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FLOWER FORMATION IN BRUSSELS SPROUTS

BY

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1. INTRODUCTION

Brussels sprouts (*Brassica oleracea gemmifera L.* var. Kolom) are day-neutral plants. The factor necessary to bring about flowering is low temperature during a certain period. Thus plants which are kept in a warm greenhouse throughout the winter can be held vegetative, and cuttings taken from such plants will likewise remain vegetative for a number of years unless exposed to cold.

It is, however, necessary that seedlings shall have reached a certain stage of development before the cold treatment is given. That is to say, there is a juvenile phase during which the plant cannot be made to flower. The juvenile and adult forms can be distinguished by physiological and morphological characteristics. Once the adult phase is reached, flowers will be formed when sufficient low temperature is given. Thus in the field, plants sown in spring have reached the adult phase during the summer, and the low temperatures of autumn and winter bring about normal flowering during the following spring.

The degree of flowering of any one plant depends upon its age and the length of cold treatment given. The rapidity of bolting is also determined by the length of cold treatment.

This paper is a partial analysis of some of the factors upon which these general statements are based.

2. MATERIAL

Results of these experiments are derived from plants of five different sowings.

Sowing 1. 1947. One set of plants was grown outside. These flowered normally, but a similar set grown throughout the winter in a warm greenhouse remained vegetative, thus showing that low temperature and not short daylength initiates flowering. Plants kept continuously in a greenhouse are liable to disease after one year, so successive generations of cuttings were made to maintain the stock of vegetative plants. Another set of plants kept in a warm greenhouse with continuous lighting also remained vegetative.

Sowing 2. November 1948. Seeds were soaked in water at room temperature for 18 hours before being put at the temperature of 2°-3 °C for vernalization treatment of 0, 1, 3, 5, 7, 9 and 11 weeks. After vernalisation the seed was sown in a cold frame and half the seed from each treatment was given continuous lighting. The remainder had ordinary daylight only. In May the plants were put out of doors. There was no flowering. Seed of variety Spiraal was also used for this experiment.

Sowing 3. April sowing 1949. Plants grew outside during all their development, flowering early in summer 1950.

