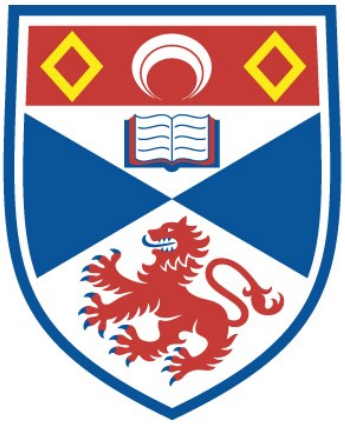
STUDIES IN THE MORPHOGENESIS OF CABBAGE WITH SPECIAL REFERENCE TO THE PHENOMENON OF HEADING

Christopher North

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



1956

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by

C. NORTH

A Thesis submitted for the Degree of
Doctor of Philosophy
in the University of St. Andrews

1956

MS 1914.0

CERTIFICATE

I certify that Christopher North has spent nine terms at research work under my direction and that he has fulfilled the conditions of Ordinance 16 (St. Andrews), so that he is qualified to submit his Thesis for the Degree of Doctor of Philosophy.

Tutor

Conway A. Wood.

DECLARATION

I declare that this Thesis records the result of experiments carried out by me; that it is my own composition; and that it has not previously been accepted for a Higher Degree.

This research was carried out at the Scottish Horticultural Research Institute, Invergowrie, by Dundee, under the direction of Dr. C. A. Wood.

Christopher North.

Education and Research Training

In 1937 I graduated (B.Sc. Horticulture) at Reading University and in 1952 I was awarded the Degree of M.Sc. at the same University for a Thesis entitled "Studies in the Vegetative Propagation of *Brassica oleracea*"

I registered as a Research Student in the University of St. Andrews in February 1952, and the work described in this Thesis was completed in March 1956.

CONTENTS

I. INTRODUCTION

Between a quarter and a fifth of the area of land used for vegetable crops throughout Europe and America is devoted to the growing of cultivated forms of Brassica oleracea L. Moreover, in many temperate climates, certain cultivars of this species such as Brussels sprouts, cabbage, savoy cabbage and horticultural kales are, together with carrots and swede turnips, the only fresh vegetables available during the six colder months of the year.

It is not surprising, therefore, that many workers have turned their attention to the study of problems arising from attempts to breed improved horticultural varieties of B. oleracea. Most of the early investigations in this field by Kristofferson (1924, 1927), Pease (1926), Detjen and McCue (1933), and others were studies of inheritance within the species, and they all led to the discovery that most, if not all, desirable horticultural characters of this species are polygenic. The situation appeared to be so complex that it was impossible to formulate any satisfactory rules by which a practical breeder could forecast the results of his work. As a result probably of these findings, very few studies of the inheritance of

B. oleracea have been made since 1934.

Shortly after Kristofferson commenced his work on inheritance, Detjen (1927), Pearson (1929) and Kakizaki (1931) began studies of compatibility within the species. Their work led to the formulation of improved methods of pollination control, designed to take advantage of the difference in combining ability of individuals or groups of plants. One of these techniques - the dialell cross method method - which has been discussed in some detail by Wellensiek (1947), and with particular reference to B. oleracea by Sneep (1948), is firmly established as a breeding method for cabbages in Denmark (Duvald 1955) and probably also in Holland. The polycross method described by Fransen and Frandsen (1948) and Wellensiek (1947) is also used in the breeding of cabbage and allied vegetables. In America most emphasis has been given to the production of F1 seed (Pearson 1932, Detjen 1944, Attia and Munger 1950) and 'hybrid' seed of cabbage is now being produced in Japan under American direction.

Even when these more advanced breeding methods are employed, the improvement of strains of cabbage and allied vegetables still depends largely on the individual worker's ability to select the most suitable genotypes. Selection is almost invariably based on a visual assessment

of the material growing under conditions which would normally be accorded to market crops. The expression of a gene complex of an individual, however, is profoundly affected by environmental conditions, and it is probable that variations in climate from year to year are sufficiently large to have marked effects on the behaviour of the genotype. It is well known for example, that early-sown cabbage may run to seed prematurely in some years and not others , and from Denmark (Duvald 1955) it is reported that in a cool wet year heads of some strains of summer cabbage are different in shape from those growing under warmer dryer conditions.

If more were known about the behaviour of forms of Brassica oleracea under different growing conditions, it might be possible to select plants for certain desirable inherent qualities under artificial conditions designed to accentuate those qualities, or to make allowance for the effect of abnormal climatic environment when selecting plants in the field.

The conditions required for flowering in cabbage (Miller 1929) and Brussels sprout (Stokes and Verkerk 1951) have been fairly thoroughly investigated. The effect of environment on the expression of morphological characters in B. oleracea which are desirable from a horticultural standpoint, however, seems to be an almost unbroken field for investigation, although a start has

been made recently by Parkinson (1951) in the form of a preliminary study of the effect of different treatments on 'curd' formation in cauliflower.

Work described in this thesis is largely a study of the phenomenon of head formation in cabbage. It forms part of a programme of research at the Scottish Horticultural Research Institute and was selected as a subject for investigation because attempts are being made there to breed a sure-heading strain of January King cabbage. This variety is extremely hardy and may be cut from the field between November and March, but a high proportion of the plants in crops of all strains fail to develop marketable heads.

II GROWTH ANALYSES

A. GROWTH OF ENKHUIZEN GLORY CABBAGE UNDER FIELD CONDITIONS

Most of the time spent on the investigation in 1953 was devoted to an exploratory examination of the growth pattern of cabbage from sowing time in Spring until the heads had burst and the plants were damaged by frost in Winter. It was intended that this analysis should give a picture of the distribution of growth in weight and the rate of formation, unfolding, and death of the leaves and the growth in length of the main axis. From this picture it was hoped to obtain a better understanding of the phenomenon of heading.

(1) Experimental

Experiment 1.

Materials. Enkhuizen Glory was chosen for analysis because nearly all strains of this variety give plants which are comparatively uniform in morphological characters and can be relied upon to grow firm heads: in addition, it was thought that the protracted growth period of Enkhuizen Glory, which matures in late summer, would permit an especially detailed study of growth features which lead to heading.

Enkhuizen Glory was found, however, to have two considerable disadvantages for the type of analysis envisaged: (i) it formed a very large plant (weighing

up to 12 lb. or more) so that measurements of weight were especially arduous; (ii) the margins of the leaves were 'wavy', and it was therefore not possible by simple methods to obtain a very accurate measurement of the leaf area.

Method Seed of Hurst's strain of Enkhuizen Glory was sown on 6 April in rows 2½ ft. apart, in land which was well-manured and had a good tilth. It germinated rapidly, and when the plants had grown 1 - 1½ in. high they were thinned to stand 2½ ft. apart in the rows. Some 200 plants were raised.

A random sample of plants was taken 44 days after sowing, and thereafter a further 13 samples - the last at 313 days after sowing. Twenty plants were collected for the first sample, 10 for the second, and 5 for all other samples. (This decrease in number of plants per sample was necessary because of the difficulty of recording details of larger plants.) In addition, at each sampling date, five main-axis growing tips were cut out and fixed and preserved in formalin-acetic-alcohol mixture. Freehand drawings of fresh growing points were also made.

The following were recorded((2) and (4) per individual plant, (1) and (3) per whole sample):-

(1) Dry weight of root, stem and leaf. (The root defined as that part of the plant below ground level; the stem as main stem and petioles;

the leaf as lamina and midrib of all sound leaves. The dry weights of folded and unfolded leaves were recorded separately - the former defined as those whose margins were classed round the younger leaves).

(2) Number of unfolded and dead leaves, and total number of leaves and leaf initials. (Dead leaves defined as those which fallen or were distinctly yellow.)

(3) Area of unfolded leaf. (Area of upper surface of lamina only.)

(4) Length of stem. (Measured as length of main axis between growing point and ground level.)

Roots were carefully lifted and washed with a strong jet of water before drying. Roots, stems and leaves were cut into small pieces and dried in a forced-draught electric oven at 100°C. for 24 hours. After drying, the material was cooled in a desiccator and weighed without delay. Until the 164th day the entire root, stem and leaf samples were dried, but on and after that day 2,000 g. samples only were died, and the total dry weights of the parts were calculated from the fresh weights and percentages of dry matter.

To prevent confusion, leaves and leaf initials were broken off as they were counted. Very small leaves and leaf initials were counted by dissecting the growing

tips under a stereo-microscope at magnifications of X 20 and X 30. Leaf scars of fallen leaves were marked with a ball-point pen to reduce the risk of counting them more than once.

Leaf area was found as follows; the leaves were lain between two sheets of plate glass which had been cut to fit over the open end of a tea chest, at the base of which were three 60 watt electric light bulbs. The outline of the leaves was traced on paper placed on the uppermost sheet of glass, and areas corresponding to the shadows given by the leaves were cut out and weighed. By comparing the weight of the cut-out areas with that of a known area of a piece of paper from the same batch, the area of the leaves was calculated. The weight per known area of paper was estimated for each sample - even when the same batch of paper was used for several samplings because it was found that the humidity of the atmosphere affected this measurement.

As the plants increased in size it became more difficult to obtain an accurate assessment of leaf area. It was often impossible to lay old leaves flat on the glass because of the folds in their margins. The later estimates of the leaf area may therefore have been somewhat low, although the recordings were partly compensated by the fact that no allowance was made for holes eaten in the leaves by insects - damage of this nature was not, however,

extensive.

The preserved main-axis growing-tips were washed, dehydrated in ethyl-butyl alcohol mixtures, embedded in paraffin wax and sectioned with a Cambridge rocking microtome. Those longitudinal sections which illustrated the morphology of the growing point about the central axis were stained with Delafield's haematoxylin, mounted in Euparal and photographed on FP3 film using daylight and a dark orange filter. These, together with freehand drawings of growing points at different samplings, provided records of the nature of the growing point at different stages of development.

Results. Appendix tables 1 and 2 show dry weights of leaf, stem and root; numbers of dead, unfolded and total leaves; lengths of stem; and areas of unfolded leaf.

From Fig. 1. it will be seen that the greatest part of the dry weight of the plant was that of the leaf. The stem portion was always less than a third of that of the leaf, and the root portion lower than that of the stem. The leaf portion increased up to the 194th day and then began to fall.

Fig. 3. shows that, between the 60th and 150th day leaves were differentiated at the high rate of about one per day. The rate of leaf initiation was greater at all times than the rate of leaf unfolding, which increased up to the 108th day and declined thereafter.

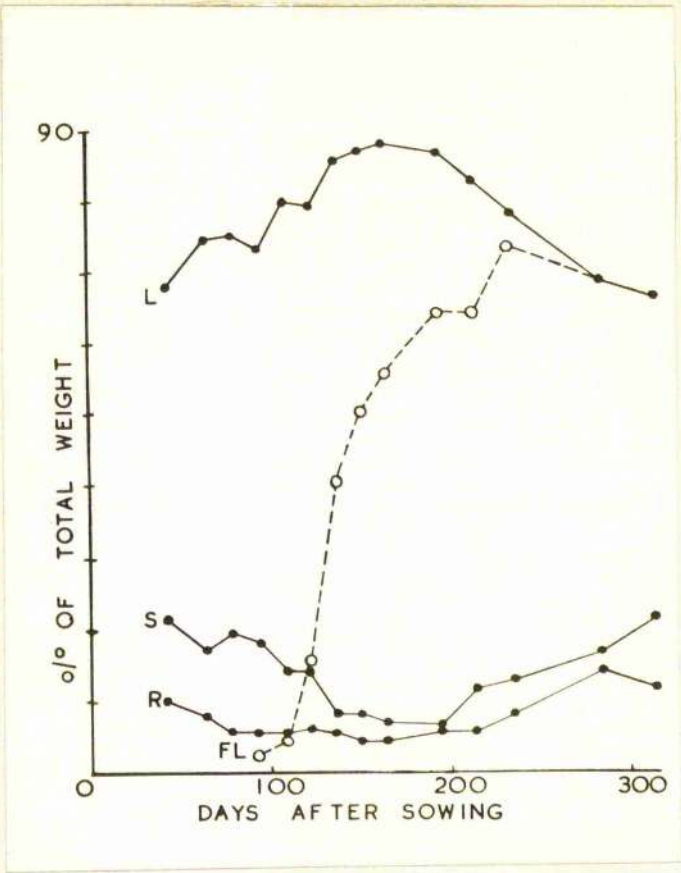

Fig. 1.

Dry weights of leaf (L), stem (S), root (R), and folded leaf (FL) expressed as percentages of total dry weight of plant. Cabbage Enkhuizen Glory.

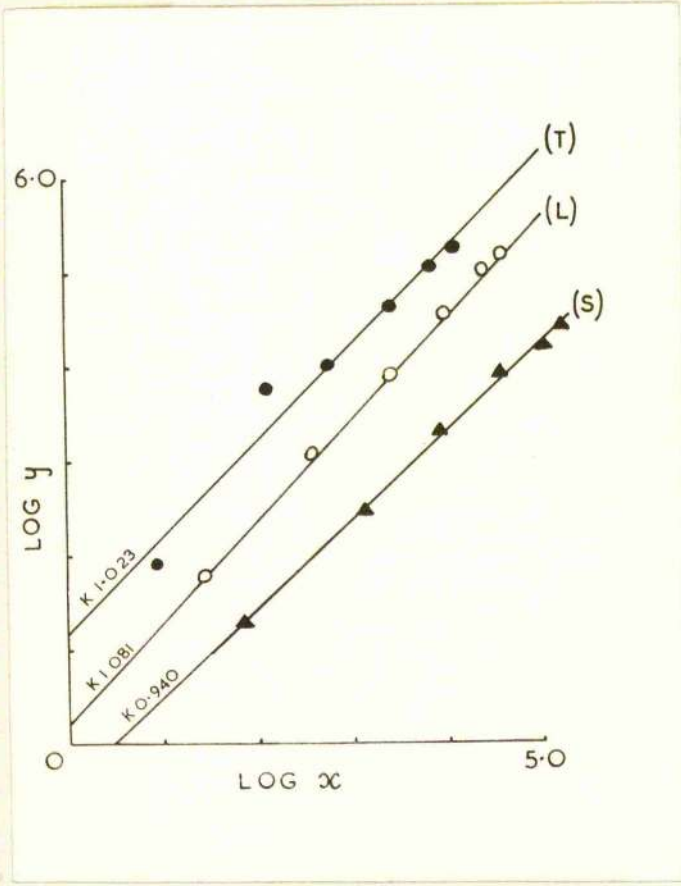

Fig 2.

Differential growth rates of shoot (T), leaf (L) and stem (S).
y = dry weight of organ.
x = dry weight of remainder of plant.
Cabbage Enkhuizen Glory.

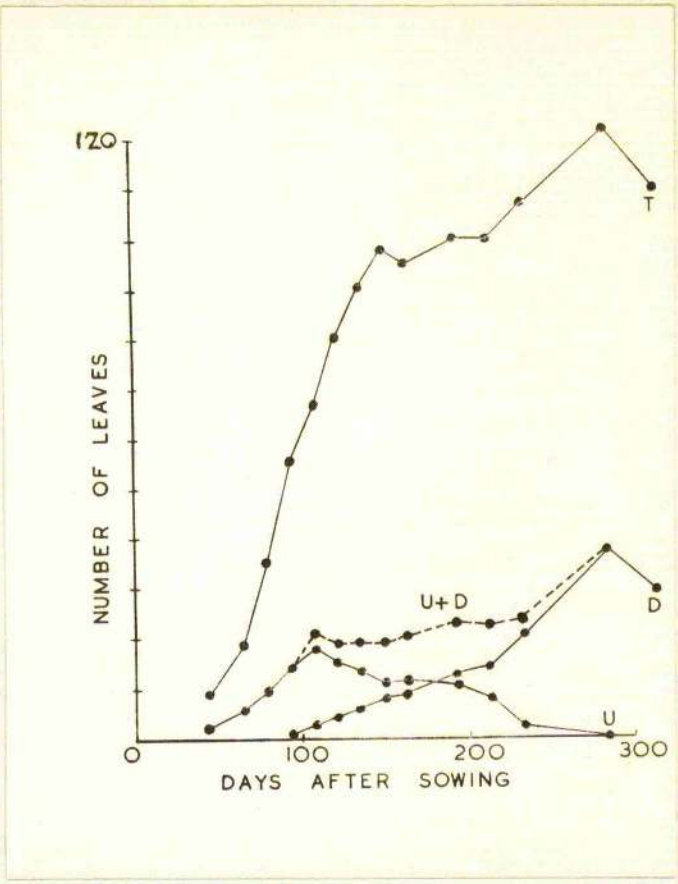

Fig. 3.
Number of leaves initiated (T), dead (D), and unfolded at different sampling dates. (U) = living unfolded leaves and (U+D) = unfolded plus dead leaves.
Cabbage Enkhuizen Glory.

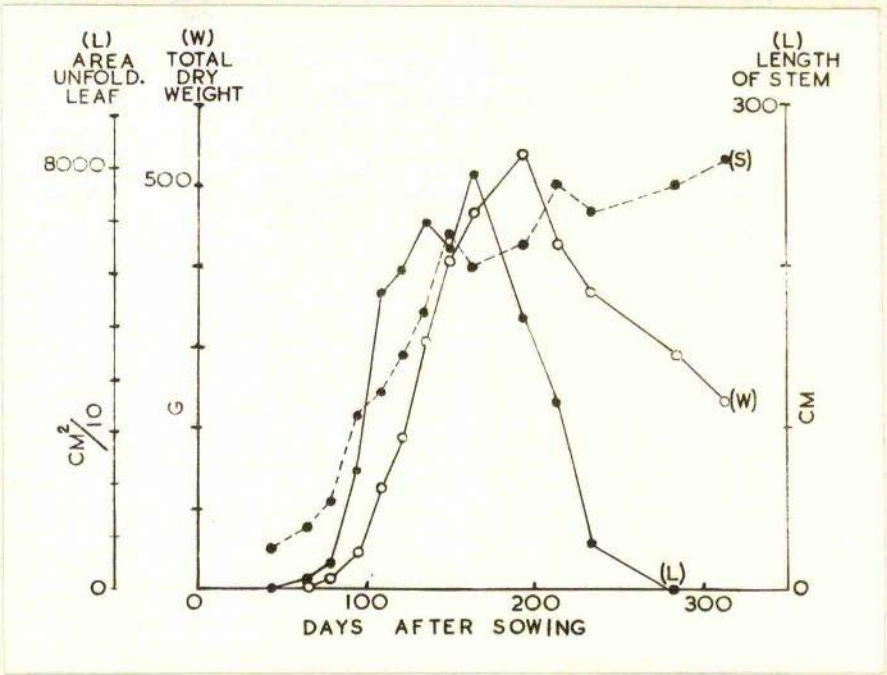

Fig. 4.
Growth in dry weight, leaf area and stem length.
Cabbage Enkhuizen Glory.

Judging from the curve for the sum of dead and unfolded leaves (U+D) it appears that one or two leaves unfolded after the 108th day, but the apparent rise in this curve between the 108th day and the 234th day may have been due to the increasing number of dead leaves, as it certainly was after the 234th day. Leaves began to die shortly after the 65th day, and the death rate became approximately 0.14 per day between the 100th and 200th day and increased thereafter.

Fig. 4. shows that the grand period of growth, as measured by the increase in total dry weight, commenced near the 90th day, about which time the rate of increase in area of unfolded leaf reached its maximum. The peak for the curve of unfolded leaf area is at about the 160th day, whilst that for the total dry weight is later - approximately the 190th day. The stem continued to increase in length throughout the period covered by the analysis.

Examination of Figs. 5 and 6a, 6b and 6c shows that there were changes in appearance of the growing point and its surrounding leaf initials. Three main stages may be recognised:-

(1) Up to the 65th day, when 18 - 20 leaf initials had been produced, the growing apex was only about 0.2 - 0.25 mm. in diameter and the leaf initials and the young leaves were held more or less upright.

