factors governing chlorophyll and anthocyanin production:-

(a) white, with or without nuances of red or green.

(b) yellow, due to plastids, in underlying tissues.

(c) green, the exposed skin being coloured uniformly with chlorophyll.

(d) red, a bright uniform pigmentation of anthocyanin on the exposed parts of the bulb.

(e) "purple" a combination of red overlying green.

(f) restricted area of anthocyanin displaying a belt of green.

These characters were investigated by KAJANUS (1913) and are described here because of the palallel that they afford to those of swede. Among the various hybridisation theories that have been advanced to account for cultivated varieties, the suggestion (STEPHEN 1908) that yellow turnip originated from a hybridisation between white turnip and yellow-fleshed swede, at some time since the introduction of the latter into Scotland 1777, is still credited.

Several workers including WILSON (1911) and KAJANUS (1913) (1917) have studied hybridisations between/

between swede and turnip and although there were indications that some of the factors governing certain characters such as flesh and skin colour were identical, strains of agricultural value were not found. The yellow fleshed turnip has a low degree of self-fertility, but is highly fertile inter se, and its pollen is well formed.

The species hybrid on the other hand produces about 50% bad pollen, and was found, by the writer, to be highly self-sterile, only two or three seeds being obtained per plant under bag isolation. KAJANUS and WILSON obtained their seed by isolating F_1 or F_2 plants in groups.

SECTION II.

(6) Summer swede-like rape (GERMAN - SOMMERRAPS) is a bulbless annual grown on the continent for the production of oil.

(7) Winter swede-like rape, rape, colza, or coleseed, is a closely related biennial form, grown in Britain as a crop. LUND and KJAERSKOU (1886) found that the swede-like rapes formed an overlapping series, sexually compatible with one another and with swede, and forming a similar series of forms to that of the turnip-like rapes and turnip. Unlike the latter, however, the swede-like rapes were self-fertile. These forms will be discussed later in connection/

connection with the 'Bulbless bolter'.

(8) Ragged Jack Kale is a plant resembling in general characters the Colza rape, but with laciniated leaves. The flowers are bright canary yellow.

(9) Asparagus Kale is also a type related to Colza rape but with distinctive leaf characters. SUTTON (1908) found these two kales to be fertile with other members of the group under discussion and he followed hybridisations between the two Kales and swedes into the F_2, where bulbed and bulbless forms segregated, the bulbed condition being dominant but the ratios uncertain.

The Swede or Swedish turnip is a cultivated biennial. It differs from the turnip in that a short stem called the 'neck' surmounts the 'bulb', the leaves are glaucous, the 'bulb' has higher dry matter content, and the plant is potentially self-fertile; but it resembles the turnip in being divided into (8) white-flesh, and (9) yellow-flesh types and these again include skin colour and shape differences.

The white fleshed swede is seldom employed in agriculture in Britain. There are several combinations of shape and colour, and certain varieties have an entire leaf character. The yellow fleshed swede or rutabaga is the type generally grown, and is the main subject of this paper. A very large number/

number of strains, termed 'varieties', have been selected and bred by seedsmen. Some of these varieties show distinctive genetical differences, but in most there is wide fluctuation or variation, and the strains are not sharply differentiated. The 'varieties' are commonly grouped according to colour as purple, bronze, or green-tops, and according to their most common shape as tankards, half-longs, and globes. An entire leaf type exists, but is not used in agriculture.

CHROMOSOME NUMBERS.

No cytological work has been attempted by the writer. The chromosome numbers found in Brassica species are given in a recent review by MALINOWSKI (1929); and it would appear from this, and from other publications, (JUNK 1926) and GALLASTEGUI (1926), that the following numbers have been established:-

Swede and swede-like rape	18 haploid
Turnip, Summer and Winter turnip-like rape..	10 haploid
Cabbage sub-spp......................	9 haploid

It will be seen from this that swede and rape have a tetraploid constitution as compared with the Cabbage group. This may be of interest in view of the fact that there are two pairs of factors each giving, when present, a similar white-flesh condition/

condition; while there is reason to suspect that a similar duplication occurs in the factors governing purple neck colour.

KARPETSCHENKO (1929) has extended his methods of obtaining artificial polyploids to swede and swede-like rape, having incorporated each of them in triple hybrids with his radish x cabbage tetraploid.

I.

BOLTING OR RUNNING TO SEED IN SWEDES.

Although the damage caused to the crop is not so serious as in the case of sugar beet, swedes are subject to loss in value on account of tendencies to 'bolt' or 'run to seed' during the first season of growth. Two problems arise in this connection:-

(A) The bolting of otherwise normal swedes.

(B) The occurrence of an aberrant, rape-like form known as the 'bulbless' or 'bastard-bolter'.

(A) BOLTING IN OTHERWISE NORMAL SWEDES.

In order to obtain the maximum yield of foodstuff, it is desirable that a strain of swede should be so far biennial in habit of growth that, when sown on a suitable date in spring or early summer, the plants will still be developing in bulb and not in stem at the end of the season. In addition it is also economically desirable that, when the seed is sown in September, the plants should be able to complete their life cycle within a period of twelve months. This is the process employed for multiplying 'stock' seed. The phenotype must, therefore, be sufficiently adaptable to conform to both methods of culture. A certain amount of selection is constantly in operation to maintain these propensities, because plants/

plants that bolt in the first summer are discarded during the selection of seed-parent roots, while if there are any types so far perennial that they fail to set seed during the multiplication generation, these too will be automatically eliminated.

Normal Winter Habit of Swedes: In the swede the first season of growth, as far as the upper parts are concerned, is terminated by the first frosts. At this period the leaves are still arranged in a rosette on a stem with undeveloped internodes known as the 'neck'. The first few leaves have already been shed, and the frosts cause all those that are fully grown to wilt and fall, leaving the young and half-grown leaves, which persist, with little or no growth, throughout the winter. The stem or 'neck' surmounting the bulb is from 2 to 10 cm. in length and 3 to 4 cm. in diameter, and the leaf scars are crowded in a spiral arrangement. The intervals between scars vary in different strains, ranging from 0.5 to 1.5 cm.

In this condition the swede plant remains outwardly dormant until early spring, when growth recommences. The first leaves to develop resemble those of the first season being lyrate,pinnatifid and apparently petiolate, though sometimes with small lobes or narrow margins of lamina extending to the leaf base. As the stem elongates and the internodes become/

become progressively longer, the leaf type changes, passing through transitional forms, in which the margin of lamina becomes wider, to a sessile, cordiform, and lanceolate type, which is found in the region of the inflorescences.

The main stem grows rapidly, ultimately reaching a height of about five feet; while side shoots also develop, though they seldom arise from the buds of the first year neck, unless the new growth is damaged.

The Bolting Habit; During the first season, under certain environmental conditions of which the occurrence of frost late in the spring seems to be the most common, a tendency to bolt is manifested. The neck commences to elongate at the expense of the bulb, and in extreme cases the plant may flower and set seed within five months from the date of sowing. Bulb formation is always present, but if bolting commences early, (which may be deduced from the small number of leaf scars at the base of the stem) the bulb may be very small. The rapidity of bolting varies greatly, and leaf scars may be only 2 to 3 cm. apart in a long-necked plant or 20 cm. in a fully bolted specimen.

In a crop exposed to conditions tending to cause bolting , the great majority of plants have long necks, but no signs of flower buds. This neck length is fairly constant within each commercial variety and may average 15 or 30 cm. according to the intensity of the weather conditions, and also to varietal response. Thus one 'variety' may always have a longer neck type than another, though the actual lengths vary greatly in different seasons. In addition to this general response, small proportions of plants may bolt completely and flower, while similar numbers may be found with very short necks.

In 1927 an experimental field containing 16 commercial varieties of swede in unreplicated 1/10th acre plots, was affected by general bolting conditions, and afforded an opportunity for observation on varietal behaviour, and inheritance of bolting tendencies. The long-necked condition has been observed, in this and other trials, in certain strains of all the types. Examples may be quoted from samples of commercial varieties:-

Purple tankard or half long.

Long necked:- "Feedwell" "Mervue"

Short necked:- "Picton" "Superlative" "Monarch"

Bronze tankard or half long.

Long necked:- "Acquisition" "Edina".

Short necked:- "Bell's improved purple-top"

Bronze/

Bronze globe.

Long necked:- "Caledonian" "Empire"

Short necked:- "Drummond's Bronze-top", a strain of "Darlington".

Green globe.

Long necked:- All the varieties so far observed. viz., "Kinaldie", "Teviotdale", Sutton's Drummond's and Bell's. "Green-top" varieties, and a Svalöf variety "Improved yellow Swede".

The above varieties are quoted to illustrate the distribution of neck-length variation, but it is realised that, since the varieties are heterogeneous, another sample of any one of them might exhibit a different neck type. As a group the Green-tops were found to be characterised by long necks, but the British varieties, which all closely resemble each other, may have been fairly recently selected out of some common green-top stock. The shortest type of neck occurs among the soft-fleshed, early maturing strains such as 'Picton' and 'Superlative'.

The occurrence of fully bolted plants in a crop might be due to an extreme environmental modification or to a hereditary variation or to both; on the other hand it might be due to hybridisation or to/

to admixture of seed. Unlike the 'Bulbless bolter' to be described later, the plants under consideration are of the same flesh and flower colour as the rest of their population, and resemble the main varietal type in regard to skin colour, shape and minor leaf characters as closely as may be expected in a cross-fertile crop. They are, therefore, segregates differing from the majority of the plants in comparatively few characters.

SELECTION OF BOLTER AND NON-BOLTER TYPES.

Pairs of selections were made in 1927 from populations of three varieties, which were characterised by very long necks, and which contained small proportions of fully bolted plants. In each pair one selection was a more or less bolted plant, while the other was the shortest-necked plant of good shape and conforming to the type of the particular variety that could be found in a 1/10th acre plot.

TABLE III. Selections from long-necked stocks.

"VARIETY"	DESCRIPTION & DEVELOPMENT		NECK LENGTH
CA	Bolter	not in flower	15 inches
CA	Non-bolter	short neck	2½ "
KW	Bolter	not in flower	24 "
KW	Non-bolter	short neck	3 "
LD	Bolter	pods developed	28 "
LD	Non-bolter	short neck	3 "

The seed obtained from these selected plants under bag isolation, was sown out in 1929, on April 26th., 17 days before the first normal sowing. The weather conditions did not prove conducive to bolting, and at the end of August there was only one fully bolted plant which occurred in the progeny of 'LD bolter', while the differences in neck lengths were too small to estimate.

On September 10th., observations were made, and the neck lengths grouped by eye into classes as **in** TABLE IV.

The growing shaws prevented accurate measurement.

TABLE/

Fig. 1. Bolting in normal swedes.

Progenies of "KW" selections, (see text)

The plants in the drills on the left are the progeny of a 'short necked' selection. Their necks will be seen to be short.

The plants in the drill on the right are the offspring of a bolted plant of the same variety. Their neck length~~s~~ exceeds eight inches, and the plant on the extreme right is fully bolted.

(Photographs by J. W. Gregor, Ph.D.)

TABLE IV. Neck lengths of progenies of selections.

PROGENY OF	1"	2"	3"-5"	6" and over	In bud.
CA, bolter	11	22	26	1	-
CA, non-bolter	142	14	-	-	-
KW, bolter	-	5	14	2	3
KW, non-bolter	-	120	-	-	-
LD, bolter	20	32	18	4	1
LD, non-bolter	150	10	-	-	-
"Bolters"	90		58	7	4
"Non-bolters"	436		-	-	-

At the end of the year the difference in neck length became more pronounced (See Figure I)

Notes were also obtained on another 'bolter' line, which was selected out of a commercial variety by the writer's predecessor. A plant of the L_1 generation of this line was selfed, and an L_2 strain (designated BOaa) was thus available in 1927. One plot of this was sown on April 18th., but the severity of Turnip 'fly' beetle (Phyllotreta undulata Kutz) attack, consequent on early sowing, reduced the population to 24. Of these, 9 had long necks (about 8"); 4 were half-bolted, with terminal flower buds (about 18"/

18"); while at the end of the first season 11 were fully bolted and in flower. A control plot, of a short-necked strain, did not exceed 3" in neck length. Two other replications of this 'bolter' strain were sown on May 17th., and 19th., of the same year, and in neither cases was there any sign of bolting, the necks being about 2" long in December.

From the early sown plot of BOaa, selections of extreme types were made, i.e. the shortest and the longest-necked plant. These plants were seeded in isolation, and their progenies were tested in 1929. One plot of each was sown on April 26th., along with the CA, KW, and LD strains already discussed (TABLE IV). Estimates of neck lengths were made on September 10th., and are given in TABLE V.

TABLE V. L_3 descendants of a swede bolter.

PROGENY OF:-	NECK LENGTH. 1"	2"	3"	4"
Extreme L_2 bolter	25	30	15	-
Least bolted L_2 plant	48	62	3	1

It will be seen that no differentiation was obtained by selecting extremes out of the L_2 population.

(2)/

(2) THE BULBLESS OR BASTARD-BOLTER.

The 'bulbless' or 'bastard-bolter' is an aberrant form which is sometimes found in crops of swede.

The proportions in which it occurs are generally small, e.g. 0.01%. Sometimes, however, this rogue is more abundant, and there is a consequent depreciation in the value of the crop, because the plant has a ligneous root, and is of little or no feeding value.

The origin of the bulbless-bolter is a matter of interest, since, among seed-growers, it is commonly believed to be a 'reversion' to an ancestral form. LAFFERTY (1929) has recently identified it with rape; and in certain crops he found both true breeding rape forms and also swede x rape hybrids. The present writer, while agreeing with LAFFERTY that there is a close structural resemblance between the bulbless-bolter and swede-like rape, cannot, at present, complete the identification on account of the bolting habit. The strain of swedelike-rape used as a control, was distinctly biennial. When seed was sown in September, both the rape and the bolter flowered early in the following summer, but when sown in May, the rape remained dwarfed throughout the first season, the stem being less than/

than 4" in length, while descendants of a bulbless bolter growing under similar conditions , reached a mean height of 3½ feet and flowered. Further samples of swede-like rape are being examined in an attempt to match the bolting character of the bulbless bolter. All the varieties of the rape grown in this country are said to be winter swede-rape, a biennial classified by HEGI (1906) as B. Napus L., var. arvensis, f. biennis. Although a certain amount of summer swede-rape seed is imported as a foodstuff for small birds, this annual form is not grown in Britain to any extent as a crop.

Observations have been made on several strains of bulbless bolters, and evidence tending to disprove the reversion theory has been collected.

<u>Comparison of yellow flesh swede and a true-breeding form of bulbless bolter.</u>

SWEDE	BOLTER
1. Foliage glaucous.	1. glaucous but darker green.
2. Bulb formed, even in small or bolted plants.	2. swelling none or only slight.
3. Bulb tissues soft with diffused fibro-vascular strands.	3. tissues interior to cambium solid wood.
4. Side roots usually thin. Sometimes fleshy "fangs" formed.	4. branching system of stout roots, termed fangs, not fleshy.

5/

5. Tissues interior to cambium yellow.	5. Internal tissues of root all white.
6. Petals dull buff.	6. Petals bright lemon.
7. Self-fertile.	7. Considerable self-fertility.
8. Pods smooth.	8. Pods wrinkled.
9. Seed dull black.	9. Seed larger, with oily seed coat.
10. Seedling habit spreading.	10. Seedling erect.

Comparison of winter swede-rape with a true-breeding form of bulbless-bolter.

Points of resemblance:-

(1) Foliage glaucous and dark green.

(2) Root bulbless, woody.

(3) The pith of the stem green ending in a cup-shaped socket of ligneous root-tissue.

(4) Roots stout and ligneous, forming a branched system.

(5) Internal tissues of root all white.

(6) Petals bright lemon yellow.

(7) Seed large with an oily seed coat.

(8) Seedling habit, erect.

Points of difference:-

(9) At the end of the first season the bulbless bolters so far collected have ranged from 10" to 4 ft. while the rape sample was only 4" in stem length.

(10) There were minor differences in tone of petal colour.

(11)/

(11) The lateral leaflets were revolute in one strain of bulbless bolter whereas in the rape sample as in swede, these were involute or flat.

Breeding.

Bulbless bolters have been found in a number of swede crops from different sources, indicating the widespread nature of their occurrence.

Breeding experiments have been carried on out on bulbless bolters obtained from three sources, viz., two commercial crops and an experimental plant.

The bolters selected out of commercial crops proved to be true-breeding, but a hybrid bolter was obtained from a swede plant exposed to natural crossing.

(1) A plant, BP, was found in a purple-top yellow fleshed swede crop in 1926. The stem was about ten inches long at the end of the first season and flowering had not then occurred. The numerous leaves were darker green that those of the swede. The flesh was white and the petals bright lemon yellow. The plant was self-fertilised, and a progeny, BPa, obtained. 96 plants of this were observed, and were found to be very uniform. They resembled swede rape and the stems did not elongate until late in the first season, when a height of about 10 inches was again reached, without flowering. The roots/

roots were white and woody.

(2) Bulbless bolters were collected from a commercial crop in 1923 and selfed in 1924. In 1925, L_1 generations were grown, and five selections were made from one of these populations (BOb). The selfed progenies of these, being the L_2 generation, were observed by the writer in 1927.

TABLE VI. Flowering in bulbless-bolter lines.

LINE	NUMBER OF PLANTS	IN FLOWER AUG. 17th.
BOba	170	37%
BObb	163	1%
BObc	162	31%
BObd	110	37%
BObe	188	9%

There was almost complete uniformity in the 800 plants examined, and much less fluctuation than is to be found in inbred lines of swede. The lines differed in two minor characters, (1) the margin of the leaf was differently indented and (2) the time of flowering was about a week later in BObb and BObe than in the others, as may be seen from the above score, (TABLE VI), taken soon after flowering commenced/

commenced; all the plants flowered before the end of the first season. Lines BObb and BObc were carried, through selfed selections, into the L_3 generation, where the difference in time of flowering was still distinct. Notes concerning the characters of these lines have been given above in the comparisons with swede and rape. The revolute leaflets were characteristic, and the bolting was pronounced, the plants growing uniformly to a height of about 3.5 ft.

(3) A bulbless bolter was obtained among seed on an exposed raceme of a purple-top yellow flesh swede, which was flowering beside swedes, turnips, and plants of the bulbless-bolter lines, BOb. This bulbless-bolter plant, SUacb, had (1) dark green foliage, (2) lemon yellow flower, (3) white woody flesh, (4) purple skin and neck, and (5) a small bulb strongly fanged; it was quite self-fertile.

The selfed progeny of this natural cross segregated in the first year of growth as follows:-

1. Bolting was pronounced in an early sown plot, most of the plants ranged between 4 ft. and 7 ft. but some were short. Strips of drill in this plot contained unbolted plants, so that the effect was partly environmental. In later sown plots the plants with one or two exceptions were not bolted, but had stems ranging up to 15 inches.

2/

2. The flowers were mostly bright lemon yellow, a few dull buff, and these colours were linked with white and yellow flesh repectively. Towards the end of the season minor differences in the lemon yellow colour were noted.

3. The roots were all much fanged and partly swollen, but varied in toughness and size. Parent types were not found.

4. <u>Flesh colours.</u>

	White	Yellow	Total
observed	276	31	307
expected (15:1)	288	19	

White flesh in swedes is governed by two unlinked factors, in the absence of both of which flesh is yellow. Here however, there is a suggestion of linkage which will be followed up in the experimental crossings.

5. <u>Skin colours.</u>

	Purple.	Non-purple.	Total
observed	233	74	307
expected (3:1)	230.3	76.8	

The swede parent was homozygous for purple skin, a simple dominant. The probable male parent, one of three similar bulbless bolters, had little or no pigment, which is the recessive condition.

Artificial hybridisations have been made between swede, winter-rape, and the true-breeding bulbless bolter, BObb; and the F_1 hybrids are compared with parent strains, all being sown in May and grown under similar conditions. F_2 generations of these hybridsations are not yet available.

<u>Swede x Winter rape.</u>

F_1... Dark green foliage, white flesh, woody fanged root (like rape).
Half-bulbed (intermediate).
Shaws spreading, pigment purple (like swede parent).

There were no indications of bolting in this hybrid, but in this connection it may be mentioned that/

Fig. 2. Swede x "Bulbless Bolter".

A. Bulbless bolter strain, (one drill only,) flowered in August, height 4 ft.

B, B' F_1 hybrid population, (two drills), flowered in September, height 4½ - 6 ft.

C. Swede parent strain, (drills to the right) not bolted, necks 1 to 2 inches in length.

that the swede parent was of a variety not inclined to elongation of the neck. (fig 3, p.33).

Swede x Bulbless Bolter (BOb)

F_1.... Foliage dark green, flesh white, roots fanged, bolted (like BOb).
Half bulbed, time of flowering later and more irregular than BOb (intermediate).
Shaw in young stages spreading, pigment purple, (like swede P_1).

The parent strain of bulbless bolter used as a control and sown at the same time as the F_1, flowered early (August), the individual plants reaching the flowering stage simultaneously and growing to a uniform height of 4 feet.

The parent strain of swede did not bolt, the necks remaining short from 1 to 2 inches in height.

The hybrid population flowered during September and grew larger than either parent, attaining heights of from 4½ feet to 6 feet. (fig 2).

Swede rape x Bulbless Bolter (BOb).

The growth of the F_1 was biennial; at the end of the first season the stems were from 6 to 8 inches high, whereas the parent strain of rape, under similar conditions, was only 3 inches, and the parent strain of bulbless bolter, which had flowered, exceeded 3½ feet in height. The secondary leaflets of the hybrid were revolute resembling those of the bulbless/

bulbless bolter parent. In other characters the hybrid appeared to resemble both parents.

The extent to which crossing between swede and bulbless bolter (BOb strain) may occur in nature was also tested. Two plants were seeded close together in natural isolation on an island where no other Brassicae were growing. The inflorescences were exposed until flowering had nearly finished, when the ripening pods were protected from birds by wide mesh muslin. The seed of each plant was harvested separately, and sown out in the following year.

The bulbless bolter was true breeding for white flesh, (a dominant character), and non-pigmented stem and root (recessive); while the swede had yellow flesh (recessive) and a purple top with pigmented shaw (dominant).

The progeny of the Bolter ♀ consisted of 51 plants, all white fleshed, of which 5 were unpigmented and bulbless, while the remaining 46 were pigmented and showed swellings or half-developed bulbs. The progeny of the swede ♀ consisted of 96 plants, all purple-top, of which 82 were yellow fleshed and normal swedes, while 14 had white flesh and other bolter characters.

Cross-fertilisation had therefore occurred

in/

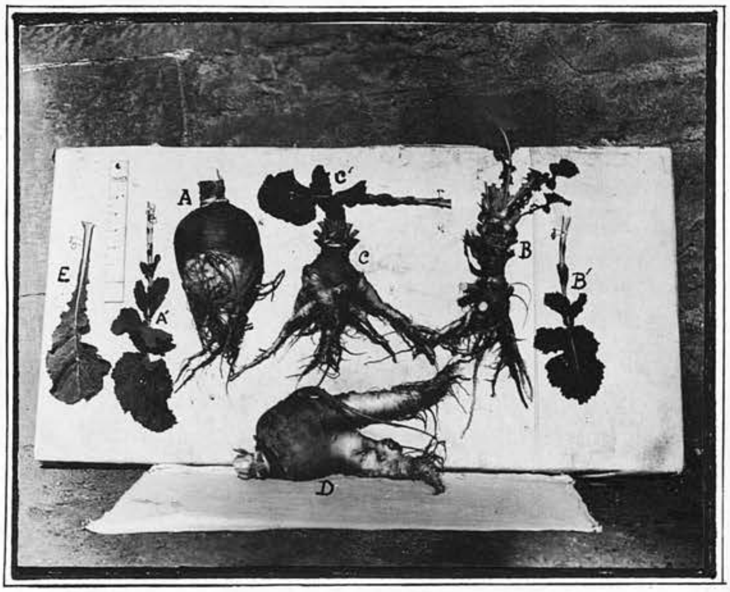

Fig. 3. Swede x Winter swede-rape.

A. Swede,fully bulbed, symmetric. A' swede leaf.

B. Winter swedelike-rape, bulbless. B' rape leaf.

C. F_1., half-bulbed, fanged roots. C' F_1 leaf.

D. Swede, misshapen bulb for comparison.

E. Swede leaf, entire form found in certain strains

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Note difference in colour between swede leaves and rape and F_1 leaves.

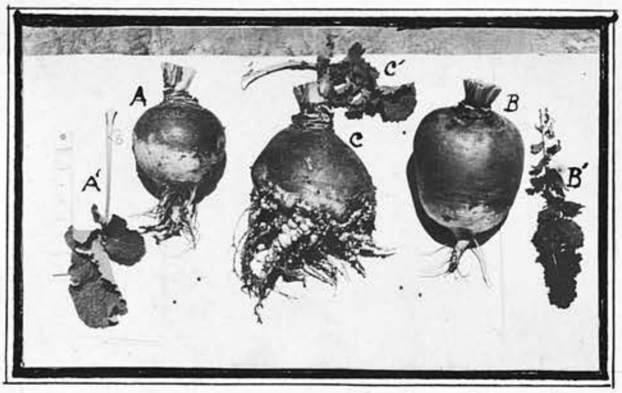

Fig. 3a. Swede x White turnip.

A. Swede of parent strain. A' leaf.
B. White fleshed turnip. B' leaf
C. F_1 hybrid, fully bulbed,frequently symmetric, but nearly always showing great development of nodules and swellings. (BARTLETT,(1928)) (KAJANUS,(1913)(1917)).

in both plants; in the bulbless bolter ♀ to the extent of 90%, but in the swede ♀ only 14.5%.

Forms with which the Bulbless Bolter may be identified.

1. Swede-like rape. This is the most probable source of bulbless bolters. It is sexually compatible with swede and the hybrids are fertile (LUND and KJAERSKOU (1886)). Varieties of the winter form are widely used in agriculture in Britain, as a catch crop for sheep feeding or green manure. Normally under this treatment rape is not allowed to seed, but occasionally seeding might occur with consequent contamination of the soil with ground-keeper seed.

It has already been mentioned that the annual form is rare in Britain, and unlikely to form a frequent source of adulteration.

2. Ragged Jack and Asparagus Kales. Although these are potential sources of fertile hybrids (SUTTON 1908) their distinctive leaf shapes have not been observed among the bulbless bolters so far examined.

3. Turnip and Turnip-like-rape. These may be eliminated on account of their distinctive leaf characters and self-sterility. Further, the hybrids of Swede x B. Rapa L., are practically sterile. The turnip itself when crossed on swede gives a fully/

fully bulbed hybrid. The turnip-like-rapes are not grown to any extent in this country.

4. Wild or Field Brassica. This is described as a slender rooted annual which should distinguish it from the bulbless bolter. Its behaviour in crossing is unknown, except that LUND and KJAERSKOU (1886) placed it with the turnip and turnip-like-rape group. Growing as a weed it might sometimes occur in fields of flowering swedes.

5. B. oleracea sub-spp. Great difficulty has been experienced in obtaining hybrids between swede and members of this species. (NELSON 1927).

6. Mustards. The wild and cultivated forms of mustards found in Britain seem to be sexually incompatible with swede. (NELSON 1927).

Duscussion - Bolting in normal swedes.

Commercial varieties of swedes exhibit different responses in the development of neck, and under certain environmental conditions some grow long and coarse stems of 15" or more in length, while others are very little affected. As a group, the winter-hardy green-tops seem most inclined to long neck formation, but this may merely indicate a comparatively close relationship. Certain soft flesh, early-maturing varieties are apparently the least responsive/

responsive to bolting conditions. Otherwise there appeared to be no connection between bolting and shape or colour.

Seedsmen select for a certain length of neck, and though it is not considered desirable to have too long a neck, yet it is advisable that there should be sufficient length to permit ease in pulling the bulb and in cutting off the shaw.

Moreover, the varieties intended for winter use should have a good shaw as protection against frost, and this may necessitate a greater coarseness in the neck.

HELWEG (1887, quoted by FABER, 1920) found that the tendency to run to seed during the first year was a character of strains of root crops and was inherited. Small experiments are described above, in which attempts were made to determine whether bolters and short-necked plants from a commercial variety possess different hereditary constitutions. Although the season in which the progenies were tested was not favourable to bolting, there was evidence that the progenies of three bolters produced on the average, longer necks than those of the short-necked plants from the same varieties.

Selection of extreme types from L_2 strain of bolter was without effect in the L_3 progenies. There/

There can therefore be wide fluctuation, ranging from 8" necks to fully developed bolters, in a population that is apparently breeding true for bolting propensities.

DUDOK VAN HEEL (1927) working with inbred strains of sugar beet, found that the tendency to bolt was hereditary, and was recessive in crosses with strains having little tendency to bolt. SUTTON (1924) observed the inheritance of bolting in cabbage. When sown in the autumn most of the varieties bolt to a very great extent in the following spring, but the 'spring' cabbage forms a heart and does not bolt.

This non-bolting character was found to be dominant. In the present experiments the breeding properties of bolter lines of normal swedes are still under examination and the results of crossing are not yet available. In crosses between bulbless bolter x swede the bolting habit is dominant.