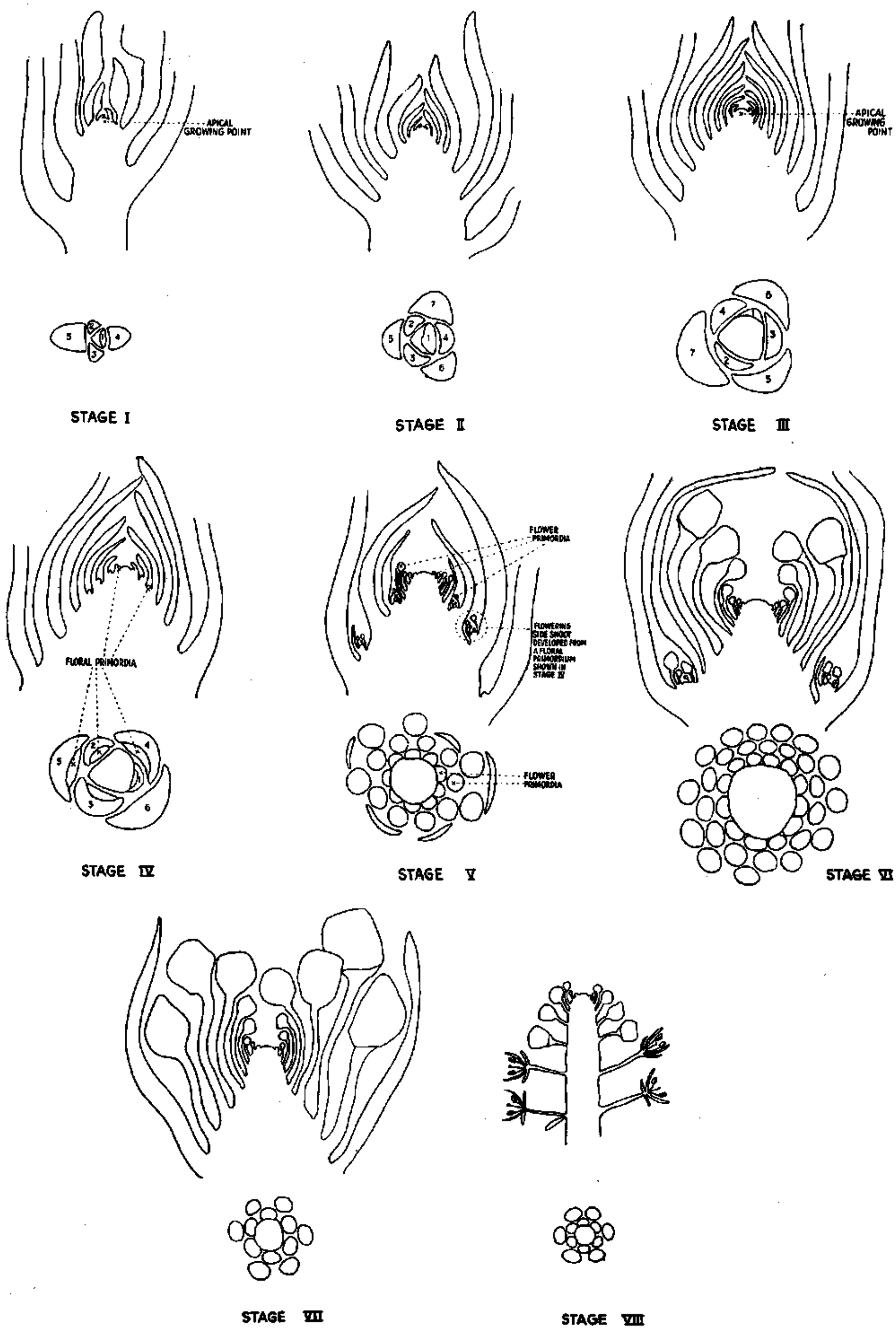

Figure 1. Diagrams of developmental stages of the apex of Brussels sprouts

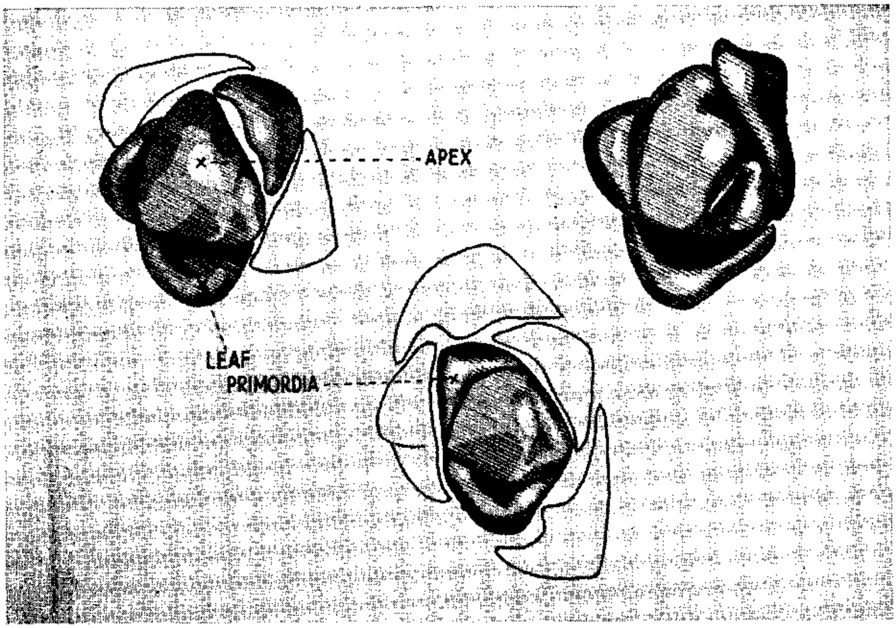

Fig. 2. Stage III. Surface view of apical growing points of adult vegetative plants. Note triangular arrangement of primordia.

Sowing 4. Summer sowing 1949. These plants were grown out of doors during the summer and were then given specific cold treatment in a cold storage room at 3 °C with short day lighting of 300 lux for 12 hours daily. After this they were kept in a warm greenhouse for flowering.

Sowing 5. December 1949. Plants were sown in a warm greenhouse and then transferred at different ages to the cold storage room for varying lengths of cold treatment. They were then returned to the warm greenhouse for flowering. In the summer they were put out of doors.

3. MORPHOLOGICAL DEVELOPMENT OF FLOWERING SHOOTS

Apices were dissected out in a watch glass and covered with a weak solution of KI. They were then examined with a binocular dissecting microscope (see figure 1).

I. Brussels sprouts seedlings pass through a juvenile phase during which they cannot be made to flower. During this time the apex of the stem is somewhat flat and the growing point itself very small. There are perhaps 4 rudimentary leaves and 3 primordia present.

II. At puberty the apex becomes more pointed, the growing point enlarges and with it the apical bud which gradually builds up a large number of leaves and primordia. After the raising of the growing point plants will flower when given a sufficiently long period at low temperature.

The other morphological changes taking place at puberty are fully described in a later section (see section 5, p. 152). These include the first appearance of lateral buds in the axils of the larger green leaves in the central section of the stem.

III. This stage marks a rapid enlargement of the growing point and top bud. The growing point itself stands up as a globular structure on the apex of the stem. The leaf primordia are also very much larger (see figure 2).

IV A. This stage is only reached after the plant has been put into the cold. The first floral primordia then become visible in the axils of the leaf primordia on the actively growing buds (see figure 3), but usually only those in the apical buds continue their full development. Those lower may develop much later. If given sufficient cold these buds will develop into flower shoots.

At this stage the triangular arrangement becomes lost, and the shape becomes round as a progressively larger number of initials are cut off round the growing point. Although this is the first appearance of potentially generative structures, they do not necessarily identify the plant as being generative, since if it is returned to the warmth before further development has taken place these buds will produce only leafy shoots. The resulting plant, therefore, has the phyllotaxis of a generative plant and may bolt but produces no flowers. The apices of the leafy shoots so produced are in stage III.

IV B. As more buds are cut off from the apex, the development of the buds gradually takes precedence over that of the leaf primordia, until the latter show only as rudimentary lobes and then finally vanish altogether (see figure 4).

V. At this stage only flower primordia are cut off from the apex (see fig. 5).

VI. The apical meristem reaches its maximum size in the bud containing a large number of flowers in all stages of development and many leaves (30 or so).