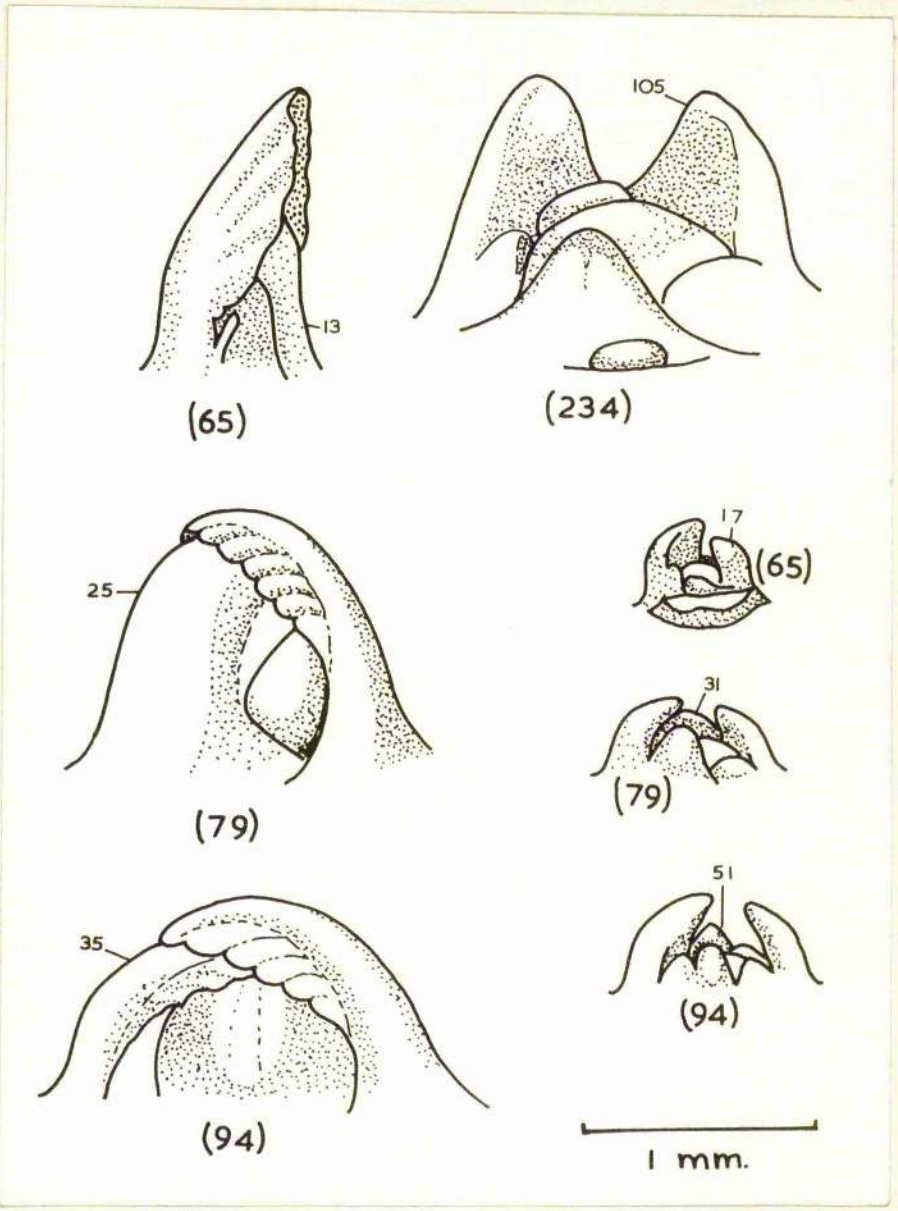

Fig. 5.
Freehand drawings showing orientation of leaves around growing point of Enkhuizen Glory cabbage. Numbers in parenthesis refer to days after sowing, and smaller figures to serial numbers of leaves. The scale shown in the bottom right hand corner refers to all drawings except the one for the 234th. day.

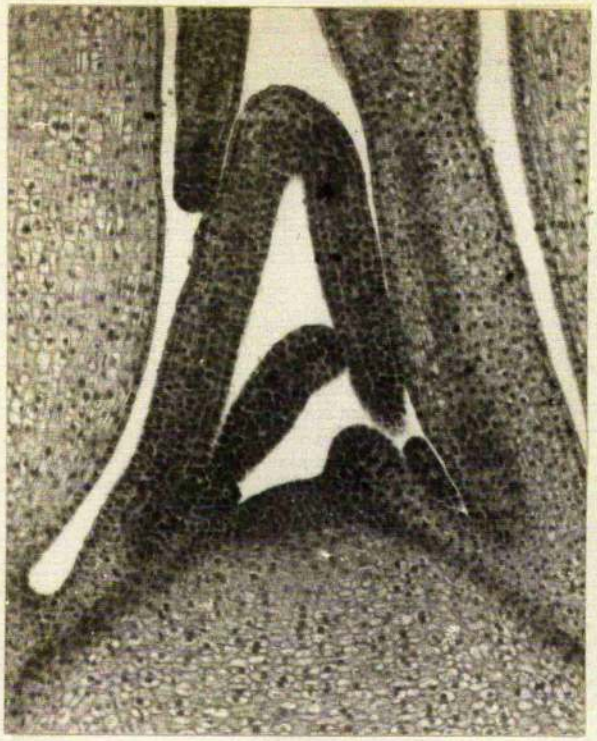

Fig. 6a.
(44 days)

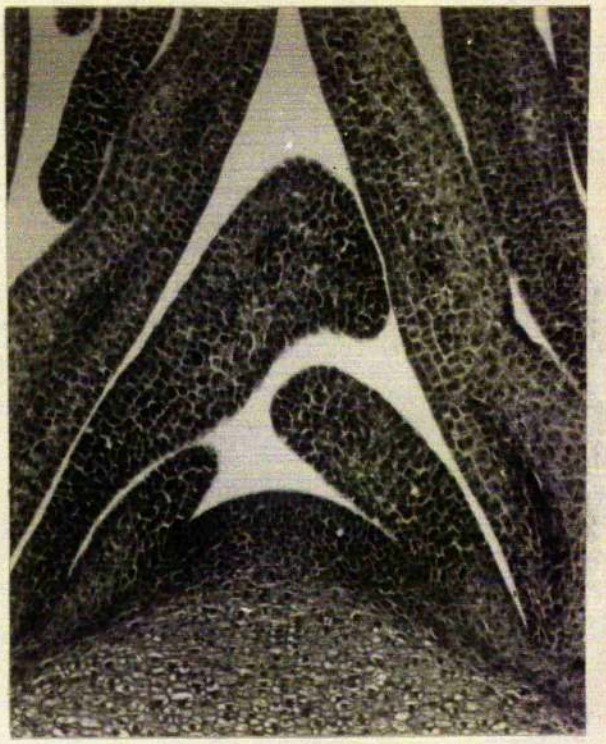

Fig. 6b.
(65 days)

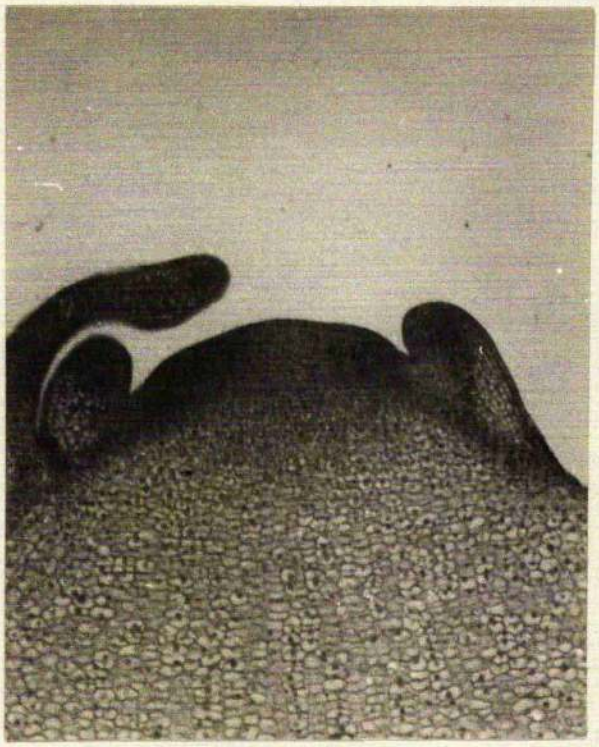

Fig. 6c.
(150 days)

Figs. 6a,6b,6c. Longitudinal sections of growing points of Enkhuizen Glory cabbage 44, 65, 150 days after sowing.

1 mm.

(2) From the 70th day, when 20 or more leaf initials had been produced, the growing point increased in diameter (up to about 0.5 mm.) and appeared to become more flattened, and the newly-formed leaves became distinctly arched over the growing point.

(3) Commencing about the 200th day (when some 100 leaf initials had been formed) the growing point began to rise within the newly-formed leaf initials, and became distinctly dome-shaped. Newly-formed leaf initials were more pointed and less arched over the growing point. Small domed swellings became visible in the axils of some leaf initials, shortly after they were formed.

(2) Discussion.

(a) Overall Growth in Weight

Fig. 4 shows a typical sigmoid curve for growth in weight of the entire plant, and a decrease in weight after the 194th day owing to the death of the older leaves. A marked feature of this curve is the late commencement of the grand period of growth in comparison with many other species.

It may be argued that the initial growth was retarde by low temperature during the months of April and May, but plants sown later in the year - and therefore under warmer conditions - as in Expt. 5 - also showed considerable delay in the onset of the grand period of

growth. The slow onset of growth can hardly be attributed to a low efficiency of the leaves as carbohydrate producers, for they were able to maintain a rate of leaf initiation of about one per day between the 60th and 150th day but it may have been due to a slow initial increase in leaf area - a hypothesis which is supported by the way the increase in overall weight closely follows the increase in functional leaf area (Fig.3). The slow initial increase in leaf area may be associated with the late development of leaf initials by the seedling, for the plumule of Brassica oleracea L. does not form leaf initials until after the cotyledons have fully expanded.

(b) Distribution of Growth

The proportions of dry weight of leaf, stem and root (Fig.1) did not remain the same throughout the life of the plant. The decrease of leaf portion and attendant increases of stem and root portions which occurred after the 194th day may be attributed to the death of the older leaves at a time when the general growth in weight of the plant was slowing down, but the increase of the leaf portion before the 194th day indicates that differential growth was taking place during that period. Fig. 1 may, however, over-emphasise the situation, for the earlier-formed leaves were petiolate and the petioles were included as stem - thus increasing the apparent stem

portion and decreasing that of the leaf.

Huxley (1932) has postulated that many organisms exhibit constant differences in growth rate of different organs, and Reeve and Huxley (1945) have coined the term allometry to describe this condition. Huxley considereas that allometric growth may be expressed mathematically as $y = bx^k$ (where y = measurement of organ; x = measurement of organism or other organ; and b and k are constants).

From this expression it can be deduced that log y is directly proportional to log x, so that the curve of y against x should be linear if logarithmic coordinates are used and growth is allometric. The curves of growth in dry weight of the stem, leaf and the complete shoot (stem and leaves)of Enkhuizen Glory cabbage in relation to that of the rest of the plant (Fig.2) have been drawn on the assumption that the relationships are allometric. (Only measurements of weights recorded up to the 122nd day were used, for after that time the death of leaves had begun to affect the total dry weight of the plant. It will be seen that the tangents of the curves approach unity, indicating that the differences in growth rates were slight.

The value of k for top/root growth rates of cabbage was 1.023. Corresponding values for turnip (Pearshall 1927) and carrot (Deleano 1907) are 0.65 and

0.55 respectively, indicating that for species which form fleshy storage roots the growth of the root is much greater than that of the stem. In respect of top/root growth rate the head of the cabbage is not therefore analogous to the storage organ of carrot and turnip, for the top does not grow at a much greater rate than the root, and it is questionable whether the 'head' of cabbage may be considered as a storage organ. A further discussion of this point appears in Section V.

Another aspect of interest in the distribution of growth is its relationship to the morphology of the growing point. The first two stages of development described on page 12 of this thesis correspond closely to stages I and II of Stokes and Verkerk (1951) for Brussels sprout. These authors associate the change from the juvenile to the adult stage, which they call puberty, with a change from stage I to stage II of the growing point, and a redistribution of growth so that the stem portion increases markedly at and after puberty. The present work with cabbage, however does not show a correspondingly linked change of growth distribution and of growing point morphology, for (Expt. 1) the stem portion continued to decrease until the 194th day, whereas the change in the growing point took place between the 65th and 70th days. It seems, therefore, that the changes in growth distribution with those in the growing point-

observed by Stokes and Verkerk for Brussels sprout are probably incidental, and not typical of Brassica oleracea as a whole.

(c) Growth of the Head

The head, which is the aggregate of the folded leaves, increases in weight in relation to the other parts of the plant (Fig. 1). This increase may be due, in part, to the 'additional' growth in weight of the leaf portion as a whole, but it largely arises from the fact that, as the plant grows older, a higher proportion of the total number of leaves are folded - a situation whoih is clearly due to leaves being initiated more rapidly than they unfold (Fig. 3).

When 16 - 22 leaves of Enkhuizen Glory had unfolded, further leaf unfolding ceased, older leaves died, and the increase in weight of the head in relation to other parts was accelerated. Growth rate of the entire plant eventually decreased - presumably because the functional leaf area was reduced (Fig. 4) to a size inadequate to maintain the previous high rate of growth - and to the eye of the practical grower, the head was mature* for cutting.

*The term "maturation" has been used throughout this thesis to denote the retardation and eventual cessation of increase in weight of the head.

On and after the 213th day it was found that some of the heads had burst. This phenomenon was probably due to the increase in volume of the younger leaves within the restricted 'skin' formed by the outer folded leaves. No doubt the continued growth in length of the stem throughout the period of investigation also assisted the bursting of the heads.

B. COMPARISON OF GROWTH OF DIFFERENT VARIETIES OF CABBAGE

The previous Section was limited to a study of the growth of one variety of cabbage. To gain a more detailed picture of the growth of the cabbage as a whole, further analyses were made with varieties which had widely differing times of maturation. The main aim of the work described in this section was to find which growth features were associated with rate of maturation.

Four experiments are described, three of a preliminary nature and one a large scale growth analysis designed on similar lines to Experiment 1.

(1) Experimental Materials. Fourteen strains of cabbage were used. They were chosen not only for their differing times of maturation but also for their range of morphological characters. Together they represent most of the main types of cabbage grown in Europe. It is appropriate therefore to describe their morphological characters and origins, and to help in this task the following publications have been consulted: Vilmorin (1925); Shoemaker (1947); Oldham (1948); Mallekote (1950); Hahn and Schmidt (1951); and Kristensen (1954). The varieties, described in their approximate order of maturation from earliest to latest are;-

Dithmasker. A selection from the German Glückstädter,

which was on the market in 1900. It belongs to the earliest-maturing type of round-headed cabbage and is probably the variety from which the widely-grown British summer cabbage Primo has been derived.

It has bright green, smooth leaves and forms a medium to small spherical or slightly ovoid head.

Copenhagen Market. A selection from Dithmasker introduced in Denmark by H. Hartman in 1909.

Very similar in morphological characters to Dithmasker, it is slightly larger and later maturing.

Early Offenham. A variety which presumably arose by selection on the part of market growers in the Offenham district of Lancashire. It is the most popular variety of 'spring' cabbage for sowing in late summer and harvesting in the following spring as 'greens' or firm heads.

The outer leaves are few in number, large, dark green and very slightly coarsely savoyed. The head is conical.

Enkhuizen Glory. A selection from Glückstäder introduced in Holland in 1902 by Sluis en Groot.

It has bluish-green leaves, frequently with wavy margins. It forms a large to very large spherical or slightly flattened head in late summer.

Christmas Drumhead. It seems likely that this variety was selected from the French Chou de Noël.

The leaves are very dark green, and the head is of medium size and distinctly flattened. Many strains are very variable in their morphological characters.

Chou de Noël. See above.

Winnigstadt. An old German variety which may have originated before 1830. It is extremely reliable in its heading ability.

The leaves are bluish-green with somewhat wavy margins, and the head is broadly conical.

Schweinfurt. An old variety, probably of Alsatian origin.

The rather pale green leaves have veins often tinted with red, and the head is very large but loose. This variety was originally grown on the continent for sauerkraut, but is now most frequently used as cattle food.

Klein's Red. Origin unknown. An early red cabbage with a medium to small spherical or ovoid head.

Amager. An old continental variety raised from strains of cabbage taken by Dutch settlers to the Danish island of Amager in 1520.

The variety exists in several strains which differ mainly in length of the stem. The strain

used in the experiments here described was Tall Amager.

The leaves are grey-green and especially smooth. The head is large, balloon-shaped and very firm.

January King. This is probably a synonym of a French savoy cabbage - Chou Milan de Pontoise - which is popular in the market gardens around Paris. It was introduced into Britain about 1920.

The outer leaves are dark green, mildly savoyed, and have many pronounced light green veins. Leaves on the outside of the head are frequently tinged red. The head is flattened.

Savoy, Drumhead and Latest of All. These two varieties are probably synonymous. They both originated from the typical Savoy cabbage which was first grown in the Piedmontese village Pancalieri.

Both have very savoyed dark green leaves with no reddish colouration. The heads are flattened.

(a) Rate of Maturation and distribution of growth Experiment 2. An attempt was made to find if there was a correlation between the relative order of maturation of varieties and their distribution of growth between root and shoot.

Seed of 11 varieties - chosen to cover as wide a season of maturation as possible - was sown outside on 14th April. Ten plants of each variety were sampled

50 days later; they were divided into root (portion below ground), and shoot, and both portions were dried simultaneously in an oven at 100°C. for 12 hours.

TABLE I. DRY WEIGHT OF SEEDLINGS OF DIFFERENT VARIETIES OF CABBAGE 50 DAYS AFTER SOWING

Variety in expected order of Maturation. (earliest first)	Total Dry Wt. of 10 plants (g).	% Dry Wt. Root of Total Dry Wt.
COPENHAGEN MKT. (ALNARP)	1.31	8.40
ENKHUIZEN GLORY (HURST)	1.71	8.19
CHRISTMAS DRUM (HARR.)	1.75	6.29
DE NOËL (S. LOUIS)	2.41	7.88
WINNIGSTADT (YATES)	1.59	6.92
SCHWEINFURT (NUTT.)	1.54	6.49
KLEINS RED (O. ENKE)	1.43	6.29
ARAGER (ALNARP)	1.88	6.38
JANUARY KING (TOZER)	1.39	7.91
SAVOY D. EARLY (HURST)	1.42	7.04
SAVOY D. LATE (CLIBRAN)	1.44	7.63

Results are given in Table I. from which it will be seen that there was no indication of a relationship between the expected order of maturation and total dry weight, or percentage root of total dry weight.

Experiment 3. Quite small seedlings had been used in Experiment 2. It was therefore decided to ascertain if there was a correlation between date of maturation and distribution of growth at a more advanced stage of developme

TABLE 2. DIFFERENCES IN LEAF NUMBER AND DRY WEIGHT OF DIFFERENT VARIETIES OF CABBAGE

Variety in Order of Maturation (earliest first)	Total No. leaves initiated sample 1st.	2nd.	No. of unfolded lvs. sample 1st.	2nd.	Sampled 92 days after sowing Total dry wt (g)	% root of total dry wt.	% stem of total dry wt	% leaf of total dry wt
DITHMASKER	51.6		13.3		38.9	5.54	14.01	80.45
COPENHAGEN MKT.	56.0	87.0	15.0	11.7	37.0	6.38	13.06	80.56
ENKHUIZEN GLORY	50.0	82.9	14.0	14.7	56.1	6.17	15.04	78.79
CHRISTMAS DRUMHEAD	50.0	76.2	15.0	16.2	43.2	5.85	12.33	81.81
WINNIGSTADT	42.6	72.7	12.6	14.7	49.2	5.04	19.55	75.40
AMAGER	44.7	82.4	14.0	21.0	42.4	6.36	22.41	71.23
JANUARY KING	41.0	75.7	13.7	18.0	38.5	5.26	19.09	75.65
SAVOY, L. OF ALL	30;7	67.7	11.7	17.7	40.1	6.51	20.53	72.95
LSD. (P = 0.05)	9.4	9.0						

the plants, and at the same time to find if rate of leaf production and leaf unfolding were related to the rate of maturation.

Plants of 8 varieties which had been sown on 14 April were sampled on 16 July and again on the 17 August using three and four plants of each variety per sampling on the respective dates. Dry weights and leaf numbers were assessed as in previous experiments. From Table 2 it will be seen that there was a strong indication from both samplings of a correlation between order of maturation and total number of leaves produced at the time the sampling was made. There was, however, no indication of a correlation between rate of leaf unfolding, total dry weight or distribution of growth between root and shoot, and order of maturation.