HALL (1928) describing BATESON'S experiments with Sugar beet and mangolds, shows how BATESON eliminated bolting for practical purposes by sowing in December, and keeping only the very few plants that did not bolt in the following summer. He writes "Bolting cannot be regarded as a simple character/

character alternative to non-bolting because it only represents a final stage of development through which all the plants must pass. The distinction between annual and biennial is one of degree rather than of kind". and "A certain small proportion is impelled to bolt under normal conditions; with earlier sowing a larger proportion responds; a January sowing under glass followed by planting out excites a still greater number; and only a small proportion can resist the drastic treatment of a December sowing. Those that do resist give rise to succeeding generations of seed that equally resist the weak stimulus of sowing in the open ground and the drastic stimulus of sowing under glass and planting out".

The present methods of raising swede seed include a generation for the purpose of multiplying up the 'élite' stock. The seed is sown in the South of England immediately after harvesting, and the plants establish themselves before winter, running to seed in the following summer without having formed large bulbs. Thus a whole year of cultivation is saved, and consequently the cost of production is lowered. To submit swedes to the drastic treatment devised by BATESON, might be successful, but would interfere with this economic practice. For districts in which bolting seriously affects the growing of swede/

swede, it might be desirable to attempt to produce non-bolting strains by this method if the extra price for the seed was justified.

DISCUSSION/

DISCUSSION - ORIGIN OF THE BULBLESS BOLTER.

There are several ways in which the bulbless bolter may originate:-

(1) Hybridisation of swede by a bulbless form of more or less annual habit.

(2) Admixed seed.

(3) Cytological abnormality.

(4) "Reversion".

(5) Chance combination of segregating factors.

The first two propositions are theoretically possible and seem to afford a sufficient explanation. LAFFERTY (1929) found both true-breeding and hybrid types of bulbless bolters in commercial crops, and the hybrid types behaved as though swede was one of the parents, for when he selfed one of the bolters he obtained two yellow-fleshed plants in a population of 31. The present writer obtained a similar segregation in the progeny of a natural hybrid between swede and true-breeding bulbless bolter. Within LAFFERTY'S population of 31 plants the bulb formation was mainly intermediate, but he distinguished two bulbed plants with flesh of swede consistency and two bulbless specimens of rape type. The present writer working with a population of 300 plants, grown under field conditions, tested each plant by cutting/

cutting the bulb and found none in which the flesh was as soft as swede. There were no symmetric bulbs and it was impossible to distinguish any truly bulbless roots. It should be noted that the plants examined by LAFFERTY were grown in pots and under such conditions bulb shape is liable to great modification.

Bulbless bolters have been observed by the writer in at least six different varieties of swede obtained from different seedsmen; the contamination of seed must therefore occur repeatedly in some ordinary agricultural operation, and 'rogue' plants must be of fairly frequent occurrence. Winter-rape certainly meets these requirements. The sample of winter-rape examined by the writer was more biennial in habit than the bulbless bolters, but LUND and KJAERSKOU (1886) found a wide and overlapping range of types in the winter- and summer-swede-like rapes.

Seed of another species may be introduced into a sample either by admixture in the threshing mill, uncleaned bags etc., or by harvesting rogue plants along with the crop. Hybrid seed might be borne on the rogue plant, but more probably on the crop plant, and in the latter case the pollen could be derived from rogue plants within the crop, or from single plants or even crops flowering in the vicinity. An experiment by the writer showed that natural/

natural crossing does occur reciprocally between swede and bulbless bolter. In the case of these Brassicae the pollen is chiefly insect carried. When "stock" seed is multiplied, the seed is sown in September and the swede plants are forced to run to seed without much bulb formation, and it is consequently difficult to distinguish, except by flower colour, any rogues which may have arisen from seed that has lain dormant in the soil. LUND and KJAERSKOU (1886) found that, when sown in the autumn, the swede, winter- and summer-like-rape all flowered at the same time early in the following summer. LAFFERTY, however, found that the bulbless bolter flowered earlier than the swede under these conditions.

Mutation, or other cytological abnormality in the swede is unlikely to account for the frequent occurrence of the true breeding bulbless bolter form; and recombination of segregating factors would not explain the dihybrid dominant white flesh colour. There is, therefore, no evidence to support the old belief in 'reversion' which is firmly held by seed-growers and which is a theory notoriously difficult to disprove.

SUTTON (1908) made reciprocal crosses between swede and Ragged Jack Kale, and attempted to explain/

explain the segregation in bulb formation as a simple mendelian ratio of 3 bulbed to 1 bulbless. The segregation obtained from the hybrid bulbless bolter was indefinite, with different degrees of bulb development. Since the parent "bulbless bolter" like winter swede-rape, had a thick root, it was difficult to determine whether segregates were slightly swollen or completely bulbless.

PEASE (1927) found that the difference between 'bulbed' Kohl rabi and 'bulbless' forms of B. oleracea involved the actions of three factors.

II.

THE STUDY OF COLOUR IN SWEDES.

The superficial layers of the above ground parts of the bulb, neck and shaw of the swede are coloured by chlorophyll, while anthocyanin is generally also present. The interior tissues of the bulb are coloured by plastids, yellow or white, and the flower colour, lemon or buff, is also due to plastids.

The variation and modification of the anthocyanin pigmentation is considerable; and the present observations were made on samples of commercial varieties and self-fertilised lines bred from them, mainly as a guide to the homozygosity of the material.

The terms 'skin' and 'flesh' are employed in this paper to denote superficial layers and internal tissues respectively. These characters are discussed, and tests made for linkage.

A. COLOUR OF THE SKIN.

(a) Chlorophyll. Chlorophyll is present in the 'skin' of the bulb and in the neck of all the commonly grown forms of swedes; though it may be partially or completedly masked by purple pigment or by a 'scurf' composed of brownish flecks or flakes on the surface. The green colour, when exposed, is uniformly intense. In the turnip this character is caused by a dominant mendelian factor, in absence of which the top of the bulb is devoid of chlorophyll, or exhibits it in nuances (KAJANUS 1913). A similar lack of chlorophyll in certain varieties of swede, both white- and yellow-fleshed, was described by VILMORIN-ANDRIEUX, (1891).

(b) Anthocyanin pigment. The skin and neck of the swede may be coloured with anthocyanin pigment, which, when freed from the scurf and waxy 'bloom' overlying it, and from the green of the chlorophyll beneath, is vinous mauve of various intensity (i.e. No. 184 in the 'Repertoire de couleurs' of the Société francaise des Chrysanthèmistes).

KAJANUS (1913) divided the anthocyanin skin colours, by simultaneous observation of neck and 'top'/

'top' into three classes:-

Red, having mainly red top and red neck.

Red-green, having red and green top and generally green neck.

Green, having green top and green neck.

This classification corresponds with the commercial grouping into 'purple-top', 'bronze-top' and 'green-top'. At first KAJANUS attributed these characters to the action of two factors P_1 and P_2; P_2 producing strong red-violet, dominant to P_1; and P_1 giving light red-violet. In absence of both factors the plants were green. These factors are still quoted by MALINOWSKI (1929) and ONSLOW (1925) but in his 1913 paper, KAJANUS abandoned factor P_1 because the segregations into red-green and green were indefinite and very irregular. He suggested instead that the recessive state of p_2 might be green or red-green, being a 'labile' modification, in contradistinction to the stable 'red' character governed by P_2.

In hybridisations, KAJANUS' 'red' segregate groups were in most cases in excess of the 75% expectation; and it is important to note that in one F2 population, from a green x red cross, a segregation of 15% red; 84% red-green; 1% green, was obtained. This seems to indicate that factor P_2 had been absent in the F_1 plant, and that brightly coloured/

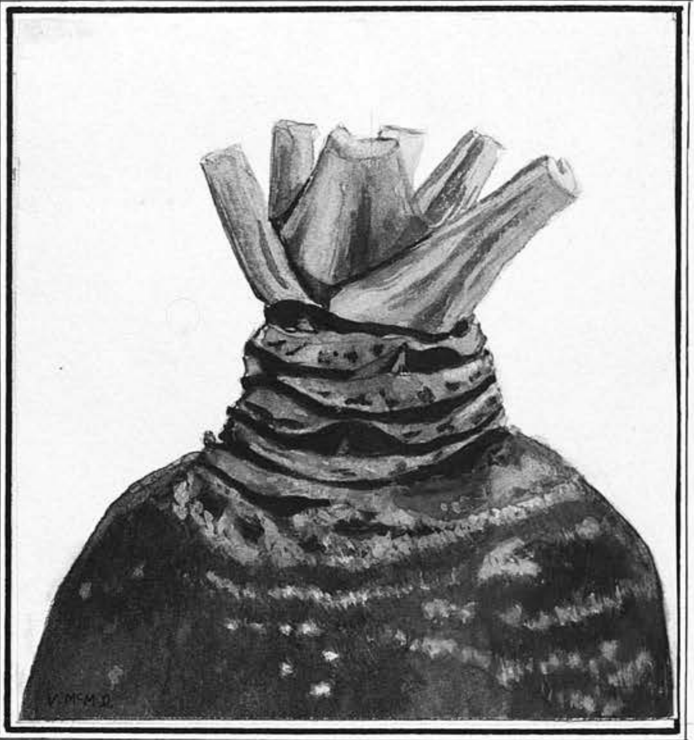

Fig. 4. Purple-necked Swede. ("Monarch")

To illustrate characters governed by the dominant factor N_1.

1. Uniform anthocyanin pigmentation of the internodes between leaf scars of the neck.
2. Pigmentation of the superficial layers of the bulb.
3. Pigment extending into the petioles in streaks.

coloured recessives were being scored as 'red'.

The writer has slightly modified the class definitions as follows:-

Purple-neck. (Fig. 4). A type in which the internodes, between the leaf-scars on the neck, are uniformly coloured with anthocyanin. Normally the pigment extends over the greater part of the surface of the 'top' (i.e. the above-ground portions of the bulb), though this is not essential. In general this class contains all the purple-top types, but excludes purple skinned plants with green on the neck.

Bronze-top. (Fig. 5). The skin is mottled with anthocyanin pigment, while the neck is green or green and mauve, but never entirely purple. The intensity of pigmentation is of no consequence.

?

cf p57 (8)

Green-top. The neck and top are normally green but capable of developing faint pigmentation in certain environments. The buds in the neck region are frequently red.

The difference between bronze and green is apparent in line breeding, but when scoring segregations no satisfactory distinction has been found. By scoring purple-neck versus non-purple-neck, an apparently discontinuous variation is obtained. A single mendelian allelomorph governing the neck colour difference and closely approximating P_2 in its/

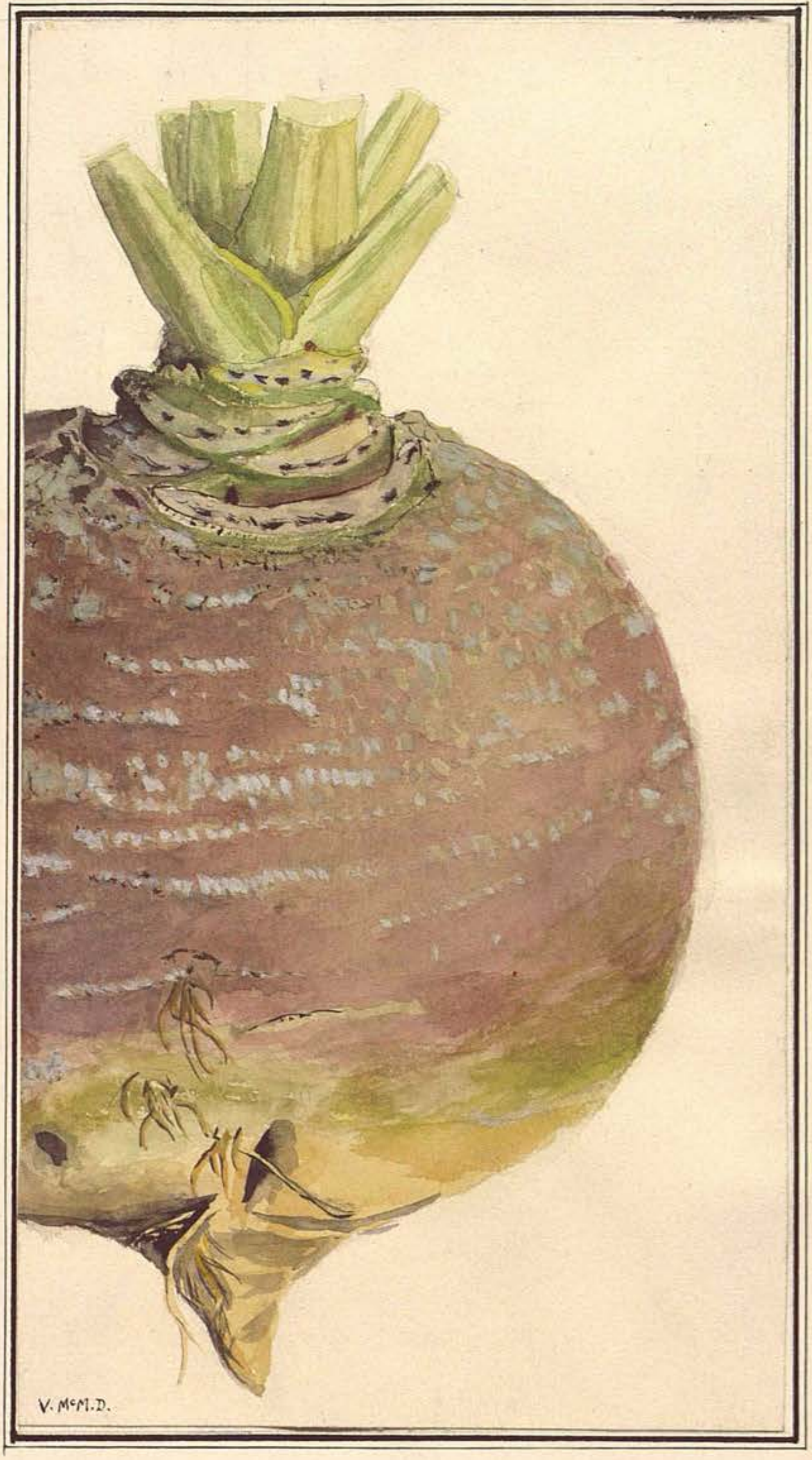

Fig. 5. Bronze-top Swede.
Characters appearing in absence of factor N_1.

1. Green and purple on internodes of the neck.
2. Green and light purple on 'skin' of the bulb.
3. White spots, which become green when wet.
4. No anthocyanin pigment in the petioles.
5. Red buds.

its action may be defined. Because of the different definition, however, it will here be named N_1. Some examples of scoring this character may be quoted.

Segregation in Best-of-all. "Best-of-all" is a purple-necked variety in which a band of green at the ground level is used as a point of selection. This character is most pronounced in the heterozygous N_1n_1 condition. A previous worker at the plant Breeding Station, selected a number of heterozygotes of this nature from a "Best-of-all" segregation, and mass-multiplied them in isolation. A large sample of seed was obtained and plots were sown out and observed by the writer in four different years. The results are given in table 7.

TABLE VII.

SEGREGATION IN BEST-OF-ALL.

	Purple neck	Non-purple neck	Total
Observed	4714	1552	6266
Expected at 3:1	4699.5	1566.5	
	+ 14.5	- 14.5	
x^2/m	0.031	0.093	0.124

Degrees of freedom 1. P between .80 and .70.

The segregation is tested for goodness of fit/

TABLE VIII.

CROSS "B". GREEN x PURPLE-NECK SWEDE.

♀ Pl. Green-top, L_1 generation, bred true.

♂ P_1. Purple-neck, L_1, bred true for neck colour.

F_1. Purple-neck, purple or purple and green skin.

5 F_1 plants selected and self-fertilised

F2 PROGENIES.

NAME	OBSERVATION		TOTAL	EXPECTATION	
	Purple	Non-purple		Purple	Non-purple
Ba	271	68	339	254.3	84.8
Bb	289	84	373	279.8	93.3
Bc	290	93	383	287.3	95.8
Bd	193	70	263	197.3	65.8
Be	212	58	270	202.5	67.5
Total	1255	373	1628	1221.0	407.0
x	+ 34	- 34			
x^2/m	0.947	2.841	3.788		

Degrees of freedom, 1.

P, lies between .10 and .05

The divergence is therefore not significant.

TABLE IX.

CROSS "C". GREEN X PURPLE-NECK..

♀ P_1 Green-top, L_1 generation, bred true.

♂ P_1 Purple-neck, L_1, bred true for neck colour.

F_1 All purple-neck, dark purple skin.

3 F_1 plants selected and self-fertilised.

F2 PROGENIES.

NAME	OBSERVATION			EXPECTATION	
	Purple	Non-purple	TOTAL	Purple	Non-purple
Ca	100	33	133	99.8	33.3
Cb	26	8	34	25.5	8.5
Cc	186	61	247	185.3	61.8
Total	312	102	414	310.5	103.5
x	+ 1.5	- 1.5			
x^2/m	0.007	0.022	0.029		

Degrees of freedom 1.

P, lies between .90 and .80

The fit is therefore good.

TABLE X.

CROSS "E" PURPLE-NECK X GREEN-TOP.

♀ P1 Purple-neck, L1, breeding unknown.

♂ P1 Green-top, L1 generation, true breeding.

F1. All purple-neck, purple and green skin.

4 F1 plants selected and self-fertilised.

F2 PROGENIES.

NAME	OBSERVATION Purple	OBSERVATION Non-purple	TOTAL	EXPECTATION Purple	EXPECTATION Non-purple
Ea	245	87	332	249	83
Eb	168	53	221	165.8	55.3
Ec	485	143	628	471	157
Ed	522	179	701	525.8	175.3
Total	1420	462	1882	1411.5	470.5
x	+ 8.5	- 8.5			
x^2/m	0.020	0.651	0.671		

Degrees of freedom 1.

P. lies between .80 and .70

The fit is therefore good.

fit by a method given by FISHER (1925) in which a value χ^2 is obtained from the formula Sx^2/m, (where x is the deviation between observation and expectation, and m is the number of individuals in the expected class). From FISHER'S table of χ^2 a probability, P, that deviations will exceed the observed divergence by chance in a certain proportion of times is obtained. In the Best-of-all segregation, P was high, and there was, therefore, no significant divergence.

Data of segregations from Green-top x Purple-neck crosses are given in tables 8,9, and 10, and it will be seen that the divergences were not[*] significant.(Probabilities of .05 or under being taken as significant). It may be added that all the selections having purple necks, so far bred, gave progenies with all or most of the necks purple. It may therefore be concluded that the purple-neck character denotes the presence of an important skin colour factor N_1, the effect of which extends over the bulb, and, as will be shown later, into the region of the shaw.

In the green-top x purple-neck crosses there were indications of the presence of other factors governing skin colour, and it is suggested that N_1 is only one factor of a series.

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[*] This was not always found in selfed progenies of heterozygous plants. cf. pp. 55 and 57.

A second factor governing purple-neck. It is suggested that a second factor, analogous in effect to N_1 has been found in a white-fleshed strain of swede. The evidence for this is at present confined to one F_2 segregation; other material being not yet available. A hybridisation between two purple-neck swedes was made in 1927, and instead of a uniform purple-top F_2, a segregation of 15 purple-neck: 1 non-purple was obtained.

It is considered that both parent plants were homozygous for purple neck colour. The female parent was of a yellow-fleshed strain (YF) and the 'skin' colour in this case was probably due to factor N_1. The male parent (WFa), was white fleshed.

The evidence is as follows:-

(1) The yellow-fleshed parent, YF, belonged to a purple-necked variety, and when selfed gave a progeny of 128 plants all purple-necked.

(2) When plant YF was crossed with another yellow-fleshed purple variety, 'Stirling Castle', an F_2 generation of 105 plants all purple-necked was obtained, indicating that the factor involved was the same as that of other yellow-fleshed varieties.

(3) The male parent, WFa, was a member of an L_1 strain out of a white-fleshed purple-neck variety. Its/

Its own generation of 142 plants was all purple-necked and when self-fertilised it gave a progeny of 54 plants, all purple. The variety is characterised by very deep shaw pigmentation, the veins and midrib being bright red purple, and the foliage somewhat resembling red cabbage; the connection between this and the neck colour has not yet been traced.

The F_1 generation consisted of 36 plants, all having purple necks and purple skin shading into green at the ground level. The F_1 plant from which the F_2 was obtained by self-fertilisation, was forced by sowing the seed in September under glass. It will be noted that, since purple is dominant, faulty isolation could not explain the presence of non-purple segregates.

167 F_2 plants were grown from the seed of this plant, and there were 8 non-purple plants. The segregation was as follows:-

TABLE XI.

F_2 of PURPLE-TOP x PURPLE-TOP

Neck	Purple		Non-purple	
Flesh	White	Yellow	white	yellow
Obtained	152	7	7	1
Expectation 225:15:15:1	146.8	9.8	9.7	0.7

The/

The presence of non-purple, white-fleshed bulbs, a very uncommon type, excludes the possibility of ground-keeper seed.

It is therefore suggested that the factors governing the neck colour of this white-fleshed variety are different from those of the yellow-fleshed strains. The "red" or purple-top varieties used by KAJANUS were all yellow-fleshed sorts, his white flesh variety having green skin. So that if the letter N_2 be used to denote the factor producing purple neck and skin in the white fleshed variety, the following factorial representation may be made:-

Fig. 6. Dihybrid skin colour segregation

P1 Yellow-flesh type $N_1N_1n_2n_2$ (purple) —— X —— White-flesh type. $n_1n_1N_2N_2$ (purple)

F_1 $N_1n_1N_2n_2$ (purple)

F_2 9 N_1N_2 (purple) 3 N_1n_2 (purple) 3 n_1N_2 (purple) 1 n_1n_2 (Non-purple)

It was observed that the white-fleshed variety had a more intensely pigmented neck than the yellow-flesh strain, and in the F_2, most of the necks were dark, though some were lighter. The difference was/

was not sufficiently distinct to score accurately.

Minor variation in skin and neck colour in swede. Observations have been made on varieties and strains to distinguish between the effects of heredity and environment.

Purple-neck types. There are several hereditary variations in skin and neck colour in purple-necked strains; so far as has been observed the anthocyanin seems to be of one colour, but differs in concentration, while the green of the chlorophyll and the brown of the scurf alter the general appearance.

(1) Light red neck. This is associated with a clear, lightly pigmented skin lacking in scurf, and is found in soft fleshed, early maturing varieties.

> Examples:- In a 1/10th acre plot of "Paragon" commercial variety a large proportion (85%) of the plants were of this type. A selection in which the character had been noted, was selfed and the progeny, PGa, bred true for neck colour in about 500 plants. The type is also found in "Best of All" and lines from a selection out of this variety bred true for light red neck in/

in the L_2 and L_3 generations.

(2) Dark red-purple neck. A neck type of more intense colouring than normal characterises certain varieties. Most of these are main-crop types and are more or less covered with scurf, and it is noticeable that the shaw pigment is strongly developed, a character that is bred for by seedgrowers.

Examples:- Plants of the white-fleshed variety already referred to have necks of this type and breed true for this character, two lines having been carried to the L_2 generation. "Monarch" and "Bangholm" are varieties having this neck colour combined with strong pigment in the petioles, while "Stirling Castle" and "Mervue" have a similar neck colour though not so much pigment in the shaw. Selfed strains from all these varieties have been examined for three generations and the dark neck colour character was seen to be inherited. Observations suggest that the intensification of pigment in the neck, shaw and bulb regions may to some extent be attributed to the same factor or factors.

(3)/

(3) Clear lightly pigmented skin. This is characteristic of soft-fleshed, early maturing varieties. The neck pigment is light or medium in intensity, and scurf is almost absent, or confined to patches.

Examples:- "Superlative", "Magnificent" and "Picton" varieties are uniform and true-breeding for this character. Lines selected from "Superlative" have been bred for four generations and a line from "Magnificent" for three generations. The type is also common in "Paragon" which has already been mentioned for its neck colour, and in the new variety "Corstorphine". Self-fertilised lines have been raised from all these varieties, and have bred true for this type of skin colour. It was noted that a type of bronze-top segregation which occurred in these varieties, is highly pigmented, and that at the end of the summer bulbs of this kind may become as brightly coloured as the main purple-top type; their necks, however, remaining green. Selections of these proved to be homozygous bronze-tops.

(4) Darker skin colours. From second-early to late maturity types, the appearance of the skin is/

is progressively more strongly pigmented, while the amount of scurf also increases.

Example:- "Best of All", "Springwood" and "Magnum Bonum" may be quoted as varieties in which the main type of skin colour is slightly more intense than that of the "Superlative" group. There is however a considerable variability and range of types especially in "Best of All" strains from different sources.

"Champion" and "Extra Improved" are distinctly darker purple than the "Superlative" group, and six lines selected out of these varieties proved to be breeding true for the character.

"Aberdeenshire Prize" is a late variety in which the skin of the bulb is almost completely covered with scurf, but where exposed it is dark purple. 13 plants of this description were selected from a sample of this variety and eight were found to be homozygous for the character (2008 plants). The other five selections, however, were heterozygotes, and their progenies segregated as follows:-

Observed	1256	purple neck and skin	339 bronze
Expectation	1197	" " " "	399 bronze

It will be noted that there was a deficiency in/

in the bronze-top class.

(5) The presence of a green band at the ground level. Green may be seen at the base of the bulb in most purple-neck varieties, but in some samples it is absent.

Examples:- A sample of "Champion" was found to be without green at the ground level and a line of that type has been bred to the L_3 generation without showing green. In "Best of All" the band is wide, and since this character is used for selection by seedsmen it is probable that heterozygous plants, which commonly have a broad green band, are frequently included, because proportions of bronze-top segregates are high in "Best of All" varying from 0.1 to 5% in 8 commercial strains. (see also TABLE VII) Nevertheless, a type of homozygous purple-top plant may exhibit the broad band as a fluctuating modification; this was found in selections of "Warrington" and "Olsgaard".

(6) Green or Bronze skin with purple neck. In segregates from Purple x Green crosses pigment may be almost absent from the skin of the bulb. Three such plants were self-fertilised, and the progeny of one (Bba, containing 315 plants) had purple necks/

necks, while the other two segregated1·8 purple neck 1 non-purple (144 purple, 80 non-purple necks).

(7) <u>Brown skin.</u> The chlorophyll sometimes shows through the pigment, giving a somewhat brown effect. This was found to be the case in F_1 hybrids between light red-purple-top x green-top and light red purple-top x bronze-top.

(8) <u>Differences of intensity in Bronze-tops.</u> Although the differences in skin colour in bronze-tops are mainly due to modification, there is also hereditary variation.

> Examples:- Light bronze strains have been selected out of "Darlington" and "XL-All" which are varieties showing considerable ranges of skin colour. In "Darlington", the strains, which have been selfed for two generations, and also mass-multiplied, have bred true to a light bronze colour, distinct from the main varietal type. In "XL-All" a light bronze segregate frequently occurs, and one such plant was selected, along with a darker type from the same sample, and pedigree lines have been bred from each for four generations. Though both were greatly modified in different seasons, the colour difference was, towards the end of the summer, always distinct/

distinct. The earlier notes on these are taken from records. An F_1 hybrid between plants of the L_3 generations was intermediate in intensity of pigment.

(9) Neck colour in Bronze-top swedes. As in the case of the skin, the colour of the neck in bronze-top swedes is subject to great modification; but there are also hereditary differences. In some strains the neck is entirely green, or with very little anthocyanin pigment on restricted areas. This is not only the case in light skin types such as the selections out of "Darlington" and "XL-All" referred to in the last paragraph, but also in a type of dark-bronze-top segregate which occurs in purple-top varieties of the soft-fleshed early-maturing and clear light-red skin type. Self-fertilised bronze-tops out of "Paragon" and "Corstorphine" yielded progenies in which the dark bronze skin colour was combined with the almost green neck.

A very dark neck type occasionally occurs, in which the neck is almost surrounded by purple pigment but is green on the north side. A plant of this type was selected out of "Keepwell" and its selfed progeny bred true for a neck type of the same/

same description. At a distance they appeared to be purple-tops, but upon examination each neck was seen to have a small area of green.

It is difficult to define any commercial varieties of bronze-tops as having green or green and mauve necks because of the great environmental modification.

MODIFICATIONS IN SKIN AND NECK COLOUR.

(1) The green band in purple-neck types. The band of green at the ground level fluctuates in width. In most strains it is restricted to the shaded part under the curve of the bulb, and may be absent altogether. Two plants of "Knockdon" were selected, one as having the broadest green band and the other as having the least. Plots of the selfed progenies were grown side by side, and while there were only traces of green to be seen in the second type, there was no green at all in the strain out of the green-banded plant. There was therefore no hereditary variation in this respect.

(2) Colour in the underground skin. The underground surfaces of the bulb are normally without green or purple colouring. If, however, a purple-neck or bronze-top bulb is pulled and left exposed, anthocyanin pigment develops, but chlorophyll does not.