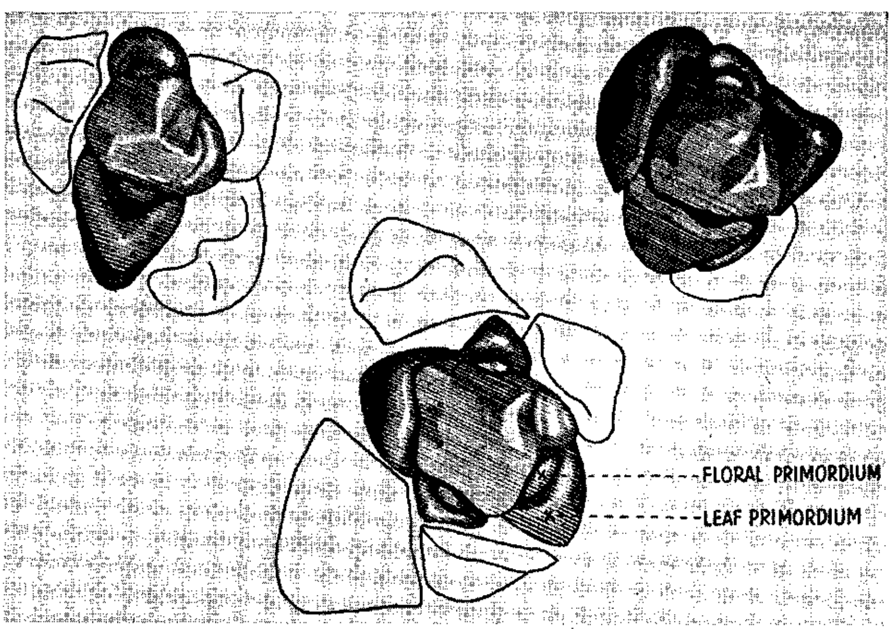

Fig. 3. Stage IV A. Surface view of apical growing points showing the first indication of the transition from vegetative to generative with the appearance of axillary buds. The triangular shape is less well-defined.

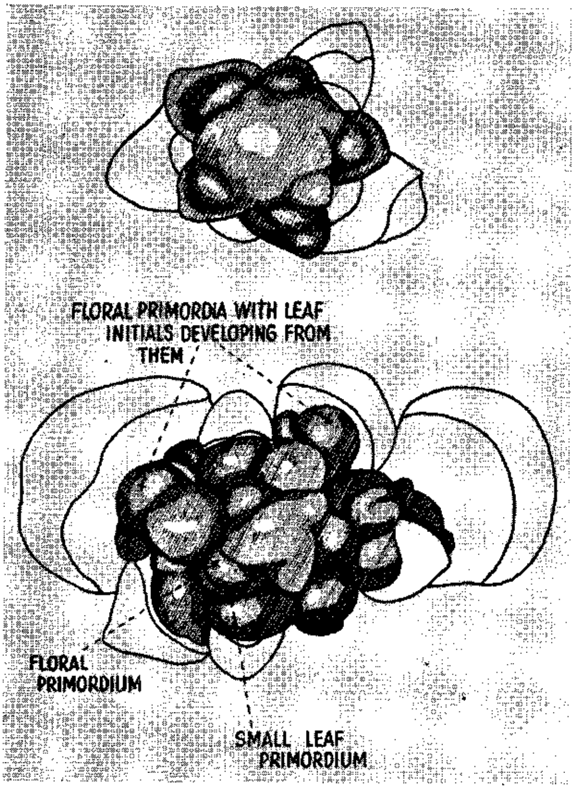

Fig. 4. Stage IV B. Surface view of potentially generative apices. Note the proportionately greater development of the buds in comparison with the leaf primordia, and loss of triangular shape.

This bud is visible to the naked eye when the surrounding leaves have been removed.

VII. Flower bud stage. Buds open out showing the individual flower buds prior to bolting. The apical meristem begins to decrease in size (see figs. 6 and 7) *).

VIII. Bolting. The apical meristem becomes very small and only few initials are cut off together, though the growing point remains permanently, no terminal flower being formed. Some primordia become arrested and never develop so that the plant eventually dies with a terminal growing point still present (see figs. 8 and 11).

The development of flowers in the apical growing point is accompanied by a general change in the appearance of the plant, due mainly to a reduction in the petiole and the production of long strap-shaped leaves towards the top of the plant, which form an increasingly large angle with the stem (see fig. 9). These features are particularly noticeable after bolting (see figs. 10 and 11). The strap-shaped leaves are referred to as "generative" leaves and seem to appear as a transition stage after subjection to low temperature.

In one plant this was clearly seen in the apical bud where some very young

*) For figures 7 – 22 see Plates I – V at the end.

structures were half leaf lamina and half stamen, half leaf lamina half carpel and no proper flowers were formed.

There was also a number of cases of plants developing a generative appearance and bolting but producing no flowers or flower initials. In such plants the apex reached stage IV but had had insufficient cold to continue the differentiation into flowers (this was after either 3 or 6 weeks cold). The apical buds then developed into a group of leafy shoots all of which had "generative" leaves and apices in stage III (adult vegetative) as already described (see fig. 12). The plant then bolted and continued a normal vegetative existence but was of a somewhat different shape from a normal plant (see fig. 13).