(b) Rate of Maturation and Rate of Leaf Initiation Experiment 4. In view of the indication of a positive correlation between rates of maturation and of leaf initiation, an experiment was planned to ascertain if a relationship of this nature could be detected in seedlings.

Seed of five varieties was sown in seed boxes on 2 September, and plants were raised in a greenhouse kept at a temperature of 60 - 75°F (as measured by a thermograph kept in a Stephenson screen on the bench where the boxes stood). Each box had 2 rows of seven seeds of each variety, the rows being arranged according

to tables of randomization. The relative positions of the boxes on the greenhouse bench were changed from time to time.

On 18 September a germination count was made so that it would be possible to ascertain if the results were related in any way to the figure of germination. Only 'normal' seedlings were counted as having germinated.

Between 24 and 30 days after sowing, four samplings were made of each variety. Two complete boxes of seedlings were taken for each sampling. By using a stereo-microscope to dissect the fresh growing tips, the total number of leaves which had been initiated was found for each seedling.

The results are given in Fig. 7. Unfortunately the figures do not lend themselves readily to a statistical analysis because, owing to differences in germination the numbers of plants of each variety in a replication were not equal. There is fair evidence, however, of a correlation between expected order of maturation and rate of the leaf initiation which cannot be accounted for by differences in germination.

(c) Growth of Five Varieties under Field Conditions.

Experiment 5. To follow up the preliminary experiments 2, 3 and 4, a large scale growth analysis of five varieties of cabbage was planned for the summer of 1954. Two sowings were made so that plants might develop both under

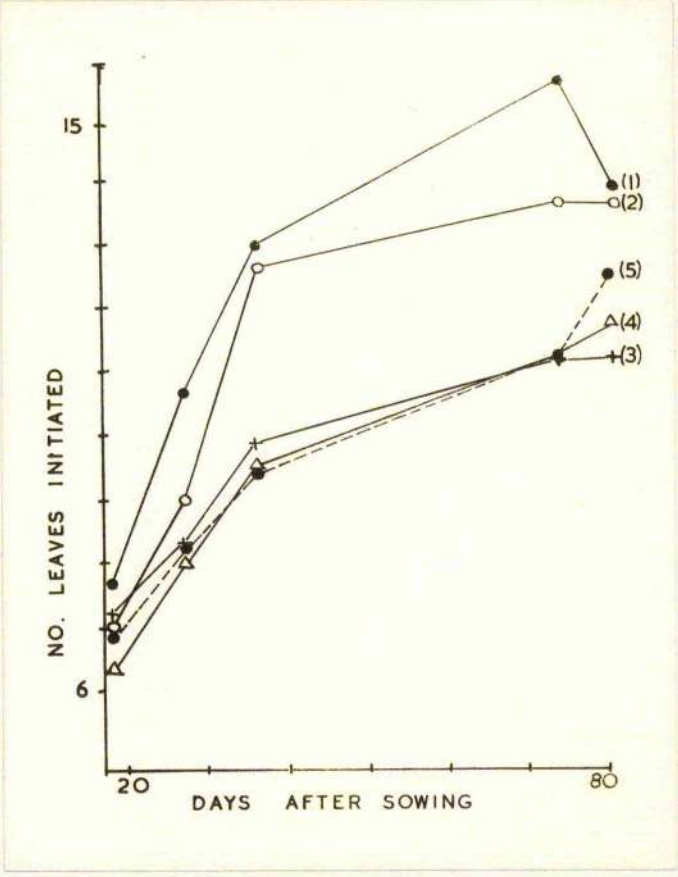

Fig. 7.
Rate of leaf initiation in five varieties of cabbage grown in a glasshouse (60 - 75°F.)

(1) Copenhagen Market.
(2) Enkhuizen Glory.
(3) Amager.
(4) January King.
(5) Savoy, Latest of All.

conditions of rising daylength and temperature, and falling daylength and temperature. An analysis similar to Experiment 1 was conducted, but samplings were made more frequently than in 1953; and to make the work practicable, fresh weights were recorded instead of dry weights, and no records of leaf area were taken.

The land was dunged and limed (as a control measure against Plasmodiophora brassicae Wor. which had caused damage to the cabbage variety trials at Invergowrie in 1953). Rows of different varieties were randomised and set at 2½ ft. apart. Small groups of seed were sown 2½ ft. apart in the rows and the plants were thinned when they were 1 - 1½ in. high so that not more than one seedling developed in each group. The first sowing was made on the 31 March and the second on 23 June. To prevent damage by Cabbage root fly(Erioischia brassicae Bouché) the seedlings were watered with a 0.3% solution of Dieldrin.

Samples of five plants were taken at intervals of 1 - 2 weeks, commencing on the 50th day after the first sowing and the 34th day after the second sowing. The following were recorded ((1) per 5 plants; (2) (3) and (4) per plant.):-

(1) Fresh weight of plant above ground level (i.e. excluding root), and fresh weights of folded and unfolded leaves. The unfolded leaf portion

did not include petioles.

(2) Numbers of unfolded and dead leaves, and total numbers of leaves and leaf initials. (Dead and unfolded leaves defined as in Experiment 1).

(3) Length of stem as in Experiment 1.

(4) State of growing point - i.e. whether (a) no sign of flower initiation, (b) flower buds visible with stereo-microscope or (c) flower buds visible with the naked eye.

From Appendix Table 3, which gives fresh weights of stem and leaf, Figures 8 and 9 have been drawn.

Fig. 8 shows curves, for the first sowing, of folded-leaf weight expressed as percentages of total leaf weight and thus gives a measure of the relative rates of head formation and maturation of the different varieties. The time of onset of head formation and date of maturation appeared to be closely associated, for varieties which commenced head formation early also matured early. Copenhagen Market and Early Offenham matured about the same time, and were followed first by Enkhuizen Glory and later by January King and Amager. There was, however, very little difference between the maturation of the two first-named varieties. Equivalent data from the second sowing were obtained only for the 118th and 181st days: from both of these samplings the order of maturation was

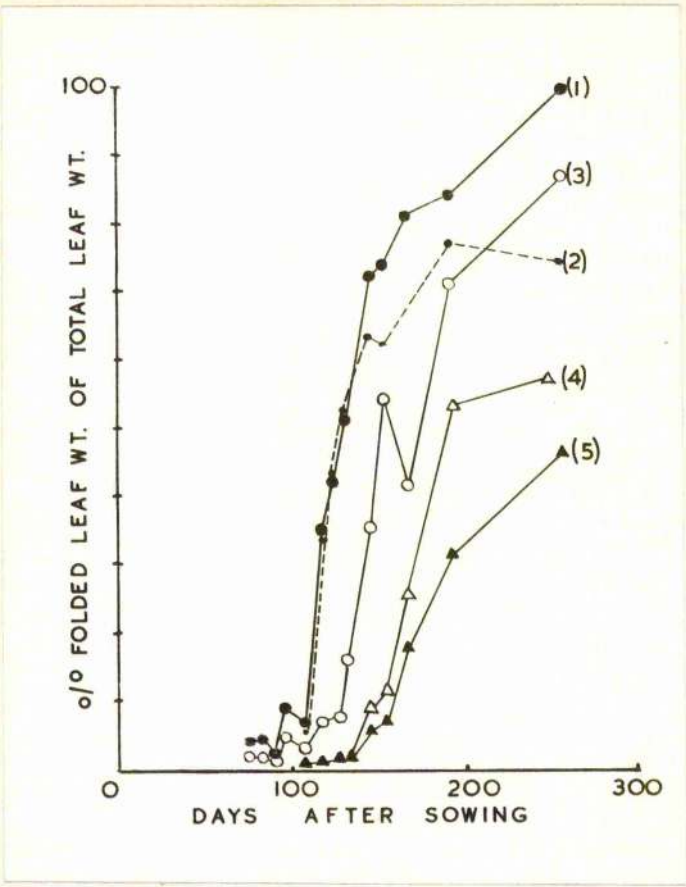

Fig. 8.
Fresh weights of folded leaf expressed as percentages of total fresh weights of leaves.
(1) Copenhagen Market.
(2) Early Offenham.
(3) Enkhuizen Glory.
(4) January King.
(5) Amager.

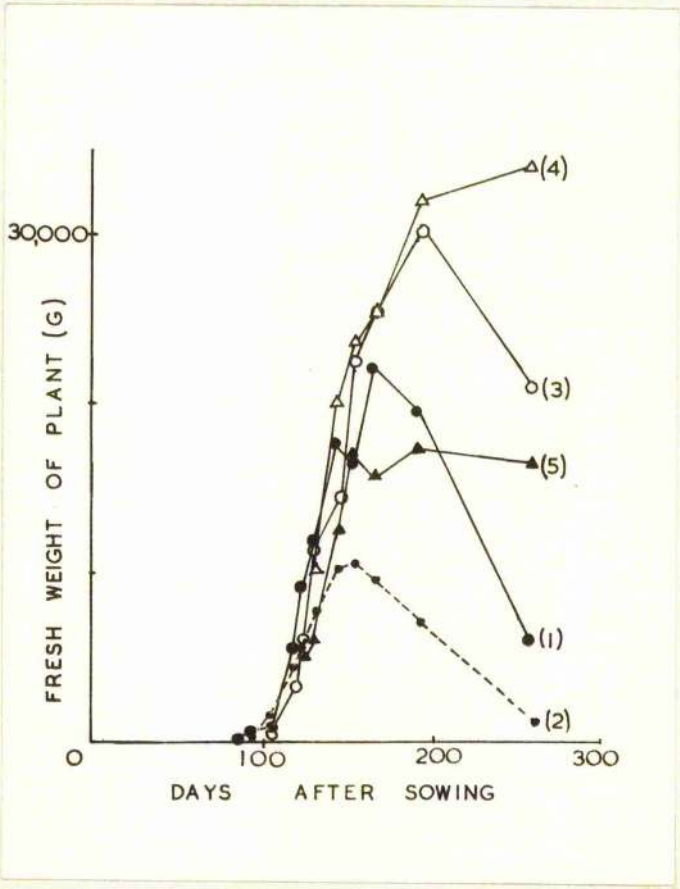

Fig. 9.
Increase in fresh weight of five varieties of cabbage. Varieties numbered as in Fig. 8.

substantially the same as from the first sowing, except that Enkhuizen Glory appeared to be maturing earlier than Early Offenham on the 181st day.

Fig. 9, showing total fresh weights, indicates that marked increases in weight occurred in all varieties 75 days after the first sowing. A similar increase in growth in weight occurred after only 50 days from the second sowing. This difference in time of onset of the grand period of growth between the first and second sowings was probably associated with differences in temperature and light. Under the same climatic conditions, however, the time of onset of the grand period of growth, and the subsequent growth rate - up to the approach of maturity - was similar for all varieties.

Appendix Table 4, which has been used to prepare Figures 10 and 11, gives the number of leaves initiated, unfolded and dead at different samplings for both sowings.

Fig. 10 shows that the relative rates of leaf initiation for the first sowing were : Copenhagen Market (highest), followed by Enkhuizen Glory and January King, then Amager, and finally Early Offenham, although there were some changes in this order after the 140th day. From the second sowing (Fig. 11) the order was the same, with the exception that Amager had a higher rate of leaf initiation than January King.

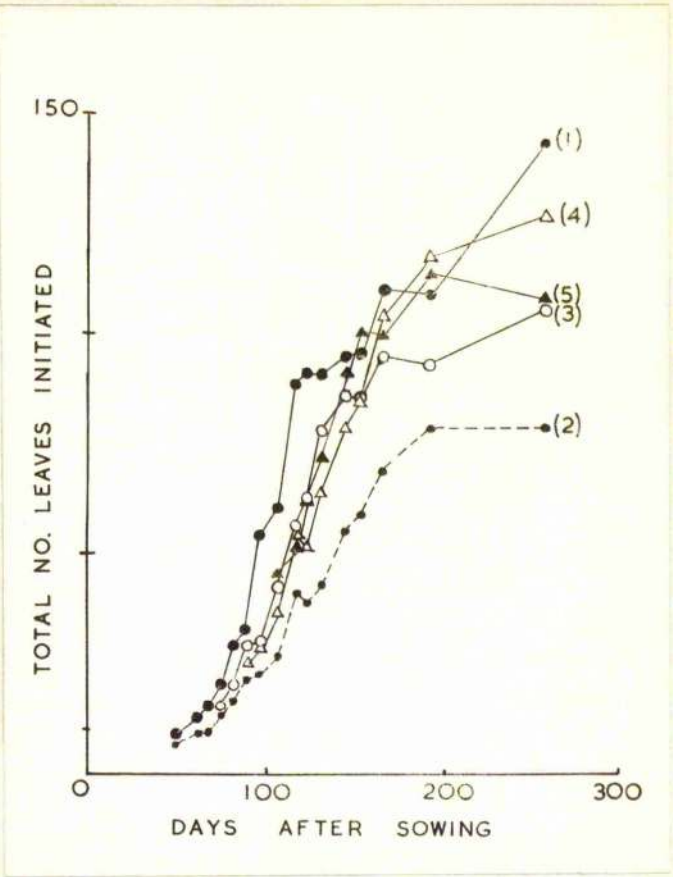

Fig. 10.
Rates of leaf initiation of five varieties of cabbage sown 31 March.
(1) Copenhagen Market.
(2) Early Offenham.
(3) Enkhuizen Glory.
(4) January King.
(5) Amager.

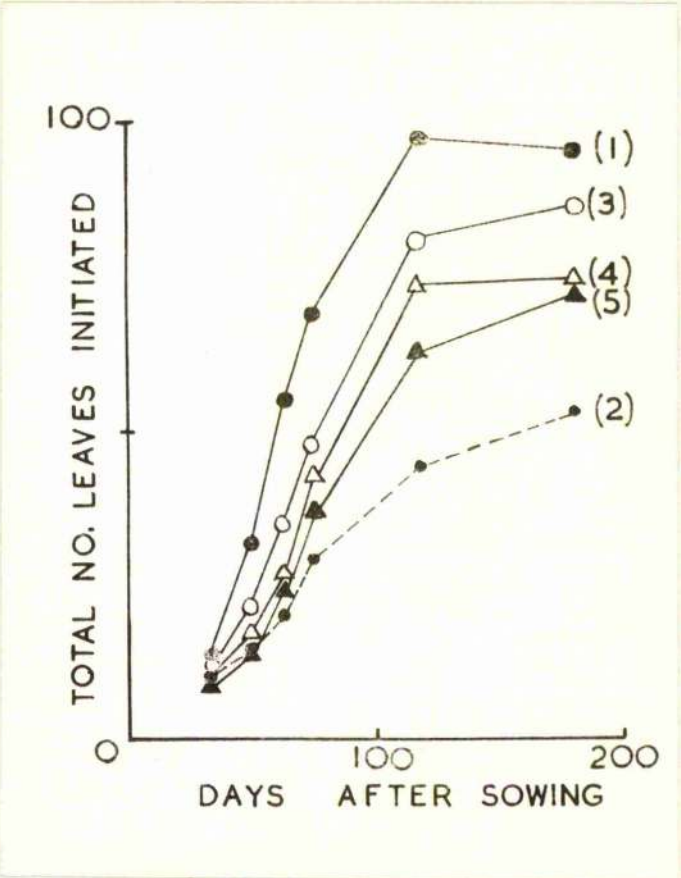

Fig. 11.
Rates of leaf initiation of five varieties of cabbage sown 23 June. Varieties numbered as in Fig. 10.

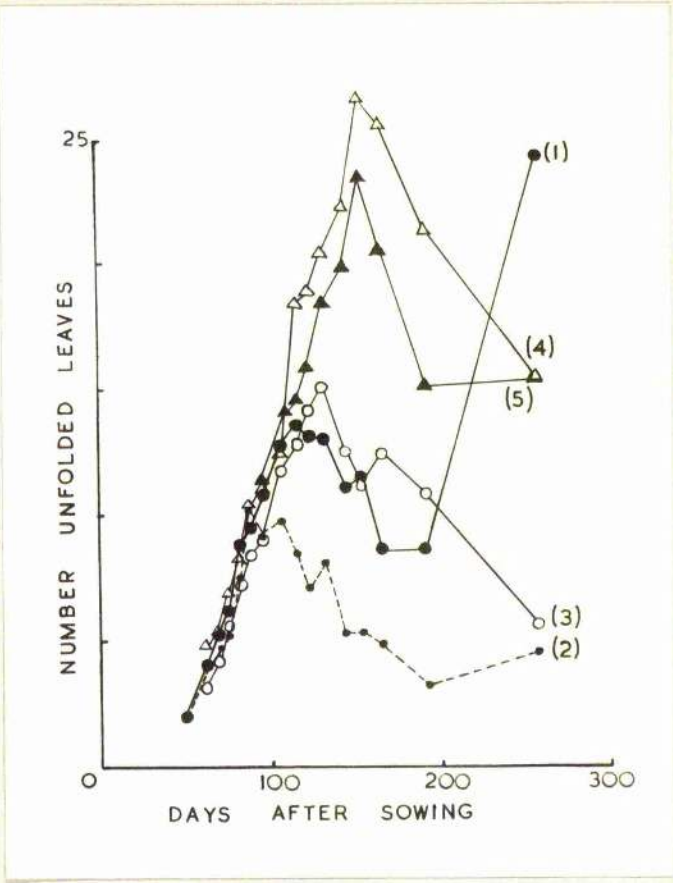

Fig. 12.
Rates of leaf unfolding of five varieties of cabbage sown 31 March.
(1) Copenhagen Market.
(2) Early Offenham.
(3) Enkhuizen Glory.
(4) January King.
(5) Amager.

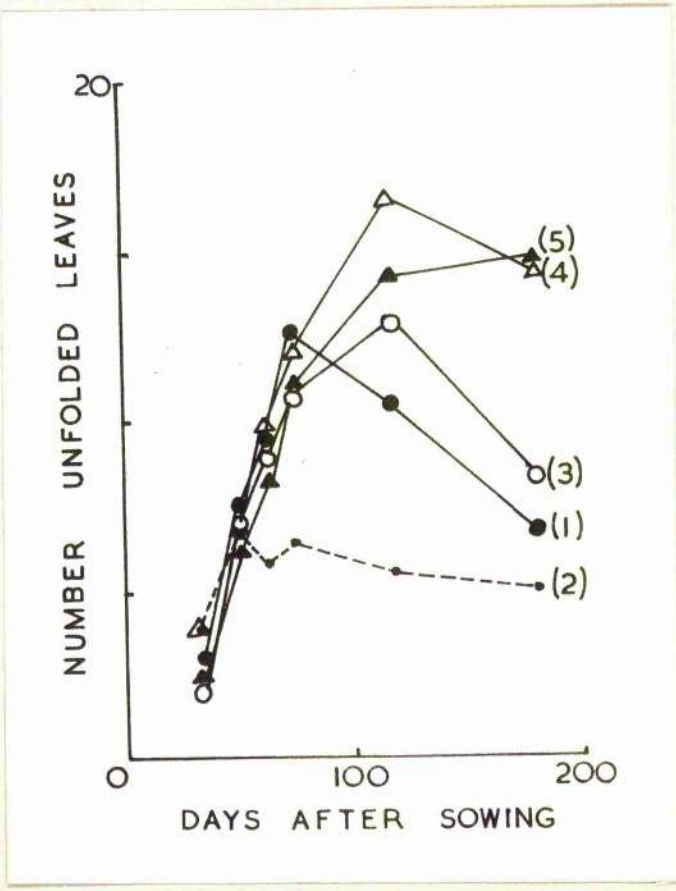

Fig. 13.
Rates of leaf unfolding of five varieties of cabbage sown 23 June. Varieties numbered as in Fig. 12.

Leaves of all varieties from both sowings unfolded at a fairly uniform rate of about one every five days (Fig. 12 and 13), but the total numbers of leaves which eventually unfolded differed with variety. Early Offenham had a maximum of 7 - 9 unfolded leaves from both sowings, Copenhagen Market about 13 and Enkhuizen Glory 13 - 15. From the first sowing January King had 23 and Amager 27; comparable figures for these two varieties are not available from the second sowing because exceptionally rapid leaf death - due, probably, to cooler conditions and poorer light - prevented the plants from unfolding their normal maximum number of leaves. The very large increase in leaf-unfolding of Copenhagen Market between the 193rd day and 258th day was due to the unfolding of young leaves on the elongating main stem which had burst through the head.