(3) Asymmetric development of pigment in the bronze-top swede. In the bronze-top swede the skin is mottled green and light vinous mauve, in splashes and horizontal streaks, usually with small spots/

spots of green in the purple areas. The intensity of the purple increases during the season and is subject to modification from year to year. The purple pigmentation becomes distinctly more intense on the southern aspect, especially when the drills are orientated East and West. While this is typical for most varieties, in some the effect of insolation is still more noticeable, for outside bulbs, unshaded by surrounding foliage, develop highly pigmented skins. (Examples "Holborn Invicta" and "Bell's Improved Bronze-top").

The pigment on the neck of the bronze-top bulb is more pronounced on the south side, and may be entirely absent from the North side.

(4) <u>Callus growths</u>. The bulb of the swede is very liable to split, with subsequent callus formation. In the purple-top the callus is as highly pigmented as the undamaged skin, but in the bronze-top it is more intensely pigmented, while in the green-top it is frequently tinted light purple. Nodules of Finger-and-toe disease (Plasmodiophora Brassica Wor.) are also frequently pigmented in green-top strains.

(5)/

(5) Green-tops. All the green-top varieties so far examined have exhibited very faint anthocyanin pigmentation, and reddish buds, at various times during the four years under observation. Thus the distinction between bronze- and green-tops, is merely one of degree. The material examined consisted of "Kinaldie", "Teviotdale" and three other green-top varieties.

(B) FLESH COLOUR IN SWEDE.

The colour of the flesh in swede is either white or yellow, the latter being the more commonly cultivated. KAJANUS (1913) hybridised the two types and found from the F_1 that white was dominant, a result which he had already observed in turnip. When his material was further bred by HALLQVIST (1916) it was found that, unlike turnip, there were two factors in swede, each causing white flesh, in the absence of both of which the flesh was yellow. The present writer has observed the breeding of the white-flesh character, in swedes from two sources.

(1) A white-fleshed, but otherwise typical plant in a commercial yellow-fleshed variety.

(2) An artificial hybridisation between plants of white- and yellow-fleshed varieties.

(1) A White-fleshed segregate. A white-fleshed plant, denoted as "PW" was found in a purple-necked, yellow-fleshed swede variety. Except for the flesh colour, the plant displayed the characters of its variety, including short neck, light purple skin, tankard shape, soft flesh and small shaw. When the plant was self-fertilised, the offspring segregated only in flesh colour. Crosses were also made with various types of swede and turnip, and the results/

TABLE XII.

BEHAVIOUR of PLANT PW in BREEDING.

Breeding	White	Yellow	Total.
Selfed progeny	104	24	128
expectation 3:1	96	32	
x yellow-fleshed swede	28	23	51
expectation at 1:1	25.5	25.5	
x white-fleshed swede	91	-	91
expectation all white	91	-	
x yellow-fleshed turnip	40	18	58
x " " "	12	11	23
	52	29	81
expectation at 1:1	40.5	40.5	
x white-fleshed turnip	63	-	63
expectation all white	63	-	

results are given in table 12.

It will be seen that the selfed progeny segregated in a ratio of 4.3 white to 1 yellow. Fitting these figures to a 3:1 expectation by the method given by FISHER (1925, p.82) a value of $\chi^2 = S(x^2/m)$ =2.67. is obtained, which is equivalent to a probability (P = .10) that the divergence is exceeded by chance once in ten times, which is not significant.

In the cross between "PW" and the recessive yellow-fleshed swede, a ratio of 1.2 white to 1 yellow was obtained and when this is fitted to a back-cross ratio of 1:1, the value of χ^2 is 0.47 and P =.50, so that there is no significant divergence here. When crossed with white-fleshed swede of a true-breeding strain, and also with white turnip, the progeny was in each case all white-fleshed. Two crosses were made with yellow-fleshed turnip, for which a 1:1 back-cross ratio might be expected. This was obtained in one progeny but in others there were 40 white and only 18 yellow, a highly significant divergence. The cause of this is not apparent and since it raises the question of interspecific relationships, is outside the scope of the present section.

From its behaviour in self-fertilisation and crossing with swedes, it would appear that the plant "PW" was heterozygous for a single factor giving/

giving white flesh. There was, however, a shortage of yellow segregates in each constituent, and especially in the cross with yellow-fleshed turnip.

(2) <u>White x Yellow-fleshed swede, Hybridisation "G"</u>

A second set of observations was made on the descendants of an artificial cross between plants of white- and yellow-fleshed varieties; the material being taken over by the writer at the F_1 stage.

The parent plants were grown in 1924-25.

♀ Pl. White-fleshed swede of commercial generation (denoted by letters WF).

♂ Pl. Yellow-fleshed swede of L_1 generation (SCe)

The F_1 hybrid generation was grown in 1926-7

F_1 described as "G". 17 plants all white-fleshed.

In 1927 seed samples were raised from the following:-

1. 12 plants mass-multiplied. F_2 named G(mx).
2. 1 plant self-fertilised. F_2 " Ga.
3. 1 " " " F_2 " Gb.
4. F_1 x yellow-fleshed swede. Back-cross GxSC
5. Yellow-fleshed swede x F_1 " " SCxG
6. F_1 x white-fleshed swede. " " GxWF
7. White-fleshed swede x F_1 " " WFxG

TABLE 13/

TABLE XIII.

SEGREGATION in FLESH COLOUR in CROSS "G".

Name	Observation			Expectation	
	White	Yellow	Total	White	Yellow
1. G(mx)	4042	280	4322	4052	270
2. Ga	67	4	71	66.6	4.4
3. Gb	50	3	53	49.7	3.3
Total	4159	287	4446	4168.1	277.9
4. G x SC	91	24	115	86.4	28.8
5. SC x G	34	12	46	34.5	11.5
	125	36	161	120.8	40.3
6. G x WF	107	-	107	all white	
7. WF x G	50	-	50	" "	

It will be seen from TABLE XIII that the F_2 segregations closely fit a 15:1 ratio; the value of χ^2 for the total observations being 0.32, and the probability lying between .70 and .50. When the F_1 was crossed with the recessive yellow-fleshed parent type, a dihybrid back-cross ratio of 3 white to 1 yellow was to be expected; and this was obtained, the value of χ^2 being 0.61, and P lying between .50 and .30, so that there was no significant divergence.

It may be concluded, therefore, that the white-fleshed parent was homozygous for the two factors M_1 and M_2, both of which were absent in the yellow-fleshed strain. When either factor was present the flesh was white. Besides confirming HALLQVIST'S observation, the figures show that there was no significant divergence from the expected ratios, and consequently that there was no linkage between the factors.

(C) RELATIONSHIPS BETWEEN FLESH AND NECK COLOURS.

The only available data by which neck and flesh colours may be tested for linkage are those for cross "G" already described for flesh colour.

Unfortunately, however, although segregation occurred in the F_2 populations, doubt exists as to the skin colour of the parents, which were not seen/

seen by the writer.

The white-fleshed parent was a commercial plant known to have been purple, but untested as to homozygosity. The male parent was an L_1 plant from a purple-necked, yellow-fleshed strain, and it was recorded as a purple-top. It is known, however, that the strain in which it occurred was segregating in skin colour, and the plant itself was not tested by selfing. The circumstantial evidence suggests that both parents were homozygous for skin colour, and that the yellow-fleshed pollen parent was a bronze-top; because the 17 F_1 plants were quite uniform in skin colour, each having a dark purple neck and the characteristic heterozygous skin colour, viz. purple on the shoulder fading into a broad green band at ground level. Had both parents been heterozygotes, the probability is slight that the F_1 would have been uniform, and that the mass-multiplied F_2 derived from 12 of these plants, should have given a segregation without excess of dominants.

It has already been recorded (page 49)that the purple neck colour in the white-fleshed strain is probably due to a different factor (N_2) from that found in the yellow-fleshed swedes (N_1), and since the female white-fleshed parent was purple-necked (a single selfed plant homozygous for purple, having been/

been bred from it) a test for linkage with flesh colour would refer to the neck and skin colour factor "N_2".

The segregation of neck colour in the mass-multiplied F_2 was as follows:-

Observed	Purple 2637;	non-purple 1008;	= 3645
Expectation	" 2773;	" 911.	

There was, therefore, an excess of 2.6% non-purple-tops and the divergence is significant ($\chi^2 = 16.66$:P = less than 0.01). The reason for this is not apparent. There were no bronze- or green-tops among the F_1 plants of this multiplication, and natural isolation was good. The purple-top seedlings may have been less vigorous at singling time, and consequently have been eliminated disproportionally.

In TABLE XIV as a test for linkage with white-flesh factors, the segregations are fitted to the ratio 45:15:3:1.

TABLE XIV/

TABLE XIV.

SKIN and FLESH COLOUR SEGREGATIONS IN F_2.

Skin Flesh	Purple white	non-P. white	Purple yellow	Non-P yellow	Total
G(mx)					
Observed	2457	941	180	67	3645
Expected	2563	854	171	57	-
deviation	-106	+87	+9	+10	
Ga					
Observed	53	14	3	1	71
Expected	50	16.6	3.3	1.1	
deviation	+3	-2.6	-0.3	-0.1	
Gb					
Observed	39	11	2	1	53
Expected	36.9	12.8	2.5	0.8	
deviation	+2.1	-1.8	-0.5	-0.2	

The two F_2 segregates from single plants i.e. "Ga" and "Gb", fit the expected ratio fairly closely. In "Ga" the value of χ^2 is 4.26, and the probability between .30 and .20, which is not significant for a divergence. In the population "Gb", χ^2 is 2.68, and P. lies between .50 and .30 which again is not significant.

As tested in TABLE XIV, the segregation of the mass-multiplied F_2 "G(mx)" shows a highly significant divergence, but this has already been traced to an excess of bronze-tops. To eliminate this cause and to examine the results for any other divergence or linkage, the data may be treated by a method given by FISHER (1925, p. 82). The totals of purple and non-purple-tops are taken and each class divided into the ratio 15:1. (See TABLE XV)

TABLE XV.

GOODNESS OF FIT IN G(mx) SEGREGATION.

	Purple		Bronze or Green		
	White	Yellow	White	Yellow	χ^2
Observed	2457	180	941	67	
Expected	2472.2	164.8	945	63	
x	- 15.2	+ 15.2	-4	+4	
x^2/m	0.934	1.400	0.017	0.254	2.605

Degrees of freedom 2 (See FISHER). P lies between .30 and .20.

There is, therefore, no significant divergence.

It/

It will be seen that, when the irregularity of the skin colour segregation has been eliminated, there is no significance in the remaining divergence.

It may be concluded, therefore, that in this material there is complete absence of linkage between the factor governing purple neck and skin colour, and either of the flesh colour factors. It has been shown that the neck and skin colour factor was probably N_2, the purple neck factor of the white-fleshed strain, but since doubt exists as to the skin colour constitution of the parents, the results need to be confirmed by observation on tested material which is being prepared.

(D) PIGMENT IN THE SHAW OF SWEDE DURING THE FIRST SEASON.

Anthocyanin pigmentation occurs in various parts of the swede shaw, the amount and distribution varying considerably in different strains. At one extreme there is complete absence of pigment, as in green-top types, while at the other there is a condition resembling that of red cabbage, found so far only in a white-fleshed strain. In this the pigment is present and intense in all parts of the shaw, colouring the veins and midrib purple, darkening the green/

green of the lamina and giving a crimson appearance to the young leaves of the main axis bud.

In most purple-top strains the anthocyanin is confined to splashes of colour at the base of the petiole and extending to some extent along the midrib. It is absent from the veins and lamina of the grown leaf, but present and frequently intense on the very young leaves. Sometimes, instead of splashes, the colour is more dilute, and evenly tints the petiole. In some strains a dot of colour occurs midway on an otherwise unpigmented midrib on the axial side, at the junction of some of the veins. A transitory condition also occurs, even in green-tops, on the flattened adaxial surface of the petiole, which during certain seasons, may become faintly tinted. The young leaves in the centre of the shaw, surrounding the main bud, also show a range of anthocyanin pigmentation, from complete absence in certain green-tops to dark crimson in some strains of purple-top.

There is great fluctuation in intensity and distribution of pigment even in pedigree L_3 lines, and so strong is the modification at different times of the season and in different years, that it would be difficult accurately to score the intensities. Towards the end of the first growing season, when shape and skin colour may best be scored, the pigment/

pigment has been partly bleached out of the petioles.

Pigmentation also occurs in the second year but the present observations refer entirely to the first season of growth.

The most obvious observation that may be made is that the shaw of bronze and green-top swedes is devoid of anthocyanin; and that bronze-top segregates in purple-neck crops may frequently be recognised by this character. This statement, however, requires qualification for the following reasons:-

1. The adaxial surface of the petiole may be faintly tinted in certain environments; and this is the case even in green-tops such as "Kinaldie". This condition is transitory and is possibly due to some physiological effect of translocation.

2. The young leaves in the centre, which are normally yellow-green, sometimes show a trace of pigment. This is common in bronze-tops, but may also occur in green-tops.

3. Occasionally bronze-top plants may have still splashes of pigment on the petioles. In the cases so far observed the areas pigmented have been small and the pigment faint; it is more probable that they are due to extreme modifications than to a genetical "cross-over".

Behaviour of shaw pigment in crosses. In

cross /

cross "G" which has already been discussed with regard to flesh and skin colours, some notes were also taken on the segregation of shaw pigment. The white-fleshed purple-top female parent had the 'red cabbage' colour of shaw already described; the male parent strain was segregating into purple-neck and bronze-top types. The purple-tops of this variety have lightly pigmented shaws, while the bronze-tops are unpigmented, but might contain some of the factors necessary for anthocyanin production.

The 17 F_1 plants were uniformly pigmented, more strongly than any of the common swede strains, but not as brightly as the white-fleshed parent. The F_2 generations from two selfed F_1 plants were examined in order to determine whether definite segregation could be obtained. The range of types of pigmentation was wide and indefinite. Four classes were made but the plants scored as 'pigmented' varied greatly, some approaching the deep pigment of the white Pl fleshed strain, and others having localised areas of pigment on the petioles.

POPULATION/

	POPULATION	
	Ga.	Gb.
Like deeply pigmented Pl	1	3
Pigmented,	19	17
Tinged with pigment,	10	19
unpigmented,	23	32

By scoring purple- and non-purple-top characters in conjunction with presence or absence of pigment in the shaw, the following segregations were obtained (TABLE XVI)

TABLE XVI.

SEGREGATION OF SKIN AND PETIOLE PIGMENT IN F_2 POPULATIONS.

SKIN	PURPLE		BRONZE or GREEN		TOTAL
PETIOLE	pigmented	unpigmented	pigmented	unpigmented	
Ga.					
Observed	29	12	1	11	53
Expected at 9:3:4	29.8	10	-	13.2	
Gb					
Observed	38	18	1	14	71
Expected at 9:3:4	39.9	13.3	-	17.7	

With/

With the exception of one plant in each constituent, the non-purple segregates were unpigmented. Some of the purple-top segregates were also unpigmented; and the proportions in which the types occur will be seen to conform roughly to a 9:3:4 ratio. Testing by FISHER'S (1925) table of χ^2 it was found that in the population "Ga" the value of χ^2 was 0.789, and the probability lay between .90 and .80 while in "Gb", X^2 was 2.525, with a probability between .50 and .30. Thus there was no significance in the divergences apart from the two pigmented shaws in non-purple-top plants. It is therefore, suggested that the production of pigment in the shaw is primarily dependent on two factors.

1. The neck colour factor, in the absence of which there is little or no pigment in the shaw, and in the presence of which pigment may occur if an e~~x~~tension factor (or factors) is present.
2. A factor extending the anthocyanin into the petioles, and acting in the presence of the purple neck factor.

It is not proposed to stress the appearance of pigment in the shaws of non-purple-top plants, because in all the cases observed, this colouring has been slightly in amount. If fully pigmented shaws/

shaws occurred in plants with bronze- or green-skins a crossing over could be stipulated. As has been noted above, however, the anthocyanin in the bulb and neck does not act as a presence or absence character, and it may be inferred that the same is the case in the region of the shaw.

With regard to the hereditary factors governing the intensity of the shaw pigment, no conclusions can be drawn, except that the 'red cabbage' type of pigmentation breeds true under self-fertilisation and is distinctly different from the most strongly pigmented of the yellow-fleshed strains.

Observations were also made on the F_2 generations of green-top x purple-top swedes, already described in TABLES VIII and X. There are no records of the pigmentation in the shaws of the actual parents, but the characters of the parent strains are known. The green-top parent was recessive for the neck colour factor N_1 and possibly for other colour factors such as KAJANUS' rejected factor P_1, but the presence or absence of the extension factor postulated above, could not, of course, be determined. The purple-top parent was dark purple homozygous for the neck and skin factor N_1, In this strain the lower proximal part of the midrib, or the petiole, is strongly pigmented. Attempts were again made/

TABLE XVII.

SEGREGATION of NECK and PETIOLE PIGMENTS in F_2 POPULATIONS.

NECK	PURPLE		BRONZE or GREEN		TOTAL.
PETIOLE	pigmented	unpigmented	pigmented	unpigmented	
Cc.					
Observed	138	21	4	49	212
Expected at 9:3:4	119.3	39.8	-	53	
Ed.					
Observed	182	54	1	74	311
Expected at 9:3:4	174.9	58.3	-	77.8	
Ec. (1927)					
Observed	190	77	-	81	348
Expected at 9:3:4	195.8	65.3	-	87	
Ec. (1928)					
Observed	88	90	-	57	235
Expected at 9:3:4	132.6	44.2	-	58.8	

made to determine whether mendelian segregation occurs by the study of the progenies of single F_1 plants.

In TABLE XVII the presence or absence of pigment is recorded in the purple and non-purple-neck segregates. Each observation is compared with a 9:3:4 expectation.

In the F_2 population "Cc" there were four pigmented shaw, non-purple-neck plants, but apart from that the fit was bad. There was an excess of pigmented shaws, and this divergence was significant, since χ^2 = 12.11. In the population "Ed" the fit to the 9:3:4 ratio was good, χ^2 being 0.79 and the probability lying between 0.70 and .50.

Two samples of "Ec" were scored, the first, in 1927, gave a segregation that fitted the 9:3:4 expectation, χ^2 being 2.68 and P lying between .30 and .20, but when another plot of the same sample was examined in 1928, there were more unpigmented than pigmented shaw types among the purple-top segregates. The 9:3:4 ratio was completely upset. This may have been due to environmental modification, such as bleaching, at the time the plants were scored. The pigment is most distinct in the younger stages, before the skin colour can accurately be determined, and there are too many deaths in the plots to correlate scores of large populations made at different times/

times.

The results to some extent, confirm the hypothesis advanced for the "Ga" and "Gb" strains, viz. that the combined action of the purple neck factor and another factor extending the area of pigment into the region of the shaw, normally control the presence or absence of shaw pigment. Whether the neck colour factor was the same in both experiments, is a matter of uncertainty. (See page 67)

Colour in the young leaves.

The young leaves in the centre of the first year shaw exhibit a range of colours due to the presence of greenish-yellow chloroplasts and varying amounts of anthocyanin pigment. In total absence of anthocyanin, the colour is greenish-yellow, but with increasing amounts of pigment, the colours may be best compared with copper coins of different ages. Sometimes, however, the light copper and dark copper change to similar intensities of crimson in the same plants observed at different times of the year. The strongest grade of pigmentation is a very deep crimson, the colour of beetroot. Although comparative distinctions may be drawn between strains observed simultaneously, there is considerable fluctuation, even in pedigree lines. It will be seen therefore, that the conditions are too variable for the accurate scoring/

TABLE XVIII.

DISTRIBUTION of CENTRAL COLOUR in YOUNG LEAVES of F_2

Neck	Colour of young leaves	F_2 populations. Cc.	Ed.	Ec.
Purple	Dark copper	3.3%	3.9%	2.6%
"	Mid copper	8.5%	20.3%	11.1%
"	Light copper	13.2%	23.2%	25.5%
"	Orange	30.7%	26.4%	33.6%
"	No pigment	19.3%	2.3%	3.0%
Green	Orange	0.5%	3.9%	3.0%
"	No pigment	24.5%	20.3%	21.3%

TABLE XIX.

DATA FROM TABLE XVIII.

NECK	PURPLE		BRONZE or GREEN		TOTAL
CENTRE	pigmented	unpigmented	pigmented	unpigmented	
Cc. Observed	118	41	1	52	212
Expected at 9:3:4	119.3	39.8	-	53	
Ed. Observed	229	7	12	63	311
Expected at 3:1	233.3	-	-	77.8	
Ec. Observed	171	7	7	50	235
Expected at 3:1	176.3	-	-	58.8	

scoring of types (cf TABLE XVIII).

The darker colours are exhibited by purple-tops, while bronze-tops may be unpigmented or tinged with anthocyanin, and green-tops are normally yellow i.e. devoid of pigment. In certain seasons, however, traces of anthocyanin have been observed even in green-tops, so that this pigmentation is only a matter of degree.

The F_2 progenies of green- x purple-top crosses, already discussed in regard to petiole pigment, were also scored for central colouration. The green-top parent strain is normally devoid of pigment in the young leaves, while the purple-top parent strain is darkly pigmented.

In TABLE XVIII the segregations are grouped according to intensity of pigment in the young leaves. The classes were by no means distinct. It will be seen that there were large proportions of plants, grouped as 'orange', in which the young leaves were yellow with traces of dilute anthocyanin, the two blending to give a light orange colour. As this condition sometimes appears in green-top or bronze-top plants which have, at another time in the season, been classed as devoid of pigment, it would appear that the division into pigmented and non-pigmented is not a hereditary variation. It will be seen that in the populations Ed and Ec there were only 2 or 3 per/

per cent. of unpigmented purple necks and similar numbers of orange non-purple tops. In population Cc, however, there was a large group of unpigmented purple necks. In TABLE XIX the population is divided into pigmented and unpigmented and into purple and non-purple-neck.

It will be seen that, apart from a single pigmented bronze top, the population Cc fits a 9:3:4 ratio, $\chi^2 = 0.07$ and $P=.95$. Since the petiole colour of this population Cc had also been fitted to a 9:3:4 ratio (TABLE XVII) though in that case with large and significant divergence, it may be of interest to correlate the two characters, and this is done in TABLE XX.

TABLE XX.

CORRELATION BETWEEN PETIOLE AND YOUNG LEAF PIGMENTATION IN F_c (Cc).

Colour of young leaves	COLOUR OF PETIOLES		
	Pigmented	Tinged	Unpigmented
Dark copper	3.3%	-	-
Mid copper	6.6%	1.9%	-
Light copper	8.0%	5.2%	-
Orange	10.8%	18.9%	1.4%
No pigment	0.9%	11.6%	31.6%

In/

In TABLE XX it will be seen that there is a positive correlation between the intensities of pigmentation in the two characters. The agreement is sufficiently close to suggest that both characters may be ascribed to the same set of causes. This however would not apply in the populations Ed and Ec where there are 2 or 3% of plants with unpigmented young leaves among the purple-neck segregates, but 25% with unpigmented petioles. No conclusions can therefore be drawn from these figures.

DISCUSSION - COLOUR IN SWEDE.

With the exception of white and yellow flesh colour, and entire and pinnatifid leaf shape, there are no sharply defined alternative characters in the first year of growth of swede. Shapes of bulb grade into one another, and are subject to great modification, while habit of growth and minor shaw characters give continuous ranges of variation, though true-breeding types may be obtained.

With regard to the anthocyanin colouring of top and neck, three classes are commonly recognised: purple-top, bronze-top and green-top. The main types of commercial varieties can easily be identified with these classes, but individual plants, and especially F2 segregates, may be difficult to define.

The purple-top class may be regarded as synonymous with the "red" group of KAJANUS (1913), who made his observations simultaneously on neck and top, and if these were mainly red attributed the character to a dominant factor P_2. The recessive condition might, according to KAJANUS, be either green or red and green. The present observations suggest however that the character difference needs to be redefined, and emphasis placed on the neck colour/

colour, uniformly pigmented neck being dominant to green or green and mauve neck. If the importance of neck colour is not stressed, there is a possibility of including very darkly coloured bronze-tops as dominants, whereas their bright skin colour may merely be due to modification by insolation. Again, if intensity of colouring is considered, some purple-necked types, especially heterozygotes, have comparatively little pigment on the skin of the bulb, and might be classed as recessives, yet their behaviour in breeding would show that the dominant factor was present. A number of 3:1 segregations were scored (TABLE 7,9 and page 55) on the basis of neck colour, and in most cases there was no significant divergence from the expected ratio. KAJANUS' factor P_2 has, therefore, been tentatively renamed N_1 in order to describe the allelomorph governing the reconstituted alternative characters, purple-neck versus non-purple-neck.

KAJANUS (1913) abandoned the use of another factor, P_1, which he had defined as giving the red-green character, because there was no discontinuous variation between red-green and green in F_2 segregates. He considered the whole group, red-green and green, to be a "labile" modification. Nevertheless, the/

the green-top phenotype gave indications of being recessive; and in the present observations the breeding of self-fertilised lines shows that green-top and at least three types of bronze, (viz.light & dark 'bulb' and very dark neck) are due to different hereditary constitutions, though subject to strong modification.

KAJANUS (1913) came to the conclusion that certain characters, including the 'skin' colour in Brassica, were not due to a mendelian mode of inheritance. Colours did not arise as immediately established mutations, but as modifications retained by continuous selection and good cultivation. Segregations occurring in crosses were explained as pseudomendelian since they did not refer to fixed genes; while the occurrence of di- and tri-hybrid segregations only illustrated the chance forces of the factors concerned.

The writer is inclined to regard the 'skin' colour of a swede as the result of strong environmental modification acting upon a genotype comprising several different colour factors. Many cases have been established in which anthocyanin has been produced by the presence of two factors, each governing the/

the production of colourless substances, and in antirrhinum, ONSLOW (1925) described one factor which produced a flavone, and another giving rise to some other substance; the presence of both being necessary for the production of anthocyanin colour. If two substances necessary for the formation of anthocyanin are denoted as "a" and "b" it is possible to suggest a series of factors to fit some of the colour variations found in swede.

1. Since, under certain environments, anthocyanin may appear in the skin or buds of the bottom recessive green-top, it may be assumed that one of the substances, "a", is always present in skin and neck; while the other "b" may be synthesised in certain environments.
2. The presence of one or more factors similar to KAJANUS' rejected factor P_1 would cause an uneven and dilute distribution of substance "b" on the skin and neck. The intensity of anthocyanin in plants of this nature is much affected by insolation.
3. Substance "a" has been assumed to be present in the neck and skin of the bulb, but not in the petioles. Another factor, E, appears to be necessary to extend "a" into the petioles, but its/

TABLE XXI.

SCHEME OF COLOUR FACTORS.

Substances present in:-

CLASS	PHENOTYPE	SKIN	NECK	SHAW
Green-top	$p_1n_1n_2e$	a	a	-
"	$p_1n_1n_2E$	a	a	a
Bronze-top	$P_1n_1n_2e$	ab	a±b	-
"	$P_1n_1n_2E$	ab	a±b	a
Purple-neck	$p_1N_1n_2e$	ab	ab	b
"	$p_1N_1n_2E$	ab	ab	ab
"	$P_1N_1n_2e$	ab	ab	b
"	$P_1N_1n_2E$	ab	ab	ab
"	$p_1n_1N_2e$	ab	ab	b
"	$p_1n_1N_2E$	ab	ab	ab

"a" is unpigmented

"b" is unpigmented

"ab" is coloured with anthocyanin

its effect cannot be seen in the bronze-top except for an occasional tinge or splash of colour.

4. When factor N_1 (KAJANUS' P_2) is present, the neck is uniformly purple, as is most of the skin of the bulb; this factor therefore, governs the production of substance "b" in these regions. Frequently, however, there is a restriction of anthocyanin at the ground level, and as this band of green is usually wide in the heterozygote, N_1n_1, it may be concluded that it is due to restriction in the distribution of substance "b" produced by factor N_1.
5. Substance "a" was absent in the shaw of the bottom recessive, and consequently the introduction of substance "b" by factor N_1 into the region of the petioles would in itself produce no colour. If, however, the extension factor E, were present it would cause a supply of "a" in the petioles, and anthocyanin would consequently develop.
6. The action of the purple-neck factor N_2, found in the white-fleshed strain, and apparently distinct from, but analogous to N_1, would be to supply substance "b" to all parts. The presence/

presence or absence of anthocyanin in the shaw may in this case also be regulated by the occurrence of factor E.

7. With regard to the colouration of the young leaves factors N_1 and N_2 probably supply substance "b" since there is little or no colour in the recessive forms. The distinction between pigmented and unpigmented is not valid because traces of pigment may develop in certain environments. The intensity of pigmentation in young leaves and petioles is, positively correlated, and may therefore be due in part at least, to the same causes.

8. There are also indications of several modifying factors, acting on bronze and purple-tops, and probably affecting skin, shaw and neck simultaneously.

The manner of inheritance of colour in the region of the shaw is complicated by considerable modification and it has so far been impossible to determine the causes governing different types of pigmentation, such as the "red cabbage" condition where strong anthocyanin extends through the lamina, and the "dark petiole" condition where petiole and midrib alone are strongly pigmented. KRISTOFFESSON (1924) established a series of colours in Brassica oleracea, in which five factors were involved, and characters such as coloured midrib or entirely pigmented leaf could be explained by different combinations of these factors.