In a later section it is shown that the action of low temperature is two-fold, the *effect on shooting being separate from the action bringing about flower initiation*, and the two are not necessarily consecutive. There is evidence to show that the tendency to bolt is genetically controlled [ERWIN (8), VAN HEEL (13), SUTTON (28) and ZIMMERLEY (33)] and the duration of cold treatment necessary varies enormously in different plants. Thus some will bolt before flowers have been developed whilst others reach the blooming stage and have still had insufficient cold to bolt

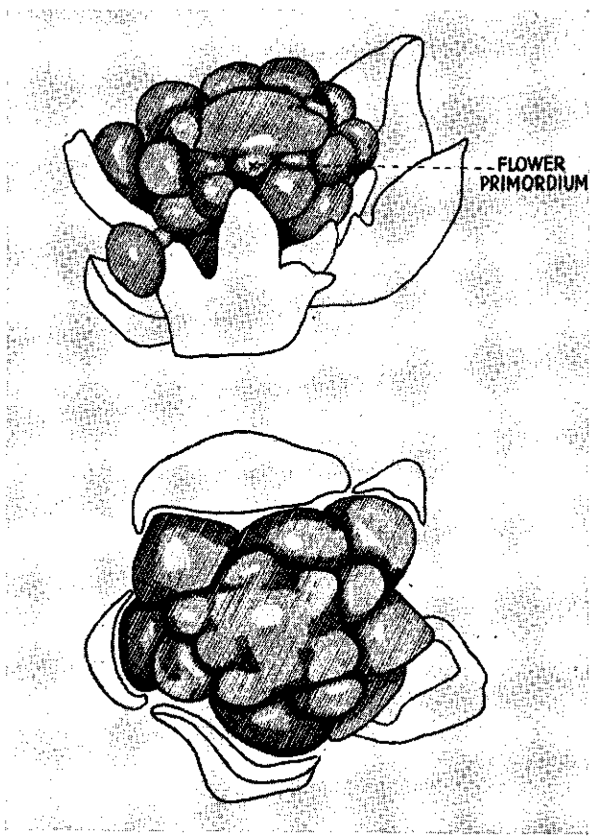

Fig. 5. Stage V. Generative apices in which only flower primordia are cut off from the apical meristem.

Fig. 6. Stage VII. Diagram to show the structure of the flower bud in stage VII.

properly (see fig. 20). A delay in bolting is therefore often found in plants which have had barely enough cold (see section 4, table 2, p. 151).

In most cases the response of the plant to cold treatment is the same throughout; that is to say the actively growing buds in all parts of the plant are in the same stage of development, although, as has been explained, full development is usually confined to the apical buds.

There were instances, however, when one or two shoots from the base of the plant flowered whilst the top remained in an ordinary vegetative condition (see figures 14, 15, 16).

A further example of this lack of uniformity of response is seen when flower buds in the leaf axils develop more quickly and are clearly visible before there is any sign of a flower bud in the apex (see figures 17 and 18). In such a case the whole stem may bolt and the flower buds in the apex only grow out later (fig. 19).

Figure 20 shows the development of two plants which had 6 weeks cold treatment. This was enough to produce flowering in plants of this age but it was insufficient to ensure the complete change to the generative state. After flowering well, these plants reverted to the vegetative habit producing a number of "generative" leaves and then returning to the development of flower initials. These did not develop (figs. 21 and 22).

4. THE INFLUENCE OF THE AGE OF THE PLANT AND DURATION OF LOW TEMPERATURE TREATMENT ON FLOWER FORMATION

Plants used were those of sowing 5 (cf. p. 145).

Flowering was recorded for 5 groups of 32 plants which were 8, 11, 14, 17 or 20 weeks of age when low temperature treatment commenced. From each of these age groups 4 sets of 8 plants each were given 0, 3, 6 and 9 weeks cold. There were thus 20 treatments and 8 plants for each treatment. After removal from the cold storage room the plants were returned to the warm greenhouse, or, when it was warm enough, put outside.

Table 1 shows the number of plants which flowered from each treatment.

TABLE 1

Number of plants which flowered from groups consisting of 8 plants each. Bracketed numbers refer to footnotes.

Age group	Weeks cold treatment			
	0	3	6	9
8	0	0	0	0
11	0	0	1 [4])	1 [11])
14	0	1 [1])	2 [5])+1 [6])	2 [11])
17	0	1 [2])	3 [7])+2 [8])	5 [11])
20	0	1 [3])	3 [9])+2 [10])	8 [11])

[1]) This plant had a group of buds in the apex resembling the arrangement of a generative shoot, but consisting only of "generative" leaves. Bolting took place as in a generative shoot (see figs. 12 and 13 and section 3 p. 148).

[2]) One plant developed flower buds in the leaf axils but not in the apex. Bolting was late. The axillary buds then developed and only one week later flowers developed in the apex.
These were very few (see figs. 17, 18, 19 and section 3, p. 149).

[3]) One plant showed "generative" leaves but there was no bolting.

[4]) Flowering was normal but there were only very few flowers.

[5]) Two plants flowered and bolted normally, though bolting was very delayed in one. Later they reverted to the vegetative condition and produced some leaves, followed again by more flower initials, but these did not develop (see figs. 20, 21 and 22).

[6]) One plant with generative arrangement of buds of "generative" leaves only, bolted as with a flowering shoot.

[7]) Three plants flowered of which two bolted normally. One did not bolt.

[8]) Two plants had the generative arrangement of buds of "generative" leaves only, bolting as with flowering shoots.

[9]) Three plants flowered normally.

[10]) Two plants had buds of "generative" leaves only; bolting was as with generative shoots.

[11]) Plants in all groups flowered normally.

The five age groups gave the following percentages of flowering plants:

8 weeks:	0 %
11 weeks:	12·5 %
14 weeks:	25 %
17 weeks:	62·5 %
20 weeks:	100 %

These percentages are derived from the number of plants which flowered after the maximum length of cold treatment, i.e. 9 weeks. The wide range of age at which plants reach the flowering stage shows the great variability of the material.

There is no flowering without cold treatment. Three weeks cold treatment were insufficient to produce proper flowering.

Six weeks cold treatment were enough to produce normal flowering in some cases. Owing to the variability of the material a number of plants developed abnormally.