There appeared to be no constant differences between the death rates of leaves of different varieties before they had matured. When the plants were mature, however, the death rate of the leaves on the outside of the head increased, and leaves in this position often died before the unfolded leaves. It was observed that a longitudinal tension was set up along the midrib and petiole of the oldest folded leaves by the expansion of the head: this may have led to premature abcission and death

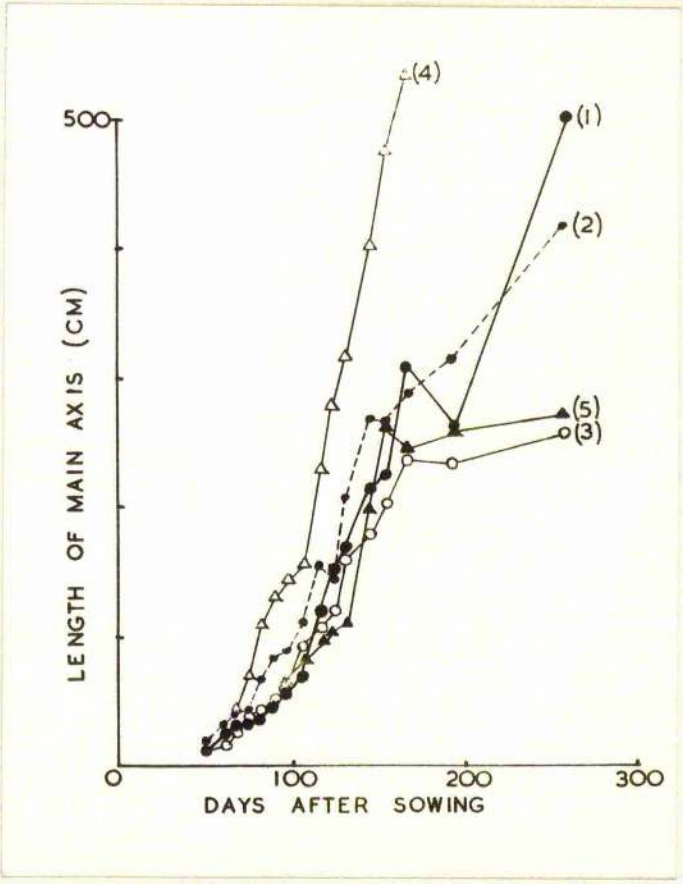

Fig. 14.
Growth in length of stem of five Varieties of cabbage sown 31 March.
(1) Copenhagen Market.
(2) Early Offenham.
(3) Enkhuizen Glory.
(4) January King.
(5) Amager.

of the leaves.

Appendix Table 3 gives stem length, and Fig.14 shows these graphically for the first sowing. Two features will be noted; first, the increase in stem length was greater for Amager than other varieties, and second, the stem in all varieties continued to increase in length throughout the period of the experiment although there was a substantial decrease in rate of stem elongation for most varieties after maturation: Copenhagen Market was an exception in this respect.

TABLE 3. STATE OF GROWING POINT OF DIFFERENT VARIETIES OF CABBAGE SAMPLED AT DIFFERENT DATES

	Days after sowing						
	1st sowing					2nd sowing	
Variety	145	154	166	193	258	118	181
COPENHAGEN MKT.					fff		ffff
ENKHUIZEN GLORY							f
AMAGER				f	FF	f	ffFFF
E. OFFENHAM					ffffF		ffff
JANUARY KING	f	fF	fF	F	ffFFF	fF	FFFFF

(Each symbol represents an apical growing point which has differentiated flower buds).

f - flower buds just visible with stereo microscope

F - flower buds visible with naked eye.

From Table 3, which summarizes the records of the state of the growing point, it will be seen that flower initiation occurred earliest in January King and

latest in Enkhuizen Glory, with the other three varieties more or less intermediate in this respect. With the exception of some individual plants of January King, which initiated flowers very much earlier than other varieties, flower initiation did not occur until after the second week in December, irrespective of whether the plants were from the first or second sowing.

(2) Discussion

Experiments described in this section give information for a study of the relationships between certain growth features of a variety and its time of maturation. The main growth features which have been examined are:-

(a) Rate of overall increase in fresh weight of the plant

(b) Shoot/root growth ratio

(c) Rate of leaf initiation

(d) Rate of leaf unfolding

(e) Time of flower initiation

The evidence for the relative effects of these factors on time of maturation will now be considered.

(a) Rate of overall increase in fresh weight of the plant

From Experiment 5 there was no evidence that early-maturing varieties increased in overall fresh weight more quickly than late-maturing varieities; indeed, Early Offenham, which was one of the first to mature, seemed to have a lower rate of growth in weight than other

varieties.

(b) Shoot/root growth ratio

Experiments 2 and 3, which recorded the distribution of shoot/root growth of different varieties, showed no pronounced correlation between this factor and rate of maturation. Both these experiments, however, were of a preliminary nature, and it is possible that further investigation might lead to the discovery of a correlation of a smaller order.

(c) Rate of leaf initiation

From the preliminary Experiments 3 and 4 it appeared that there might be a correlation between rate of maturation and rate of leaf initiation of a variety. In experiment 5, however, Early Offenham had the lowest rate of leaf initiation and yet matured first. This variety differs from the other four tested in Experiment 5 in having a pointed head, and it may be that whereas rate of maturation and rate of leaf initiation are correlated within groups of closely-related varieties, no such relationship exists among varieties belonging to groups with widely-differing morphological characters.

The ability to detect the relative rates of maturation of batches of seedlings would be of considerable practical value to the plant breeder, and on these grounds the possibility of a correlation between rate of leaf initiation and maturation within groups of varieties merits

further investigation.

(d) Rate of leaf unfolding

Rate of leaf unfolding during the period of maximum growth in 1954 (approximately 1 every 5 days in Experiment 5)was remarkably close for all five varieties tested at both samplings, and it was near to that for Enkhuizen Glory in 1953 (approximately 1 every 4½ days in Experiment 1). The time when leaves ceased to unfold was, however, closely related to rate of maturation. It seems therefore that under given environmental conditions, leaves continue to unfold at about the same rate in all varieties, until some factor intervenes to prevent leaf unfolding, and that the time of operation of this factor is related to the rate of maturation of the variety. Leaves may cease to unfold because maturation - the slowing down of growth in weight - has commenced through the intervention of some other factor, but cessation of leaf unfolding precedes maturation and it seems probable that maturation is a result rather than the cause of cessation of leaf unfolding.

(e) Time of flower initiation

Miller (1929) found that flowering could be induced in Cabbage by a period of cold treatment after the plants had passed a certain juvenile stage of their development, but he was unable to influence flowering by

day-length treatments. Stokes and Verkerk (1951) found similar results with Brussels sprouts and noted that flower initiation occurred during or very soon after the requisite cold treatment had been given. They were also the first to use the term puberty to denote the change from the juvenile to the adult stage when plants could be induced to flower by cold treatment.

From Table 3 it will be seen that varieties differed in their time of flower initiation. The plants in the first sowing were older than those in the second, and yet, with the exception of January King they did not produce flower initials earlier. This suggests that the difference observed between varieties was not one of differing ages of puberty, but rather a difference in the threshold temperature required for flowering. From the experiments described in this section there was no indication of a relationship between threshold temperature and rate of maturation of a variety.

January King appears to be very prone to early flower initiation and it is interesting to speculate whether this character is linked with the poor heading capacity of this variety.

C. COMPARISON BETWEEN ROSETTE ROGUES AND HEADED PLANTS OF JANUARY KING CABBAGE.

January King is a late-maturing variety of cabbage, and all strains show considerable variation in the inherent rate of maturation of individual plants. Thus, during a poor growing season, many individuals do not make sufficient growth to mature before the onset of cold weather and a large proportion of plants are found without heads. Early-sown crops, and those which enjoy good growing conditions, produce the highest number of headed plants. All stocks of the variety at present available, however, give some plants which will not form heads even when they are afforded excellent conditions for growth, and Finch (1952) has found that the proportion of these non-heading plants is relatively constant for a range of sowing dates. Rogues of this type resemble a conventional rosette in form (see Figs. 15 and 16) and have become known as 'rosette rogues' - a term which was probably first used by Miller (1929).

(1) Experimental

(a) Differences in weight, leaf number, length of main axis and flower initiation.

Experiment 6. As a preliminary experiment, three typical rosette rogues found at Mylnefield on January 1 1954 were compared with headed plants from the same batch.

Fig. 15.
Rosette rogue (left) and headed plant (right) of January King cabbage.

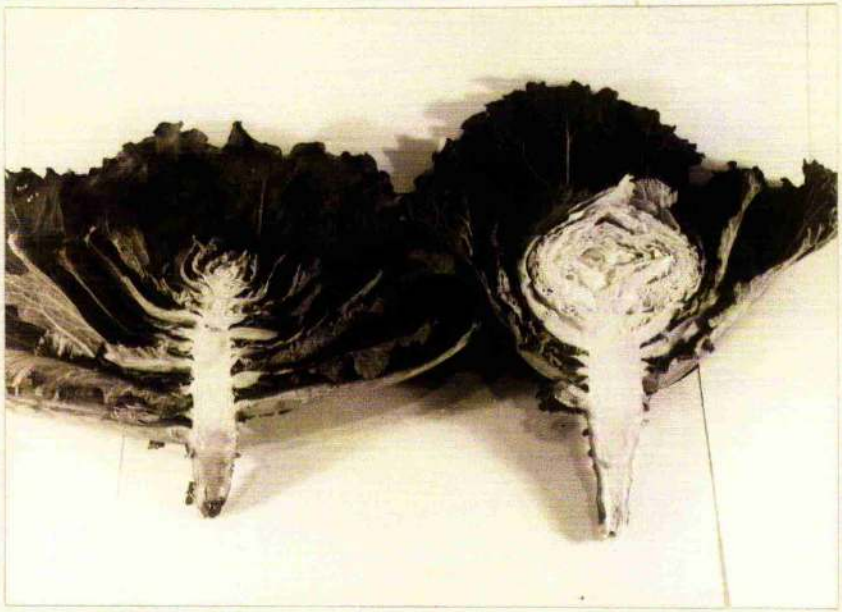

Fig. 16.
Longitudihal sections of rosette rogue (left) and headed plant (right) of January King cabbage.

TABLE 4. COMPARISON BETWEEN ROSETTE ROGUES AND HEADED PLANTS OF JANUARY KING (MEAN PER PLANT).

	Fresh wt (g)	Dead leaves	Total no of leaves initiated	Length of stem (mm)
Rogues	2128	17.6	114.6	314
Headed	3801	22.6	106.6	357

Results in Table 4 show that there was very little difference in the length of stem, total number of leaves, or number of dead leaves of headed and rogue plants. All the headed plants were heavier than the rogues. Each of the six plants had initiated flower buds, but whereas those of the rogues were visible with the naked eye, flower buds of headed plants were only just visible with a stereo-microscope.

Experiment 7. Two growers' crops of January King at Inverkeithing and Musselburgh were sampled on 9 and 10 January 1956 and twenty rogues and twenty headed plants selected from each. The plants at Inverkeithing had been raised from Suttings' strain sown 30 April and transplanted 29 June and those at Musselburgh from seed of Clucas' strain sown direct in the field during April and thinned.

Fresh weight; number of dead, unfolded, and folded leaves; length of stem and state of flower differentiation were recorded. Flower differentiation

was recorded according to the following scale:-

0.	No signs of flower initiation	As viewed with stereo-microscope
1.	Many axillary buds forming	
2.	Flower buds just differentiated	
3.	Flower buds small	
4.	Flower buds readily visible	
5.	Flower buds just visible	With naked eye
6.	Flower buds readily visible	

The length and width of each sixth successive leaf of eight normal and eight rogue plants from the Musselburgh crop were also recorded.

The results, with the exception of the leaf measurements, are given in Table 5: they confirmed those of the preliminary experiment, for there was no significant difference between rogue and headdplants in the length of the stem, total number of leaves or number of dead leaves. The headed plants again weighed more than rogue plants, although the difference in the mean figures for the Musselburgh crop was not significant. Flower initiation had occurred in all but two of the forty plants, but the state of flower development was again moreadvanced in the rogue than the headed plants.

Leaf measurements are given in Table 6 and Fig. 17. The length/width ratio of the oldest leaves of both rogues and headed plants was comparatively high. It fell with successively younger leaves to a minimum between the 30th and 50th, and then began to rise. For any given serial number, however, the ratio was higher for rogues than headed plants.

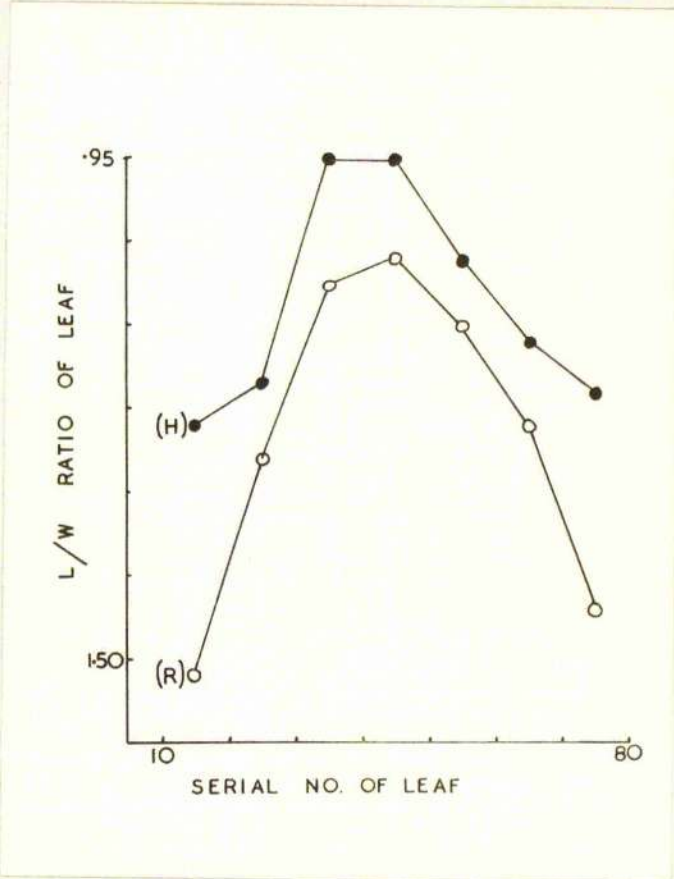

Fig. 17.
Length/width ratio of successive leaves of rogues and headed plants of January King cabbage.

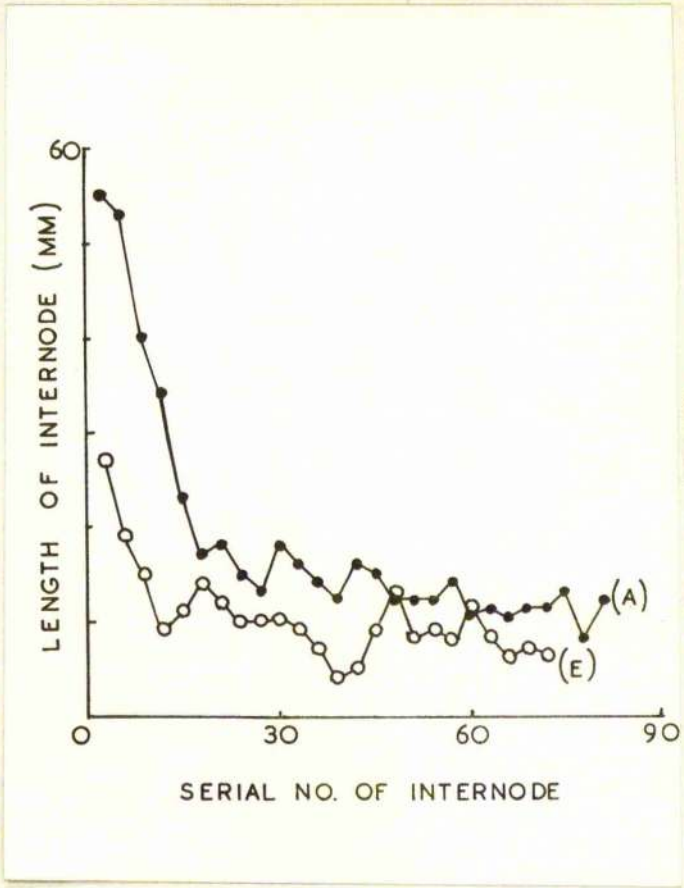

Fig. 18.
Lengths of internodes of Amager (A) and Enkhuizen Glory (E) cabbages.

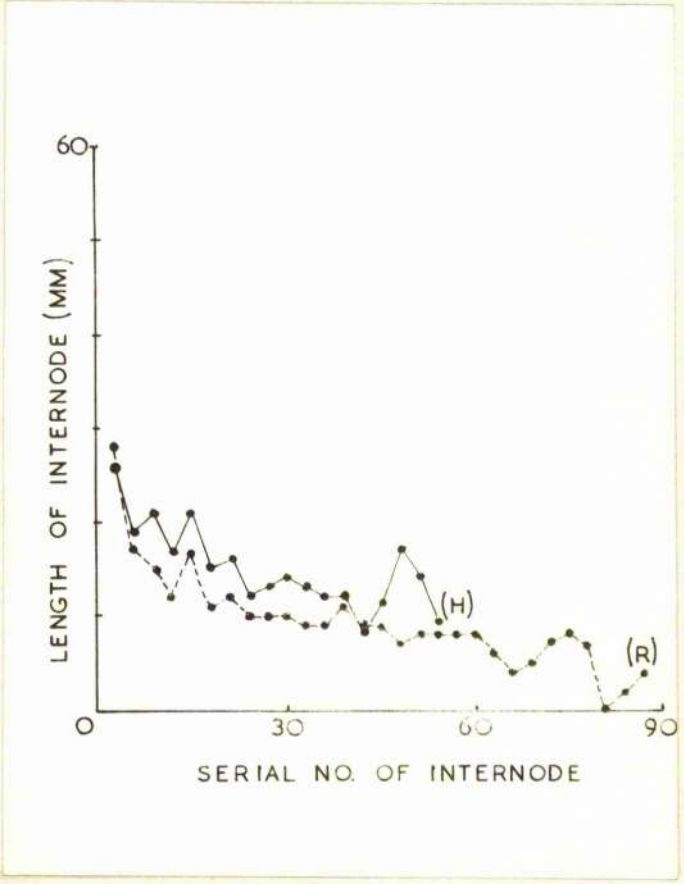

Fig. 19.
Lengths of internodes of rosette rogues (R) and headed plants (H) of January King cabbage.

With the exception of the 21 - 30th leaf, the mean leaf width of rogues was lower than that of leaves of similar age from headed plants.

(b) Length of internodes

On 19 January measurements were made of the internode lengths of headed plants of Enkhuizen Glory and Tall Amager, and headed plants and rogues of January King.

The stem was cut at ground level - as near as possible at right angles to its axis. A pinwas stuck into the centre of the axillary bud of the oldest leaf, and the distance measured between this and the cut surface of the stem. The pin was then removed to the next highest axillary bud and the operation repeated.

It was noted that the phyllotaxy was a simple spiral with an angle of 135° between successive leaves, so that every eighth leaf lay above another. Spirals of different plants were both left - and right-handed, and an examination of seedlings of different typesand varieties of B. oleracea showed that the numbers of each kind of spiral were nearly always equal. Allard (1951) has found that many other species have random distribution of the direction of the spiral of leaf arrangement.

By subtracting the measurements for successive leaves, a negative value was sometimes obtained for internode length. This was presumably due to the fact that the stem was bent, or had not been cut at right-angles

to its axis. The sums of each three successive measurements of internode length were therefore plotted to indicate relative internode length, and the results are shown in Figs. 18 and 19.

It will be seen that the earliest-formed internodes of all varieties tend to be longest, and that there is a continuous decrease in internode length with successively older leaves. At first this decrease is rapid, but it changes suddenly before the 15th node to a slower rate - a phenomenon which is especially marked with the long-stemmed Amager variety. There is no indication that the internodes of rogues are longer than those of headed January King plants - in fact, they were slightly shorter.

(2) Discussion

Folded leaves have a higher moisture content than unfolded leaves (p.105) and it is likely that the proportion differences in dry weight between rogue and headed plants of a comparable age are less than that of their fresh weights. Even if this is so, it seems probable from the fresh weight data in Table 5 that, at the time of sampling, the headed plants from Inverkeithing had a significantly higher dry weight than the rogues, and there is therefore an indication that rogues may have a lower overall growth in dry weight than plants which form heads.