FLESH COLOUR

HALLQVIST (1915-6) obtained monohybrid and dihybrid ratios in flesh colour segregations, white being completely dominant to yellow. Experiments in the present paper confirm these results, and show that the two factors M_1 and M_2 were not linked. The presence of a heterozygous white-fleshed plant in a yellow-fleshed crop is of interest. White flesh rogues generally denote bulbless bolters, but here the plant was a typical swede. Cross-fertilisation by/

by a white fleshed swede is a probable explanation, yet the white flesh gene must have been present within the commercial variety for several generations, because other characters of the plant were typical of the variety. KAJANUS noted that the colour of the flesh, which was due to plastids, was completely linked with the colour of the petals, and concluded that both characters were manifestations of the same factor. White-fleshed plants, not only of swede but also of turnip had bright lemon yellow petals, while yellow-fleshed individuals exhibited a dull buff, or light orange petal colour. The bright lemon petal colours are similar in both species but there are differences between the buff flowers of yellow-fleshed swedes and turnips. In swede-like rape four types of petal colour ranging from light yellow to orange were found by SYLVÉN (1927)

III.

INHERITANCE OF YIELD AND COMPOSITION IN SWEDES.

HISTORY.

Improvement of the swede crop has mainly been effected by selection for size and shape of bulb; and although the breeding of new varieties has been extensively carried out in this country since the middle of the 19th century, no qualifying test as to composition has come into general use. At an early date the Marquess of Tweeddale attempted to improve turnips by means of the specific gravity of the whole bulb, and his methods were investigated by ANDERSON (1855-7) who reported that the specific gravity tests on whole bulbs, and on portions of bulbs, were very irregular on account of air cavities in the tissues. He recommended that specific gravity of the juice would afford a more reliable guide to feeding value, and at about that time this test was adopted by sugar beet growers who used it until the introduction of the polariscope (DOWLING 1928); it has been little used in swede breeding, however, except by Danish breeders for the selection of seed parents (FRUWIRTH 1922). The invention of the polariscope was of no value/

value to swede breeders, since the carbohydrates in swede are of several kinds and consequently have little rotatory power. Sugar estimations have long been used for the determination of plot yields and an improved method for that purpose was devised by WOOD and BERRY (1902-4). For seed-parent selection however these analyses were found to be too lengthy HENDRICK (1905), ROBB and WISHART (1911).

In 1888, **FJORD*** demonstrated the value of dry-matter in mangels and swedes, by a series of feeding experiments. He found that the dry matter was equivalent in feeding value to an equal weight of corn(FABER (1920).). Since it was possible to produce two and a half times as much dry-matter by growing roots as by growing barley, the Danish agriculturists changed their cropping system by greatly increasing the proportions of root crops, and this led to the most comprehensive scheme of yield trials that has been undertaken with root crops, other than sugar beet. Taking yield of dry-matter as the standard of comparison, HELWEG, who conducted these trials, completely altered the nature of the root crops by persuading the seed-growers first to eliminate all but a few of the commercial varieties, and later to discard inferior strains of these varieties (FABER (1920).). As a result the strains of swede and/

*(1890)

and other root crops at present grown in Denmark are few in number, being the best of a recent trial; but although systematically named and issued under guarantee of purity, they can not yet be regarded as true breeding, and are capable of further sub-division. In Danish yield trials these specially selected strains yield greater amounts of dry-matter per acre than varieties from other countries.

At the end of the last century three important investigations into the composition of root crops were proceeding in Britain. WOOD and BERRY (1902-4) (1905) were working with swedes and mangels at Cambridge; COLLINS (1905-6) with swedes and turnips in Northumberland, and HENDRICK and GREIG (1906) with swedes and turnips in Aberdeenshire. The variation in dry-matter percentage between individual bulbs of a population, and the number of plants needed to give a representative sample of a plot were determined, and yield trials were carried out by all three groups. COLLINS devised a formula whereby the separate effects, upon dry-matter percentage, of season, variety, locality and bulb size could be estimated. This formula met with some criticism on statistical grounds (HALL (1902-4), COLLINS (1902-4 page 375).

The distribution of solids in the bulb tissues/

tissues was investigated by both HENDRICK and WOOD, and methods of sampling were devised. HENDRICK applied dry-matter and soluble solids tests to breeding, and selected seed parents on the basis of these tests. He found that the determination of the soluble solids in the juice was a valuable aid in the selection of turnips, because "foggy" or "fozy" roots occurred which were high in total dry matter, but contained dry, corky, spongy tissues and were of inferior quality. It is not stated what methods of isolation he employed; the turnips at least must have been open to cross-pollination. It is understood (from DR. HENDRICK) that these breeding experiments were terminated prematurely by Finger-and-toe disease.

In 1911, ROBB and WISHART (1915) working with DR. T. WILSON at St. Andrews, commenced breeding experiments with swedes, in which they tested plots for dry-matter and sugar content, and selected their seed parents on the basis of dry-matter of a single core. The inclusion of fibrous bulbs was checked by examination of progenies. They considered that improvement could be effected by this means, but the work was interrupted by the War and had just been recommenced when the death of DR. WILSON occurred. Some of the inbred material was/

was transferred to the Scottish Plant Breeding Station where it was further examined by SANSOME (1926). Certain observations in the present paper relate to descendants of these strains.

In 1922, a concerted investigation into swede and turnip problems was commenced. Under the Department (then the Board) of Agriculture for Scotland, a committee representative of the Scottish Agricultural Colleges and Research Institutes was formed, with a sub-committee of chemists from the three Colleges, - Edinburgh, Glasgow and Aberdeen. At these three centres the composition of the swede was investigated, and the methods of analysis were revised. The yield and composition of a number of varieties were estimated each year at experimental farms in Aberdeenshire, Ayrshire and Midlothian. It was noted(LAUDER (1926) (1927))that:-

(a) Varieties exhibited greatly different yields and compositions at the various centres, and in different years. This indicated the effect of environment since the same strains of varieties were used throughout.

(b) The varieties exhibited comparatively small relative differences in dry-matter percentage, and the same order was maintained under different environments, indicating hereditary variations.

(c) On account of the inverse correlation between yield and dry-matter percentage, the yield of dry-matter per acre was very similar in all the varieties of a yield trial.

A sheep-feeding experiment (LAUDER (1927)) was carried out in which high- and low-dry-matter varieties of swede were tested; equal quantities of dry-matter being consumed in each case. The quality of the dry-matter as a foodstuff appeared to be the same in both types of swede.

When these investigations were started in 1922 the Scottish Plant Breeding Station had newly been opened, and in that year initial observations and yield trials were carried out there on varieties and strains from many sources. It was found that a lack of uniformity prevailed among the strains sold under a "varietal" name, and that there were many synonyms employed for similar strains. As a consequence it was decided that the Plant Breeding Station should examine the material by breeding self-fertilised lines, and await the findings of the chemists' sub-committee before proceeding upon any elaborate scheme of selection on the basis of composition. Experiments with dry-matter in swedes were made, however, by SANSOME (1926), and as the number of pedigree lines increased it became desirable to lay/

lay out yield trials and determine dry-matter and sugar.

In 1927 the Edinburgh and East of Scotland College of Agriculture co-operated with the Scottish Plant-Breeding Station in a scheme for testing the value of soluble solids and dry-matter determinations, as applied to seed-parent selection, a line of investigation which had been recommended by the above mentioned sub-committee of chemists.

The Object of Breeding for Composition.

WARRINGTON (1919) states an average percentage composition of swedes as follows:-

Water 89.3%; Albuminoids 0.7%; Amides 0.7%.
Fat 0.2%; Soluble carbohydrates 7.2%.
Fibre 1.1%; Ash 0.8%.

The percentage of total solids may, however; vary in individual plants from 9% to 17%.

The chief consideration, therefore, is the advisability of breeding for high total solids, (i.e. dry-matter). It has already been mentioned that a recent feeding experiment (LAUDER (1927)) showed that there was no difference in the feeding value of strains of high and low dry-matter percentage. HENDRICK (1911) found that a bullock fed on

112/

112 lbs of turnips per day, and thereby consuming over 100 lbs of water, thrived equally well on a ration which contained only 50 lbs of water. Hence it may be concluded that the water content was more than sufficient for the animal's needs. HENDRICK also showed that a large consumption of water by animals in courts was deleterious to the quality of the farmyard manure.

On account of an inverse correlation between bulb weight and dry-matter percentage, varieties high in the latter generally give relatively small yields. Economically there would be a saving in costs, such as cartage, in a small crop. On the other hand, the palatability of the swede is probably an important factor in determining a ration, and the nature of additional dry-matter may be of importance. In certain extreme cases, such as "foggy" turnips or swede x rape hybrids, this is known to consist of lignified tissues and to be undesirable.

The Danish swede varieties, as has been mentioned, yield the largest quantities of dry-matter per acre. They have been tried in this country, but were not appreciated by Scottish agriculturists who considered that the bulbs were unpalatable/

unpalatable, fibrous, ugly and relatively small. In breeding agricultural crops popular fancies, such as white flesh in potatoes, must be taken into consideration, and here it would appear that, unless feeding trials should alter farming opinion, size in swede must not be sacrificed for richer composition.

The total solids may be readily ascertained by dry-matter determination, but a rapid test for the digestible constituents is needed. The nitrogenous substances are present in small quantity, and improvement of these has not yet been undertaken. The carbohydrates, which form the main foodstuff of the swede, cannot be tested rapidly. The lengthy sugar analysis may be employed profitably in certain circumstances, such as tests of a few whole bulbs already selected by dry-matter tests from a large population. But in such cases difficulty arises in sexual propagation, for though the "neck" may be grown, it will only yield a few hundred seed.

Caldwell's method applies it!

In lieu of carbohydrates, the solids soluble in the juice may be estimated (HENDRICK (1906).) Determinations of these may be readily effected by specific gravity or dry-matter tests. Besides the actual soluble solid content of the bulb, it is desirable to note the proportions in which soluble and insoluble solids occur, for this may indicate the digestibility of the material.

PROBLEMS/

PROBLEMS ARISING OUT OF SELECTION FOR COMPOSITION.

When attempts are made to improve the yield and composition of swedes the main difficulties encountered are the variability of response in these characters, and the correlations between them. It is consequently a problem of importance to trace variability and correlation to hereditary or environmental causes.

The greatest variability is exhibited in the weight of the bulb. Here the importance of environmental modifications may be seen when plots of the same sample are sown under different conditions: e.g. in 1926 a strain was grown in yield trials in Midlothian, Aberdeenshire and Ayrshire, and yielded 15, 21 and 31 tons per acre respectively (LAUDER (1927)). The effect of hereditary variation may be seen when several varieties are grown under a series of comparable conditions, thus in the above mentioned trials one variety exceeded another by 2.8, 2.2 and 3.5 tons per acre. The figures are quoted to draw attention to the small effect of heredity, as compared with environment, in yield trials.

Among/

Among individual plants of a population the variability is very great, bulbs ranging from a few ounces to many pounds, and it is the object of the present experiments to determine the causes. It may here be noted that the frequency distribution is not normal, because certain of the extreme types are caused by special environments. The very small plants are frequently found close under well developed specimens which adversely affect their growth, while very large plants are often associated with blank spaces in the drill.

The variability of dry matter percentage is small compared with that of bulb weight, but here again the effects of environment and heredity may be discerned by experiment, for a variety receiving different treatments shows differences in dry-matter percentage, while a group of varieties may exhibit a relative order of percentages which is maintained throughout a series of trials. LAUDER (1927).

Correlation. It has long been recognised that the dry-matter percentage is correlated inversely with the bulb weight. This is manifest not only among different strains, but also among individual plants of a population. The nature of this relationship is of importance in view of the possibility of combining high dry-matter percentage with heavy/

heavy bulb weight.

The experimentation was arranged in the following order:-

(1) Comparison of inbred and outbred populations.

(2) Examination of groups of graded bulbs.

(3) Comparison of selections, made from the material of the second experiment, with their selfed progenies.

(4) Examination of lines in L_2 and L_3 generations.

(1) COMPARISON OF INBRED AND OUTBRED POPULATIONS.

If environment alone controls the differences of development of a population, the co-efficient of variability should differ only with the diversity of the local environment, and should not be influenced by the degree of inbreeding. If, on the other hand, hereditary variation alters the composition of individuals to any considerable extent, it might be expected that outbred populations, such as F_2 generations, would exhibit greater variability than pedigree lines or F_1 generations.

The extent to which dry-matter percentage and bulb weight can be developed independently in the plant must regulate the degree of inverse correlation. If the causes governing independent development are entirely environmental the co-efficient of correlation should differ with the uniformity of the environment, but not with the degree of inbreeding. If however there is hereditary variation governing combinations of high dry-matter percentage with large bulb weight, and low percentage with small weight, the presence of these types might be expected to lessen the correlation in outbred stocks, as compared with inbred strains where variation has been reduced.

<u>Material/</u>

Material. Ten populations of from 37 to 100 plants were employed. These strains (TABLE XXII) included three F_2 populations, as examples of outbred stock, and three pedigree lines, L_2 L_3 and L_5, which, together with an F_1 constituent, may be taken as representative of material with reduced variation. Three L_1 generations are also included, but the genetic constitution of these is uncertain, since, being progenies of commercial plants, they may be either F_2 generations from natural crosses, or more highly inbred strains.

Method. Each population was grown in a single plot of two or more rows on the flat at 36" intervals. Three or four plants at the end of each row were discarded, and outside rows were not employed. Despite these precautions, and care in cultivation, the bulb weights were found to range from 0.6 lb to 7 lbs, though extreme types were not so numerous as under ordinary field conditions. Every plant was tested in these experiments, consecutive bulbs being cored horizontally and the dry-matter percentage of each estimated. The bulbs were then pulled, cleaned and weighed separately to the nearest 0.1 lb. The analysis of each population was carried out expeditiously in order that there might be a minimum/

TABLE XXII.

CORRELATION AND VARIABILITY IN SWEDE POPULATIONS.

NAME	GENERATION	CO-EFFICIENT OF VARIABILITY		CO-EFFICIENT OF CORRELATION	NUMBER OF PLANTS
AAMa	F2	53·7% ± 4·57	9·30% ± 0·70	-0·67 ± 0·059	89
AAVa	F2	49·9% ± 3·94	7·71% ± 0·55	-0·61 ± 0·063	100
ACMa	F2	47·4% ± 5·12	6·18% ± 0·60	-0·39 ± 0·114	55
SAa	L1	38·2% ± 4·08	4·64% ± 0·47	-0·36 ± 0·126	48
SAb	L1	36·2% ± 3·85	3·65% ± 0·37	-0·46 ± 0·112	50
SAc	L1	41·1% ± 4·44	5·15% ± 0·52	-0·39 ± 0·120	50
WMaa	L2	42·1% ± 4·57	7·57% ± 0·76	-0·62 ± 0·086	50
IGaab	L3	44·0% ± 4·54	6·21% ± 0·59	-0·34 ± 0·118	56
KOaaaaa	L5	34·3% ± 3·62	2·83% ± 0·28	-0·48 ± 0·109	50
ABA	F1	62·3% ± 8·55	11·73% ± 1·36	-0·57 ± 0·111	37
Mean		45%	6·5%	-0·49	

minimum of metabolic change (CALDWELL (1927)) during the period of sampling, and for this reason the populations were restricted in numbers.

The names and states of breeding of the ten populations are given in the left hand columns of TABLE XXII. The two F_2 populations named AAMa and AAVa were the progenies of hybrids between swede varieties which were known to have significantly different dry-matter values. KOaaaaa was a strain which had been selected for high dry-matter for five generations and was very uniform in botanical appearance.

Results. In TABLE XXII statistics are given for the co-efficients of variability in bulb weight and dry matter percentage, and for the co-efficient of correlation between these two characters. The variability of the bulb weight was found to be seven times as great as that of the dry matter.

Bulb weight. (TABLE XXII). It will be seen that there was a slight reduction in variability of bulb weight in all the selfed strains as compared with the three F_2 populations. The difference, however, between the most inbred line, KOaaaaa, and the least variable of the F2 generations, ACMa, was 13.1% ± 6.27 which was slightly more than twice its error, so that significant differences occurred in/

in this case. The L_2 and L3 strains, however, were not significantly less variable than the F_2 populations. Since the parents of ABA, the F_1, had each been inbred for two generations, the genetic constitution of the hybrid population might be expected to be more or less uniform, but the coefficient of variability in it was over 60%, being the greatest of the ten. Local dissimilarity in soil conditions may have been responsible for this one instance, but it should be mentioned that in two other F_1 populations, where the bulbs were weighed but not analysed, the coefficients of variability were 49.8% ± 6.54 and 59.5 ± 5.53. There seems therefore to be no reduction of variability in the F_1 as compared with the F_2 generation, and since only one of the pedigree lines, the L_5, showed definite reduction, the influence of heredity was not proved.

Dry-matter percentage. (TABLE XXII). In dry matter percentage the L_5 strain, KOaaaaa, again showed less variability than any of the F_2 populations, since it differed from the least of these (ACMa) by 3.35% + 0.66. The L2 and L_3 strains, WMaa and IGaaa, were equal in variability with two of the F_2 populations, AAVa and ACMa, while the F_1 population, ABA, exceeded all the strains in the magnitude/

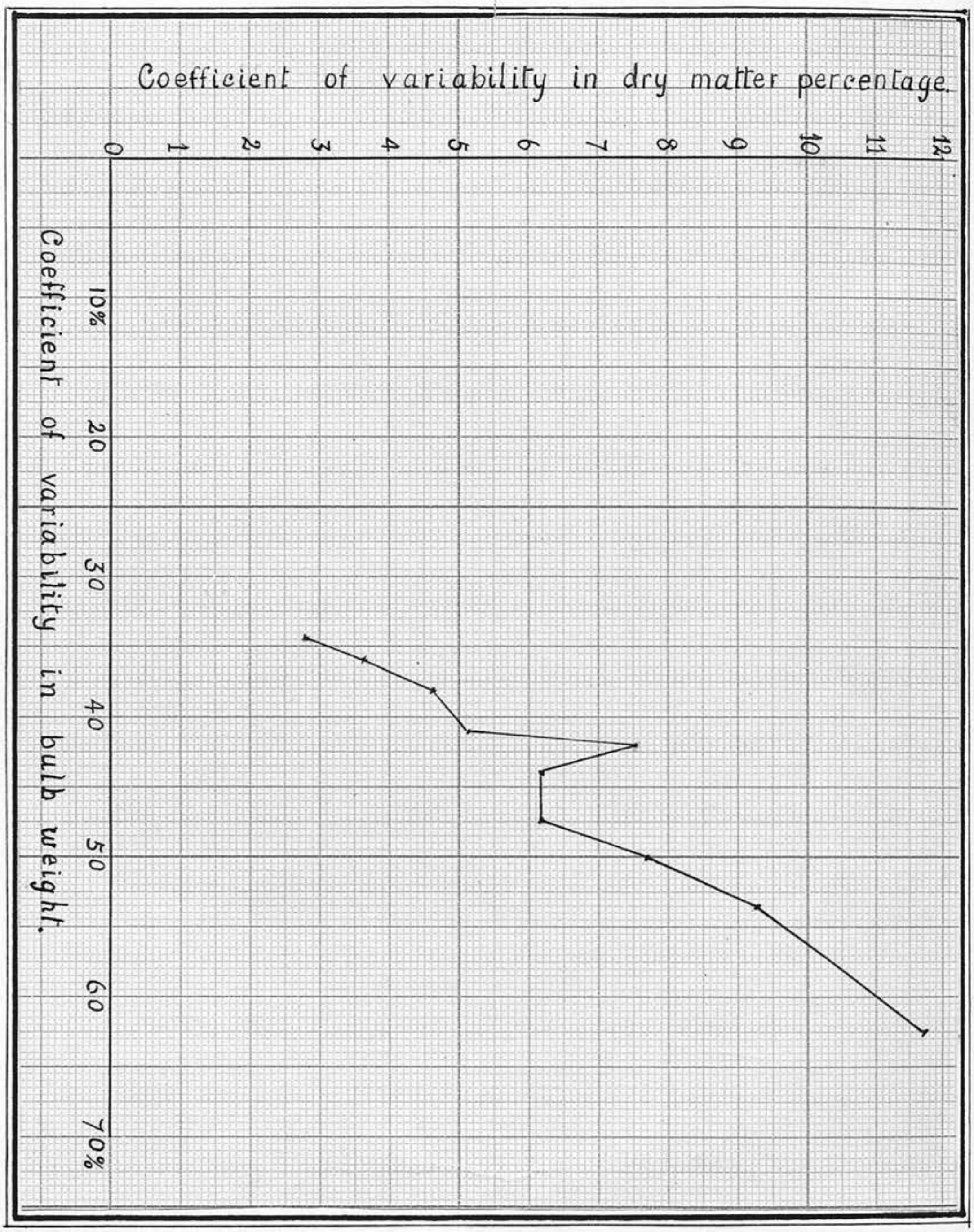


Fig. 7. Graph to show a positive correlation between the coefficients of variability.

magnitude of its variability. There is therefore no proof that the variability in dry matter percentage can be reduced by inbreeding, though this is suggested in the case of KOaaaaa.

Correlation. (TABLE XXII). The coefficients of correlation ranged from -0.34 in an L_3 strain to -0.67 in an F_2, a reversal of the expected order. While the difference between these extremes, 0.33 ± 0.127 was more than twice its error, there was little significance among the other results. In both inbred and outbred groups there were good and poor correlations, so that there was no indication of the effect of heredity.

When the coefficients of variability in TABLE XXII were under examination, another aspect of the correlation between dry-matter percentage and bulb weight was noted. If an individual bulb weight deviates greatly from the mean, the dry-matter percentage in that plant will also show a relatively large deviation, though in the opposite direction. Consequently high variability in bulb weight of a population implies high variability in dry matter percentage also. In FIG. 7, the two sets of coefficients are plotted on a graph and it will be seen that there was a strong positive correlation between them. This was calculated and found to be/

be + 0.96 ± 0.024.

(2) EXAMINATION OF GROUPS OF GRADED BULBS.

In the preceding experiment samples representative of whole populations were under consideration; every plant in a given area being tested. It is proposed here to discuss analyses of groups of graded plants; large plots being examined, and only those bulbs which exhibited good shape, and average or large size being employed for analysis. Two groups of these will be compared, one drawn from a commercial variety named Buffalo (denoted as BF) and the other from an L_3 pedigree line out of Superlative variety (named SUaca). The following determinations were made:-

1. Bulb weight.
2. Total solids percentage, i.e. total dry-matter percentage.
3. Soluble solids percentage, i.e. soluble dry-matter percentage,

and from these were calculated:-

4. Insoluble solids percentage.
5. Ratio Soluble/Insoluble-solids.
6. Soluble solids content of the bulb.

The/

The analyses formed part of a co-operative scheme for the trial of the soluble solids test as a method of selecting seed-parents. The two populations under consideration were analysed by the writer, and other commercial varieties were tested in a similar way by Mr. A. COMRIE of the Edinburgh and East of Scotland College of Agriculture.

Methods of analysis.

(1) The bulbs were chosen for shape and size, the smallest being equal to the average weight of the crop. Outside plants and those adjoining blanks in the drill were discarded, and it was the aim in selection to obtain large bulbs growing at 9 inch intervals from adjacent plants. The chosen bulbs were cored, weighed and labelled. (In weighing plants which may be kept for breeding, the side roots are cut off and the mud removed, and the shaw is cut just above the neck, which has to be preserved in an undamaged condition).

(2) The total dry-matter percentage was estimated on a diagonal core.

(3) Soluble solids percentage was calculated from a dry-matter determination of the juice extracted from a second core bored horizontally. The formula used was devised by HENDRICK (1906).

(4) Insoluble solids were calculated by difference between total- and soluble-solids.

(5) The ratio soluble/insoluble solids percentage was calculated, since it was considered to be an indication of the quality of the dry-matter. HENDRICK(1906).

(6) The soluble solids content was also calculated since it affords a suitable criterion for selection of seed parents.

A difficulty arose with regard to the method of treating the core prior to the expression of the juice. In the writer's analyses this was carried out as follows:-

The core was reduced to pulp on a coarse rasp, and the pulp was wrapped in a strong linen bag, and placed in a specially constructed press. The juice was expressed not only through the linen bag, but also through a filter paper, and another piece of linen, fitted into the outlet of the press. The juice so obtained was slightly turbid and yellow, and would not pass readily through filter paper by gravity. Most of the cells appeared to be ruptured by this rasping process.

COMRIE tried an alternative method of preparation/

preparation. He sliced the core into thin sections, and expressed the juice (in a press of the same pattern) under high pressure. The cells of the tissue were mostly intact at the time of pressing, and very little juice could be obtained. The extract was a clear and colourless liquid, and contained smaller percentages of solids. COMRIE compared the two methods of preparation by testing 33 cores halved longitudinally. The difference was as follows:-

"Rasped" ½ cores 8.14% ± 0.102

"Sliced" ½ cores 7.82% ± 0.100

The correlation between individual results was

$$r = + 0.93 \pm 0.021$$

These figures, which were calculated from COMRIE'S data by the writer, are included here to show that the soluble solids percentage is not based on a definite compound, but depends largely upon the proportion of cells ruptured and the consequent liberation of colloids. Comparisons could only be made by maintaining a standard procedure in preparing and pressing the cores.

Neither [illegible]
is [illegible]

With bulk samples the practice has been to extract the juice from material that has been passed through a mincing machine, and the tissues are broken up and more or less bruised according to the type/

type of machine, so that the prepared material is in a condition intermediate between rasping and slicing. Estimations on the progeny strains, described in a later experiment, were performed in this manner.

Material. One hundred bulbs were chosen from a large plot of "Buffalo purple-top swede", "BF", a commercial variety which was observed to be lacking in uniformity in respect of shape, skin, colour and length of neck.

Fifty plants were chosen from a plot of an L_3 line bred from Superlative and named SUaca (the three small letters "aca" denote the number of inbred generations). This strain was of a completely different type from BF, and it was observed to be uniform in appearance, except a fluctuation in bulb shape which is a feature common to pedigree lines of Superlative and is known to be of no hereditary significance, since extreme modifications have been tested by breeding.

Results. The means and coefficients of variability for the several estimations are given in TABLE XXIII. If the mean values are examined it will be seen that the bulb weight and composition of the two strains were dissimilar, but the ratios of soluble/

TABLE XXIII.

STATISTICS OF ANALYSES ON SELECTED GROUPS OF BULBS.

DETERMINATION	"BF." A COMMERCIAL SAMPLE		"SU aca." AN L_3 LINE	
	MEAN	Co-efficient of VARIABILITY	MEAN	Co-efficient of VARIABILITY
Total dry matter %	11·19% ± 0·067	5·99% ± 0·427	10·63% ± 0·078	5·20% ± 0·520
Soluble solids %	8·71% ± 0·063	7·25% ± 0·513	8·24% ± 0·070	5·97% ± 0·597
Insoluble solids %	2·46% ± 0·036	14·42% ± 1·041	2·38% ± 0·037	11·01% ± 1·114
Ratio $\frac{\text{soluble}}{\text{insoluble}}$ Solids	3·62% ± 0·058	15·93% ± 1·16	3·52% ± 0·069	13·93% ± 1·42
Bulb weight	4·56 lbs ± 0·087	19·19% ± 1·381	3·88 lbs ± 0·115	20·34% ± 2·11
Soluble solids in bulb	0·40 lbs ± 0·007	18·72% ± 1·369	0·32 lbs ± 0·009	19·33% ± 2·00
Number of plants tested.	100		50	

soluble/insoluble solids were not significantly different. The average composition of the dry-matter was, thus, the same in both, being 78% soluble and 22% insoluble in each case.

<u>Variability (TABLE XXIII)</u>. In the previous experiment where bulbs of all sizes were employed, the average coefficient of variability was 45%, but here it was reduced to about 20% by the selection of bulbs. The variability in dry matter percentage, on the other hand, is as great in this as in the last experiment.

Comparing the two groups, BF and SUaca, it will be seen that there was no significant difference in variability of bulb weight. Thus the two groups were not differently chosen. The variability of the amount of soluble solids per bulb was slightly greater in SUaca, but in total, soluble and insoluble solids percentage there were slight reductions of variability in the inbred strain. None of these differences were significant, so that, as in the case of the bulb to bulb analyses, this comparison fails to prove any reduction in variability due to inbreeding.

In TABLE XXIV, the coefficients of correlation between the several determinations are given for/

TABLE XXIV.

CO-EFFICIENTS OF CORRELATION BETWEEN DETERMINATIONS

CORRELATION BETWEEN	"BUFFALO" VARIETY	"SUaca L_3 STRAIN
Bulb weight & Total solids %	- 0·22 ± 0.051	- 0·44 ± 0·115
" " Soluble solids %	- 0·31 ± 0·090	- 0·45 ± 0·113
" " Insoluble solids %	- 0·08 ± 0·099	- 0·22 ± 0·135
Total solids % & Soluble solids %	+ 0·81 ± 0·035	+ 0·90 ± 0·027
" " Insoluble solids %	+ 0·36 ± 0·087	+ 0·37 ± 0·122
Soluble solids % & Insoluble solids %	- 0·08 ± 0·099	± 0·00 ± 0·141

for both strains while in FIG. 8 they are displayed diagramatically. The correlation between bulb weight and dry matter percentage is considerably less in these groups than in the preceding experiment with whole populations.