Nine weeks cold were sufficient to bring about normal flowering in all cases where plants were old enough to flower at all (see fig. 10).

Table 2 shows the rate of growth of plants after removal from the cold storage room.

TABLE 2

Showing the rate of growth of flowering plants in the warmth as it varies with age and duration of cold treatment.

Morphological stage	Weeks warmth following cold treatment															
	1		1½		3		4		5		6		7		10	
	Age	Weeks cold	Age	Weeks cold	Age	Weeks cold	Age	Weeks cold	Age	Weeks cold	Age	Weeks cold	Age	Weeks cold	Age	Weeks cold
VII. Flower bud stage	11 14 17 20	6 [1] 9 9 9			11 14 17 20	9 6 6 6	14	6	17	3						
VIII. Bolting			11	6	11 14 17 20	9 9 9 9					14 17 20	6 6 6	17	3		
Whorls of "generative" leaves and generative phyllotaxis					17 17	3 6			20	6			14 14	3 6		
Bolting of "generative" leafy shoot											17 20	6 6			14 14 17	3 6 3

[1]) N.B. This group which is irregular was represented by only one flowering plant.

The longer cold treatment brings about the most rapid growth. The rate of growth depends entirely on the length of cold treatment and is irrespective of age.

The development of abnormal transitional plants is very slow, which is to be expected since they are the result of too little cold. In these cases age does appear to have some effect.

The degree of flowering of individual plants is determined by:
1. The age of the plant at the onset of low temperature. Older plants have a larger number of side buds and therefore produce more flowering shoots.
2. The length of the subjection to low temperature. Cold accelerates the rate of bolting. Plants given a long period of cold shoot more quickly and produce more flowers *ipso facto* than plants given the minimum amount of cold necessary for flowering.

These factors form an important consideration in seed production.

5. DEFINITION OF JUVENILE AND ADULT FORMS

Results from table 1 show that, with such variable material, age expressed as a number of weeks is a useless criterion for defining when a plant is old enough to flower.

In an attempt to define this stage more fully, data were collected of the number of nodes, the number of green leaves, the dry weights of stem, leaves, and roots on samples of 20 plants of different age groups, before cold treatment and on removal

TABLE 3

Showing the development of the apical growing point of Brussels sprouts with age at different temperatures.

Morphological stage	Duration of cold treatment (weeks)							
	0		3		6		9	
	Age group	%	Age group	%	Age group	%	Age group	%
I. Apex flat; growing point very small. Vegetative. Juvenile.	8 11 14 17 20	100 100 75 50 33	8 11 14 17 20	100 100 75 12 0	8 11 14 17 20	100 90 50 50 12	8 11 14 17 20	100 75 100 0 0
II. Growing point raised. Vegetative adult.	14 17	25 50	14 20	25 100	14 17	12 12	17	25
III. Growing point globular. Vegetative adult.	20	66	17	88	17	25		
IV. Buds in axils of leaf primordia. Generative.					14 17 20	25 12 50	11 17 20	12 12 34
V. Flower buds cut off directly from apex.					11	10	17	65
VI. Very large head of flower primordia.					14 20	12 38	11 20	12 66

from the cold storage room. Microscopical examination of the apical growing points and a morphological description were also made simultaneously.

From the data obtained, it is shown that on reaching the stage of development when they are sensitive to low temperature as a flower inducing factor, Brussels sprouts plants undergo physiological and morphological changes whereby the juvenile and adult forms may be distinguished.

Measurements were also made of leaf area and stem length but these results showed nothing of interest.

5.1. *The morphology of the growing point*

Table 3 is an analysis of the morphological development of the growing point as already described, made from samples of 16 plants from each treatment immediately before entering the cold storage room, and immediately upon removal.

This shows that the growing point actually changes from vegetative to generative at the low temperature and that the flowers are developed in the cold after 9 weeks. One additional set which was left in the cold storage room for 12 weeks, had well developed flower buds in nearly all plants, and many had bolted before being returned to the warmth.

It is also clearly shown that there are no generative apices formed with 3 weeks cold or less, which is in agreement with the data for flowering given in table 1.

By comparing the stage of development of the apices before cold treatment (table 3, 0 weeks treatment) with the percentage flowering obtained for each age group as shown in table 4, there is seen to be a very close connection between the percentage of plants with apices in the developmental stage II and the percentage of plants flowering after cold treatment. This shows that the raising of the growing point is a structural change associated with the attainment of the ability to flower after cold treatment, which we may call puberty.

5.2. *The morphology of the plant*

At the time of the raising of the growing point, there is a very rapid change in the appearance of the plant due mainly to an increase in the stem size. The upper portion of the stem swells and becomes very fleshy looking, and it is considerably thicker than the lower half. There is a sudden increase in length, accompanied by the first visible appearance of buds in the axils of the larger green leaves in the central section of the stem. The buds in the lower nodes remain dormant and

TABLE 4

Comparison of development of the apex before cold treatment, with flowering.

Age group in weeks	% adult plants at onset of cold treatment	Total % of plants flowering after sufficiently long cold treatment, i.e. after 6 and 9 weeks cold.	% flowering after maximum cold only i.e. after 9 weeks
8	0	0	0
11	0	12·5	12·5
14	25	30	25
17	50	50	62·5
20	66	69	100

undeveloped, and the buds in the axils of the young leaves at the top of the stem are too rudimentary to show.

Puberty comes when the number of green leaves is approximately 15 and the total number of nodes is about 30 (i.e. number of leaves fallen + approximately 15 green leaves + leaf initials in the apical bud) but this is only a general indication and by no means a fixed number.