There is evidence, from the larger number of headed plants at Musselburgh, that the crop there was at

TABLE 5. COMPARISON BETWEEN HEADED AND ROSETTE ROGUE PLANTS OF JANUARY KING. (MEAN PER PLANT).

	Fresh wt (g)	Dead leaves	Unfolded leaves	Folded leaves	Total No of leaf initials	Length of stem (cm)	State of growing point
MUSSELBURGH			**	**			
Rogues	1180	16.5	59.0	35.1	110.5	23.0	4.7
Headed	1502	14.0	18.4	77.7	110.1	21.7	2.9
INVERKEITHING	**		**	**			
Rogues	849	14.7	51.5	23.3	81.5	19.5	4.1
Headed	1369	14.0	18.5	64.3	86.8	22.4	2.6

**Significant at 1% level

‡ See page 45

TABLE 6. LEAF MEASUREMENTS OF HEADED & ROGUE PLANTS OF JANUARY KING

Serial No of leaf	Length/width ratio.		Width (cm)		% Width rogue leaves of leaves of headed plants.
	Rogue	Headed	Rogue	Headed	
11-20	1.52	1.22	20.9	23.9	88
21-30	1.26	1.17	19.3	16.3	118
31-40	1.05	0.95	16.1	19.2	84
41-50	1.02	0.95	12.1	17.3	70
51-60	1.10	1.02	9.7	13.5	72
61-70	1.22	1.12	6.8	8.0	85
71-80	1.44	1.18	3.8	5.0	76

a more advanced stage of growth than that at Inverkeithing (the proportion of headed plants was very low at Inverkeithing - even for a poor strain), and the headed plants in this crop had probably been in a mature state longer than at Inverkeithing. This condition would explain why the difference in weight of the two types was less at Musselburgh than Inverkeithing, for growth in weight of the whole plant is considerably slowed down or ceases at maturation of the head, but presumably no corresponding retardation occurs in non-heading plants; thus rogues had probably been growing for a relatively longer period than headed plants at Musselburgh than Inverkeithing.

Clearly the main difference between rogues and headed plants is that leaf unfolding in the former is not arrested. It is also possible that the rate of leaf unfolding is greater in rogues than in heading plants.

All samples showed that flower development was further advanced in rogue than headed plants. This may have been due either to an earlier initiation of flowers in rogues, or to a delay in their subsequent development in headed plants. If heading leads to a delay in flower development, it is unlikely that it operates through pressure on the growing point, for headed plants showing comparatively lose arrangement of the leaves did not have

flowers in a more advanced state of development than those with firm heads. It is possible that the difference in flower differentiation may result from insulation of the growing point of a headed plant from extremes of low temperature.

The difference in shape between leaves of rogues and normal plants is very interesting. Its implication is considered in the final discussion to this thesis.

III MANIPULATION EXPERIMENTS

A. GRAFTING AND LEAF REMOVAL

The experiments described in previous sections were analyses of plants allowed to develop unhindered. This section describes experiments planned to test the reaction of plants to an upset in their normal growth balance induced by grafting and leaf removal.

The purpose of the grafting experiments was twofold, namely to discover whether (1) cabbage would form a head when grafted to a root system of a non-heading form of B. oleracea; (2) the root/shoot ratio could be altered by grafting, and if such an alteration would affect heading.

Leaves were removed to find if such treatment increased the rate of unfolding of those which were left, or permitted the unfolding of leaves which normally remained in the head.

(1) Experimental

(a) Grafting Experiments. A first attempt to unite cabbage (January King) to roots of kale and cauliflower was made by cleft grafting cabbage to roots of established pot-grown seedlings which had been raised in the glass-house. The grafts were bound with Lassotape (adhesive tape used at the Station for binding inarch grafts of raspberry for virus investigation work), and stood in a heated frame. This attempt was not successful, for the

high temperature lowered the viscosity of the adhesive of the tape and the scions fell away from the stocks.

Further grafts of similar plant material were made using Crepex bandage (thin crepe rubber strip without adhesive) for binding. These grafts did not fall out, but very few united well. Stocks which had been raised on an outdoor seedbed, and which were dug up and grafted before being planted in the propagating frame, however, gave more promising results. January King cabbage united more readily with Marrow stem Kale than with cauliflower. The method used is illustrated in Fig. 20.

Experiment 8. By the time a suitable grafting technique had been discovered it was too late in the season to set out a planned experiment, but five successfully-grafted plants of January King cabbage on Marrow stem kale roots were planted in the field for comparison with January King seedlings of a comparable size.

Owing to the advanced state of the season, none of the plants formed heads, but records were made of weights of stem, leaf and root and numbers of leaves initiated. Fibrous and total roots were separately recorded.

It will be seen from the results in Table 7 that although the weight of the plants raised from seed was considerably greater than that of the grafted plants, there was no significant difference between the numbers

TABLE 7. COMPARISON BETWEEN PLANTS OF JANUARY KING CABBAGE GRAFTED ONTO MARROW STEM KALE ROOTS AND SEEDLING PLANTS OF JANUARY KING.

	Seedling	Grafted	
Number of leaves initiated per plant	61.4	70.6	NS
Fresh wt. per plant (g)	728	463	**
% Side roots of total wt. of plant	0.74	2.68	*
% 'Root' of total wt. of plant	3.65	7.28	*

**,* Significant for P = 0.01 and 0.05 respectively.

of leaves initiated. The proportion of roots - whether measured as fibrous roots or total root - was higher for the grafted than the ungrafted plants, the difference being significant at the 5% level. Thus grafting had affected the root/top ratio.

Experiment 9. Seed of Enkhuizen Glory cabbage, marrow stem kale and the cauliflower variety Cambridge No. 7 was sown outside on 31 March. Grafts of Enkhuizen Glory were made, as previously described, to marrow stem kale, cauliflower and other plants of Enkhuizen Glory. Twenty-four grafts of each of the three types were prepared, but many died and only six of each were planted in the field. Only four of the cabbage/cauliflower plants survived, and consequently only four plants of each treatment were examined on 28 October.

The grafts united well (Fig. 21) and all the plants formed heads, but none of the recorded differences between the plants (see Table 8) were significant.

TABLE 8 COMPARISON BETWEEN ENKHUIZEN GLORY PLANTS GRAFTED ONTO ROOTS OF ENKHUIZEN GLORY CABBAGE, MARROW STEM KALE AND CAULIFLOWER.

	Rootstock		
	Cabbage	Kale	Cauliflower
No. leaves initiated per plant	94.0	94.7	96.2
No. dead leaves per plant	11.7	12.5	12.2
No. unfolded leaves per plant	12.0	11.7	14.2
Fresh wt. per plant (g)	2271	2552	2121
% 'root' of total wt. of plant	0.97	1.57	1.59
% folded leaves of total leaf wt.	44.9	54.4	31.3

(b) Leaf-Removal Experiments

Experiment 10. Some of the Enkhuizen Glory plants raised for Experiment 1 were used for a leaf-removal experiment.

On 12 August (128 days after sowing and when about 86 leaves had been initiated and maturation had commenced) ten plants were selected for uniformity of size. All unfolded leaves were removed from five of the plants i.e., 13, 12, 14, 15, 14; Mean 13.6). On 19 October, 196 days after sowing, the number of unfolded leaves was recorded (i.e. 5, 8, 9, 8, 9; Mean 7.8) for untouched plants, and for those from which all the outer leaves had previously been removed (i.e. 4, 3, 3, 3, 3, Mean 3.2).

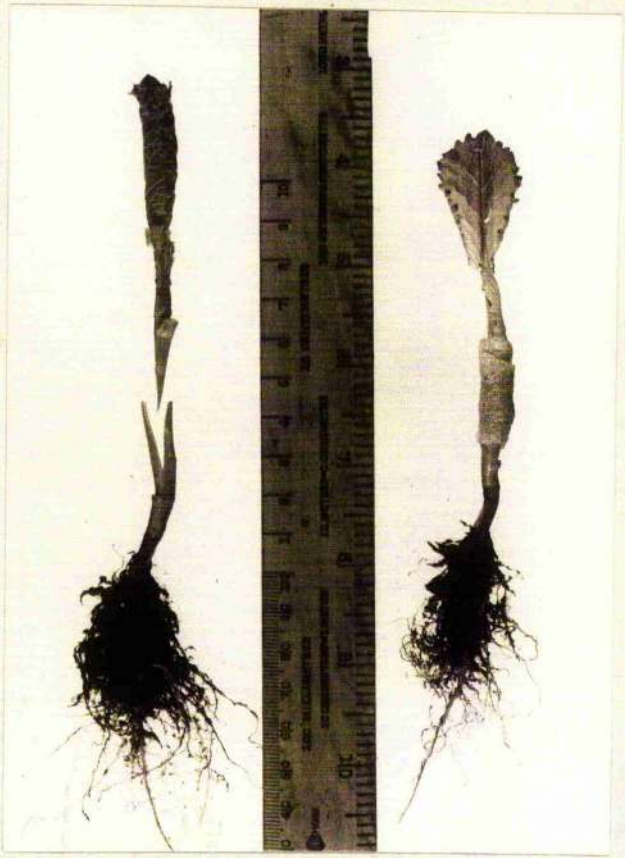

Fig. 20.
Type of graft used for uniting cabbage to othe varieties of B. olerace

Fig. 21.
Graft union of Enk, Glory cabbage on root of marrow-stemmed kale. Paper arrows indicate union.

Unfortunately no records of the number of dead leaves was made for the individual plants used in the experiment, but judging from the growth analysis (Experiment 1) an average of 8 (i.e. 13 - 5) of the older leaves must have died between the 128th and 196th day on the untouched plants. It is unlikely that any of the leaves would have died on the treated plants because 13.6 of the oldest leaves had been removed. Thus 2.2 (i.e. 7.8 + 8 - 13.6) leaves had unfolded from the untreated, and 3.2 from the treated plants.

Experiment 11. In the previous experiment leaves were removed when maturation had commenced and the rate of leaf unfolding of untreated plants had passed its peak and was considerably reduced. Experiment 11 was carried out to study the effect of removing leaves when the rate of leaf unfolding was at its peak.

Seed of Enkhuizen Glory was sown on the earth floor of an unheated glasshouse on 20 April. The purpose of sowing under glass was to reduce the risk of wind-drying, for a previous attempt to study the effect of removal of small leaves had failed because the poorly-protected growing points died through desication.

On 3 July twelve plants were selected for uniformity of size and the first 12 folded leaves removed from four plants - one of which had to be discarded later because

TABLE 9 EFFECT OF LEAF REMOVAL (ENKHUIZEN GLORY)

No. of leaves removed	No. of leaves on 10 Sept. Dead	Unfolded	Unfolded since treatment	Serial No. of youngest expanded leaf	
12	12	22	19	46	Mean 36.7
12	11	9	8	32	
12	8	12	9	32	
15	9	12	6	36	35.0
15	10	10	4	35	
15	11	10	6	36	
15	7	11	4	33	
0	7	13	-	20	19.2
0	7	8	-	15	
0	7	10	-	17	
0	8	12	-	20	

the growing-point died. When the leaves were removed a small severed leaf was laid over the growing point for about a week to reduce the risk of dessiccation. On 16 July the first fifteen folded leaves were removed from a further four plants.

The number of dead and unfolded leaves were counted on all plants on 10 September. Leaves which had unfolded since the treatments were applied were readily distinguishable by their brighter green colour, but apart from this characteristic they appeared similar to the unfolded leaves of untreated plants.

The results (see Table 9) showed that when 12 or 15 folded leaves were removed at an early stage of their development the 32nd to 46th leaf was the last to expand up to the 10 September, whereas, if no leaves were removed, the 15th to 20th leaf was the oldest to unfold.

(2) Discussion

The differences in root/shoot ratio of the plants in Experiment 9 were not significant, but the ratios for individual plants of Enkhuizen Glory on roots of the same variety were, with one exception, all lower than those for the eight plants of Enkhuizen Glory on roots of another variety of Brassica oleracea. It is reasonable to assume therefore that a similar experiment with more replications might have shown a significant difference in the root/shoot ratio, especially in view of the results of Experiment 8.

It must be admitted that even if the results had been significant there would be no clear evidence of a change in the differential growth rates of root and top. The difference in root/shoot proportion observed at one sampl-ing might have been due to alteration in the proportions when the grafts were made.

From Experiment 9 it is clear that a cabbage shoot grafted onto roots of kale or cauliflower, neither of which form heads, is capable of forming a head. This suggests that the root has no fundamental affect on heading and that any affects it might have are indirect - for example,

nutritional effects.

The removal of all the unfolded leaves from plants which had commenced to mature did not induce a marked increase in the rate of leaf unfolding - the increase (calculated from Experiment 8) of 1.0 per plant in 68 days is small in comparison with the rate of about 1 in every five days reached during the period of maximum rate of leaf expansion. This result is not surprising however, in view of the fact that on untreated plants leaves which die shortly after the onset of maturation are not replaced by others unfolding from the head.

Nevertheless in Experiment 11 the removal of leaves at an early stage of development permitted the unfolding of leaves which, on untreated plants, would have died without unfolding. It seems therefore that all leaves may have the capacity to unfold, but that some lose that capacity through an effect of the older leaves immediately surrounding them.

B. EFFECT OF MECHANICAL CONSTRICTION ON THE CAPACITY OF A LEAF TO UNFOLD.

Experiment 11 indicated that successive leaves gradually lost their capacity to unfold through the effects of older leaves immediately surrounding them. One such effect might simply be the mechanical constriction of growth in certain planes, moulding the leaves into shape until they lose their capacity to unfold. The experiment described in this section was therefore designed to find what degree of effect a temporary mechanical constriction might have on the eventual unfolding of a Brassica leaf.

(1) Experimental

Experiment 12. Glasshouse-raised seedlings of Brussels Sprout were used: Ashwell's variety was chosen because leaves on the main axis of this form always unfold, whereas some strains occasionally form a cabbage-like terminal head.

On 19 July the third unfolded leaf of each of three plants was rolled into a cigar-shape and rubber bands were placed round the treated leaves to keep them rolled (Fig. 22). Ten days later the rubber bands were removed. After a further ten days there were no signs of the treated leaves unfolding, although they were then the oldest living leaves and their neighbours were fully expanded, (Fig. 23). Within a further week all the treated leaves had died and been shed without unfolding. Thus the leaves

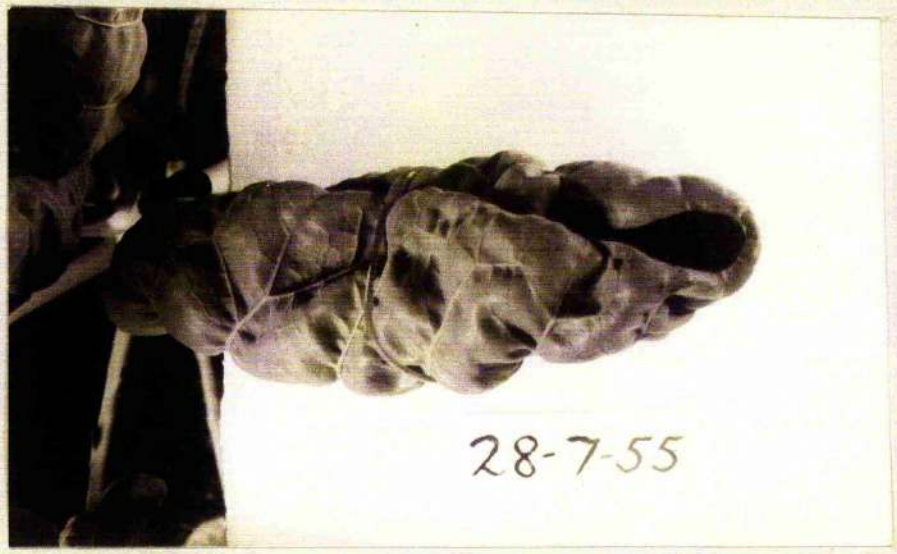

Fig. 22.
Rubber band placed round leaf of Brussels sprout plant to keep it folded.

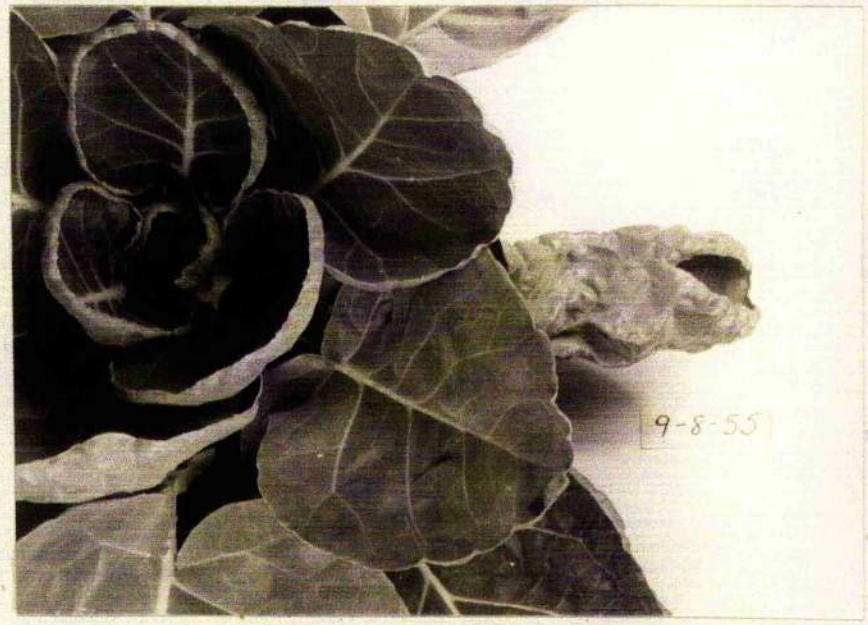

Fig. 23.
The same Brussels sprout leaf as in Fig. 22. It has remained folded after being temporarily constricted with a rubber band.

had, during the period of constriction lost the capacity to unfold.

(2) Discussion.

This small-scale experiment clearly showed that a temporary mechanical constriction of Brassica leaves, during the time they would normally unfold, could prevent their ultimate unfolding.

Cabbage leaves are formed in such a way that during the early stages of their development the lateral margins or both the lateral and apical margins (in pointed and round headed types respectively) are clasped round one another. This could lead to a temporary constriction of the leaves - the period of constriction extending as the constrictive effect becomes cumulative through an increase in the number of leaves crowded on a short stem. Successive leaves might thus loose their capacity to unfold.

C. RELATIONSHIP BETWEEN LEAF UNFOLDING AND CELL SIZE.

The results of several of the experiments on the phenomenon of heading so far described have emphasised the need for an explanation of the loss of capacity of leaves to unfold. It was thought that leaf unfolding might be related to cell size and experiments were accordingly planned to examine this aspect of the problem.

(1) Experimental.

The cabbage varieties Enkhuizen Glory and Copenhagen Market were chosen for this work because their leaf surfaces are comparatively smooth.

The areas of the large faces of epidermal cells from the ventral surfaces of leaves were measured. Cells from the distal end of the leaf were chosen and areas near large veins were avoided.

Two techniques for cell measurement were employed, namely epidermal stripping and a cellulose film technique.

(a) Epidermal stripping technique.

First attempts to measure cell area were made by assessing the greatest length of adjacent epidermal cells with a microscope fitted with an eyepiece graticule. The measurements were squared to give figures equivalent to areas.

The surface of the leaf was first wiped with cotton wool soaked in ether - to remove the cuticle - and

a portion of the epidermis was lifted and stripped with a pair of fine-pointed forceps. It was easier to strip the epidermis from young leaves if it was first lifted with a razor blade. The tissue was mounted in a dilute aqueous solution of methylene blue.

(b) Cellulose acetate film technique.