Bulb weight and composition (TABLE XXIV). Weak negative correlations were found between bulb weight and the various solids. In the case of insoluble solids the coefficients were not significant. With total and with soluble solids the correlations were significant, and similar in value. The coefficients obtained for the inbred line SUaca, were in each case greater than those of the commercial sample, but not significantly greater.

Total solids. (TABLE XXIV). Both soluble and insoluble solids percentages were positively and significantly correlated with total solids percentage. Since these two estimates together comprise the total solids their behaviour is of interest. Theoretically one of these estimations, for example the insoluble solids forming the frame work of the storage organ, might have remained as a fixed percentage of the bulb weight, irrespective of the total solids percentage. In such a case there would be no correlation between total/

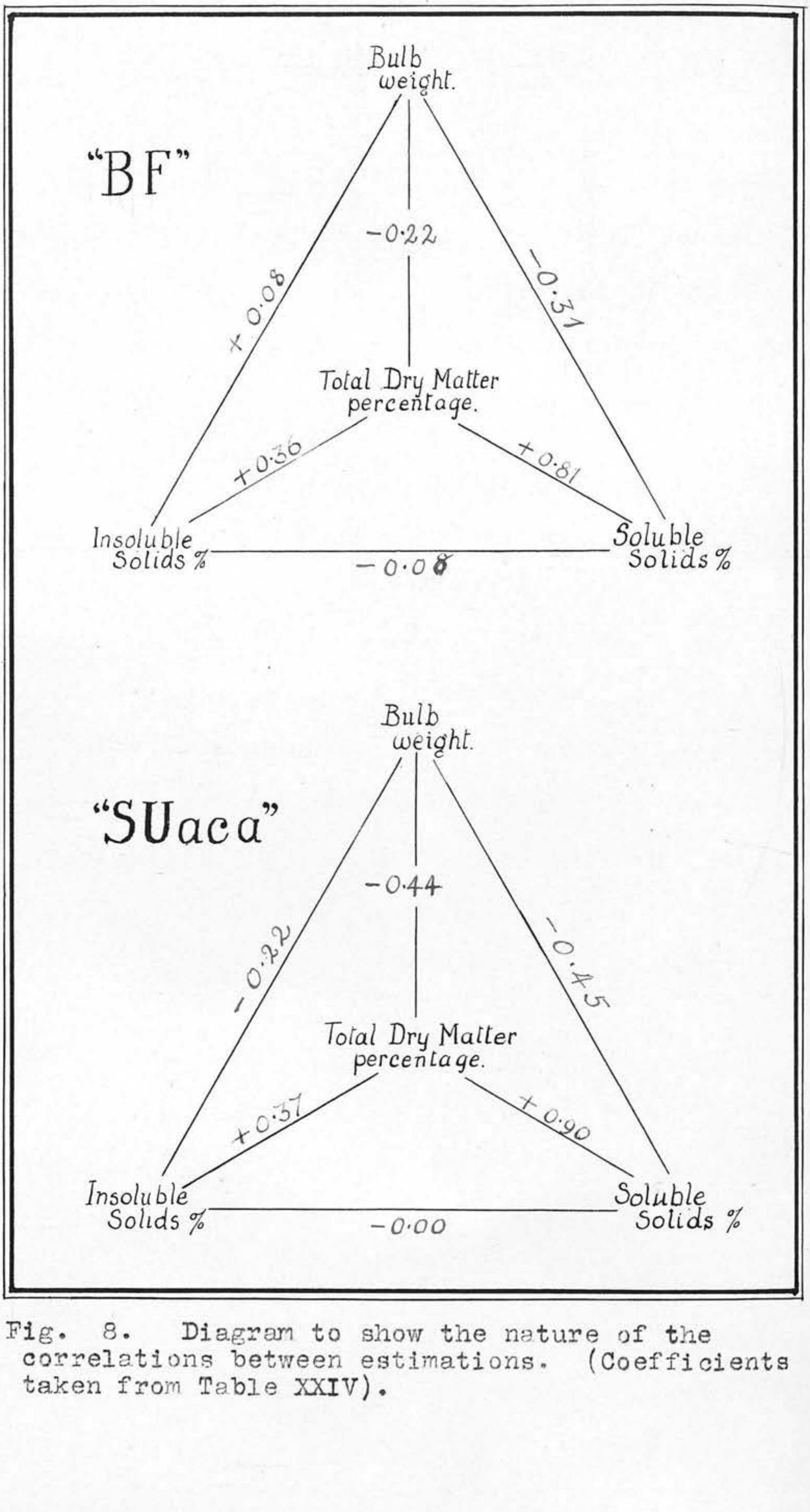


Fig. 8. Diagram to show the nature of the correlations between estimations. (Coefficients taken from Table XXIV).

total and insoluble solids, and strong correlation between total and soluble solids percentage. It was found however, that both the estimations were positively correlated with total solids percentage. Increases in percentage of total solids are therefore due to increases in percentage both of soluble and of insoluble solids, though the former substance plays the more important part.

Soluble and Insoluble solids. (TABLE XXIV).

There was no correlation between the soluble and insoluble solids percentages. If increases in percentage of total solids were always due to formation of both soluble and insoluble substances there would have been a positive correlation between them, but this was not found. Sometimes the extra solids were due to a deposit of soluble substances, sometimes to an increase in the insoluble substances, and sometimes to increase in both.

3./

3. Comparison of selected plants with their offspring.

In the last experiment two groups of large sized bulbs, designated SUaca and BF, were tested individually for bulb weight, dry-matter percentage and soluble solids percentage, while from these data the soluble solids content of each bulb and the ratio of soluble insoluble solids were calculated.

The results were examined and plants exhibiting outstanding differences in composition were selected and self-fertilised. Some of these plants were destroyed by disease, and only twelve gave sufficient seed to sow small yield trials.

The progenies thus obtained were denoted by the addition of a small letter to the parent name. Thus from plants of SUaca, the L_3 strain of Superlative, four progenies, named SUacaa, SUacab, SUacac and SUacad, were bred and tested in yield trial; these strains being of the L_4 generation. From BF, the commercial variety "Buffalo", eight selfed progenies were raised; and these were described as BFa, BFb... BFh. These L_1 strains were tested in another yield trial, with plots of the original BF variety as control. One strain, BFg, has had to be omitted from this discussion, because some plots of it failed/

failed, and the errors of the remainder were too large for fair comparison.

In tables XXV and XXVI data are collected from the original single bulb analyses and from the progeny trials, and are converted, for purposes of comparison, into percentage deviations. From such figures it may be seen at a glance how a constituent behaved in respect to any character of composition. These deviations were calculated as follows:-

(a) For the parent bulbs the results of analyses were expressed in terms of the mean values of the populations from which they were selected.

(b) For the SUaca progenies, the mean value of each determination was obtained from the results of the four strains and from this the deviations of the individual strains were calculated. The absence of a suitable control necessitated this change in procedure.

(c) For the progenies of BF, the results are expressed in terms of the mean values of five plots of the parent variety, BF, which had been included in that trial.

In table XXV three determinations are examined/

TABLE XXV.

EFFECTS OF SELECTION FOR COMPOSITION.

NAME of PROGENY	PARENT BULB			PROGENY STRAIN		
	BULB Wt.	D.M. %	S.S. %	BULB Wt.	D.M. %	S.S. %
SU acaa	+ 16	± 0	+ 2	- 1	- 1	- 1
SU acab	+ 10	+ 4	+ 5	+ 4	+ 1	+ 1
SU acac	+ 10	- 6	- 12	+ 4	- 1	- 1
SU acad	+ 16	- 6	- 2	- 6	+ 1	+ 1
$S.E._d$				±3·7	±1·4	±1·9
BFa	+ 1	+ 5	+ 11	+ 17	- 1	- 2
BFb	+ 10	- 6	- 11	+ 7	- 2	- 2
BFc	+ 10	+ 17	+ 20	- 14	+ 10	+ 2
BFd	+ 21	+ 12	+ 2	+ 25	- 7	- 4
BFe	- 18	+ 7	+ 13	+ 6	- 0	± 0
BFf	- 22	+ 9	+ 20	- 2	+ 2	+ 1
BFh	+ 1	- 3	+ 5	+ 25	- 3	+ 1
$S.E._d$				±4·8	±0·7	±1·0

D.M. % = Dry Matter percentage.

S.S. % = Soluble solids percentage.

$S.E._d$ = Standard Error of mean difference.

examined.

Bulb Weight

Dry-matter percentage, and

Soluble solids percentage.

The values of the parent bulbs are recorded On the left, while those of their respective progenies are set out opposite on the right. As a guage of the significance of the results of the progenies, errors of mean difference, expressed as percentages, are included below each set of progeny deviations. These errors are approximately correct for the SUaca strains, each of which was tested in quadruplicate, but in the case of Buffalo, some strains were in quintuplicate, and others quadruplicate, so that each error, based on four plot differences, was too great in certain comparisons.

A difference between the two groups of progenies may readily be seen. The L_1 strains of BF, exhibited large deviations, while the progenies of SUaca varied little in the different estimations. In dry-matter and soluble solids percentages, the differences between SUaca progenies were insignificant, but in bulb weight the strain SUacad, obtained ~~from~~ a large bulb, was significantly lower than two of/

of the others. It is doubtful whether any hereditary variation existed among the four parent plants; and selection for various characters of composition was certainly without effect. It had been intended to include progenies of small bulbs of SUaca for contrast, but the parent plants were destroyed by disease.

Correlation (TABLE XXV). The inverse correlation between bulb weight and percentage of dry-matter may be observed by noting the plus and minus deviations. It will be seen that this correlation was not entirely absent in the results of the parent bulbs, but was very noticeable in those of the progenies. For example, the parents of BFc had been chosen as high both in dry-matter percentage (+17%) and in bulb weight (+10%). In the progeny the high dry-matter percentage (+7%) was to some extent maintained, but the bulb weight was very low (-14%). In the parent of BFd, the bulb weight (+21%) and dry-matter percentage (+12%) were also high, but in this case it was not the bulb weight (+25%) but the dry-matter percentage (-7%) that failed to reappear in the offspring. Thus in these two selections a variation and a modification had been exhibited with the result that in each progeny, the inverse correlation between/

between weight and dry-matter percentage reappeared. Correlations between soluble solids and weight may likewise be observed.

Bulb weight. (TABLE XXV). The differences between mean bulb weights of progenies were as great as those between parent bulb weights. *With regard to SUaca* a slight difference in the strain in the SUacad has already been noted. *Among Buffalo progenies* differences of good significance were obtained. In BFb and BFd, parent and offspring were alike in bulb production, while in BFc they were dissimilar. BFa and BFh were found to be good croppers, whereas their parents were mediocre bulbs. Progenies BFe and BFf were average, though their parents had been small. It must be noted however, that a small parent bulb was as large as the average of the plot from which it was chosen.

Dry matter percentage (TABLE XXV). The deviations in dry-matter percentage between progenies were not so great as those between parent plants. *In SUaca*, all the progenies reverted to similar values. *In Buffalo* BFb, BFc and BFh exhibited some resemblance in behaviour between parent and offspring. In BFd the two generations were vary dissimilar.

Soluble/

TABLE XXVI.

EFFECTS OF SELECTION FOR COMPOSITION (Continued)

NAME of PROGENY	PARENT BULB D.M. per bulb			PROGENY STRAIN D.M. per bulb		
	D.M. per bulb	S.S. per bulb	$\frac{S}{I}$	D.M. per bulb	S.S. per bulb	$\frac{S}{I}$
SU acaa	+ 16	+ 19	+ 29	- 2	+ 5	- 3
SU acab	+ 14	+ 16	+ 11	+ 5	- 3	+ 2
SU acac	+ 3	- 3	- 25	+ 3	- 1	+ 2
SU acad	+ 10	+ 16	+ 23	- 5	- 1	- 1
$S.E._d$				±3·7	±4·5	±6·6
BFa	+ 6	+ 8	+ 22	+ 16	+ 15	- 3
BFb	+ 3	- 8	- 30	+ 6	+ 6	+ 1
BFc	+ 28	+ 28	- 7	- 5	- 12	- 24
BFd	+ 35	+ 20	- 41	+ 18	+ 21	+ 10
BFe	- 12	- 8	+ 11	- 6	- 5	+ 1
BFf	- 15	- 10	+ 40	+ 1	± 0	- 6
BFh	- 1	+ 3	+ 30	+ 22	+ 27	+ 19
$S.E._d$				±5·0	±4·8	±2·6

D.M. per bulb = Dry matter content

S.S. per bulb = Soluble solids content

S/I = Ratio Soluble / Insoluble solids

$S.E._d$ = Standard Error of mean difference

<u>Soluble solids percentage</u> (TABLE XXV.) The differences in soluble solids percentage among the progenies were small. <u>In SUaca</u>, the progenies exhibited no significant differences, showing that the values of the parent plants were merely due to modification. <u>In Buffalo</u> the only deviation of any importance was that of BFd and it was dissimilar to the value of the parent plant. In four cases parent and offspring deviated in the same direction but whereas the parents showed differences from mean of 11% or 20%, their offspring had negligible divergences of 1% or 2%. Selection for soluble solids percentage was consequently of no economic value.

In TABLE XXVI, three sets of derived data are displayed in the same manner as in TABLE XXV. These estimates are:-

Dry matter content
Soluble solids content
Ratio soluble/Insoluble solids.

The first two are intended to measure the value of the plant or crop; while the ratio is believed to indicate the quality of the dry matter with regard to digestibility.

<u>Dry-matter and soluble solids contents</u> (TABLE XXVI) <u>In SUaca</u> there were no significant differences/

differences in soluble solids content among the progenies, but the small bulb weight previously noted in SUacad gave this progeny a lower dry-matter content than either SUacab or SUacac. Though the parent plants differed considerably, it was not on account of hereditary variations. <u>In the Buffalo</u> progenies, however, there were several significant differences. Judged on both dry matter and soluble solids contents it would appear that:-

1. In BFd the value of the parent bulb was to a considerable extent maintained in the offspring, and a hereditary variation was probably disclosed by the original analysis.

2. In two cases, BFa and BFh, valuable strains appeared from the selection of bulbs of average value, though these latter were, of course, larger than the mean bulb size of the original Buffalo plot.

3. In the case of BFc, the high bulb weight of the parent plant was entirely due to modification, and the heredity of this type was completely different.

<u>Ratio Soluble/Insuluble solids</u> (TABLE XXVI)

The width of the ratio of soluble/insoluble solids is an indication of the proportion of digestible foodstuffs/

foodstuffs (the wider the ratio the better the quality).

In SUaca it will be seen that three of the parent plants had wide ratios, and one the P_1 of SUacac, had a very narrow ratio. Among the progenies there were no significant differences. Selection in the L_3 generation, had therefore failed to isolate variation.

In Buffalo significant differences were obtained among the progenies. BFh was the only strain that maintained a wide ratio in both P_1 and L_1, and there the value dropped by 11%. BFd unexpectedly gave a good ratio while BFa and BFf failed to show the wide ratios of their parent plants. The parent of BFc was somewhat narrow in ratio, but its progeny was 24% below average. BFc was in fact the only bad strain derived from the seven selections. Its parent must have been growing under exceptionally favourable conditions and consequently developed a large bulb. The progeny had small, fibrous and fanged bulbs.

Conclusions. (1) Selection in an L_3, SUaca, was of no economic value, and it is doubtful whether any hereditary variation in composition occurred in the four selections.

(2) Selection in the commercial variety was mainly/

mainly successful, for the content, both of dry-matter and of soluble solids was maintained or improved and the quality as determined by the ratio soluble/Insoluble solids was likewise maintained or improved. One selection of the seven was however decidedly inferior.

A description of the progeny trials, together with statistical data of means and errors is appended for reference.

The trials were laid out as follows:-

(1) Four strains from selected bulbs of SUaca were included with three other strains, which are not under discussion, in a block yield trial. The quantities of seed were small, but by hand sowing in dibble holes spaced at nine inches on drills, it was possible to lay out four plots of each, and to obtain about 150 plants in each plot. Dry matter and soluble solids tests were performed on bulk samples of 100 cores, drawn from each plot. Each plot consisted of three drills 16 yards long. At the time of weighing these were reduced to 14 yard lengths so that the outside effect and uneven ends of the drills might be eliminated. The bulbs in 42 yards of drill thus obtained were topped and tailed, and weighed in bulk, while a record was kept of the numbers of plants.

By/

TABLE XXVII.

STATISTICS OF SUPERLATIVE (SU aca) PROGENY TRIALS.

DETERMINATION	PROGENIES OF SELECTED BULBS SU acaa	SU acab	SU acac	SU acad	S.E. of DIFF.	COEFFICIENT of VARIABILITY
Number of plants per plot.	138·5	132·0	138·8	136·3	4·48	4·3% ± 0·58
Dry matter %	10·69	10·81%	10·59%	10·87%	0·15	1·8% ± 0·25
Soluble Solids %	7·90%	8·10%	7·93%	8·10%	0·15	2·4% ± 0·33
Weight of 100 bulbs.	245 lbs	256 lbs	259 lbs	233 lbs	9·06	4·8% ± 0·64
Dry matter per 100 bulbs	26·2 lbs	27·9 lbs	27·4 lbs	25·4 lbs	1·00	4·9% ± 0·66
Soluble solids per 100 bulbs.	20·1 lbs	18·4 lbs	18·8 lbs	18·9 lbs	0·86	5·9% ± 0·79
Ratio $\frac{\text{Soluble}}{\text{Insoluble}}$ solids.	2·85	3·00	2·99	2·92	0·19	4·3% ± 0·58

7 strains (three not quoted); 4 replications of each strain, sown in blocks.

By this means the yield per acre, and the weight of a hundred bulbs could be estimated. The latter determination has been dealt with here, because it is less subject to the effect of density of population. Even in bulb weight, however, a sparse population may have an enhanced value on account of the more favourable conditions of growth; this source of error was not appreciable in the SUaca trial. It was possible, therefore, to calculate all the statistics by the block method described by ENGLEDOW and YULE (1926), reducing the magnitude of the variance by eliminating variance due to local differences between blocks. The statistics obtained from this trial are given in TABLE XXVII.

(2) A number of progenies of BF selections were laid out in another trial. On account of shortage of seed some of the plots in different blocks failed, and consequently it was impossible to apply the correction for local soil conditions. The errors for eight strains and the commercial variety control, each having two, four or five replications, had to be calculated irrespective of blocks, and are therefore somewhat larger than would otherwise have been the case, but, despite this, significant differences were obtained. The plots and determinations were similar to/

TABLE XXVIII.

STATISTICS OF 'BUFFALO' PROGENY TRIAL.

STRAIN	Number of bulbs per plot		Dry matter percentage		Soluble Solids percentage	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Commercial	138	± 4.2	10.96%	± 0.047	8.06%	± 0.052
BFa	127	± 4.7	10.89%	± 0.052	7.94%	± 0.058
BFb	134	± 4.7	10.72%	± 0.052	7.90%	± 0.058
BFc	118	± 4.2	12.05%	± 0.047	8.18%	± 0.052
BFd	131	± 4.7	10.24%	± 0.047	7.71%	± 0.052
BFe	138	± 5.5	10.95%	± 0.047	8.07%	± 0.052
BFf	115	± 4.2	11.21%	± 0.047	8.11%	± 0.052
BFg	131	± 6.7	10.76%	± 0.074	7.86%	± 0.082
BFh	127	± 4.2	10.64%	± 0.047	8.16%	± 0.052
S.D.	9.43	± 1.10	0.11%	± 0.012	0.12%	± 1.013
Co-eff of var.	7.3%	± 0.85	0.96%	± 0.106	1.45%	± 0.16

TABLE XXVIII (CONTINUED)

STATISTICS OF 'BUFFALO' PROGENY TRIAL

	Weight of 100 bulbs in lbs.		Ratio Soluble / Insoluble solids		Dry Matter per 100 in lbs.		Soluble solids per 100	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
BF	228	± 7.5	2.78	± 0.045	24.9	± 0.83	18.3	± 0.60
BFa	266	± 8.4	2.70	± 0.052	29.0	± 0.92	21.1	± 0.67
BFb	245	± 8.4	2.81	± 0.052	26.3	± 0.92	19.4	± 0.67
BFc	196	± 7.5	2.11	± 0.045	23.7	± 0.83	16.1	± 0.67
BFd	286	± 8.4	3.06	± 0.045	29.3	± 0.92	22.1	± 0.67
BFe	215	± 8.4	2.81	± 0.045	23.5	± 0.92	17.4	± 0.67
BFf	224	± 7.5	2.61	± 0.045	25.1	± 0.83	18.2	± 0.60
BFg	258	±11.8	2.71	± 0.071	27.8	± 1.31	20.4	± 0.94
BFh	286	± 7.5	3.31	± 0.045	30.4	± 0.83	23.3	± 0.60
S.D.	16.8	±1.92	0.10	± 0.011	1.85	± 0.212	1.33	±0.15
C.	6.8%	±0.79	3.7%	± 0.41	6.9%	± 0.80	6.8%	± 0.78

to those of the SUaca trial. The statistics of the BF trial are included in TABLE XXVIII.

4. Comparison of L_2 tests and progeny yield trials.

The Stirling Castle Trials.

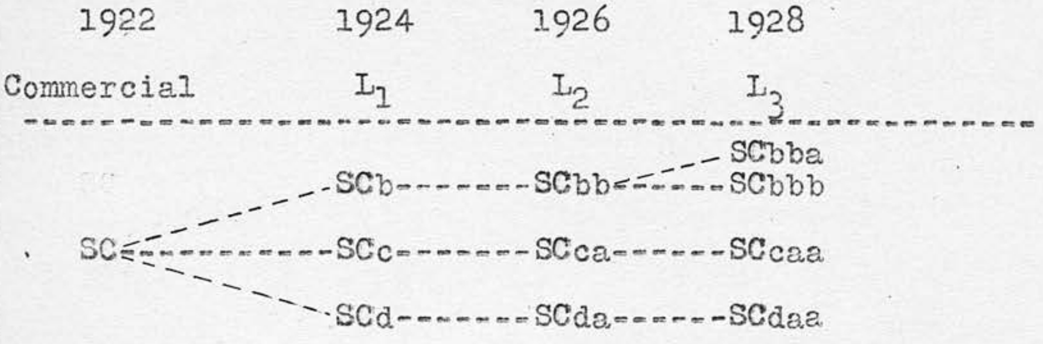
In the previous experiments, strains were examined during two generations, first by the analysis of a number of individual plants, while a second generation consisting of selfed progenies, was tested in yield trials. In the present experiment the procedure was somewhat different. Selections had already been made from a commercial stock, and were undergoing intensive inbreeding by continued selection and self-fertilisation. Weighings of small plots, and a few single bulb analyses were carried out on the L_2 generation, and these tests are considered in relation to a more elaborate yield trial in the L_3.

From a purple-top swede variety known as "Stirling Castle" three plants were selected, for botanical characters, in 1922. The points of difference between these selections were shown by breeding to have been mostly modifications, though small hereditary differences were also noted, as for example a somewhat brighter skin colour which persisted throughout the SCb line. (See FIG. 9 pedigree chart). Compared/

Compared with the "Buffalo" variety employed in the last experiments, "Stirling Castle" exhibits little external variability, the proportion of bronze-top segregates to be found is extremely small, while there is comparatively little diversity in shape and neck length.

In the pedigree chart (FIG. 9) the various populations are denoted, as elsewhere, by letters. The two block letters "SC" are employed to indicate samples of the commercial variety; and in order to describe a line, a small letter is suffixed for each self-fertilised generation that has been effected.

FIG 9 Pedigree chart of Stirling Castle lines



Tests in the L_2 generation. (TABLE XXIX left). In 1926, three L_2 lines, SCbb, SCca and SCda were sown out in two replications of small plots. A new sample of commercial seed, SC, being included in each case as a control. The plots consisted of two or/

TABLE XXIX. "STIRLING CASTLE" TRIALS.

L_2 GENERATION.								Deviations, from means of L_2 Strains, exhibited by			L_3 GENERATION.										
Single plot weighings.				Bulb to bulb tests on Rod row plots				L_2 Selections.			Mean values of Yield Trial.										
Name of L_2 strain	Number of plants per row.	Yield per acre	Weight of 100 bulbs	Number of plants per row.	Dry matter percentage	Mean bulb weight	Dry matter per bulb	Dry matter percentage.	Bulb weight.	Dry matter per bulb	Name of L_3 strain.	Number of plants per plot.	Dry matter percentage	Yield per acre	Dry matter per acre	Weight of 100 bulbs	Dry matter per 100 bulbs	"Sugars" percentage	'Sugar' per acre.	'Sugar' per 100 bulbs	Actual number of plots
SCbb.	100	101	107	133	94	94	88	+2·0	+18·4	+21·2	SCbba	104	95·5	114	109	111	106	103	117	115	5
								−0·9	+22·5	+23·1	SCbbb	103	96·3	114	110	111	107	100	114	105	6
SCca	110	100	95	133	102	73	73	+2·3	+5·3	+6·8	SCcaa	108	107·7	98	106	91	98	114	116	102	5
SCda	-	80	79	No analysis				—	—	—	SCdaa	119	94·3	124.	117	105	99	97	123	102	5

Value of each strain stated as a percentage, when that of the control, SC, is taken as 100%.

or more "rod-row" strips, sown on the flat at 36" spacing, with nine inch intervalz between plants.

The plots of one replication, were weighed in bulk, (about 100 plants per plot) and the yields per plot, and mean bulb weights are given on the left of TABLE XXIX In order to obtain comparable results, the values are expressed as percentages, where the value of the control is taken as 100%.

Tests for dry matter percentage were made on individual bulbs of single "rod rows". The bulbs were weighed separately, and the data derived from these tests are included in the second part of TABLE XXIX.

Selections from the L_2 strains. TABLE XXIX Centre) Two plants from SCbb, and one from SCca were selected from the tested rod rows and seeded in bag isolation in 1927. The individual results of these bulbs are expressed as percentage deviations from the mean values of the strains out of which they were selected. (see TABLE XXIX centre). The three bulbs were relatively large, but in dry matter percentage they did not differ significantly from the means of their strains. A selection from SCda was also seeded, but no tests had been made in this case.

Yield/

Fig. 10. Plan of 'Stirling Castle' L_3 Trial.

Swede strains	not employed	in trials.
SC	SC	SC
SCbba	SCbbb	SCdaa
SC	SC	SC
SCcaa	SCbba	SCdaa
SC	SC	SC
SCbbb	SCcaa	SCdaa
SC	SC	SC
SCbba	SCbbb	SCdaa
SC	SC	SC
SCcaa	SCbba	SCdaa
SC	SC	SC
SCbbb	SCcaa	SCbbb
SC	SC	SC
SCbba	SCbbb	SCcaa
Swede strain	not employed	in trials.
1st break	2nd break	3rd break.

Plots 20 yards long, two drills, 27" intervals.

Yield trials on L_3 progenies, 1928.

TABLE XXIX right) In 1928 the progenies of the three tested plants and the botanical selection from SCda were sown out in yield trial with a sample of SC as control. The results are summarised on the right of TABLE XXIX. In this trial a systematised alternate plot method was employed which did not prove very satisfactory. Pairs of drills of SC were sown through three breaks, leaving two drills between each SC pair, and into these the L_3 strains SCbba, SCbbb and SCcaa were scattered in quintuplicate or sextuplicate. (See FIG 10). The five plots of the strain SCdaa were not scattered but were concentrated in one break, with a plot of the control, as usual, between each of them. This arrangement was successfully employed in swede trials by PARKER (1927) and was adopted here in order that the strain might be omitted from the trial if necessary. It so happened, however, that the break in which these SCdaa plots were grouped, was badly infected with dry-rot (Phoma lingam (Tode) Desmeziere) and the commercial control failed; being very deficient both in number and weight of bulb. The superiority of SCdaa must, therefore, be ascribed to disease resistance rather than to cropping power.

Estimations. Dry-matter analyses were made on bulk samples of 100 cores drawn from each plot. Weighings were made on 32 yard lengths of drill the size of the plots before trimming being two drills of 20 yards. Bulbs were weighed in bulk and counted, calculations of yield and weight of 100 bulbs being made.

The result of each plot of pedigree line was expressed as a percentage of the mean value of two adjacent control plots of SC and in this manner comparable percentages were obtained for the estimations of number of plants per plot, dry-matter percentage, yield per acre, dry-matter per acre, weight of 100 bulbs and dry -matter per 100 bulbs.

Sugar determinations* were made on a few of the bulk samples. Only 3 or 4 plots of each strain were tested and 5 of the control SC. The relative values in percentages were therefore calculated from the mean values, and the errors were computed direct, instead of using the alternative plot method.

Comparision of L_3 lines with commercial control. In TABLE XXX the four pedigree lines are compared with SC, the differences in percentages being expressed as "plus" when line exceeds control. As an estimate/

---

* By a modified form of the Wood-Öst method (Wood(1902 -1904))

T A B L E XXX.

L3 STRAINS COMPARED WITH STIRLING CASTLE CONTROL.