5.3. *Distribution of growth*

Analysis of the dry weights of stem, leaves, and roots for plants of different ages before cold treatment, shows that there is a very significant change in the distribution of growth with puberty.

Whilst the growth of the whole plant is as shown in figure 23, the ratios of the dry weights of leaves and roots to stems, plotted in figure 24, show that during the juvenile phase there is an increasingly large proportion of dry matter being transferred into the stem and that the swelling seen at puberty is indeed a very real accumulation of storage materials. The ratios of dry weights of leaves and roots to stem dry weight reach a minimum at puberty, and then remain approximately constant in the adult vegetative stage in plants of the ages investigated, but old plants were not examined in this respect.

It is significant that puberty, the appearance of axillary buds and the change in the morphology of the apical growing point, come with the maximum accumulation of materials in the stem.

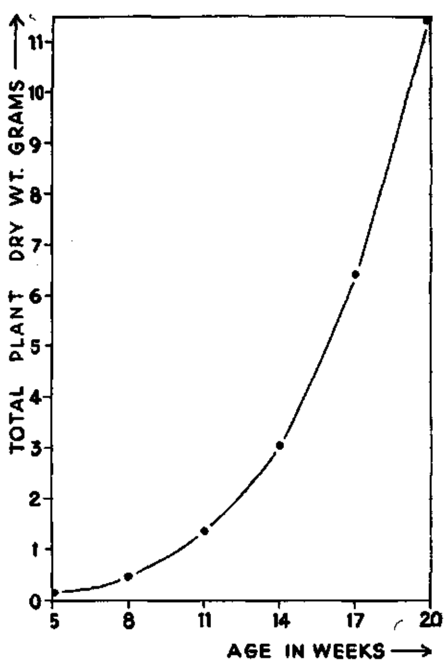

Figure 23. Graph to show the growth of vegetative plants expressed as total dry weight.

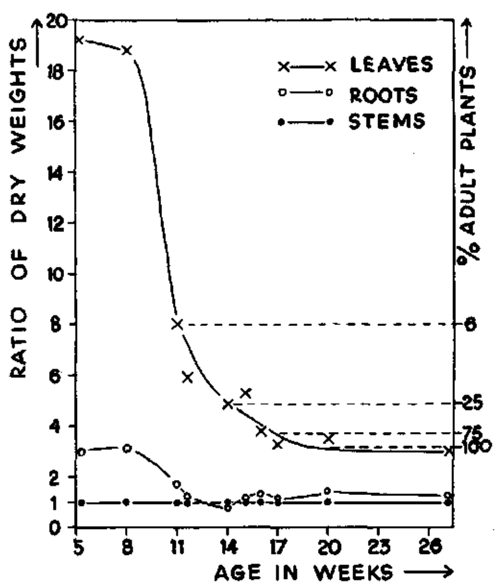

Figure 24. Graph showing dry weights of leaves and roots plotted as multiples of the stem dry weight in juvenile and vegetative adult plants.

6. DISCUSSION

There are two features of particular interest arising from the study of Brussels sprouts.

Firstly, it has been shown that there exists a "juvenile" phase during which seedlings cannot be made to flower. In itself this is now new conception, since it is well-known that many plants (if not all) must reach a certain size or phase of development before they can flower. KLEBS (14) called the attainment of such a stage "ripeness to flower" and this term has been widely used. PURVIS (24) for example, showed that in winter rye "ripeness to flower" is never found before the plant has produced a minimum of seven leaves, but the number varies according to the environment and as yet the only identification of "ripeness to flower" has been the visible initiation of the flower primordia themselves.

"Before ripeness to flower has been attained no change in the external factors can induce flower initiation; this therefore corresponds with the stage of puberty" [GREGORY (11)]. Since puberty is accompanied by marked morphological and physiological characteristics in Brussels sprouts, it is proposed to discard the term "ripe to flower" and use only the terms "juvenile" and "adult" in describing the developmental condition of the plant with regard to flowering.

During the juvenile phase, there is, in Brussels sprouts, a progressively larger accumulation of materials in the stem which reaches a maximum at puberty, and then remains more or less constant in relation to the size of the plant in vegetative individuals (see fig. 25).

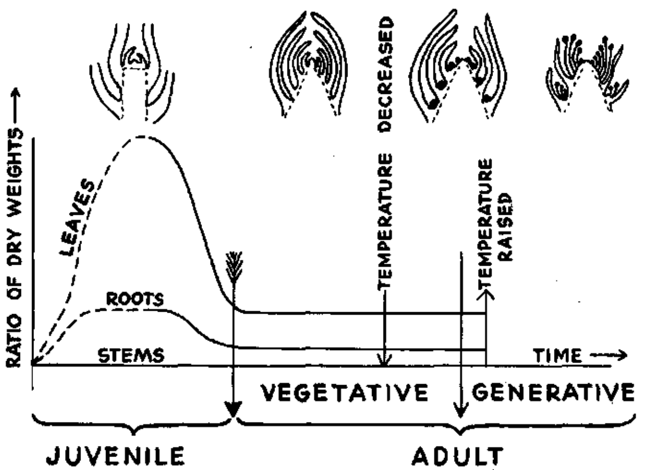

Figure 25. Diagram to show the changes in the structure of the apical growing point and the distribution of growth during the junevile, vegetative adult and generative plants. Dry weights of leaves and roots are represented as multiples of the stem dry weight.