It was often difficult to observe areas of epidermis sufficiently large for measurement, and even when this was achieved the presence of mesophyll cells frequently confused the appearance of the tissue. To overcome the failings of the stripping technique the following method for assessment of cell area was evolved:-

A saturated solution of cellulose acetate and Night Blue (B.D.H. bacteriological stain) in acetone was prepared. With a small wad of cotton wool dipped in the solution and held with forceps, a thin film was smeared onto the leaf. Practice was required to obtain a film of optimum thickness, and the best results were obtained if the solution was diluted with acetone. (It was not possible to select an optimum initial concentration of the solution for the evaporation of acetone led to changes in concentration). When the film was dry it was painted with a 10% solution of Teepol (a detergent), drawn from the leaf, and spread out and mounted in a 1% aqueous solution of orange G. . This stain formed a sharp colour contrast with the film, the thicker parts of which appeared

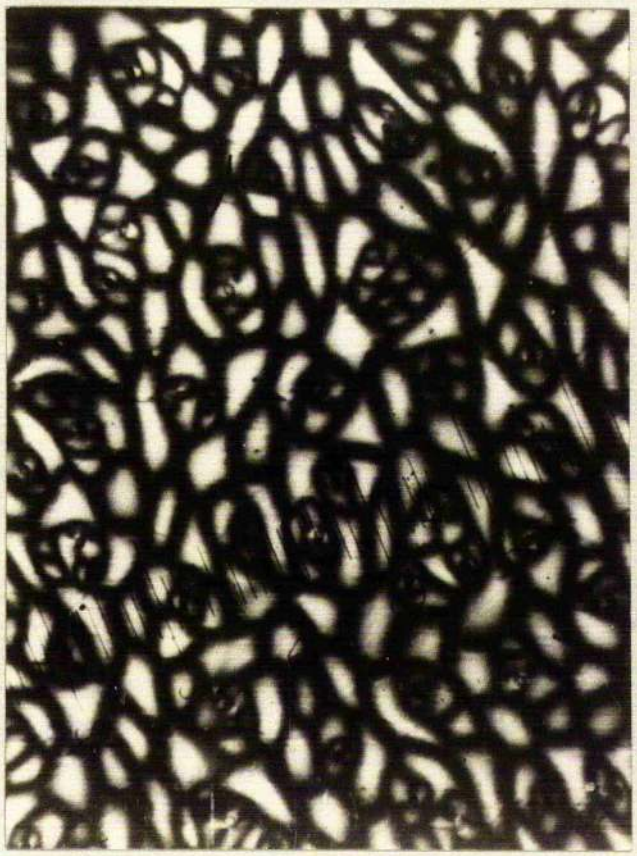

Fig. 24.
Photomicrograph of cellulose acetate film from epidermis of cabbage leaf.

as an almost black image on a light orange ground. A slight improvement in definition of the image was obtained by using phase-contrast. Fig. 24 shows a photomicrograph of a typical cellulose acetate film.

The mean cell area was measured by counting the number of cells in a known area. Two square holes were cut in a piece of black paper so that when they were viewed through a camera lucida one was equivalent to 0.5 mm^2 and the other 0.25 mm^2 at the objective stage of the microscope. The black paper was laid over a sheet of white paper and viewed at the same time as an epidermal film and a cross corresponding to each complete cell marked on the white paper within one of the square holes in the black paper. For small cells the small hole was used and vice versa.

Films representing areas of the epidermis one cm^2 or larger could be obtained quickly with this technique. Moreover, the shrinkage of the films was negligible, and of the same order for different leaves. The technique did not, however, give very good results when the leaves were covered with a thick layer of wax, and when this was removed the acetone solution would not flow uniformly over the treated surfaces; incomplete films were then obtained.

The technique was developed entirely independently,

but is similar to that described by Buscalioni and Pollacci (1902) and Long and Clements (1934). These workers preferred colloidin films, and did not use the technique described above for removal of the films from the leaf.

(c) Cell size of successive leaves.

Experiment 13. The cells of alternate leaves of a plant of Enkhuizen Glory (sown 20 April) were measured by technique (1). Forty measurements were made for each leaf examined.

From Fig. 25, which shows the calculated cell area plotted against the serial number of the leaf, it appears that there may be a marked change in the rate of increase in cell area of a leaf about the time it commences to unfold. The ordinate for serial number of the leaf is not, however, a true linear measurement of the time factor, for leaves are produced more slowly in early than in later stages of development.

Experiment 14. Measurements of cell size of successive leaves of two plants of Copenhagen Market (which had been sown outside on 31 March) were made 119 days after sowing by technique (1). Information on the rate of leaf formation was available from the growth analysis (Experiment 5), and it was therefore possible to draw Fig. 26 to show the relationship between cell area and leaf age.

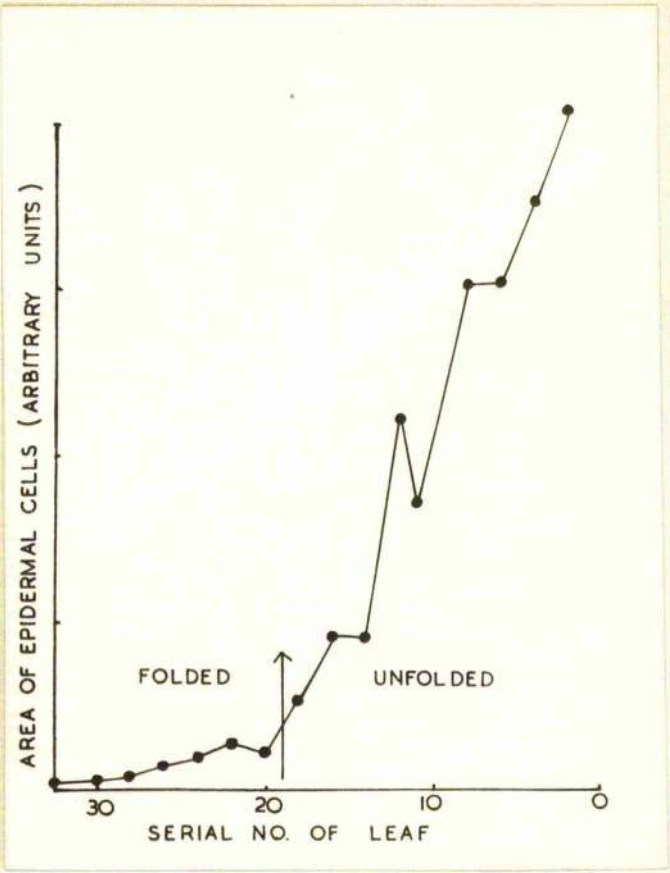

Fig. 25.
Areas of epidermal cell
of successive leaves of
Enk. Glory cabbage.

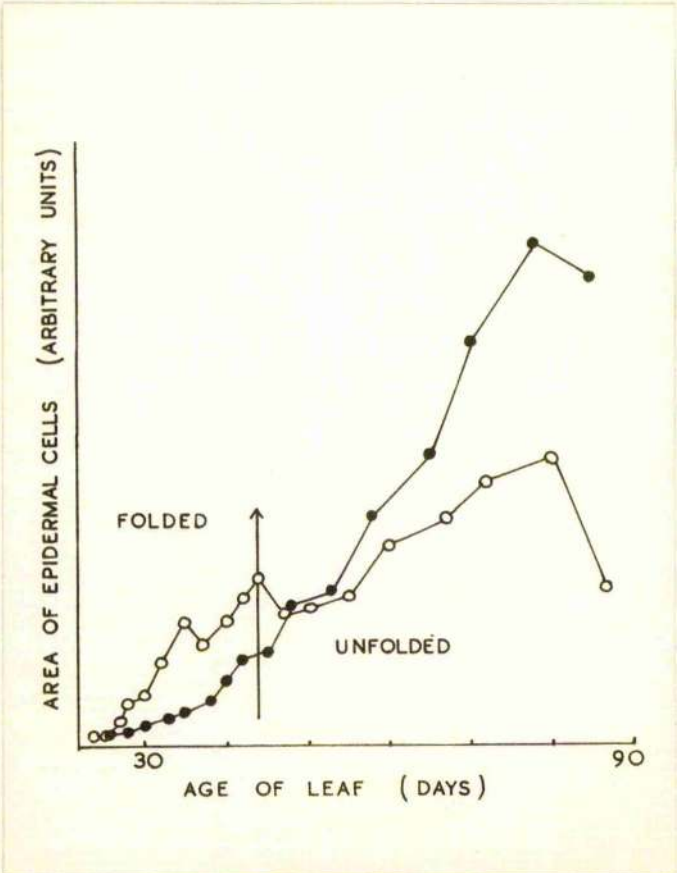

Fig. 26.
Areas of epidermal cell
of two plants of
Copenhagen Market cabba

Fig. 26 shows a marked difference in the greatest area of epidermal cells of two apparently similar cabbages from the same batch. (A similar difference was noted by Arney (1952) for kale (Brassica oleracea L. acephala)). There was a marked increase in the size of cells of leaves when they were 25 - 35 days old, but this did not coincide with leaf unfolding which occurred when leaves were 40 - 45 days old. Another feature of the curve is the apparent shrinkage of leaves before they died.

Experiment 15. As a preliminary trial, technique (2) was used to measure the cell size of leaves of a seedling Enkhuizen Glory cabbage. The results are shown in Fig. 27.

The change in rate of cell expansion occurred about the same time as leaf unfolding in this plant and the curve showed again that the cells of the oldest leaf were smaller than those of the second oldest leaf.

Experiment 16. This experiment was planned to find if the smaller size of cells of the oldest leaves could be attributed to shrinkage.

A plant from the same batch as that used for Experiment 15 was selected. On three occasions six counts were made of the area of the epidermal cells of the oldest and second oldest living leaves, using Technique 2. Results are given in Table 10. There was a

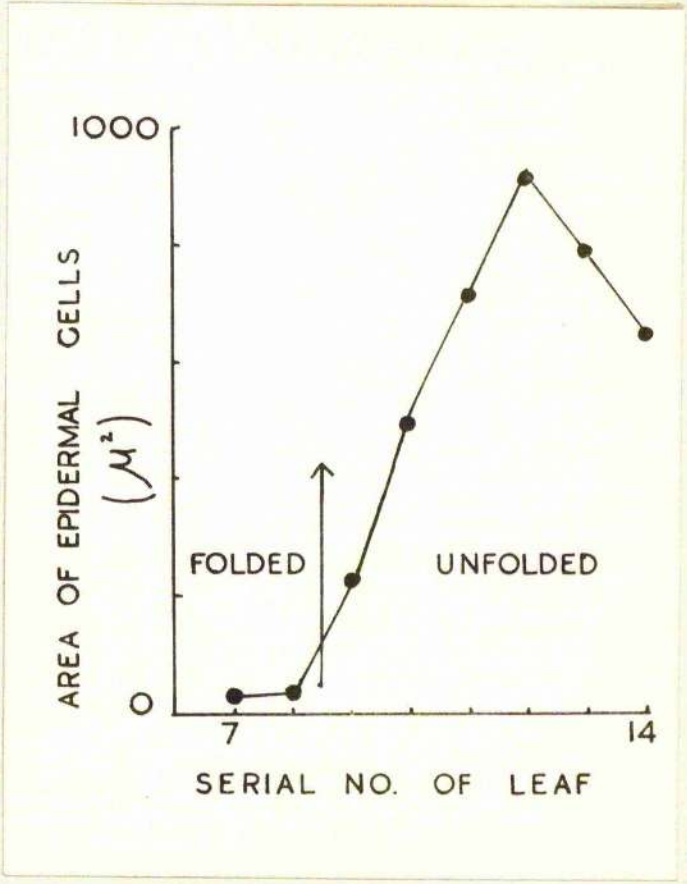

Fig. 27.
Areas of epidermal cells of seedlings of Enkhuizen Glory cabbage.

significant increase in the number of cells per given area of the second oldest leaf, showing that the cells of this leaf had shrunk during the experiment. The area of the cells of the oldest leaf did not alter appreciably in size during the experiment, probably because they had already shrunk to the minimum size before counts were made.

TABLE 10. CHANGE IN CELL AREA OF AGEING LEAVES

	No. of cells per unit area			LSD
	25 March	29 March	4 April	P = 0.05
OLDEST LEAF	99	95	98	NS.
2ND OLDEST LEAF	109	128	145	16

(d) Degree of cell expansion of oldest folded leaf Experiment 17. From Experiments 13 and 15 it appeared that leaf unfolding might correspond with a marked increase in the rate of cell expansion in young plants, but Experiment 14 suggested that such a relationship did not always exist with older plants. Experiment 17 was therefore planned to examine the degree of cell expansion of the oldest folded leaf of plants of different ages.

Seed of Copenhagen Market was sown outside on 5 April in rows 2½ ft. apart, and the seedlings were eventually thinned to 2 ft. apart in the rows. On 24 May five plants were sampled and the following data recorded:-

(1) Mean cell area of epidermis of oldest folded leaf using Technique 2.

(2) Mean cell area of oldest living leaf.

(3) Mean cell area of second oldest living leaf.

(4) Number of leaves initiated, unfolded and dead.

Three counts for cell area were made for each leaf. A further six samplings were made at intervals of 1 - 3 weeks. Results are given in Table 11. The figures for percentage of expansion of the cells of the oldest folded leaf were obtained by expressing the cell size of this leaf as a % of that of the oldest or second oldest leaf - whichever was the larger.

The cells of the oldest folded leaf were larger as the plant grew older, and their percentage expansion was also greater. There was a marked rise in the degree of expansion between the 87th and 100th days, which coincided with a slowing down and eventual cessation of leaf unfolding.

(2) Discussion. The experiments described in this section indicate that there are three main stages in the growth in size of cells of the cabbage leaf. In the first stage, after leaf initiation, cell expansion is slow and probably accompanied by a high degree of cell division. Then follows a second stage during which cell expansion is much more rapid, and cell division is very infrequent or does not occur. (Examination of leaf sections showed

TABLE 11. RELATIONSHIP BETWEEN LEAF CELL AREA AND LEAF UNFOLDING OF PLANTS OF DIFFERENT AGES.

	Mean cell area (μ^2)				No. of leaves		
Days after sowing	Oldest folded leaf	2nd oldest folded leaf	Oldest leaf	% Max cell expansion	Total	Unfolded	Dead + unfolded
49	682		2513	27.1	13.2	2.7	2.7
63	702		3145	22.3	32.6	6.2	6.2
70	841	2475	2762	31.0	44.4	7.2	8.0
87	822	2433	2451	33.5	75.8	12.2	15.2
100	985	2457	2105	40.1	88.0	14.0	17.4
112 (1)	1300	1905	1996	65.1	105.0	15.8	20.4
128 (2)	1613	2004	1988	80.5	109.0	14.2	20.0

(1) Most plants mature. (2) Many heads bursting.

no indication of mitotic divisions in this stage). Finally the third stage is reached when cells begin to shrink - a phenomenon which may result from a reduction in water supply to the leaf owing to the formation of an abcission layer.

Experiments 13 and 15 indicate that, in the early stages of growth of the plant, leaf unfolding takes place at about the time of the change from the first to the second stages of cell expansion. It is suggested that leaves would continue to unfold at this stage throughout the life of the plant if some factor did not operate to prevent unfolding.

Whatever the factor is which prevents successive leaves from unfolding, it is clear from Experiment 17 that cell expansion continues in the outer leaves of the head whether they are prevented from unfolding or not.

Unfolding of the leaf necessitates a change in form, and must therefore be accompanied by a change in the number or size of cells, or both, and the greater the degree of cell expansion of a leaf the less will be its capacity to alter shape and unfold. Whilst it must be admitted that the degree of expansion of epidermal cells does not necessar represent the potentiality for expansion of all cells of the leaf and petiole, it seems reasonable, without contrary evidence, to regard this as a fair assumption. Experiment 1 therefore suggests that with increasing age of the plant the

outer leaves of the head in undergoing expansion of their cells, loose their capacity to unfold and cannot therefore replace the unfolded leaves which die when the head is reaching maturity.

IV. EFFECTS OF LIGHT AND TEMPERATURE ON HEADING.

Light and temperature have profound effects on growth and development in cabbage, but the extent to which these factors differentially affect growth features associated with heading was not known. Experiments were therefore planned to obtain some information on this aspect of the problem.

A. CONTINUOUS LIGHT

Miller (1929) found no evidence that daylength affected flowering of cabbage. It was thought by the writer nevertheless, that this factor might influence head formation as in lettuce (Bensink 1955).

Plans to grow cabbage under reduced daylength conditions, whilst at the same time maintaining comparable temperatures for treated and control plants, necessitated the raising of plants in pots. Atempts to grow cabbage tp maturity in pots were unsuccessful, for the plants invariably suffered from drought and nitrogen starvation. It was decided, therefore, first to examine the effect of continuous light on cabbage plants which, for this purpose, could be grown on the earth floor of a greenhouse.

(1) Experimental

Experiment 18. Seed of Enkhuizen Glory cabbage was sown in an unheated glasshouse on 20 April in rows 2½ ft. apart. The seedlings were thinned to 2 ft. apart in the rows. The

sole purpose of using a greenhouse was to protect the lighting equipment from rain.

The glasshouse was divided transversely with a curtain of several thicknesses of hessian, and one of the compartments was illuminated between 7 p.m. and 8 a.m. so that it received continuous light. Two sets of six 4 ft. 'daylight' type flourescent tubes with tungsten ballast lamps were suspendedfive feet from the ground to illuminate an area of about 10 x 15 ft. This type of lighting was used, instead of tungsten filament lamps alone, because it emits more light from the blue end of the spectrum; Wassink and others (1950) have shown that several members of the Cruciferae differ from most plants in being more sensitive to increases in daylength by blue rather than red light.

The light intensity was measured with a photometer at 11 p.m. on 8 June, when there was a thick layer of cloud. Along the central row of plants and directly below the banks of lights, the intensity ranged from 20 - 50 lumens, whilst the outermost rows received 12 - 30 lumens. The intensity in the non-illuminated compartment was less than 0.1 lumens throughout.

The plants were sampled on four occasions, using five plants per sampling. On each occasion the fresh weight of leaves was recorded, and also the numbers of dead, unfolded and total leaves and the length of the stem.

TABLE 12. EFFECT OF CONTINUOUS LIGHT

			Days after sowing			
			32	43	58	128
No. of leaves	Dead	Control	0	0	0	7.6
		Illuminated	0	0	0	6.8
	Unfolded	Control	2.0	3.3	6.8	10.2
		Illuminated	2.0	3.5	6.4	9.2
	Total	Control	6.7	12.4	23.5	84.0
		Illuminated	6.5	12.6	22.9	79.0
Fresh wt of plant (g)		Control	2.2	17.9	163.2	2414.6
		Illuminated	2.3	19.5	153.5	2475.1
Length of stem (cm)		Control	17.8	36.1	74.5	245.0
		Illuminated	24.3 **	42.8	90.1 **	239.0

** Difference Significant (P = 0.01)

Results given in Table 12 show that the only significant difference between the treated and untreated plants was that the former had slightly longer stems at all sampling dates except the latest. At the sampling on the 128th day the fresh weight of folded leaves was 32% of that of all leaves for the control plants, and 36% for the treated plants - the difference was not significant.

(2) Discussion. Although the differences at all samplings were not significant, there was a strong indicatio that increase in daylength had induced an increase in stem length. This did not, however, lead to any measurable delay in time of heading.

These results do not cover the full possible effects

of daylength on head formation, for the natural daylength to which the plants were subjected - some 16½ - 17½ hours - may well have been above the minimum required for most formative effects.

B. SHADING.

Early in 1953 it was decided to investigate the effect of shading on the growth and development of cabbage. At the time little was known about heading, but it was thought that a moderate reduction in light intensity would result in a relative increase in leaf areas and that such an increase might take place through a greater rate of leaf unfolding and a consequent slowing down of the rate of head formation.

(1) Experimental

Enkhuizen Glory was used for Experiment 19. It was intended to use Copenhagen Market for Experiment 20, but seed was obtained locally and the strain was found to be incorrectly named; it formed small cabbages with rather loose conical heads, and is thought to have been a strain of the Durham Early type.

Seed was sown in the open and the seedlings were thinned and then watered with Dieldrin solution.

Plants were shaded with cages made of a metal framework 9 ft. long x 6 ft. wide and 2¾ ft. high covered with 40 mesh galvanised iron wire. Measurement of the light intensity under the cage with a photometer showed that light was reduced to ⅓ - ¼ of full light intensity on a bright but cloudy day, and fell to slightly less than ¼ when the angle of the sun was low during the evening

and early morning.

Experiment 19. Some plants from seed sown 6 April were shaded 44 days after sowing and others 94 days after sowing. The first batch of plants were quite small seedlings when covered and had initiated less than 10 leaves and had only two small unfolded leaves. Plants covered on the 94th day had already commenced to nature.