DETERMINATION	SC bba.		SC bbb.		SC caa.		SC daa.	
	Diff.	Diff. S.E.	Diff.	Diff. S.E.	Diff.	Diff. S.E.	Diff.	Diff. S.E.
Number of plants per plot	+ 4%	0·5	+ 3%	0·5	+ 8%	1·3	+ 19%	3·1
Dry matter %	- 5%	10·5	- 4%	9·4	+ 8%	17·9	- 4%	13·3
Yield per acre	+ 14%	4·1	+ 14%	4·6	- 2%	0·5	+ 24%	7·2
Dry matter per acre	+ 9%	2·5	+ 10%	2·6	+ 6%	1·6	+ 17%	4·6
Weight of 100 bulbs	+ 11%	2·3	+ 11%	2·6	- 9%	1·9	+ 5	1·1
Dry matter per 100	+ 6%	1·3	+ 7%	1·5	- 2%	0·4	- 1%	0·1
Sugar %	+ 3%	1·7	± 0	-	+ 14%	9·7	- 3%	1·6
Sugar per acre	+ 17%	5·4	+ 14%	4·0	+ 16%	5·0	+ 23%	6·7
Sugar per 100 bulbs.	+ 15%	3·0	+ 5%	0·9	+ 2%	0·3	+ 2%	0·3

estimate of significance the calculated "difference/ standard error of mean difference" is stated.

Density of population. SCdaa had 19% more plants per plot than the control and the significant difference was too great to permit fair comparison; the large yield of SCdaa being due to plant numbers. It may be noted however that the mean bulb weight was 5% greater than that of SC; and this insignificant, but unexpected result was probably due to better resistance to dry-rot disease. The plant numbers in the other three strains were not significantly greater than the control, yet the figures for yield were probably to some extent affected.

Correlation TABLE XXX). In each strain the effect of inverse correlation between bulb weight and dry-matter percentage may be observed by noting the plus and minus deviations.

Dry-matter percentage (TABLE XXX.) On account of the small standard error (see TABLE XXXI) all the differences in dry-matter percentage were significant.

In Yield and dry-matter yield. SCbba and SCbbb were significantly higher than SC, while SCcaa showed no significant differences.

In/

<u>In bulb weight and dry-matter content</u> the same order persisted, but, while the bulb weights showed significance, in"dry matter per 100 bulbs" all significance was lost.

<u>The Sugar determinations</u> (TABLE XXX) are chiefly remarkable for the high percentage of carbohydrates in line SCcaa, but while the superior value of the strain is maintained in the yield of sugar, significance is lost in the sugar content. ("Yield" refers to amount per plot or per acre while "content" refers to amount per bulb or per 100 bulbs.)

<u>Conclusions.</u> It may be concluded that though the three strains SCbba, SCbbb and SCcaa differed from the commercial control in detail, yet when they are compared bulb for bulb in dry-matter or sugar content the results are not significant (with the exception of sugar content in SCbba.)

In TABLE XXXI comparisions between strains are drawn, while the standard error, which in this case is also the coefficient of variability, is given on the right of the TABLE.

The first set of figures deals with the differences in composition between progenies of sister plants SCbbb and SCbba. In appearance these two/

TABLE XXXI.

COMPARISON OF SCbbb AND SCcaa WITH SCbba.

DETERMINATION	SCbbb.		SCcaa		STANDARD ERROR or COEFF. of VARIABILITY
	diff.	$\frac{\text{diff.}}{\text{S.E.}}$	diff.	$\frac{\text{diff.}}{\text{S.E.}}$	
Number of plants per plot	±0	0.1	+4%	0.8	9.7% ± 1.43
Dry matter %	+1%	1.8	+12%	28.3	0.68% ± 0.11
Yield per acre	±0	-	-16%	4.6	5.3% ± 0.79
Drymatter per acre	+1%	0.1	- 3%	2.4	5.9% ± 0.91
Weight of 100 bulbs	+1%	0.1	-20%	4.2	7.4% ± 1.09
Dry matter per 100	±0	0.1	- 8%	1.7	7.5% ± 1.16
Sugar %	-3%	1.5	+11%	7.5	2.2% ± 0.36
Sugar per acre	-3%	0.9	- 1%	0.4	4.8% ± 0.78
Sugar per 100 bulbs	-10%	1.8	-13%	2.4	7.4% ± 1.20

two plants were dissimilar, the first being of the varietal type while the other was asymmetric and somewhat ugly. The analyses of these parent plants have already been shown in TABLE XXIX. It will be seen from TABLE XXXI that the two progenies were not noticeably different. The numbers of plants per plot were practically identical, and in no determination was a significant difference found, while in several estimations the strains were identical to the nearest 1%. It may thus be concluded that no hereditary variation was isolated from SUbb by these selections, and there is a suggestion that the L_2 parent strain SCbb had been reduced in hereditary variation.

<u>Comparison of SCcaa and SCbba TABLE XXXI</u>.

In the centre of TABLE XXXI SCcaa is contrasted with SCbba. These two lines were unrelated as far back as the commercial bulbs from which they originated. It will be seen that there was a 4% difference in number of bulbs which did not however, affect the yield. SCcaa was significantly higher in dry-matter percentage and sugar percentage and significantly lower in yield per acre and bulb weight. Since the latter determinations were the more important, the net result was unfavourable for SCcaa, for the dry-matter per acre and sugar per 100 bulbs, were significantly less than in SCbba.

Thus/

TABLE XXXII.

COMPARISON OF 'STIRLING CASTLE' STRAINS IN L2 and L3 GENERATIONS.

NAME		DRY MATTER %		YIELD		BULB WEIGHT			DRY MATTER PER BULB	
L2	L3	L2	L3	L2	L3	L2 (a) *	L2 (b)	L3	L2	L3
SCbb		94%		101%		107%	94%		88%	
	SCbba		96%		114%			111%		106%
	SCbbb		96%		114%			111%		107%
SCca		102%		100%		95%	73%		75%	
	SCcaa		108%		98%			91%		98%
Control SC.		100%	100%	100%	100%	100%	100%	100%	100%	100%

* (a) = Plot weighings. (b) = rod row analyses.

Thus while two L_3 progenies from the same L_2 population showed no differences; two L_3 strains from different commercial plants of a variety, showed significant differences. A reduction in the total potential variability seems therefore to have been effected by inbreeding.

Comparison of L_2 and L_3 strains.

In TABLE XXXII the data from TABLE XXIX are rearranged so that the results of two generations may be compared.

The figures are all expressed as percentages of SC, which was grown as a control in each case; and it will readily be seen that the two generations, except as regards dry-matter percentage, compared very differently with the control. This may have been partly due to difference in cropping powers of the samples of SC used in the two generations and partly to differences in numbers of plants per plot in the L_2 tests. (see Table XXIX for these data.)

In order to compare SCbb lines with the SCca line the differences in percentage values may be calculated.

In dry matter percentage SCbb (94%) was less than SCca (102%) by -8%. The progenies SCbba and/

and SCbbb (96%) were less than SCcaa (108%) by -12%, The difference between strains was thus somewhat in the two generations. <u>In yield</u> the difference in the L_2 generation was + 1% but in the L_3 it was +16% Thus the small plot, being greatly affected by differences in density of population, is valueless as an indication of the yielding powers of a strain.

<u>In mean bulb weight</u> two replications (a) and (b) were weighed, with dissimilar results; the differences between strains being respectively +12% and +21%. In the L_3, the difference was +20%.

<u>In drymatter per bulb</u> the difference between L_2 strains was +13%, and between L_3 strains it +8% or +9%.

It may be concluded, therefore, that though the yields of small plots are valueless, the dry matter percentage and mean bulb weights may indicate the nature of strains to some extent, provided that the density of population is approximately the same for each strain tested.

The "rod-row" was found to be too small for the purpose of selecting types, and in the following years, 50 or more plants per strain were employed for such tests.

The/

<u>The plan of SC yield trial</u>. The alternate plot method of planning a yield trial was adopted here, in the hope that the large errors obtained in measurements of yield and bulb weight might be reduced. The coefficients of variability (TABLE XXXI) were, however, in most cases greater than those obtained by the chequer board method of ENGLEDOW and YULE (1926) which was employed in the SUaca trial (TABLE XXVII) while twice the number of determinations had to be made.

GENERAL DISCUSSION AND CONCLUSIONS ON BREEDING OF VARIETIES AND PEDIGREE LINES.

The term 'variety' is applied by seed growers to any sub-division of a cultivated plant form that may conveniently be reproduced and maintained to conform to an arbitrary economic standard. Genetically the varietal unit may be a clone, as in the potato; a pure line, as in the more recent cereal varieties; or a collection of pure lines as in the older cereals; on the other hand it may be a mass-multiplied population, which is the case in those plants that are normally cross-fertilised, including the swede.

In swede the seed-grower may derive a new 'variety' from the offspring of a hybridisation, or by selection from an existing 'variety'. He selects phenotypes approximating some desirable standard, and when the strain is considered sufficiently true to type, it is put on the market. There are two harvests necessary for the production of each sample of commercial seed, in the first of which a comparatively few, carefully selected plants are seeded in natural isolation; while in the second, the progenies are seeded with similar precautions. These operations have/

have to be repeated year after year, and since the type is never fixed, the quality of the variety is largely dependant upon the skill of the selector. WATSON (1925) compares the root crop variety with a herd of livestock, in which deterioration will occur if selection is neglected. There is, however, a certain amount of self-fertility in root crops, especially in the swede, so that inbreeding may occur to an extent greater than is possible in animals.

The number of genes in respect to which an individual, or group of individuals is not pure or homozygous, was termed by HAGEDOORN (1921) the "total potential variability"; and he considered that even the isolation of a random sample of a population would cause some reduction of total potential variability, because crossing would be restricted to some extent, and some factors might have been excluded. With mass-selection there would be considerable reduction of total potential variability, because undesirable dominant characters could be permanently eliminated, and a concentration of desirable characters obtained. Although recessive characters can be established, in a true breeding condition, recessive factors cannot be artifically eradicated, unless the appearance of the heterozygote is distinctive. Moreover heterozygotes may be more desirable than dominant homozygotes; and since selection cannot be carried out in/

in the multiplying generation, the commercial mass-selected sample may exhibit a considerable lack of uniformity on account of segregation and recombination.

If it is desired to breed a strain of swedes to conform to any specified character, whether it be a certain shape or a high yield of dry matter, considerable success may be achieved by strict selection and mass-multiplication. These methods, together with a general discarding of inferior strains, proved satisfactory in the Danish trials (FABER (1920)). After the initial increase in value however, progress becomes slow. Indeed, RASMUSSON (1928), reporting on N.H.NILSSON'S experiments, stated that the Scandinavian seed growers, despite constant mass-selection, had merely kept up the yields of strains to certain standards during a period of 20 years, and that there was little promise of real advance. Consequently NILSSON and RASMUSSON commenced self-fertilisation experiments with swedes, finding that there was little danger of depression due to inbreeding.

FRUERGAARD (1923) also tested the effect of self-fertilisation, and found that in swedes, unlike other root-crops, there was no marked loss of vigour due to inbreeding. In only two, out of 35 selfed lines, did he find appreciable decrease in/

in cropping power.

The present writer crossed pedigree lines of different types, and compared small plots of the F_1 hybrids with adjacent plots of selfed progenies of the parent plants. The dry matter percentages of the hybrids were equal to the mean values of the respective pairs of parents, but the bulb weight was greater, suggesting heterosis. There was not sufficient material to obtain significance, however, and the experiments are not included in this paper.

The breeding of 'pure lines'. The effect of selection and self-fertilisation has been observed. External characters were found generally to breed true from the original selection. In many cases the varieties concerned, were observed to be already uniform for these characters, especially in the case of recessives such as non-purple-neck, and yellow flesh. In the recessive bronze-top varieties, the few purple necked plants found, were either rogues of distinctive type, or heterozygotes. In recessive yellow flesh strains, white fleshed plants were generally of the bulbless bolter type, with one exception (See page 63) where a heterozygous white fleshed plant was otherwise typical of its variety.

In dominant purple-neck varieties, where a small percentage of recessives occur, plants of the main/

main type that have been bred, were usually found to be homozygotes, but occasionally a large proportion of heterozygotes was selected, (as in the case of Aberdeenshire Prize, p.55). Numerous minor characters such as shape of leaf, arrangement of leaflets, margin pattern and habit of growth, were found to be true breeding in progenies of single plants; though the parent varieties exhibited a range of forms. It would appear, therefore, that plants in the commercial variety are frequently of self-fertilised origin.

With regard to cropping powers, it is almost impossible to estimate the value of a line without yield trial, unless some obviously undesirable character, such as fanged bulbs is present. Yield trials to be really conclusive need to be repeated in diffirent years and with large plots(ENGLEDOW and YULE (1926)) in order to assess the place variation (CLARK (1910))and to minimise the differences in density of population.

These conditions are impracticable in the early stages of breeding, because the seed from a single plant is very limited. If a strain is mass-multiplied for the purpose of yield trial, two years of pedigree breeding are lost, while the strain, on account of its mass-selected nature, does not give

a/

a true representation, either of the P_1 population, or of the P_2 plant.

The chief difficulty encountered in the small plot yield trials, was the difference between numbers of plants per plot. TOCKER (1922) found similar trouble with small plots of the same variety under different treatments; for he found that sets of replications gave widely different densities of population, which were not directly attributable to the manurial treatments. In the case of variety trials, there may possibly be a differential susceptibility to diseases in the young stages, due either to hereditary causes, or to the vigour and condition of the seed. Plots may be similar in density of population immediately after singling, but in each replication differences between strains may be found at the end of the season. Besides the obvious losses due to Dry rot and finger-and toe, when these diseases are present, it is possible that seedlings may be destroyed by other diseases such as Olphidium radicicolum, de Wildem, which has been investigated by BARTLETT (1928)

The commercial "variety" does not afford a precise control, because samples of it may differ in hereditary constitution, even when they are obtained from the same grower. If seed from different sources were/

were used the populations might be of completely different type (McROSTIE (1927)).

The seed of commercial varieties may also be old and lacking in vigour.

Lines selected from commercial varieties (Stirling Castle and Buffalo) were, with one exception, of equal or greater value than the varieties. The characters of bulb weight and composition exhibited by the parent bulbs were mostly modifications however, though the preliminary choice of large bulbs seems to have been of value. (It must be noted, however, that all these characters were subject to "place variation" (CLARK (1910)) and that the differences in response to a particular environment, and not the actual values obtained were under consideration).

There are indications that inbreeding causes reduction in hereditary variation in repsect of the bulb weight and composition. This may be deduced from the selection of plants out of L2 and L_3 populations (Stirling Castle and Superlative trials) the progenies of such selections showing practically no significant differences.

Attempts to discover the effects of inbreeding on the variability in individual plants of populations were not conclusive. The only L_5 strain available/

available was decidedly less variable than the F_2 populations, but since this was a single case, the result may have been due to an exceptionally uniform environment. The F_1 population was remarkable in being slightly more variable than the F_2 populations.

The inverse correlation between dry matter percentage and bulb weight has been noted by many workers. FRUWIRTH (1922) quotes HELLRIEGEN, BUHLERT, HELWEG, ZIELSTORFF and BERGER as having found it in various types of experiments. HENDRICK (1906) gave a table in which the dry matter percentages were grouped according to bulb weight. A small proportion did not adhere to the inverse correlation, and he considered that these might be hereditary variations.

Breeding experiments described in this paper indicated that bulbs high in both dry matter percentage and bulb weight, were modified in one or other of these characters, (TABLE XXV, BFc and BFd). The extent of correlation in different populations was apparently due to the uniformity of envoronmental conditions. Even the L_5 strain showed no higher coefficient of correlation than the F_2.

The effect of correlation on variability is noticable. Great variability in bulb weight being accompanied/

accompanied by relatively great variability in dry matter percentage. It was found, however, that when the bulbs were selected for size, though the variability in weight was reduced by half, the variability in dry matter percentage was not affected.

From an examination of correlations, it may be concluded that an increase in the total dry matter percentage of a plant may be caused by independant increments of both soluble and insoluble solids.

EXPERIMENTS IN METHODS OF SAMPLING.

In order to obtain samples for dry matter or other analyses many investigators employ a cylindrical core, bored out of the swede bulb. This method may be used when collecting composite samples for determining plot yields, and also when selecting single bulbs out of large populations for breeding purposes. In the latter case a core is favoured because it causes comparatively little damage to the plant tissues. Although unreplicated estimates are not normally countenanced, it is impossible in this case to duplicate cores through identical tissues; and, in the following section, the writer has attempted to estimate the reliability and to measure the error of dry matter tests on unreplicated cores. The effect of direction of coring, the influence of irregular concentrations of solids in the bulb, and the relationship of dry matter estimates made on cores to the composition of the whole root have also been investigated.

Variability of results in single core dry-

matter/

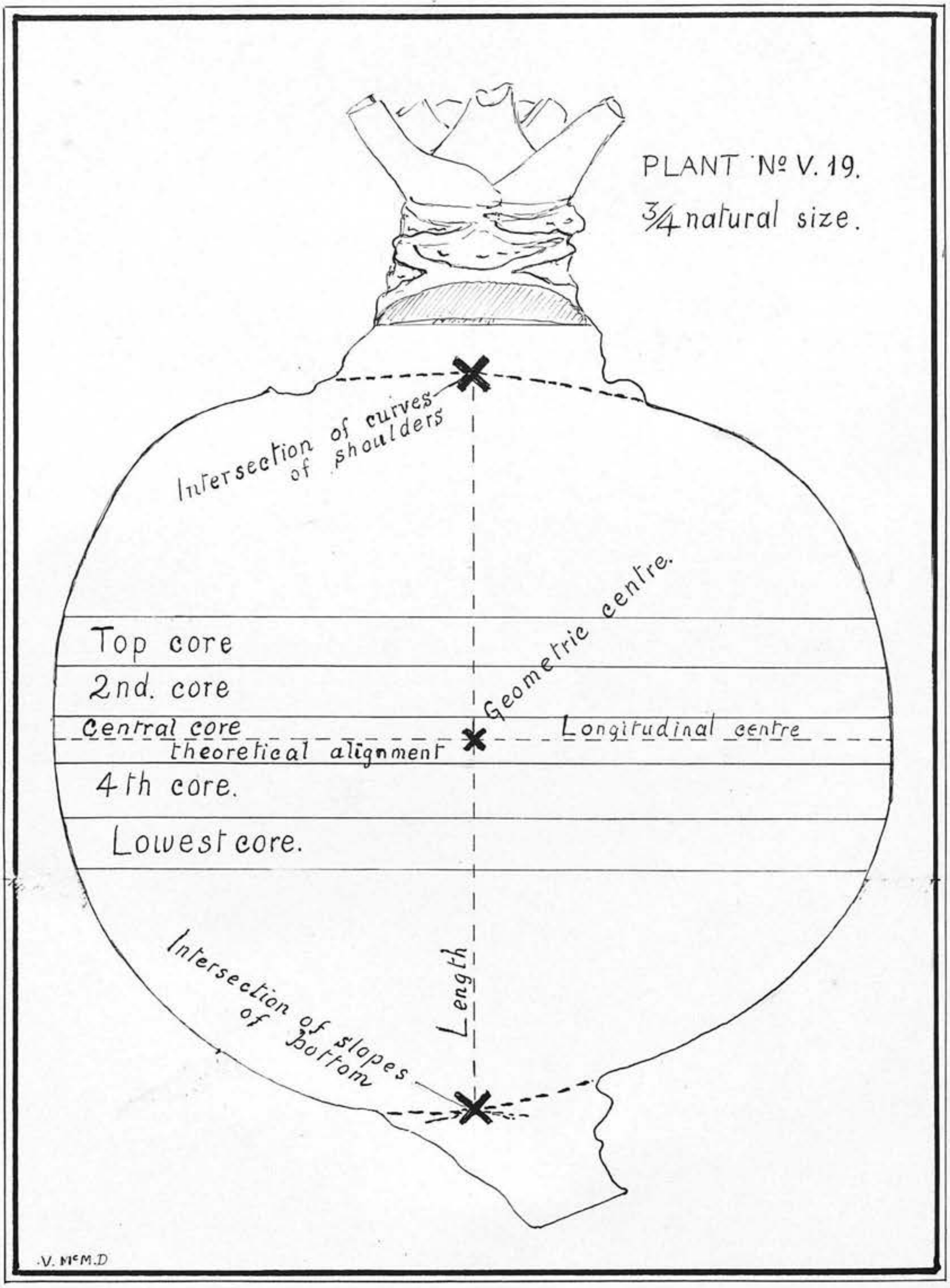


Fig. 11. Deflections of horizontal cores in a vertical plane.
Diagram to show method of cutting the cores.
(See page 152).

matter analyses may be due to several causes:-

(i) Errors of analysis.

(ii) Errors due to deflections of borer from a theoretical alignment.

(iii) Errors due to asymmetric concentrations of dry matter in the bulb.

Before dealing with these experiments it is advisable to give certain definitions. In the first place, when boring bulbs of different shapes and sizes, it is necessary to gauge certain points by eye. A longitudinal centre is found by estimating the distance between two points of intersection, (1) where the curves of the shoulders would meet if produced into the neck tissue and (2) where the slopes of the bottom would meet if produced into the tissue of the tap root. (FIGS 11 & 12) This distance is taken as the length of the bulb, and the mid point as the longitudinal centre. The middle point of a transverse plane at the level of the longitudinal centre is taken as the geometric centre. In a shouldered bulb the point of the shoulder is the point where the curvature is greatest; in a globe however, there is no physical feature to determine this point. It will be seen therefore that there may/

may be a considerable variation in core alignments. A diagonal core is here taken to mean one in which the borer is driven from the point of the shoulder diagonally through the geometric centre, and out at the bottom on the further side. A horizontal core is one in which the borer is driven horizontally through the geometric centre, from side to side. Some workers core horizontally through the greatest diameter.

Returning to the estimations of variability:-

(i) ERRORS OF ANALYSIS. Because the dry matter is unevenly distributed through the tissues of the swede bulb, uniform material is not available for replicated tests, and errors occurring during analysis must therefore remain an unknown factor and must be included in estimates of other errors. Replicated determinations on samples drawn from mixtures of swede pulp cannot be taken as analogous, since an ununiform mixture may increase the error in these. Replications of bulk samples of swede material were frequently found to give results identical to 0.01% of the fresh material weight, i.e. about 0.12% of the dry-matter value.

Care was taken in all the dry-matter determinations to maintain similar conditions of temperature, time etc.

(ii) DEFLECTION OF CORE FROM A THEORETICAL ALIGNMENT.

In order to obtain information as to the magnitude of errors due to deflections from the theoretical alignment of a core, a number of small experiments were carried out. Rectangular cores were carved out of slabs of swede bulb, so that a carefully cut central core might be compared with a pair of parallel adjacent cores as an estimate of minor deflections; and, since larger deflections might be expected if the bulb is in the ground and partly hidden, another core was cut on either side of the three, to indicate the effect of major deflections. There were three sets of these experiments:-

(a) diagonal cores lying in a longitudinal plane,

(b) **horizontal** cores lying in a longitudinal plane, i.e. two above and two below the theoretical central core, and

(c) horizontal cores lying in a horizontal plane, i.e. on either side of the true core.

In practice the deflection and the theoretical alignment would generally not be parallel, and might frequently intersect.

The/

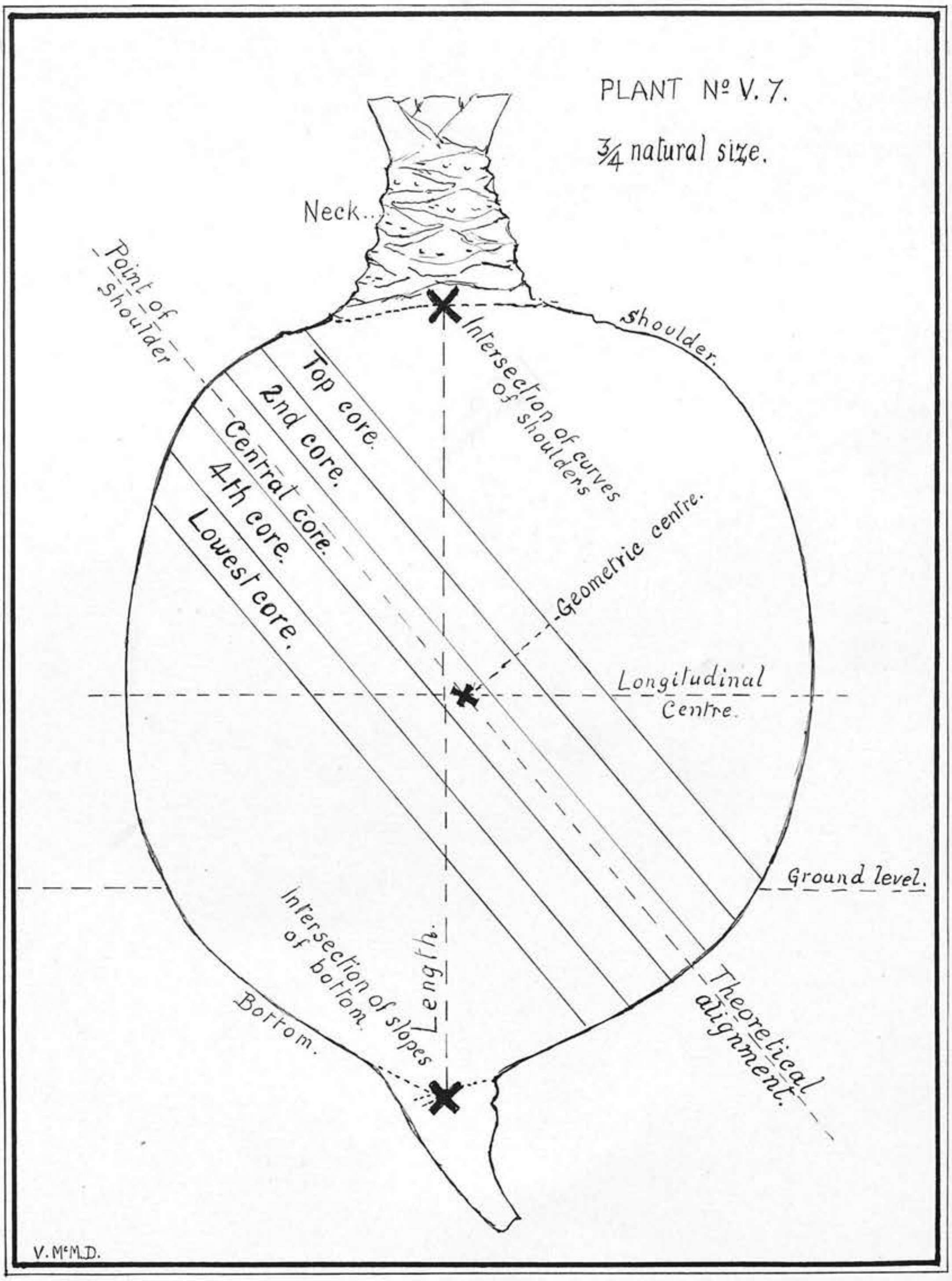


Fig. 12. Deflections, in a vertical plane, of diagonal cores.
Diagram to show method of cutting the cores.

The material included roots of different shape and size analysed at different times during the season. The results of dry matter analyses were converted to percentages for comparison.

(ii a) DEFLECTIONS IN A VERTICAL PLANE OF DIAGONAL CORES.

The bulb, having been washed and dried, was sawn longitudinally so that a central slab, 1 cm. thick, passing from neck to tap root was obtained, care being taken to avoid the diarch side root system. From this slab five cores were sliced, the central one being cut in the theoretical diagonal alignment, and the others parallel and adjacent. (FIG. 12). The cores, which were 1 sq. cm. in cross section, were then tested separately for dry matter percentage. Ten bulbs were thus treated.

In order to convert results to comparable percentages, a standard had to be chosen, and since the true central core result might contain an error of analysis, it was decided to take the mean value of the centre and adjacent cores as 100, and to compute the relative values of all five cores on this basis. In TABLE 33. the actual mean values of the central three cores are given in the third column, and/

TABLE XXXIII.

50 DIAGONAL CORES.								
Ref. No.	Description.	Ratio Length/Breadth	Actual D.M. mean value of 3 inner cores	Value of core, when mean of 3 inner cores=100				
				Top core 2 cm above.	1 cm. above	Central core.	1 cm below	Lowest 2 cm below
V. 1	Tankard.	1·9	12·00%	101·5	101·0	100·3	98·7	98·1
2	"	1·8	10·86	100·0	99·8	100·1	100·1	100·7
3	Globe	1·2	10·63	102·8	100·3	100·6	99·3	99·3
4	"	1·2	10·90	102·3	100·0	99·6	100·6	100·0
5	"	1·1	10·56	104·2	101·6	100·7	97·7	97·1
6	"	1·1	10·91	100·7	100·7	99·7	99·6	99·3
7	Half-long	1·1	12·15	100·8	100·7	99·1	100·2	101·6
8	Globe.	1·0	10·42	104·2	100·9	100·6	98·4	100·7
9	"	0·9	12·39	103·1	100·7	99·3	99·9	99·1
10	"	0·9	10·96	102·0	101·7	99·2	99·1	99·4
			Mean	102·2	100·7	99·9	99·4	99·5
	Deflections				Within 3 cm.	...	Within 5 cm.	
	Co-efficient of Variability ...				0·89% ± 0·115	...	1·45% ± 0·145	
	Standard error of mean difference. ...				± 0·40	...	± 0·65	

VARIABILITY IN DRY MATTER PERCENTAGE DUE TO VERTICAL DEFLECTIONS IN BORING DIAGONAL CORES.

and the values of the various cores are set out as percentages. The ratio length/breadth is given as an indication of the proportions of each bulb.