Puberty is recognized by a swelling of the upper portion of the stem, the appearance of axillary buds and a raising of the apical growing point. Plants having reached puberty are then vegetative adults, as they do not flower until they are subjected to cold, but adult plants, or cuttings made from adult plants, can be made to flower at any time by this means.

Some growers of cabbage claim that in autumn, before the onset of low temperatures, they can predict which plants will flower early in the winter by the size and appearance of the stem in relation to the rest of the plant. MILLER (18) found no correlation between stem diameter and "ripeness to flower" and dismissed the possibility of distinguishing what are here called "juvenile" and "adult" plants. It will be realised, however, that experienced growers can very likely recognize the difference since the features of puberty are essentially those of development and not size. Here it is important to appreciate the distinction between growth in size and development made by LYSENKO (17) and emphasized by WHYTE (32). The actual size of the plants at puberty varies, and depends upon the genetical constitution and environment, but is immaterial.

BOSWELL (4), in a study of flowering in cabbage, described the raising of the growing point in some plants in autumn and remarked that these plants would probably be generative in winter, but he made no more than a hint at any connection between the raised growing point and the ability to flower.

Distinction between juvenile and adult forms has also been made for woody species, though no other mention has been found with reference to non-woody plants.

FURR et al. (10) describe a juvenile form in species of citrus and give details of grafting experiments in which juvenile wood was grafted onto adult flowering trees. Similar experiments done by FRITZSCHE with apple and pear agree with the conclusions of FURR et al. that juvenile wood could not be made to flower before its normal time by this means. A few grafting experiments with sprout plants, in which the tops of flowering plants were exchanged with those of juvenile plants, also gave no flowering in the juvenile parts, but it is interesting that in the cold requiring *Dianthus barbatus*, the exchange of generative tops with those of adult vegetative plants produced flowering in all the previously vegetative plants within two weeks (WATERSCHOOT, unpublished).

FRITZSCHE (9) defines juvenile forms of apple and pear by morphological, anatomical, chemical and physiological characters. Juvenile forms for apricot and ivy are described by PASSECKER (20) and other examples of juvenile forms are found in many coniferous species [BEISNER (2) and BEISNER-FITSCHEN (3)]. These morphological forms are quite distinct, but no work has been done on them from the physiological point of view.

Literature on this conception of puberty is scanty as yet, but it is suggested that changes such as those in Brussels sprouts may be found to be more common than is supposed.

Secondly, there is the consideration of the necessary action of low temperature in flower initiation.

Flowering is no simple process. Flower initiation is generally quite different in its requirements of light and temperature from the process of shooting, and it is necessary to distinguish clearly between these different phases when discussing the influence of a particular factor on flowering.

Needless to say, species vary in their response to external factors; in some a particular condition of lighting is necessary for one or both phases – sometimes in combination with a particular range of temperature [ROBERTS & STRUCKMEYER (26)] – whereas other plants are insensitive to light in this respect, and temperature alone determines the development of flowers. In yet other plants the external conditions may effect the rate of flowering, but it is impossible to prevent flowering under any condition after a certain age [PURVIS (24)].

The rôles of low temperature in flowering may be discussed under the following headings:

1. Flower initiation

1.1. Direct (Brassicas, Biennial Beets).

1.2. Delayed action as in Annual Beets and *Hyoscyamus*, where seed vernalization brings about flowering later, in the appropriate day length.

Where low temperature brings about flower initiation, it has not been found possible to replace it by any other treatment.

2. Shooting

2.1. Direct and irreplaceable (Tulip and Hyacinth bulbs).

2.2. Direct but not essential (*Campanula*).

2.3. Delayed and not essential as in vernalisation of winter Rye.

This classification will now be discussed in more detail.

1.1. There is only a small number of species known to require low temperature for flower initiation. These include in addition to Brussels sprouts: Cabbage (*Brassica oleracea capitata*) [BOSWELL (4), MILLER (18), STUCKEY (27)]; Sweet turnip (*Brassica napus* var. *napobrassica*) [PETO (21)]; Foxglove (*Digitalis purpurea*) [ARTHUR & HARVILL (1)]; Stocks (*Matthiola*) [POST (22, 23), EMSWELLER & BORTHWICK (7)]; Sweet William (*Dianthus barbatus*) (WELLENSIEK, unpublished).

All these plants are known to have to reach a certain minimum age before they can be made to flower, and the indications are that they are day-neutral.

Beets treated as biennials also come into this group [CHROBOCZEK (5), OWEN et al. (19), WELLENSIEK and VERKERK (31)].

1.2. Low temperature is necessary for flower initiation in *Hyoscyamus* [LANG & MELCHERS (15)], and Annual Beets [CHROBOCZEK (5), OWEN et al. (19), WELLENSIEK and VERKERK (31)], but in these light sensitive plants it may be given in the juvenile phase at seed germination. The action is then delayed and flowering takes place later in higher temperatures.

2.1. In Tulips [HARTSEMA, LUYTEN & BLAAUW (12)], and Hyacinths [WATERSCHOOT (30)], flower initiation takes place in the warmth. It is then necessary for bulbs to be stored at a low temperature after initiation if the flowers are to be able to shoot. The actual shooting process is quicker at a higher temperature, but previous cold is essential. In temperate latitudes this is given naturally in the soil, but in the tropics these bulbs will not shoot unless they are stored in a cool place, or taken to the mountains after flower initiation until the "nose" is two inches long (HARTSEMA, private communication).

2.2. In *Campanula medium*, flower initiation is brought about by short days. Low temperature, given during the short day, is without effect on the initiation, but the subsequent shooting in the warmth is much accelerated in comparison with plants maintained in the warmth throughout (WELLENSIEK, unpublished).