On five occasions five plants from each treatment were sampled and the same data were recorded as in Experiment 1.

Table 13 and 14 show that shading resulted in a considerable reduction in the toal growth in weight of the plant. It also led to a smaller number of leaves being initiated at each sampling, but this effect was apparently due to a check in the rate of leaf initiation immediately after shading, followed by a resumption of a rate similar to that of unshaded plants, (See Fig. 28) rather than an overall decrease in the rate of leaf initiation.

Shading gave a significant increase in the growth in length of the stem and an overall increase in the proportion of stem weight to that of root and leaf. The rate of leaf unfolding was slightly reduced immediately after shading, but following a period of adjustment the rate of unfolding was regained or exceeded, so that on the 150th day there was a significantly higher number

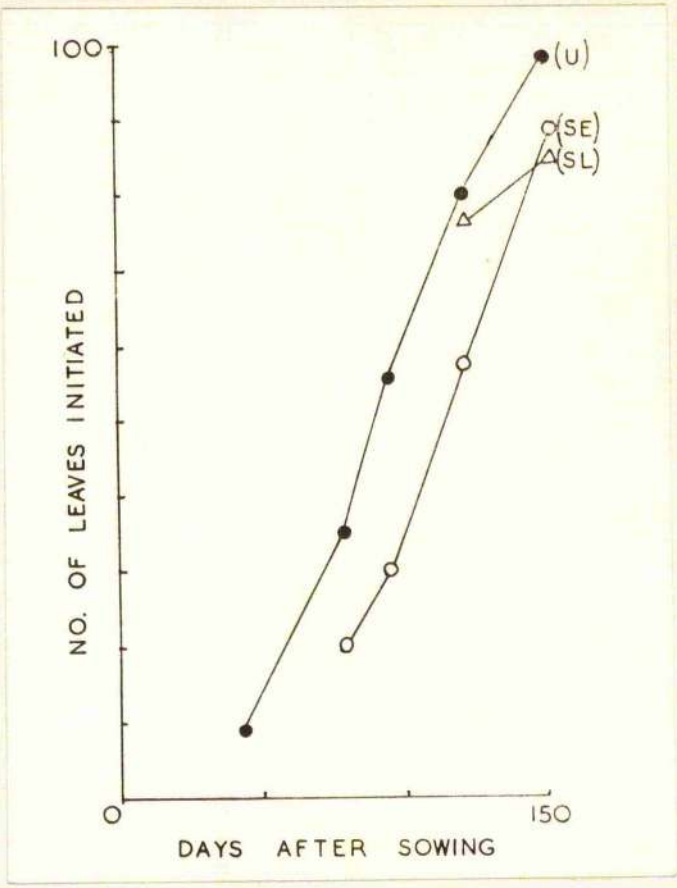

Fig. 28.
Effect of shading on rate of leaf initiation in Enkhuizen Glory cabbage. (U) unshaded; (SE) shaded from 44th. day; (SL) shaded from 94th day.

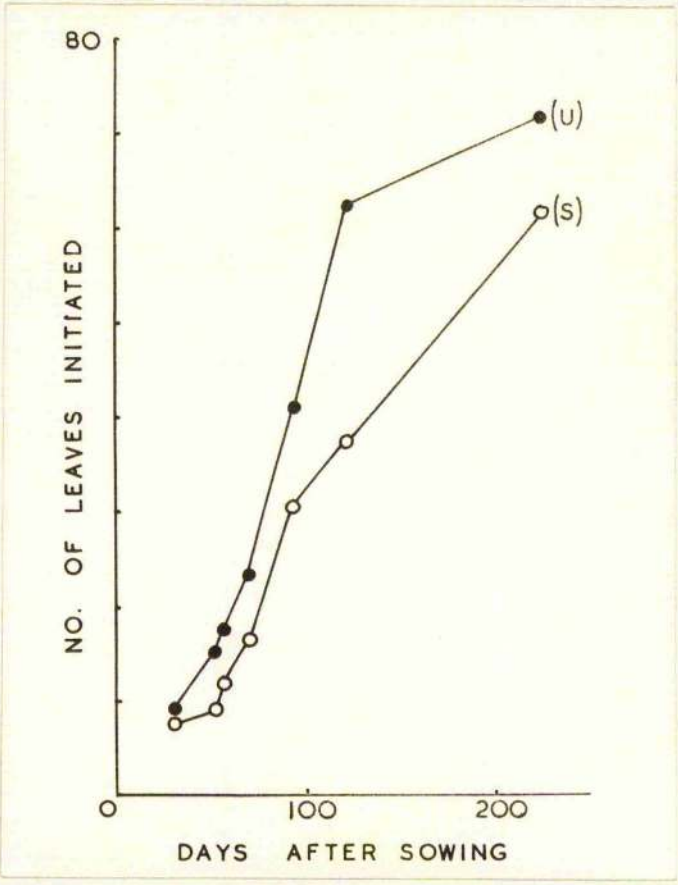

Fig. 29.
Effect of shading on rate of leaf initiation in unknown cabbage variety. (U) unshaded; (S) shaded.

TABLE 13. EFFECT OF SHADING ON LEAF NUMBERS

	Treatment	Days after sowing: 44	79	94	122	150
Total no. of leaves	(Unshaded	9.0	35.4	55.8	80.4	98.0
	(Shaded from 44th day		20.0	30.2	57.4	88.8
	(Shaded from 94th day				76.8	85.4
	(LSD (P = 0.05)		NS	20.0	12.6	NS
No. of leaves unfolded	(Unshaded	2.0	9.6	14.2	15.2	11.2
	(Shaded from 44th day		7.8	11.0	14.2	16.2
	(Shaded from 94th day				13.2	12.4
	(LSD (P = 0.05)		0.9	2.4	NS	2.15
No. of dead leaves	(Unshaded	0	0.4	0.6	4.4	8.3
	(Shaded from 44th day		0.2	2.0	4.8	7.6
	(Shaded from 94th day				8.8	8.4
	(LSD (P = 0.05)		NS	0.5	1.2	NS

TABLE 14. EFFECT OF SHADING

	Treatment*	Days after sowing 44	79	94	122	150
Total dry wt. per plant (g)	(I	0.08	10.5	46.5	188.1	403.9
	(II			8.4	54.6	137.4
	(III				87.7	117.6
% dry wt of stem of total dry wt.	(I	21.3	19.8	17.9	14.1	8.5
	(II		24.7	25.3	17.7	16.1
	(III				14.1	11.8
Area of unfolded leaf per plant (cm^2)	(I	3	950	4545	12183	12946
	(II		411	1519	6786	11271
	(III				8919	10715
Dry wt. of unfolded leaf per cm^2 (mg)	(I		8.29	7.80	9.86	11.53
	(II		4.19	3.90	5.79	6.41
	(III				6.77	5.94
Length of main axis (cm)	(I	23.4	53.6	106.0	145.0	233.8
	(II		86.4	111.4	191.2	277.2
	(III				166.0	188.0
	LSD (P=0.05)		22.7	NS	32.0	48.7

*As for Table 13

of unfolded leaves on the plants shaded from the 44th day than on the controls.

Shading led to a reduction in functional leaf area, but this was not proportional to the reduction in growth in weight. For a given weight of total plant the leaf area of shaded plants was generally greater than that of unshaded plants in spite of the fact that shading resulted in a smaller growth in weight of the leaf relative to that of the stem. This relative increase of leaf area of the

shaded plants was attained by a reduction in thickness of the leaf, for the weight per unit area was lower than in controls.

There was a slight but significant increase in the death of leaves shortly after a reduction in light intensity.

Experiment 20. On 11 May seed was sown outside, and some of the rows were covered with the shading cage immediately after sowing. Records were made of total numbers of leaves, fresh weights of leaves and lengths of stem.

Table 15 shows that shading led to a reduction of growth in weight and of numbers of leaves initiated. A close examination of the figures for leaf initiation (Fig. 29) suggests. however, that the differences in leaf numbers at sampling dates up to the 93rd day may have results from differences in the time of onset of the maximum rate of leaf initiation, rather than from an overall reduction in the rate of leaf initiation. This explanation does not hold after the 93rd day, when temperatu and daylength were falling rapidly.

The differences in numbers of dead and unfolded leaves between shaded and unshaded plants were not significant.

(2) Discussion. The cabbage plants were able to compensate to a certain extent for reduced light intensity by a thinning of the leaf and consequent increase in

relative leaf area. In this respect they behaved similarly to the bluebell (Blackman and Rutter (1948)) and the sunflower (Blackman and Wilson (1951)). The degree of compensation was not, however, sufficient to prevent a considerable reduction of growth in weight; in fact, the weight of shaded plants was between ½ and ¼ of that of unshaded plants at all samplings. The light intensity on a dull day may be quarter of that on a sunny day (Lundegårdh (1925)), and the differences of growth in weight during a sunny and a dull week in summer could be appreciable with a plant, like the cabbage, which doubles its dry weight every ten days in the grand period of growth.

Shading apparently causes a delay in the onset of the maximum rate of leaf initiation, but it has rather less effect on leaf unfolding. It may thus delay heading by decreasing the rates of folded to unfolded leaves.

It is clear that shading, by reducing the rate of growth, and probably by inducing lengthening of the stem, may delay or even prevent heading. The reduction in light intensity in late summer may therefore be one of the most important of the factors which prevent some late-maturing varieties from heading after cold and dull summers. The falling light intensity would also cause prenature death of the older leaves, and so reduce the

functional leaf area and accentuate the fall of growth in weight.

C COLD TREATMENT.

In section IIc the comparisons between 'rosette' rogues and heading plants of January King showed that the rogues were more advanced in flower formation than headed plants. From this it might be inferred that inability to form a head could be related to premature flower formation, and experiments were therefore carried out to find the effect upon heading of conditions favouring flower initiation.

Full details of the time when cabbage plants reach the stage of puberty, the threshold temperature required to induce flower initiation, and the requisite length of cold treatment, are not known. It was therefore necessary to give a range of treatments in order to be able to observe the effect of those which were marginal and yet not sufficient to induce such a complete flowering condition that all effects on heading would be masked.

(1) Experimental.

(a) Exposure to cold weather.

Experiment 21. Seedlings of January King and Enkhuizen Glory were raised in a glasshouse kept at 55 - 60°F. Three seeds were sown in each 3 - inch pot on 18 December and 10 days later the plants were thinned to one per pot. In order to counterbalance low winter light intensity the seedlings were irradiated with mercury-vapour lamps during

daylight hours. The growth of plants treated in this manner appeared to be normal, whereas a few non-irradiated plants from the same batch grew slowly and had long stems and petioles.

Batches of 60 plants of each variety were removed to an unheated frame on 18 February and 9 March, and these, together with a further batch taken direct from the glasshouse, were planted in the open field on 14 April. These constituted treatments 1, 2 and 3 respectively (see Table 16).

A number of plants from the first batch of Enkhuizen Glory transferred to the frame were killed by a severe frost shortly after their removal from the glasshouse. No plants of January King were killed. Only 45 plants of each batch of each variety were planted in the field.

On 9 March, Enkhuizen Glory plants in the glasshouse had initiated 18.2 leaves and those of January King 18.0 leaves, as recorded on 4 plant samples. Plants of both varieties had 7 - 9 unfolded leaves.

On each of the dates 16 June, 8 July, 20 July and 12 August, five plants of each variety were sampled and lengths of stem, fresh weights and numbers of dead, unfolded and total leaves were recorded. The numbers of plants which had initiated flowers was also noted.

TABLE 16 EFFECT OF EXPOSURE TO COLD WEATHER

	Exposure treatment	Length of stem (cm)	Fresh wt (g)	No. of leaves Dead	Unfold	Total	% Wt of folded leaf of total leaf wt
January King	(1 Long	194.8	1591	5.4	19.0	79.7	16.4
	(2	159.7	1293	6.1	19.2	82.6	16.0
	(3 Short	152.2	1186	7.4	18.7	82.1	22.5
Enkhuizen Glory	(1 Long	267.8	1819	4.7	18.2	74.9	40.3
	(2	169.1	1401	6.4	16.0	78.2	37.0
	(3 Short	153.9	1494	8.4	14.2	90.7	48.7
LSD. (P =0.05)		39.3	320	0.94	NS	7.5	NS

Except for the figures for total leaves, it is not possible to calculate the significant differences for comparison between all sampling date and cold treatment means, because most of the interactions were not significant. Table 16 therefore excludes the sampling date effect.

Lower cold treatment resulted in :-

(1) Greater weight. - The difference between treatments 1 and 3 was significant for both varieties and that between 1 and 2 for Enkhuizen Glory.

(2) Longer stems - The difference between treatments 1 and 2, and 1 and 3 were significant for both varieties.

(3) A smaller percentage (by weight) of folded leaves - Treatments 1 and 2 were significantly lower than 3.

(4) Fewer leaves initiated. - The difference between the effects of treatments 1 and 2 was significantly lower than3 in Enkhuizen Glory.

(5) Fewer dead leaves. - All the differences between the effects of consecutively-numbered treatments were significant, except between treatments 1 and 2 in January King. Treatment 3 led to a significantly higher number of dead leaves in Enkhuizen Glory than in January King.

From Table 17 it will be seen that more plants of Enkhuizen Glory than of January King initiated flowers, and that cold treatments 1 and 2 both gave increased

numbers of Enkhuizen Glory plants with flower buds.

A final visual assessment of the remaining plants made on 12 October (Table 17) showed that the only non-heading plants were those which had bolted early and produced seed Some plants had formed heads and then burst and bolted, or had sent up flowering shoots from the stem below a firm head.

TABLE 17. EFFECTS OF EXPOSURE TO COLD WEATHER RECORDED 12 OCTOBER.

Treatment		No. of plants with head*	
January King	(1	24	1 bolted and with seed pods
	(2	22	3 bolted, seed stems short and much-branche
	(3	22	3 bolted and 1 headed plant with flowering shoots from base
Enkhuizen Glory	(1	17	8 bolted and with seed pods
	(2	25	4 headed plants had burst and bolted
	(3	25	None bolted

*Maximum of 25 plants.

(b) Treatment at 44°F

Experiment 22. Small plants of January King and Copenhagen Market which had been raised from seed sown in the open on 28 March, were transferred to a butcher's refrigerator which had been converted into an experimental plant growth cabinet. The chamber was a 6 ft. cube. It was illuminated

by 8 daylight-type flourescent tubes and tungsten filament lamps. Heat was removed by a thermostatically - controlled 2 h.p. refrigerating plant, and a 60 watt heating tube was fitted in the chamber to counteract a sudden fall in temperature due to the cooling of the air by the liquid remaining in the pipes after the refrigerating pump had switched off. With this equipment the temperature was maintained at 44 F± 1 F.

Strips of hessian, hung so that the lower ends dipped in trays of water, were fitted to counteract the reduction in air humidity resulting from removal of moisture by condensation on the cooling pipes.

The plants were placed on metal benches about 3 ft. from the flourescent tubes, and the light at plant level, as measured by a photometer, was between 500 and 700 lumens. The duration of the light period was 18 hours daily.

Four treatments were given in the growth cabinet at 44°F: these were 30 days cold at one plant age, and 15 days cold at three different plant ages. Untreated plants were grown as controls. Plants were transferred to the open field immediately after treatment.

Records were made of the number of leaves and dry weight of five representative plants from the glasshouse before each batch of plants was transferred to the cold chamber. Details of the treatments are given in Table 18.

TABLE 18. CONDITION OF PLANTS AT TIMES OF TREATMENTS IN EXPERIMENT 22.

	Treatment	No. days cold	Date of start of cold treatment	No. of leaves per plant at start of treatment: Dead	Unfold.	Total	Dry wt per plant (g)
Copenhagen Market	A	30	6 June	0	8.0	27.8	11.15
	B	15	7 July	3.2	12.4	46.2	54.4
	C	15	21 June	2.4	10.2	37.2	34.8
	D	15	6 June	0	8.0	27.8	11.15
	E	0	-	-	-	-	-
January King	A	30	6 June	0	8.0	21.4	9.60
	B	15	7 July	2.2	12.0	43.4	71.4
	C	15	21 June	2.0	9.2	30.2	36.3
	D	15	6 June	0	8.0	21.4	9.60
	E	0	-	-	-	-	-

The plants were sampled on 17 - 20 August when five plants of each treatment were examined in the same way as in the previous experiment.

Results are given in Table 19. The significant differences for fresh weight, unfolded leaves and percentage folded leaf of total leaf weight may be compared both within and between varieties, but those for the other features apply only within the varieties, because the variety x cold treatment interactions in these cases are not significant.

Copenhagen Market gave significantly higher figures for overall fresh weight, number of leaves initiated and percentage of folded leaf of total leaf than January King.

Comparison of the effects of treatments A & D shows that the longer cold period resulted in significantly less weight, fewer dead leaves, fewer leaves initiated and lower percentage of folded leaf in both varieties. There is no indication that longer cold treatment affected the rate of leaf unfolding.

Comparison of the plants which had 15 days cold treatment shows that the later the treatment was applied the less was the weight, the shorter the stem (Significant in Copenhagen Market only between the treatments B and D), the fewer the leaves initiated and the lower the percentage of folded leaf. Treatments B and C for Copenhagen Market gave significantly more unfolded leaves than when the cold

TABLE 19. EFFECT OF COLD TREATMENT (44°F)

	Treatment	Length of stem (cm)	Fresh wt. (g)	No. of leaves Dead	Unfolded	Total	% wt. of folded leaves of total leaf wt.
January King	A	12.2	295	2.8	20.0	35.6	3.8
	B	10.6	280	2.8	21.8	68.8	8.7
	C	17.2	1005	4.2	20.6	92.8	19.5
	D	19.2	2022	6.4	20.6	103.8	21.5
	E	16.0	1597	6.4	20.6	106.2	18.9
Copenhagen Market	A	11.8	279	3.8	19.2	50.6	3.7
	B	12.0	431	5.4	24.2	87.8	15.5
	C	14.2	1081	5.2	23.4	101.4	41.5
	D	22.8	2857	6.4	17.6	107.2	63.9
	E	29.0	3841	7.6	19.0	120.6	67.9
LSD (P = 0.05)		11.7	391	1.6	2.6	10.54	8.3

Fig. 30.
Plant of ~~Enkhuizen Glory~~ Copenhagen Market cabbage which has initiated flowers after cold treatment.

was applied when the plants were younger (Treatment D).

Flower buds were visible with the naked eye on 4 plants of Copenhagen Market (Fig. 30) and 5 of January King which had been treated for 30 days. None of the 15-day cold treatments, or the controls showed flower initiation.

(2) Discussion. Some of the cold treatments resulted in flower initiation. The treatments were more effective with Enkhuizen Glory than January King, probably because the latter reaches puberty later than the former, for Experiment 5 showed that plants of January King that had passed puberty stage tended to initiate flowers more readily in autumn temperature conditions than those of Enkhuizen Glory.

Puberty had been reached in most plants of Enkhuizen Glory when 18 or even fewer leaves were initiated, but at this stage many of the January King plants were not responsiv to cold treatment. Puberty was reached in January King before the plants had formed 23 leaves. Thus, if puberty is dependent on leaf number, it probably occurs in January King when 20 - 25 leaves, and in Enkhuizen Glory when 16 - 20 leaves, are formed.

Once January King had passed puberty, cold treatment at 44 F for 30 days resulted in flower initiation; 15 days cold treatment at this temperature was inadequate.

When a treatment induced flowering in some plants,

heads were produced by those plants of the same batch which did not flower, and none grew into plants resembling rosette rogues. It seems unlikely, therefore, that the rosette rogue form is an expression of a higher threshold temperature for flower initiation.

Cold treatment led to a delay in head formation, for the percentage weight of folded leaves was generally lower in treated than in untreated plants. That this delay was not necessarily the result of a decreased growth in weight may be seen from Table 16, for the plants which had received the longest cold treatment gave a significantly higher fresh weight, but significantly lower percentage of folded leaves than those which had been kept longest in the heated glasshouse. The reason for the association between longer cold treatment and greater weight is not clear, but it is thought that it may have resulted from the plants kept longest in the glasshouse becoming potbound, through greater relative growth of the root portion in the higher temperature.

The delay in heading does not seem to be related to an increase in leaf unfolding - although there is a suggestion of a slight increase in rate of leaf unfolding through cold treatments B and C in experiment 22. There was, however, a strong indication, throughout the experiments described in this section.that delay in heading might be

associated with a depression in the rate of leaf initiation due to cold treatment.