Statistics have been compiled to show the variability within the central three cores, and it will be seen that the co-efficient of variability was 0.9% ± 0.12, from which it may be inferred that the standard error due to minor deflections of the borer in a single estimation on a bulb of 12% dry matter would be ± 0.11% of the fresh weight.

Similar statistics are given for all five sets of cores, the variability of which was greater, being 1.5% ± 0.15, so that a series of cores, in which deflections of 2 cm. from the theoretical alignment were common, must be assigned a standard deviation of about 0.18% of the fresh weight in bulbs containing 12% dry matter.

The mean values of the sets of cores form a gradient diminishing in dry matter from above downwards. The individual results for the lowest set of cores are variable, some being relatively high and others low. If twice the standard error is taken as significant, it will be seen that the top set is significantly higher than all the others, while/

TABLE XXXIV.

50 HORIZONTAL CORES.

Ref Nº.	Description.	Ratio Length / Breadth	Actual D.M. mean value of 3 inner cores	Value of core, when mean of 3 inner cores = 100				
				Top core 2 cm above	1 cm above	Central core	1 cm below	Lowest 2 cm below
V.11	Tankard	1·9	11·86%	99·5	100·5	$\boxed{98{\cdot}3}$	101·2	97·3
12	"	1·8	12·29	$\boxed{99{\cdot}0}$	99·8	100·0	100·2	100·8
13	Half-long	1·2	11·15	100·3	$\boxed{99{\cdot}6}$	99·5	101·0	101·3
14	Globe	1·2	10·38	106·1	$\boxed{100{\cdot}2}$	100·9	98·9	99·1
15	"	1·1	10·86	$\boxed{101{\cdot}1}$	100·4	100·2	99·3	99·5
16	Half-long	1·1	10·95	104·0	101·3	$\boxed{99{\cdot}4}$	99·3	98·1
17	Tapering Globe.	1·1	14·18	$\boxed{97{\cdot}3}$	98·0	100·5	101·7	101·6
18	" "	1·0	14·42	100·0	$\boxed{99{\cdot}9}$	98·4	101·7	102·9
19	Round.	0·9	10·61	101·4	$\boxed{99{\cdot}9}$	99·8	100·2	102·6
20	"	0·8	12·51	101·5	$\boxed{100{\cdot}4}$	100·0	99·7	100·8
			Mean.	101·0	100·0	99·7	100·3	100·4

Deflections................................	Within 3 cm.	...	Within 5 cm.
Coefficient of Variability..............	0·9% ± 0·118	...	1·58% ± 0·158
Standard error of mean difference.........	± 0·40	...	± 0·71

VARIABILITY IN DRY MATTER PERCENTAGE DUE TO VERTICAL DEFLECTIONS IN BORING HORIZONTAL CORES.

while the second set exceeds the two lowest.

(ii^{b}) DEFLECTIONS IN VERTICAL PLANE OF HORIZONTAL CORES.

The preparation of a longitudinal slab of bulb was carried out as in the previous experiment (ii^{a}), and five cores were sliced out of it in a horizontal direction, one in the theoretical alignment, two immediately above, and two below. (See FIG. II).

Dry matter determinations were carried out on the cores, ten roots being thus treated.

In TABLE 34. the dry matter values of the 50 cores are stated as percentages where the average value of the three central cores of each set was taken as 100.

The co-efficient of variability within the central three cm. was 0.9% ± 0.12, and that for all five was 1.6% ± 0.16. There was no significant difference between sets of cores and no general gradient of dry matter distribution was observed, but the results of individual roots showed different tendencies. Thus Nos. 14,15 and 16 exhibit fairly uniform gradients decreasing from above downwards, while in Nos. 13,18,19 and 20 there is a tendency for/

for an increase in the lowest cores. In Plant No. 17 the above ground portion was wide and flat, while the bottom tapered uniformly to a deep tap root, which may explain the results obtained in this case. The behaviour of the tankards (Nos. 11 and 12) seems to be uncertain.

In TABLE 34. the longest core of each bulb has been marked by surrounding its value with a thick line. The effect of coring with the greatest diameter instead of the longitudinal centre as a theoretical alignment may thus be ascertained. The ten cores coinciding with the greatest diameters had relative values as follows;- 98.3%; 99.0%; 99.6%; 100.2%; 101.1%; 99.4%; 97.3%; 99.9%; 99.9% and 100.4%. The mean value was 99.5% and the difference between mean values of longitudinal centre and greatest diameter cores was 0.5%±0.37, which is not significant. The co-efficient of variability of greatest diameter core values was 1.04% ± 0.23, which closely approximates the variability found for minor deflections..

It appears that the concentration of dry matter at different levels depends to a large extent upon shape. The longitudinal centre, as previously defined does not coincide with similar tissues/

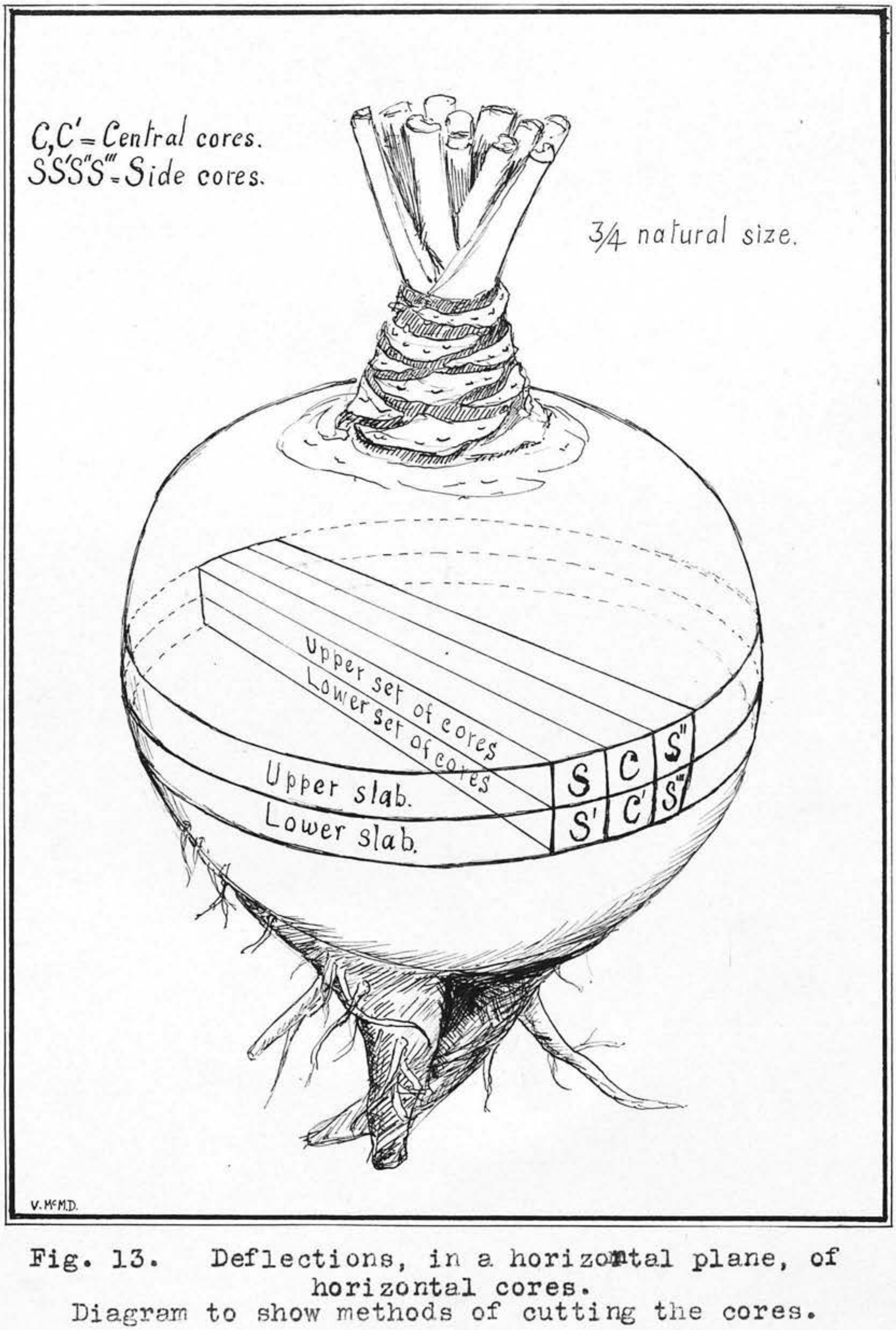


Fig. 13. Deflections, in a horizontal plane, of horizontal cores.
Diagram to show methods of cutting the cores.

tissues in roots of different shape, while the greatest diameter in the above ground portion of the bulb may be situated very differently in globes, tankards, bulbs with wide shoulders, and bulbs that slope from shoulder to ground level. It is seen, therefore, that neither the longitudinal centre nor the greatest diameter affords precision when coring horizontally.

(iic) DEFLECTIONS IN A HORIZONTAL PLANE OF HORIZONTAL CORES.

The washed bulb was sawn in half transversely through the longitudinal centre, and from each cut surface slabs 1 cm. thick were sawn; the top and bottom portions of the root were then discarded. The upper slab was replaced on the lower slab in its original position and three cores were cut from each in such a way that corresponding cores lay in the same longitudinal plans, (see Fig. 13.). Of these, one core conformed to the theoretical alignment, while the other two lay on either side of this central core. Ten bulbs were treated in this way, and the sixty cores so obtained were tested for dry matter percentage.

It was considered unnecessary to take

cores/

TABLE XXXV.

60 HORIZONTAL CORES.											
	CORES VARIOUSLY ORIENTATED.					CORES ORIENTATED, EAST TO WEST.					
Ref. Nº.	Position.	Mean D.M%	expressed as %age of mean.			Ref Nº.	Position.	Mean D.M.%	expressed as %age of mean.		
			Side	Centre	Side				North	Centre	South.
V.21	Upper	11·46%	100·2	99·1	100·8	V.26	Upper	10·88%	99·6	99·6	100·8
	Lower	11·20	99·4	99·9	100·7		Lower	10·54	99·6	99·4	100·9
22	Upper	12·24	98·0	100·3	101·6	27	Upper	12·35	97·9	99·8	102·3
	Lower	11·69	95·8	100·4	103·9		Lower	11·91	98·8	99·7	101·6
23	Upper	12·53	98·4	99·8	101·7	28	Upper	8·45	99·3	99·2	101·4
	Lower	12·50	97·8	100·1	102·1		Lower	8·61	100·0	99·3	100·7
24	Upper	11·49	100·4	99·7	99·9	29	Upper	8·84	99·9	99·5	100·6
	Lower	11·46	99·6	99·9	100·6		Lower	8·62	100·1	99·1	100·7
25	Upper	11·89	99·5	99·8	100·6	30	Upper	9·55	100·8	99·6	99·5
	Lower	11·48	99·7	99·3	101·2		Lower	9·54	103·4	98·5	98·0
	Mean			99·8			MEAN		99·9	99·4	100·7

Orientation	Various (left side)	East to West	Both sets.
Co-efficient of Variability	1·41% ± 0·182	1·17% ± 0·151	1·29% ± 0·118
Standard error of mean difference.	—	± 0·78	—

VARIABILITY IN DRY MATTER PERCENTAGE DUE TO HORIZONTAL DEFLECTIONS IN BORING HORIZONTAL CORES.

cores at 2 cm. from the centre, since deflections are not likely to be as great in a horizontal plane, where the whole circumference may be seen, as in a vertical plane, where part of the bulb may be hidden underground. In the first five bulbs no note was taken of the orientation of the cores (TABLE 35 left side) except that they were cut at right angles to the diarch side root systems; since however, as gradients of dry matter appeared in some of these, the last five (TABLE 35right side) were cut in an east to west direction, and the side cores were distinguished according to whether they lay to North or South of the centre.

In TABLE 35 the actual mean value of each set of three cores is given, and taking this as 100, the values of individual cores of the set are expressed as percentages. The duplicate sets of cores were not averaged, but were treated as separate tests.

The coefficient of variability for the last five plants, cored East to West, was 1.2% ± 0.15, which is slightly less than that of the first five plants, 1.4% ± 0.18. A general co-efficient of variability, compiled from all the figures was 1.3% ± 0.12. It may be noted that while the dry matter percentage/

percentage was higher in the south than in the north cores of plants Nos. 26, 27, 28 and 29, the reverse was the case in bulb No. 30. There is no significant difference in dry matter value between cores to North and to South of the centre in the few bulbs tested. The duplicate tests carried out on each plant indicate that, in the main, the differences found were due to asymmetric concentration of dry matter in the bulb.

The estimates of variability found in the preceding sections may be summarised as follows:-

TABLE. XXXVI.

VARIABILITY OF DRY MATTER PERCENTAGE DUE TO DEFLECTIONS OF CORE FROM THEORETICAL ALIGNMENT.

CORING METHOD	DIRECTION of DEFLECTIONS	MINOR DEFLECTIONS	MAJOR DEFLECTIONS.
Diagonal	Vertical	0.9% ± 0.12	1.5% ± 0.15
Horizontal	Vertical	0.9% ± 0.12	1.6% ± 0.16
Horizontal	Horizontal	1.3% ± 0.12	- -

CONCLUSIONS. From the co-efficients of variability given in TABLE 36 , it may be concluded that/

that, in bulbs of average dry-matter percentage, e.g. 12%, a difference exceeding 0.5% of the fresh matter weight might be taken as significant, i.e. due to causes other than sampling, but that if the plants are sampled while in the ground this might be increased to 0.55%.

(iii) ASYMMETRIC CONCENTRATIONS OF DRY MATTER IN THE BULB.

Several investigators have traced dry matter concentrations and gradients in swede and other 'roots', and some of their results will be mentioned in the discussion below; the present experiments are confined to three or four points which may be of importance when taking samples by single core methods these are:-

(a) The presence of a slender column of very low dry matter which FRUWIRTH (1922) found to pass down the centre of the bulb from the heck to a point near ground level. If this should extend so far down it would greatly affect single core determinations, since cores might or might not pass through this region of low dry matter.

(b) Greater concentration of dry matter in the southern half of a core cut horizontally from/

from North to South, was demonstrated by SANSOME (1926) who also suggested that this was due to a displacement towards the North of FRUWIRTH'S low dry matter column. It was necessary, therefore, to test the concentrations of dry matter at various points along the line of a horizontal core.

(c) FABER (1920) quotes KRISTENSEN (1911) as having shown that, in beet, a side of the root which bore rootlets was higher in dry matter than a smooth side. It was, therefore, necessary to note this effect in swede and to estimate the amount of difference, if any, between horizontal cores cut low along the radii of the diarch side roots, and cores cut at right angles.

(iii) a & b. AN EXPERIMENT TO DETERMINE THE RELATIVE DRY MATTER VALUES OF DIFFERENT PORTIONS OF A HORIZONTAL CORE ORIENTED NORTH AND SOUTH.

In a horizontal core there are several types of tissue. On the outside there is a layer of "bark", about 0.4 cm. thick, which can be detached from the interior tissue of "flesh" at a cambial/

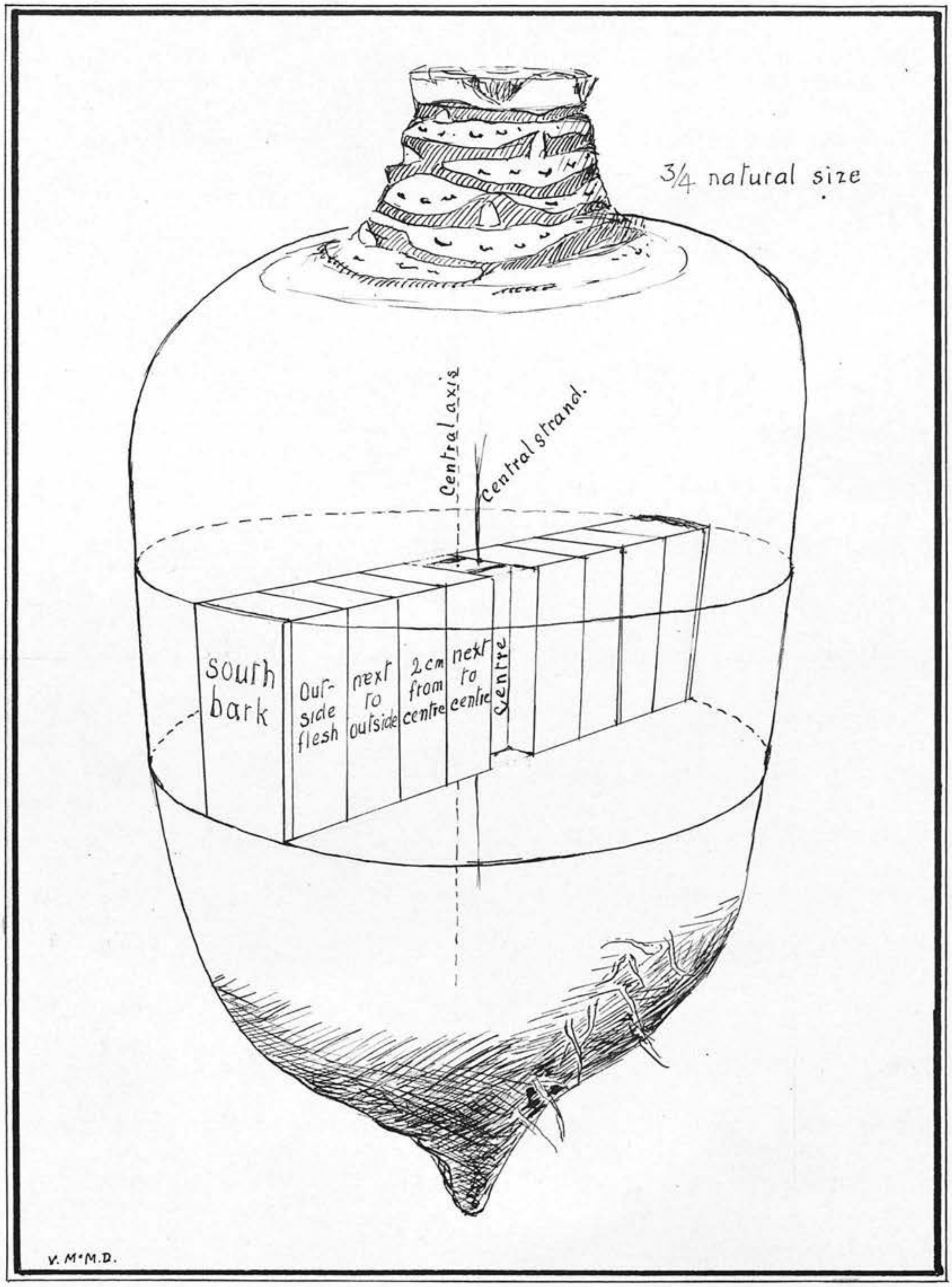


Fig. 14. Diagram to show method of cutting the bulb in order to determine the relative dry matter values of different portions of a horizontal core.

cambial region. The consistency of the "flesh", which according to PERCIVAL (1926) is composed mainly of degenerate wood, varies in different parts, the surface layer being largely composed of fibrous tissue, while the interior is mainly xylem-parenchyma with diffused fibro-vascular strands. (HABERLANDT 1914) A stouter lignified strand extends from the tap root along the central axis.

Since there is not sufficient material in an ordinary core to provide for analysis of different sections, a larger strip, 2 cm. wide and 4 cm. deep, was cut across the centre of the root, from North to South. (Fig. 14.)This strip was cut tangentially into sections 1 cm. thick, so as to afford information as to each centimetre length in a horizontal core. The "bark", however, was stripped off and tested separately. Straight sided and erect growing bulbs were chosen for this purpose, and the north point was marked while each plant was still in the ground. In cutting up the strip of material the following procedure was adopted. The centre was first ascertained by measurement, and a section cut to include the central axis. In this central section the sides were shaved down so as not to include too much tissue on the East and West. The north/

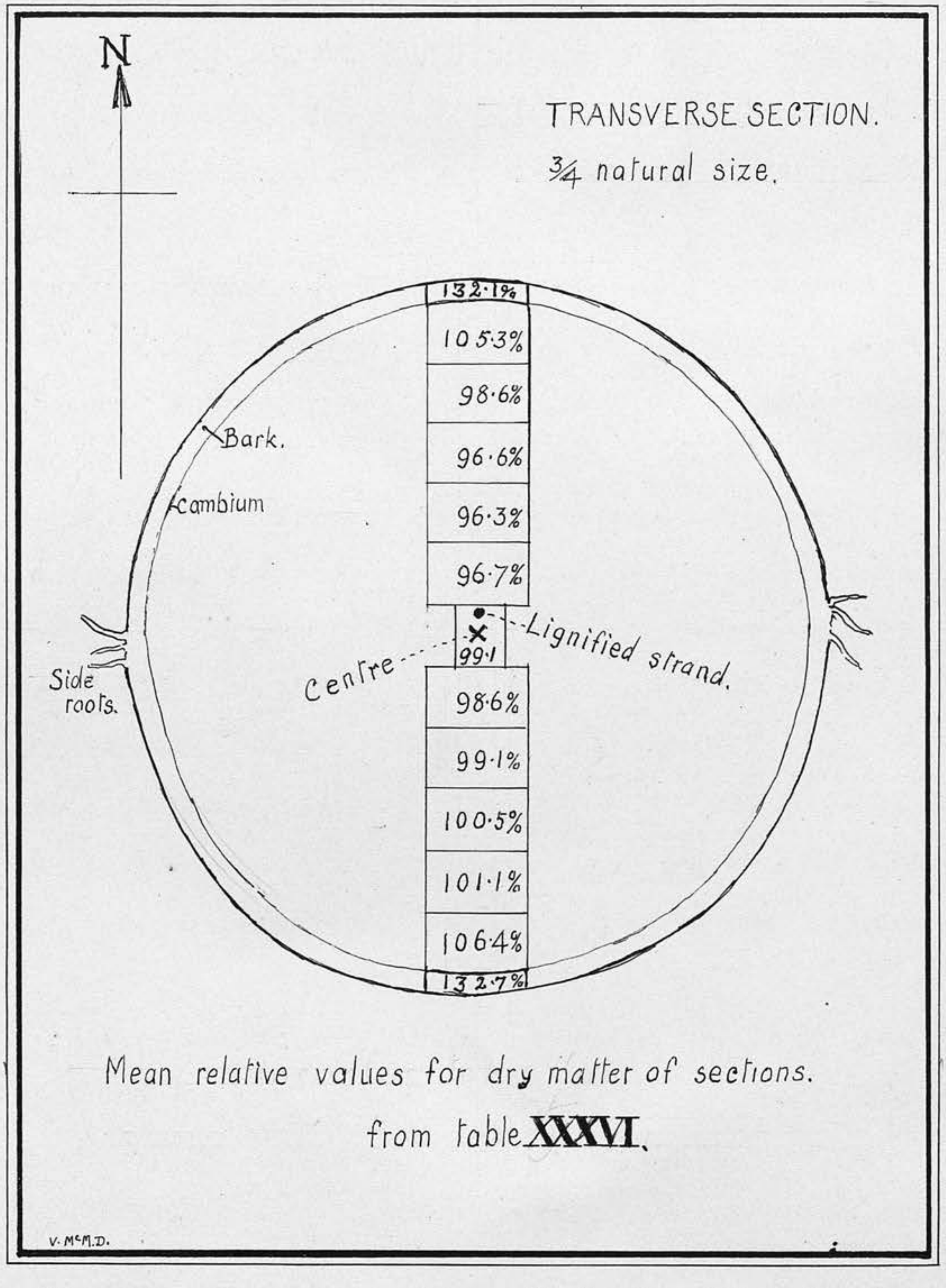


Fig. 15. Diagram to show method of cutting the bulb in order to determine the relative dry matter values of different portions of a horizontal core.

north and south "barks" were then stripped off and analysed separately. Next the remaining pieces of flesh were measured and cut into equal numbers of sections, about 1 cm. in radial thickness, so that corresponding portions to North and South could be contrasted. The central lignified strand usually fell half into the central section and half into the adjacent northern section. Each section was marked on a diagram (Fig. 15) and tested separately for dry matter percentage. Ten bulbs were thus treated.

Four of the bulbs were larger in diameter than the others, and, in order to treat the data statistically the following grouping was made. The five middle sections of each bulb were arranged in columns (See TABLE 37) The "bark" sections and the two outer pairs of flesh sections were also entered in columns. This left four pairs of sections midway between bark & centre, belonging to the four larger roots; and these were grouped by themselves.

The mean dry matter value for the flesh of each bulb was calculated, and, taking this as 100; each section, including the "bark", was set out as a percentage of this value. Thus, the figures in different bulbs can be compared. (TABLE XXXVII)

In estimating a general standard error for the flesh sections it was necessary to eliminate variance/

TABLE XXXVII.

DISTRIBUTION OF DRY MATTER ALONG CORE.														
		NORTH SECTIONS.							SOUTH SECTIONS.					
			"FLESH" SECTIONS						"FLESH" SECTIONS					
Ref. Nº.	Mean D.M. percentages of Flesh sections	BARK	Outside	Next to outside	3 cm. from centre.	2 cm. from centre	Next to centre	Centre axis	Next to centre	2 cm. from centre	3 cm from centre	Next to outside	Outside.	BARK.
1	11·61	140·9	106·4	95·7		94·2	94·1	97·9	100·0	100·9		103·1	107·2	141·7
2	12·08	124·7	102·8	100·4		99·0	98·4	100·2	98·7	99·9		99·5	101·4	123·3
3	12·21	138·2	108·0	97·9		95·7	93·7	101·4	98·5	96·9		99·4	108·1	145·2
4	11·78	131·8	105·8	100·9		99·6	97·9	98·0	97·6	98·2		97·5	104·1	136·0
5	11·29	123·9	103·5	98·2		95·1	95·3	101·4	98·1	99·7		102·3	106·8	134·8
6	9·66	136·1	107·4	99·7		93·2	97·1	98·1	97·2	99·6		100·7	107·1	127·4
7	12·33	124·6	105·4	100·3	97·9	96·5	97·8	99·9	100·4	98·0	98·2	100·2	105·2	128·0
8	12·32	136·1	103·5	94·6	95·9	98·5	101·2	101·1	99·6	101·1	100·5	100·2	103·9	133·0
9	11·39	130·0	108·6	100·4	96·3	94·3	92·6	94·3	96·4	96·4	101·6	104·6	114·1	134·5
10	11·23	134·2	101·2	97·8	96·3	96·8	98·5	98·9	99·6	100·2	101·5	103·0	106·0	123·0
Totals.		1320·5	1052·6	985·9	386·4	962·9	966·6	991·2	986·1	990·9	401·8	1010·5	1063·9	1326·9
Means.		132·1	105·3	98·6	96·6	96·3	96·7	99·1	98·6	99·1	100·5	101·1	106·4	132·7

STATISTICS FOR THESE DATA ARE GIVEN IN TABLE XXXVIII.

DISTRIBUTION OF DRY MATTER CONCENTRATION ALONG HORIZONTAL CORES ORIENTATED NORTH AND SOUTH.

variance due to treatments, i.e. due to the different mean values of the sets of sections. This was effected by a method given by FISHER (1925) (page 227). For the estimation of variance due to treatment, only the nine full columns could be employed. (See TABLE)

TABLE XXXVIII.

STATISTICS FOR DRY MATTER DETERMINATIONS OF SECTIONS (EXCLUDING BARK) GIVEN IN TABLE 5.

Variance due to:-	Sum of Squares	Degrees of Freedom	Mean Square	S.D.
Uncorrected deviations	1484.67	97	15.31.	
Treatment	1000.25	8	125.03	
Experimental error	484.42	89	5.44	2.33%

S.E. of difference for groups of 10 tests = ± 1.04%

" " " " " " 4 tests = ± 1.65%

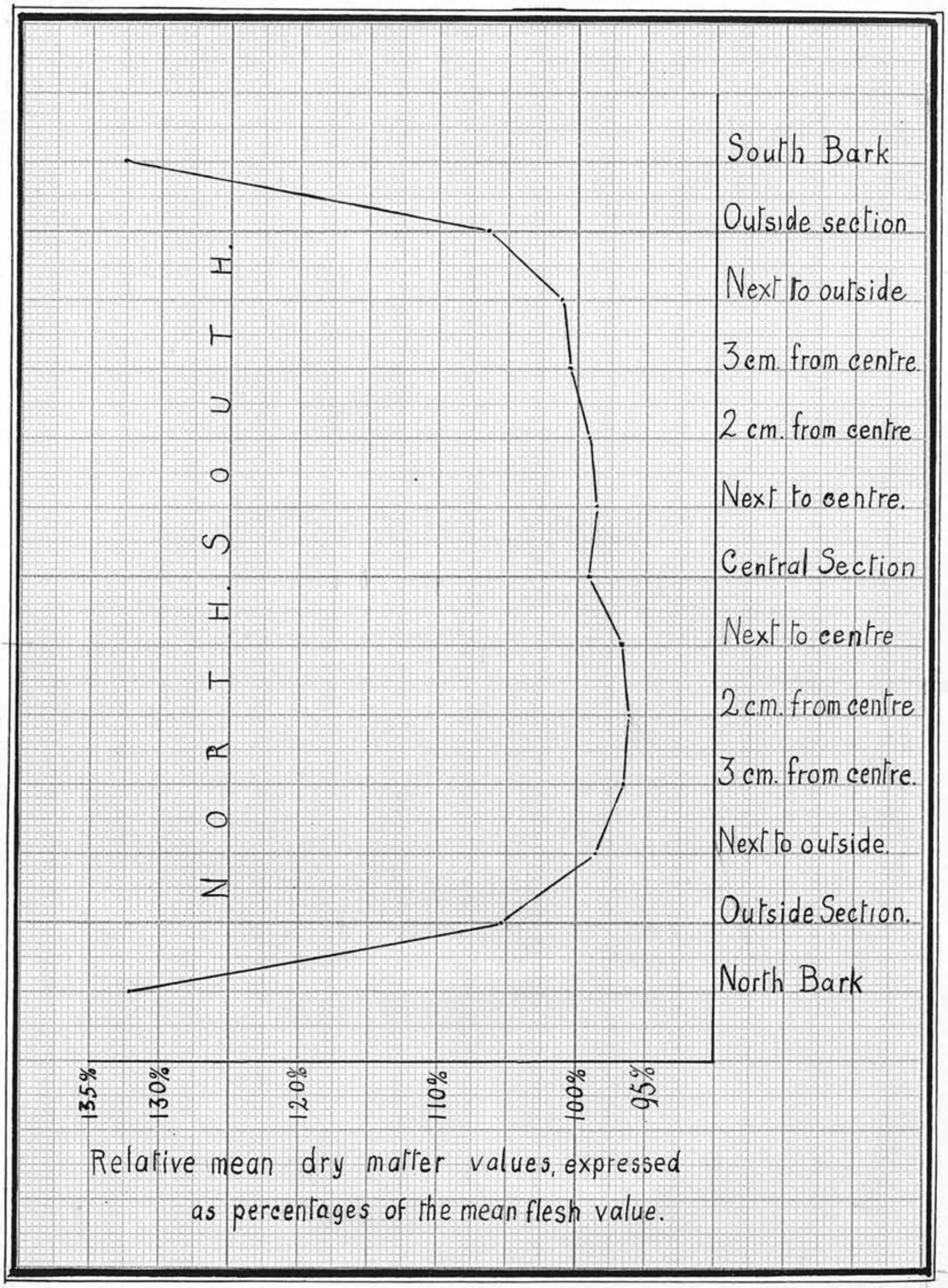
By separate estimations.

S.D. of Dry matter determinations in bark =±6.4 %

S.E. of difference for groups of 10 tests =±2.9%

CONCLUSIONS/

FIGURE 16.


South Bark
Outside section
Next to outside
3 cm. from centre.
2 cm. from centre
Next to centre.
Central Section
Next to centre
2 cm. from centre
3 cm. from centre.
Next to outside.
Outside Section.
North Bark
NORTH. SOUTH.
135%
130%
120%
110%
100%
95%
Relative mean dry matter values, expressed as percentages of the mean flesh value.

CONCLUSIONS.

The presence of tissues of low dry matter value in, or near the central axis of the bulb was not observed in any of the ten plants analysed. FRUWIRTH (1922) obtained a column 1.5 cm. wide with a dry matter value equivalent to 47% of that found in the surrounding tissues. The lowest section value found in the present experiment was only a drop of 7.4% below average.

SANSOME'S (1926) suggestion that the displacement of a central area of very low dry matter accounted for the greater dry matter value which he found in the southern halves of horizontal cores, was not confirmed. It is true, however, that swede bulbs grow asymmetrically. In particular, it is found that, when a bulb has been knocked over, which frequently occurs during cultivation, the upper side develops more rapidly, and the central strand is closer to the lower surface. But even when the bulbs are growing erect, and not crowded in the drill, there is a slight displacement, for it was found in the above material, that in seven cases the strand was about 0.5 cm. to the north of the measured centre while in the other three cases it was central.

It will be seen from Figure 16 that there was/

was a symmetrical arrangement of dry matter in the bulb. The bark was about 33% richer than the average flesh. The outside flesh sections were about 6% above the average, and there were no great differences between the interior sections. When corresponding sections to North and South of the centre are compared (TAB.39) however, it will be seen that there was higher dry matter percentage in every south section. This superiority was negligible in the bark, and not significant in the outside and innermost pairs of sections, but was significant in the remainder.

TABLE XXXIX.

COMPARISON OF MEANS OF NORTH AND SOUTH SECTIONS.

Section	Excess of South over North	S.E. of difference	$\frac{\text{Dif.}}{\text{S.E. of dif.}}$
Bark	0.7%	±2.9	0.2
Outside section	1.1%	±1.04	1.1
Next within	2.5%	±1.04	2.4
3 cm. from centre	3.9%	±1.65	2.3
2 cm. from centre	2.8%	±1.04	2.7
Next to centre	1.9%	±1.04	1.9

Comparing/

Comparing the mean difference of flesh sections (as calculated from the four full columns on each side in TABLE 37) it was found that the south side was richer than the north by 2.08% ± 0.52 which is fully significant, and confirms SANSOME'S observations. It may be concluded, therefore, that a greater concentration of dry matter is deposited throughout the flesh tissues in the southern half of the bulb, and that this is fairly uniformly distributed within the peripheral region, but less marked towards the centre.

(iii)c. EFFECT OF VASCULAR TISSUE FEEDING SIDE ROOTS.

The swede "bulb" is a storage organ composed of shoot, hypocotyl and true root tissues. The positions of the lowest leaves are marked by scars on the somewhat flattened top of the bulb; and there is a considerable distance between these scars and the uppermost side roots; this part of the bulb is said to have originated in the hypocotyl region. The first side roots frequently arise from points an inch or more above ground level. This is probably accounted for by the fact that the soil is pared away from the roots at the seedling stage. It is ,therefore,possible when boring a core to include some of the vascular tissues which feed the upper side roots, and which, being/

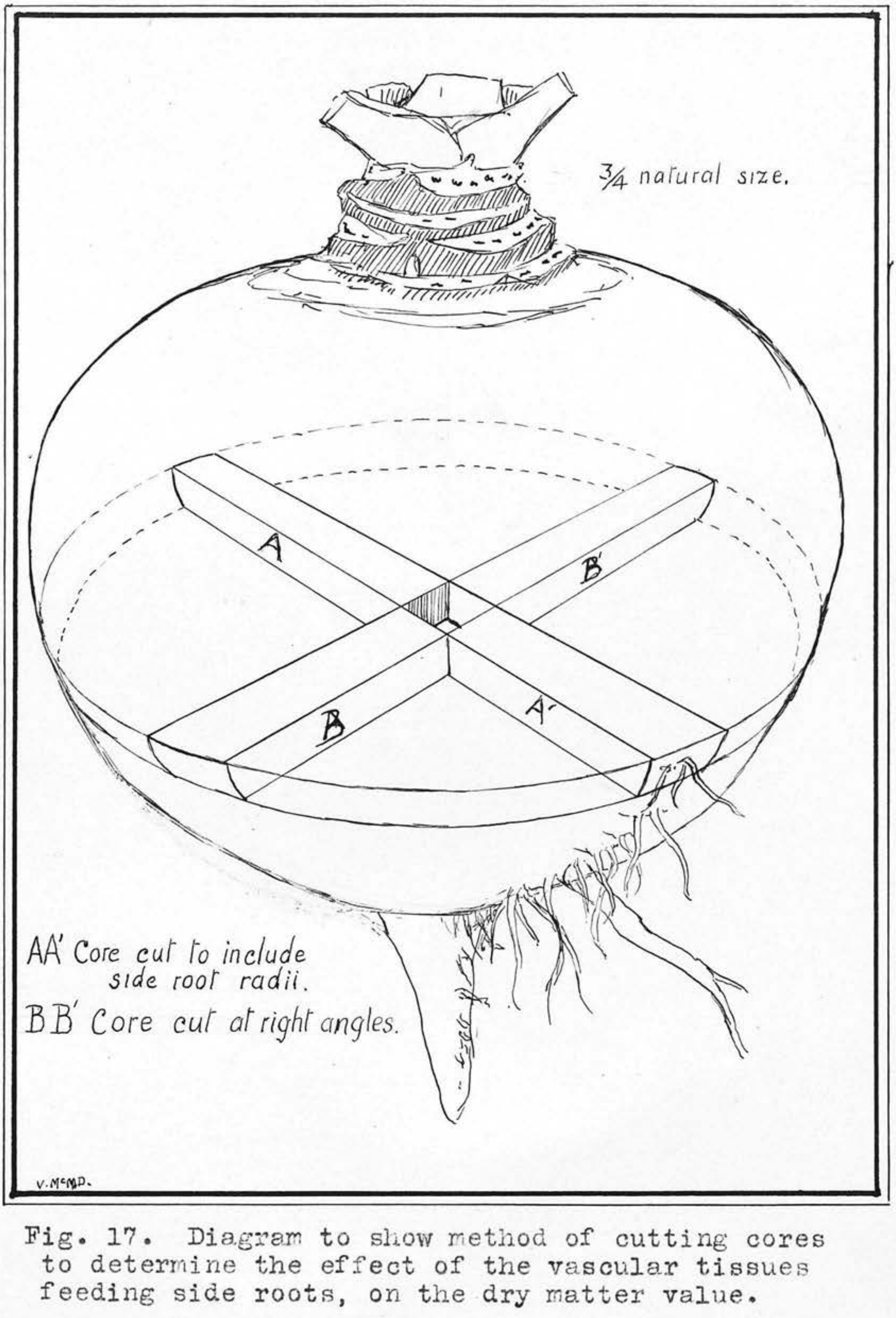


Fig. 17. Diagram to show method of cutting cores to determine the effect of the vascular tissues feeding side roots, on the dry matter value.

being deep seated, run to the centre of the bulb.

It was considered desirable to discover what effect such boring would have on the dry matter value.

Method:- A transverse slab, one centimetre thick was cut from a swede bulb somewhat below the middle but above ground level so that side roots were included. A square core was cut across the centre of the slab to include the radii of the side roots, and a second similar core was cut from the same slab at right angles to the first. The small cube of central tissue common to both was discarded, and the cores were tested separately for dry matter value. (See Fig. 17) Sixteen such tests were made.

The values found for cores including side root tissue were expressed as percentages of the normal values, i.e. of those at right angles. Results ranged from 97.9% to 102.3%. The mean value was 99.77%, and the difference 0.23% ± 0.43. There was therefore no significant difference between tissues which included vascular strands, and those at the same level which did not. The co-efficient of variability for the difference was 1.7% ± 0.31, which is comparable to the variability of major deflections (See TABLE XXXVI)

COMPARISON/

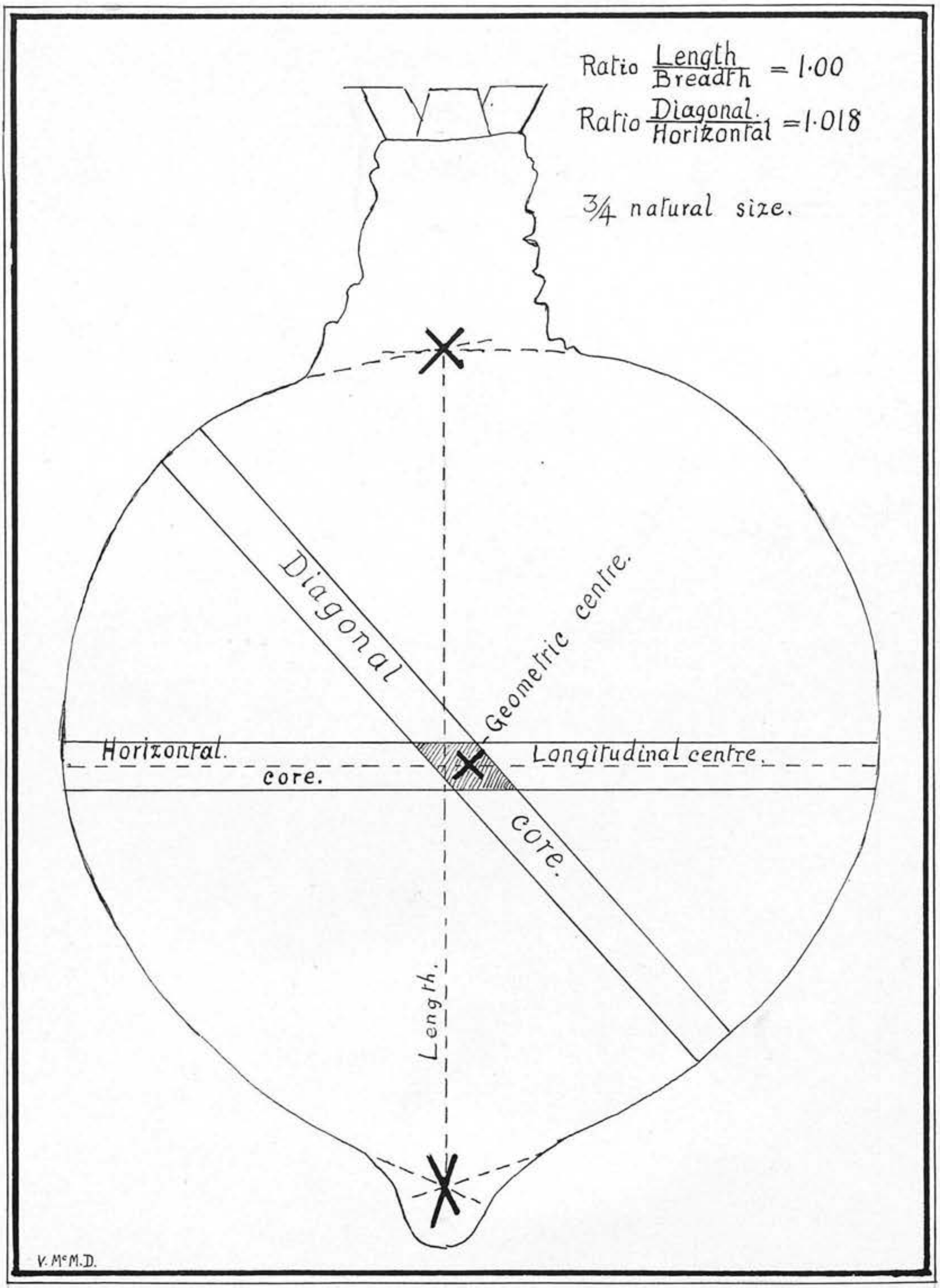


Fig. 18. Diagram to show method of cutting horizontal and diagonal cores for comparison.

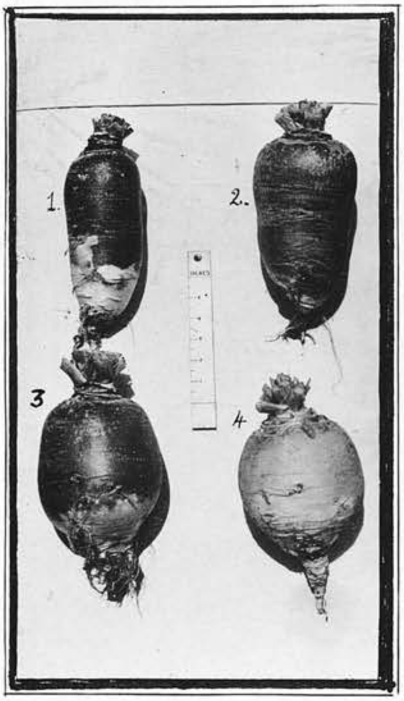
COMPARISON OF HORIZONTAL AND DIAGONAL CORES.

A small experiment was performed to estimate the relationship of horizontal and diagonal cores.

S.H. COLLINS (1906) referring to the sampling of plots by coring a large number of bulbs, considered that cores might be taken in any direction, so long as they passed through the centres, without altering the composition of the bulk sample to any great extent. With single root determinations, however, it is necessary to take every precaution to obtain comparable results.

Method:- The washed swede bulb was sawn longitudinally so that a slab 1 cm. thick was obtained, passing from neck to tap root through the central plane (Fig. 18) From this slab two cores were sliced, one diagonally and one horizontally, the central cube common to both cores was discarded, and the cores were tested separately for dry matter value. The ratio length/breadth of the bulb was noted since it was thought possible that different shapes might give different results. Sixteen roots of different shapes were thus treated.

The dry matter value of the diagonal core was expressed as a percentage when that of the horizontal core was taken as 100. The relative values of diagonal/



1. Tankard.
2. Tankard, slightly waisted.
3. Half-long,
4. Long globe, oval.

5. Globe, spherical.
6. Globe, sloping shoulders.
7. Globe, short axis.
8. Flat at shoulder, with deep, tapering bottom.
9. Shouldered globe.
10. Flat, (Milan turnip) an extreme type, not found in swedes.

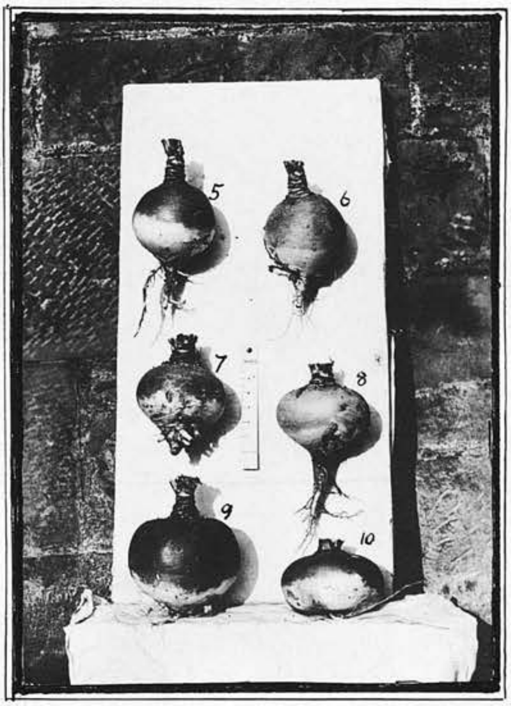


Fig. 19. Photographs to illustrate the range of shapes found in swedes.

diagonal cores ranged from 99.3% to 104.9%. The mean value was 101.76%. Diagonal cores exceeded horizontal cores by 1.8% ± 0.39, which may be regarded as a significant difference. The ratio diagonal/horizontal core dry matter value, as found above, was compared with the ratio length/greatest breadth of the bulb in order to determine whether any correlation existed between long roots and relatively high dry matter in the diagonal core. The roots employed ranged from tankards with a ratio length/breadth of 1.9 to rounds in which the axis was shorter than the breadth (0.8). The co-efficient of correlation was found to be + 0.19 ± 0.241, which was not significant.

COMPARISON OF DRY MATTER PERCENTAGE AS ESTIMATED BY SINGLE CORE WITH REPLICATED TESTS OF PULPED BULB.

The sampling of a bulb by means of a single core is an arbitrary method, justified only by the relatively slight damage done to the plant. It is unlikely that the composition of the tissues included in the core will be identical with that of the whole bulb; and since the cylindrical core contains relatively much central and little peripheral tissue, it is to be expected that the dry matter value of a core will be less than that of the whole bulb. An experiment was made to determine the amount of this difference, and the variability of a single core when used as an expression of the dry matter value of the bulb from which it was cut.

Thirty roots were cored horizontally at different times, and, after the necks had been cut off for breeding purposes, the remainder of each bulb was pulped.

Dry matter estimations were made on single cores and upon replicate samples of pulp.

The dry matter value given by the single core was expressed as a percentage of the whole root value/

value. The relative core values ranged from 90.8% to 98.2%, the mean value being 95.1% of the whole root value. The mean difference was 4.9% ± 0.53 which is significant. The co-effecient of variability of the difference was 2.0% ± 0.26.

Conclusion. When sampling a bulb by a single horizontal core the dry matter value is about 5% less than the actual value of the whole bulb, i.e. in a bulb of 12% dry matter, a horizontal core would have a value of about 11.4%.

Since the diagonal core has been shown to be nearly 2% higher in dry matter than the horizontal core, the difference between diagonal core and whole root might be taken as approximately 3% on the average.

DISCUSSION ON THE DISTRIBUTION OF DRY MATTER IN SWEDES.

In the bulb of the swede, turnip, mangel etc., the solids are distributed unevenly, and since there is great variability in shape, it is questionable whether any method could be devised whereby a small piece might be drawn with composition proportionally identical to the whole root.

In the swede the distribution of dry matter percentage varies in several ways.

(1) The high dry matter value of the "bark" compared with any other tissue was shown by FRUWIRTH (1922) and his colleagues. He found that "bark" varied in different regions, notably richest on the shoulder and decreasing towards the bottom. In an experiment detailed above (Section iii) (a) the dry matter percentage of the "bark" in the middle region was 32% higher than that of the flesh in the same region.

(2) HENDRICK (1906) found that the peripheral part of the flesh of turnip was richest and that the dry matter percentage decreased towards the centre. WOOD and BERRY (1902-4) (1905) obtained similar results with swede and mangel. It has been/

been found in the present experiment, that in the middle region of the bulb the outer shell of flesh one centimetre thick was 6% above average, while in the tissues interior to it the variation between points was not great.

(3) Transverse sections of turnip were found by HENDRICK (1906) to exhibit a gradient, from high dry matter at the level of the shoulder to low dry matter at the bottom. Similar results were found in swede, by WOOD and BERRY (1902-4) but FRUWIRTH (1922), also working with swede, found that there was a grade from high at the shoulder, decreasing towards the ground level but rising again in the true root portion of the bulb. In an experiment in which horizontal cores were cut one below the other in the middle region, indications of rising concentrations of dry matter both towards the neck and towards the tap root were observed. (Section (ii) b).

(4) In beet the tissues interior to the diarch side roots were found to be relatively high in dry matter (KRISTENSEN (1911) quoted by FABER (1920)). No significant difference could be found in swede between horizontal cores cut to include side root tissues and others on the same transverse plane. (Section (iii)c)

(5)/

(5) FRUWIRTH (1922) demonstrated a central column of very low dry matter, associated with the pith, which is most marked in the neck. He found this column to descend (according to his illustration) to ground level. In the roots tested by the writer, which were admittedly much longer in the axis, there was no indication of such a column in the middle region.

(6) SANSOME (1926) found the southern portion of the bulb to be richer in dry matter than the northern. The present experiments show that this difference is significant in the central region of the bulb; SANSOME'S explanation that this was due to a displacement of an area of very low dry matter towards the North was not confirmed. The distribution of dry matter along radii running North and South was examined and it was found that the extra concentration on the South side was distributed over a wide area extending from within the peripheral region to near the centre. It was noted that a slightly greater development of tissue usually occurred on the south side.

(7) CALDWELL (1930) suggests that foodstuffs descending the petiole are accumulated on the side of the swede bulb below the point of entry. He/

He found that the bulb tissues grew less rapidly on a side from which the leaves were continuously removed. Bulbs that have been knocked over develop mainly on the upper side, and he attributes this to the better functioning of the leaves, on the upper side of the neck, which are exposed. Bulbs of the tankard type are very liable to be knocked down, and are often asymmetric and misshapen; globes, on the other hand grow more erect and are more symmetric.

DISCUSSION ON METHODS OF SAMPLING.

Various methods have been adopted for the taking of samples for estimation of composition.

(1) Pulping the whole bulb. In the last century it was sometimes the practise to pulp a few bulbs as an estimate of a plot yield (quoted from WOOD 1905). For the selection of single plants for breeding the whole bulb may be pulped and samples drawn for analysis, but in this case the neck which can be grown in a pot, will yield only a few hundred seeds. As a means of confirming differences obtained in single core analysis of a large population, this method may be employed.

(2) A wedge shaped sample. A longitudinal sector or wedge may be cut out of the side of a bulb, and a revolving rasp has been devised to cut and pulp simultaneously. FRUWIRTH (1922) recommends the method but states that the damage to the bulb is considerable. The Danish workers rejected it, because of the difference in composition between the sides bearing side roots and smooth sides (KRISTENSEN (1911)) quoted by FABER (1920)). This difference has not been found in swedes in the present experiments.

(3)

(3) <u>Pulp obtained by sawing</u>. The Danes devised a method by which a litre of pulp was obtained by saw cuts in 50 bulbs; a special circular saw being employed (HELWEG (1893)) quoted by FABER (1920)). This method has been adopted in several countries, but since the bulbs are cut up, it is not suited for breeding work.

(4) <u>Coring.</u> Coring has been employed by a number of workers; FRUWIRTH (1922) recommends the method; and in sugar beet breeding it is highly developed, pulping drills being used. For swedes, an experiment, detailed above, indicated that the dry matter value of a horizontal core is roughly 95% of the value of the whole bulb, while a diagonal core will probably give a result slightly closer to the true value. There has been much difference of opinion as to the alignment of the core. COLLINS (1905-6) considered that it might be taken in any direction so long as it passed through the centre of the bulb. HENDRICK (1906) used diagonal cores, and introduced a method of single root selection on this basis; his coring methods have been adopted in the Scottish Colleges Trials. WOOD and BERRY (1902-4) (1905) working with swede and mangels/

mangels, cored horizontally through the greatest diameter. They found that diagonal cores were unsuitable since they included too much central tissue in long bulbs. ROBB and WISHART (1915) and SANSOME (1926) used horizontal cores. The latter cored from North to South to eliminate differences in composition between the two sides.

It has been seen (TABLE 36) that the variability due to deflections from the theoretical alignment is approximately the same in both methods; preference may be given therefore, to whichever boring can be the more accurately gauged; and since there are no exact guiding points, this is a matter of opinion.

SUMMARY.

I. In the first season of growth the stem, or "neck" of the swede had undeveloped internodes, but the intervals between leaf scars varied in different strains.

II. Under certain environmental conditions, e.g. late frosts, the majority of plants in a variety developed longer stems. The response in some varieties was a general lengthening to 10 or 15 inches, in others it was hardly appreciable.

III. In long-necked varieties, fully bolted and very short-necked plants were found in small proportions. These types when bred, were found to have had different hereditary tendencies.

IV. Great modification in stem length was found in plants of a true-breeding swede 'bolter' strain.

V./

V. The "bulbless bolter" is a rogue found in swede crops. It was similar in appearance to winter swede-like rape, but was sometimes completely annual in life term.

VI. Progenies of bulbless bolters were found to be very uniform and true breeding.

VII. Hybrids obtained from swede x bulbless bolter were strongly developed annuals having partly developed ligneous bulbs, white flesh and lemon flowers. A purple-neck, white-fleshed hybrid, segregated 8.6 white to 1 yellow and 3 purple-neck to 1 bronze. The white flesh of the bulbless bolter was probably due to two pairs of dominant factors.

VIII. Swede and bulbless bolter hybridised reciprocally when grown together.

IX. The main anthocyanin colour difference on the superficial layers of the swede was found to be determined by either of two allelomorphs N_1 and N_2, the dominant character/

character being detected by the uniform colouring of the internodes of the neck.

X. Production of anthocyanin in the region of the shaw was found to depend mainly on the presence of two factors -

(1) a purple-neck factor,

and (2) a factor extending the area of pigmentation.

XI. A number of modifications and minor variations in anthocyanin pigmentation were noted.

XII. The two factors governing flesh colour were found to be unlinked. F_2 segregations of 15 white to 1 yellow-flesh were obtained.

XIII. There was absence of linkage between flesh and neck colours.

XIV. Variability in individual bulb weight was very great. It was subject to modification, but the influence of "total potential variability" of the strain was not proved.

XV./

XV. Variability in individual dry-matter percentage was comparatively small. It was positively correlated with variability in bulb weight. The influence of "total potential variability" of the strain could not be proved.

XVI. The inverse correlation between bulb weight and dry-matter percentage was found to be subject to considerable modification. It was not affected by the "total potential variability" of the strain.

XVII. Increase in total solids percentages of bulbs were due to independant increments of both soluble and insoluble substances, the former being more strongly correlated with total solids percentage.

XVIII. Hereditary variations were isolated by selection from commercial strains, but not from twice or thrice-selfed lines.

XIX./

XIX. Individual plants high in bulb weight and dry-matter percentage were found to have been modified in one or other of these characters.

XX. When bulbs were sampled by boring cores, deflections from the true alignment caused certain experimental errors which were estimated. The variability of horizontal and diagonal core results was similar.

XXI. In the middle region of the bulb the bark was 32% richer in dry-matter than the flesh. The peripheral shell of flesh 1 cm. deep was 6% above average. There were no great differences between portions nearer the centre in the equatorial plane, though those from the South side were slightly richer than those from corresponding positions on the North.

XXII. Cores containing the vascular tissues feeding side roots were not significantly different in dry-matter percentage from other cores in the same transverse plane.

XXIII. Diagonal cores were slightly higher in dry-matter percentage than horizontal cores. Both types of core gave lower values than the whole bulb.

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