V ESTIMATION OF SUGARS IN CABBAGE LEAVES

It was indicated in Section II that the relative growth rate of leaves of cabbage in relation to that of the rest of the plant was much lower than that of the storage organs of beet and carrot, and it was questionable whether the cabbage head should be considered as a storage organ. It seemed pertinent therefore to ascertain whether the cabbage head contains food reserves.

Preliminary tests, whilst showing that head leaves contained reducing sugars, gave no evidence for the presence of starch or stored proteins. An analysis was made to determine the amount of sugar in head leaves and to compare this with the quantity in unfolded leaves.

(1) Experimental

Experiment 23.

Method. On 4 - 6 January, samples of fresh outer and head leaves of two plants of January King cabbage were shredded and into weighed stoppered flasks containing enough 95 % ethyl alcohol to cover the material. The flasks were then reweighed and the weights of the samples calculated.

The samples were boiled in alcohol for 20 minutes under reflux. They were filtered and 30 cc. of distilled water was added to each filtrate, which was then boiled under reduced pressure to remove the alcohol. After the second boiling the liquid was filtered, 1-2 g. of basic lead acetate was added, and the liquid was again filtered

under reduced pressure. Three to four grams of sodium carbonate were added and the liquid was filtered by gravity through a No. 5 filter paper. The extract was quite clear and of a very pale straw-yellow colour. Distilled water was added to make the volume of extract from each sample to 120 ml. Three extracts of head and three of unfolded leaves were made from each of two firm-headed plants.

Half of each extract was boiled slowly with conc. HCl for ten minutes in a thermostatically-controlled heating unit to hydrolise dissolved carbohydrates and it was then neutralised with solid sodium carbonate.

The amount of sugar per sample was estimated by Bertrand's method. The extract was boiled with Fehling's solution (equal parts of : I, 40 g. in 1000 ml water and II, 200 g. sodium potassium tartrate and 150 g. sodium hydroxide in 1000 ml water) for 20 minutes. It was filtered through a sintered glass funnel and the precipitate of cupric oxide was washed until the filtrate was no longer blue. The cupric oxide was then dissolved with a solution of 50 g. Ferric sulphate (Prepared by dissolving in water and then adding 200 ml. concentrated sulphuric acid and diluting to 1000 ml.)

The dissolved copper filtrate was titrated against potassium permanganate solution (which had been

standardised against ammonium oxalate) until the green colour changed to pink. One millilitre of 0.1 N potassium permanaganate was taken to be equivalent to 6.36 mg. copper. The corresponding sugar equivalents were obtained from Bertho and Grassman (1938).

Three samples of head leaves and three of unfolded leaves from each cabbage were dried and the percentage dry weight ascertained.

Table 20 gives the figures for dry weight and percentage of sugars in the samples.

(2) Discussion

The figures for total sugars are lower than those estimated for the variety Enkhuizen Glory by Janes (1950), who found 34 - 42% dry weight of reducing sugars and 8.6 - 10% dry weight of acid-hydrolysable carbohydrates in cabbage 'heads' in April. The difference may be both seasonal and varietal.

It is evident that the head leaves contained more sugar than the outer leaves, whether this was measured as percentage of the dry weight or fresh weight, and that the greater part of the sugar in the head leaves consisted of reducing sugars; in this last respect the results agree with Janes (1950).

There is some evidence therefore that the 'head' of a cabbage functions as a storage organ, and the

proportion of sugar stored in some varieties may be appreciable.

TABLE 20. SUGAR CONTENT OF JANUARY KING CABBAGE LEAVES

		Unfolded leaves	Head leaves	
% of fresh wt.	Reducing sugars as glucose	0.342	0.700	**
	Non-reducing sugars as sucrose	0.306	0.279	NS
	Total sugars	0.648	0.979	**
% of dry wt.	Reducing sugars as glucose	2.395	7.368	**
	Non-reducing sugars as sucrose	2.030	2.970	NS
	Total sugars	4.420	10.340	
% dry wt. of fresh wt.		16.01	9.49	*

VI GENERAL DISCUSSION AND CONCLUSIONS.

The head of a cabbage is a mass of compacted leaves, and the internodes must be short to permit the necessary degree of leaf crowding. A head could not form, for example, on the normal kale (Brassica oleracea L. acephala) plant because the distance between successive leaves is too great. Now internode length is determined by rate of growth in length of the stem and by rate of leaf initiation. The main axes of all cabbages have an inherent slow rate of growth in length and a high rate of leaf initiation as compared with other forms of B. oleracea, but external conditions may affect these rates.

Experiments described in this thesis have shown that, within certain limits, the following external conditions may lead to an increased growth in length of the stem:-

(1) Increased daylength

(2) Reduced light intensity

(3) Cold treatment

Daylength treatment gave a slight significant increase in stem length, but this was not sufficient to delay heading. A reduction in light intensity resulted in a considerable delay in heading, but it was difficult to separate the effect on an increase in stem length from that arising through a general reduction in metabolism.

Adequate cold treatment eventually leads to flowering and if the stimulus is given after puberty and yet at an early stage of development of the plant, the internodes will be long and heading will be completely prevented. Cold treatment insufficient to induce full flowering may, nevertheless, result in an increased growth in length of the stem and thus delay heading - a condition which probably occurred in Experiment 21 - or give rise to incompact or 'puffy' heads as described by Miller (1936).

Rate of leaf initiation seems to be most sensitive to temperature, for in Experiment 21 the cold treatment gave a decrease in number of leaves initiated but an increased growth in weight.

It seems probable that the decrease in light intensity and temperature which occur during autumn may lead to an increase in internode length and thus to either delayed heading or to 'puffiness' irrespective of their effect on overall growth in weight.

Crowding of the leaves on the main axis is not the only requirement for head formation, for rosette rogues have as many leaves and as short stems as headed plants and yet produce no heads. In order that a compact head may form, the rate of leaf unfolding must slow down or cease; the partially - developed leaves then continue to increase in volume within the 'skin' formed by the

older folded leaves, and a firm head develops.

There is an indication that leaves normally unfold shortly after their cells begin to expand rapidly. Evidence from Brussels sprouts indicates that if unfolding is prevented during this stage, the leaf can lose its capacity to change form and eventually die without unfolding. The prevention of unfolding may be attributed to the leaves surrounding those about to unfold; their effect may result from;-

(1) Shading

(2) Growth substances

(3) Mechanical constriction

Experiments with shading did not reduce the rate of leaf unfolding. Instead, there was an indication that reduced light intensity might increase the rate of leaf unfolding. The possibility of a growth-substance effect has not been examined, but it is conceivable that plant growth-substances may be involved in the maintenance of a balance between expanded green-leaf area and absorptive capacity of the root, although grafting of cabbage onto roots of other forms of B. oleracea - which might have different absorptive capacities - had no measurable effect on head formation.

Temporary mechanical constriction of a Brassica leaf (Experiment 12) is able to prevent it from unfolding,

and it seems probable that a self-imposed constriction of cabbage leaves may result in their loss of capacity to unfold and thus induce heading. A mechanical constriction of this nature might occur through the interlocking of the margins of the leaves - the lateral margins in pointed-headed types and both lateral and apical margins in round-headed types. There is evidence that the degree of constriction of the lateral margins in rosette-rogue plants of January King is less than in potential heading plants, for the leaves in the former are narrower. A parallel phenomenon may be observed in the lettuce, where a non-heading condition which Bensink (1955) associates with the formation of narrow leaves can be induced as a photoperiodic response.

It is suggested that a self-imposed constriction of the leaves of cabbage would be gradual, with each successive leaf constricting its younger neighbour and the effect becoming cumulative. It is not easy to visualise how the operation of such a principle could lead to the different relative rates of maturation of varieties, but such differences might well be associated with width of leaves and rates of leaf initiation. The examination of leaf width of 'rosette' rogues was the last experiment of the present investigation, and it suggests that a further study of leaf width of different varieties may

illuminate the problem.

In some respects, 'rosette rogues resemble 'bolters'. The narrow leaves of rogues are reminiscent of those found at the base of the flowering stem, and the apparent lack of apical constriction of young leaves is another feature of plants in a reproductive condition. This last-mentioned feature is illustrated in Fig. 5, which shows the young leaves of plants approaching flower initiation (234th day) held more upright than those of the plant in fully vegetative condition, and with no tendency to grow over one another as on the 79th and 94th days. A period of cold treatment did not give rise to rogue-like plants, but it is possible that subjection to cool growing conditions may yet reveal a relationship between the rogue type and flower initiation.

Rogues probably have a slower growth in weight than potential heading plants. In that case since the rate of leaf initiation is similar for both types, rogues would have lighter leaves than headed plants. Such a condition could arise bhrough a smaller degree of cell division in the leaves. Rogues in crops occur interspersed amongst headed plants, so it is unlikely that they result from stunted growth owing to unfavourable local soil conditions; although non-heading rogue-like plants may result from minor-element deficiencies (Kimbrough 1936).

It is interesting to speculate if the probable difference in growth rate of rogues is related to inbreeding depression for it is known that individual plants of a strain vary greatly in their breeding characteristics and that inbreeding in cabbage can result is severe depression of growth rate.

Although the cabbage head may function as a storage organ for sugars, it is a disadvantage to the plant in natural competition. It is common knowledge amonst seed growers that cabbage plants with firm heads are very prone to damage by winter frosts and pathogens. To raise a satisfactory crop of seed of some varieties in Britain it is nesessary to set small plants in the field during late summer so that they overwinter as non-headed plants and flower without heading the following spring. The headingg strains of cabbage should therefore be looked upon as aberrant types of the species, maintained by artificial selection.

Most of the work in this thesis is of a preliminary nature and many aspects merit further investigation. In particular, a study of leaf shape might profitably be undertaken and also a study of the effect of growth substances and nutritional differences on heading. The work also indicates the value of a closer investigation into the factors influencing flowering - especially the

differences between varieties in time taken to reach puberty, and the threshold temperatures necessary to induce flowering.

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APPENDIX TABLE I. DRY WEIGHTS OF LEAF, STEM AND ROOT OF ENKHUIZEN GLORY CABBAGE.

Dry weight of living material per plant (g).

Days after sowing	Root	Stem	Unfolded leaf	Folded leaf	Total plant
44	0.01	0.02	0.06	0	0.1
65	0.13	0.29	1.24	0	1.7
79	0.62	2.00	7.95	0	10.6
94	2.71	8.34	34.17	1.30	46.5
108	7.38	17.50	95.89	6.56	127.3
122	11.81	26.52	123.47	29.68	188.1
136	16.70	26.63	138.98	122.90	305.2
150	17.54	34.51	149.21	202.69	403.9
164	21.76	33.97	151.06	260.05	466.8
194	32.67	36.21	125.15	343.00	537.0
213	24.09	48.81	17.37	271.95	425.1
234	30.89	47.52	0	271.86	367.6
283	41.30	49.00	0	200.40	290.7
313	27.20	50.20	0	155.25	232.6

APPENDIX TABLE II. NUMBERS OF LEAVES, LENGTH OF STEM AND AREA OF LEAF OF ENKHUIZEN GLORY CABBAGE. Experiment 1.

Days after sowing	Numbers of leaves: Total	Unfolded	Dead	Length of stem (cm)	Area of unfolded leaf per plant (cm^2)
44	9.0	2.1	0	24.1	16
65	18.8	5.9	0	39.1	205
79	35.4	9.6	0.4	53.6	4799
94	55.8	14.2	0.6	106.0	22722
108	66.7	18.2	3.2	122.0	56894
122	80.4	15.2	4.4	145.0	60915
136	90.4	13.4	6.0	171.4	69710
150	98.0	11.2	8.3	233.8	64729
164	95.3	11.8	8.8	199.0	79091
194	100.4	10.6	12.6	214.4	51706
213	100.0	8.0	14.4	250.0	35470
234	107.4	2.6	20.8	233.4	8880
283	122.2	0	37.8	250.8	0
313	110.4	0	29.8	266.0	0

APPENDIX TABLE III. FRESH WEIGHTS OF LEAF AND STEM, AND LENGTH OF STEM OF FIVE VARIETIES OF CABBAGE. Experiment 5.

First sowing.

Variety	Days after sowing	Fresh weights of 5 plants (g) Unfolded leaf	Folded leaf	Total plant	Length of stem (cm)
Copenhagen Market	50	-	-	3	10.6
	62	-	-	9	25.4
	68	-	-	19	27.8
	75	28	1	38	28.0
	82	64	2	87	35.8
	89	146	3	165	45.8
	96	479	47	686	55.6
	106	673	55	965	64.6
	117	2981	1581	5613	111.4
	123	4388	3156	9207	150.4
	131	5184	5423	12188	171.8
	145	4216	11034	17897	215.6
	154	3944	10983	16150	226.0
	166	3796	16497	22190	311.0
	193	3027	15560	19749	269.0
	258	10	1841	6083	508.0
Amager	50	-	-	2	12.8
	62	-	-	11	40.2
	68	-	-	22	44.4
	75	33	1	47	71.6
	82	132	2	192	109.0
	89	358	4	436	134.4
	96	571	15	836	144.4
	106	1288	13	1743	155.0
	117	3814	43	5392	236.4
	123	4352	46	6088	280.4
	131	7662	141	10347	317.0
	145	14815	1017	20100	405.8
	154	18969	1422	23848	488.2
	166	17827	3944	25651	534.0
	193	19231	9810	32194	518.0
	258	9851	19566	34336	652.0

APPENDIX TABLE III continued

First sowing.

Variety	Days after sowing	Fresh weights of 5 plants (g) Unfolded leaf	Folded leaf	Total plant	Length of stem (cm)
Enkhuizen Glory	50	-	-	2	10.6
	62	-	-	4	16.8
	68	-	-	13	34.8
	75	17	0	23	37.4
	82	45	1	62	42.8
	89	150	3	171	51.4
	96	295	16	407	59.2
	106	733	21	983	83.6
	117	2441	177	3479	109.2
	123	3911	320	5681	121.8
	131	6113	1163	11793	159.6
	145	4619	8300	14528	189.0
	154	10107	12891	22700	203.0
	166	8463	16281	25558	237.0
	193	8264	20558	30493	234.0
	258	2487	17078	21145	262.0
Early Offenham	50	-	-	2	10.6
	62	-	-	11	32.0
	68	-	-	19	39.8
	75	32	1	44	43.4
	82	80	2	113	67.8
	89	323	3	365	85.2
	96	293	19	433	87.8
	106	989	64	1475	111.8
	117	2222	1161	4415	155.0
	123	2446	1886	5445	140.8
	131	3124	3457	7765	208.6
	145	3541	6032	10450	270.4
	154	3355	5561	10582	268.0
	166	2233	5002	9640	290.0
	193	1387	4720	7180	318.0
	258	185	520	1953	420.0
January King	50	-	-	2	10.6
	62	-	-	7	19.4
	68	-	-	13	26.4
	75	26	1	38	40.6
	82	68	1	96	44.6
	89	182	2	203	61.2
	96	302	6	410	62.8
	106	1194	25	1642	82.0
	117	2278	62	32640	98.0
	123	4067	93	5907	107.6
	131	4884	231	6123	112.6
	145	10542	1025	12620	197.0
	154	13597	1738	17142	263.0
	193	7587	8551	17809	260.0
	258	6460	8487	16574	274.0

APPENDIX TABLE III continued

Second sowing.

Variety	Days after sowing	Fresh weights of 5 plants (g) Unfolded leaf	Folded leaf	Total plant	Length of stem (cm)
Copenhagen Market	34	-	-	17	30.2
	50	-	-	151	52.6
	63	-	-	846	77.6
	75	-	-	1916	128.0
	118	2526	5160	8356	205.0
	181	1472	4725	6877	216.0
Enkhuizen Glory	34	-	-	14	35.8
	50	-	-	120	63.2
	63	-	-	526	87.4
	75	-	-	1542	126.1
	118	4994	1967	7611	193.0
	181	3096	3769	7691	241.0
Amager	34	-	-	15	35.8
	50	-	-	86	49.6
	63	-	-	550	93.5
	75	-	-	1448	131.0
	118	4769	340	5633	217.0
	181	4371	422	5527	245.0
Early Offenham	34	-	-	16	44.6
	50	-	-	136	63.8
	63	-	-	352	77.2
	75	-	-	1651	125.0
	118	2075	2086	4601	190.0
	181	1460	1670	3474	200.0
January King	34	-	-	13	36.2
	50	-	-	94	57.6
	63	-	-	356	82.6
	75	-	-	1416	127.0
	118	3733	285	4384	180.0
	181	4300	835	5805	224.0

APPENDIX TABLE IV. NUMBER OF LEAVES OF FIVE VARIETIES OF CABBAGE. Experiment 5

First sowing.

Days after sowing	Copenhagen Market No. of leaves			Enkhuizen Glory No. of leaves			Early Offenham No. of leaves		
	Initiated	Unfolded	Dead	Initiated	Unfolded	Dead	Initiated	Unfolded	Dead
50	8.8	2.0	0	7.4	2.0	0	7.0	2.0	0
62	13.0	4.0	0	10.6	3.4	0	11.0	4.2	0
68	15.8	5.2	0	12.2	4.2	0	11.4	4.8	0
75	20.2	6.2	0	14.4	5.6	0	13.6	5.2	0
82	29.0	8.8	0	20.0	7.4	0	16.2	7.4	0
89	33.2	9.5	0	25.2	8.4	0	21.4	10.2	0
96	54.4	10.8	1.0	30.2	9.0	0.6	22.8	9.0	1.2
106	60.4	12.8	1.8	43.2	11.8	0.6	26.6	9.6	1.6
117	88.6	13.6	2.8	57.2	12.8	2.2	41.0	8.4	3.8
123	91.0	13.2	4.6	63.2	14.2	3.4	38.4	7.0	3.2
131	91.4	13.0	5.6	78.2	15.0	4.8	43.2	8.0	3.2
145	95.0	11.0	8.6	85.8	12.4	6.8	55.4	5.2	7.4
154	96.0	11.4	9.8	85.8	11.2	9.2	58.8	5.2	8.0
166	110.2	8.6	12.6	95.2	12.4	8.6	69.4	4.8	12.2
193	109.8	8.6	12.8	93.8	10.8	11.0	78.8	3.2	18.8
258	144.4	24.2	77.8	106.8	5.6	17.8	79.2	4.4	39.0

	Amager			January King		
50	7.6	2.0	0	7.4	2.0	0
62	12.2	4.8	0	11.4	4.2	0
68	13.2	5.2	0	12.6	4.6	0
75	15.0	6.8	0	15.4	6.0	0
82	19.2	8.2	0	20.2	8.4	0
89	24.6	10.2	0	23.8	9.8	0
96	29.8	11.0	1.2	32.0	11.2	6.4
106	36.6	12.6	1.6	44.6	14.0	1.2
117	56.8	18.4	2.6	52.8	14.4	2.4
123	51.8	18.8	2.8	62.8	15.8	3.2
131	64.0	20.4	4.4	71.8	18.4	5.2
145	78.6	22.2	7.2	91.8	19.8	7.7
154	84.6	26.6	7.8	100.4	23.4	8.2

APPENDIX TABLE IV continued

Second sowing.

Days after sowing	Copenhagen Market No. of leaves Initiated	Unfolded	Dead	Enkhuizen Glory No. of leaves Initiated	Unfolded	Dead	Early Offenheim No. of leaves Initiated	Unfolded	Dead
34	13.8	3.0	0	11.2	2.0	0	10.4	3.8	0
50	32.0	7.4	1.0	21.8	6.8	0.2	15.0	6.6	0.6
63	55.6	9.4	2.8	35.4	9.0	2.0	20.2	5.8	2.8
75	69.4	12.6	3.0	48.0	10.6	2.6	29.8	6.4	3.4
118	98.0	10.4	8.0	81.6	12.8	6.8	44.6	5.4	7.2
181	96.2	6.6	16.4	87.2	8.2	12.2	53.6	5.0	12.2

	Amager			January King		
34	10.8	3.8	0	9.2	2.4	0
50	17.0	6.6	0	16.8	6.2	0
63	27.4	9.8	2.0	24.6	8.2	2.0
75	43.0	12.0	2.4	37.8	11.0	3.0
118	74.6	16.4	7.6	63.2	14.2	6.0
181	74.7	14.2	11.2	72.4	14.6	10.8