2.3. In winter rye sown in spring flowers can be initiated without low temperature, but in nature the shooting is delayed until too late in the autumn to provide a harvest. Seed vernalization accelerates the growing out of the flowers and thus enables a summer crop to be obtained from spring sowing [LOJKIN (16), PURVIS (24), PURVIS & GREGORY (25), VOSS (29)].

Low temperature is also instrumental in the shooting of Brussels sprouts, but this is independent of the effect on initiation and not necessarily a secondary action, as after insufficient cold some plants flower without bolting whilst others bolt without flowering. Genetical differences may come into account here since in Beets the rapidity of bolting is known to be genetically determined [ERWIN (8), VAN HEEL (13), SUTTON (28), ZIMMERLEY (33)].

In this way, the duration of low temperature also determines the degree of flowering of the individual plants, since rapid bolting causes more flowers to open out *ipso facto*.

The following scheme is proposed for the rôles of low temperature in flowering:

Low temperature

- *Qualitative*, *Essential*, *Irreplaceable*
  - 1. *Flower initiation*
    - 1.1. *Direct initiation* of flower primordia in adult plants. *Brassicas*. Biennial beets.
    - 1.2. *Delayed. Vernalization* of seed. *Hyoscyamus*. Annual beets.
  - 2. *Shooting*
    - 2.1. *Direct*. Effect upon flower primordia. Tulip. Hyacinth.
- *Quantitative*, *Not essential*
  - 2. *Shooting*
    - 2.2. *Direct accelerating*. Effect on the flower primordia. *Campanulas*. *Brassicas*.
    - 2.3. *Delayed accelerating*. Effect after seed vernalization. Winter rye.

This is only intended as a skeleton scheme on which to base comparisons with other examples, and for simplicity only one or two species have been cited for each type from the vast numbers of references in the literature which apply to group 2. Species requiring cold for flower initiation are very few and therein lies their particular interest.

It would seem probable that the action of low temperature in seed vernalisation is of a different nature from the immediate action which is necessary for flower initiation in Brussels sprouts. *Hyoscyamus* and Beets treated as biennials respond to the immediate action of cold in the adult stage, but when given seed vernalization the subsequent flowering is also effected by conditions of day length, and it would appear to be general that those plants of which the seeds can be vernalized are also sensitive to day length. This fact puts the problem of seed-vernalization on a different basis from that of Brussels sprouts.

Perhaps one might describe seed-vernalization as preparing the plant to react to the reception of a light effect acting in the leaves, whereas the direct action of cold is on the growing point itself [CURTIS & CHANG (6)].

Nevertheless, from the point of view of phasic development, both Beets and Sprouts have this in common: that at some time during the development there is an obligatory period of low temperature before the complete life cycle can be fulfilled by flowering.

SUMMARY

1. Brussels sprouts' seed cannot be vernalised.
2. Brussels sprouts plants are day-neutral.
3. There is a juvenile phase during which Brussels sprouts seedlings cannot be

made to flower. This is distinguished from the adult form by physiological and morphological characters which change with the attainment of the ability to flower.

4. The morphological changes throughout the development of the plant are described together with the forms transitional between vegetative and generative.
5. A period of subjection to low temperature is necessary for flower initiation in adult vegetative plants.
6. Six to nine weeks cold is necessary to bring about full flowering in all plants.
7. Flower primordia are initiated and developed in the cold.
8. These results are discussed in connection with the literature and a scheme is suggested for the rôles of low temperature in flowering.

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Fig. 7. Stage VII. Flower bud stage.

Fig. 8. Stage VIII. Bolting. Note change in leaf shape towards the top of the stem.

Fig. 9. Vegetative and generative plants showing the general change in appearance of a generative plant before flower buds are visible. Note the change in the axillary angle of "generative" leaves.

Fig. 10. Plants of the same age which have received 0,6 and 9 weeks cold treatment respectively. The left hand one is vegetative. Note the angle of the leaves round the crown in comparison with the "generative" leaves of the transitional form produced after 6 weeks cold.

Fig. 11. Heads of flowering plants. The left hand plant was older than the other when cold treatment commenced so there are more leaves around the lateral flower shoots.

Fig. 12. Transitional plant with a group of vegetative shoots in the apex. These have "generative" leaves. For explanation see text, p. 148.

Fig. 13. The same plant as in figure 12 during bolting.

Fig. 14. For explanation see text, p. 149.

Fig. 15. For explanation see text, p. 149.

PLATE IV

Fig. 16. For explanation see text, p. 149.

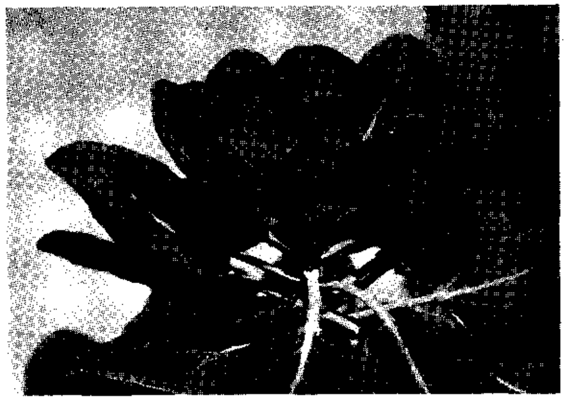

Fig. 17. Generative plant showing well developed flower buds in the leaf axils.

Fig. 18. The same plant as in figure 17 showing the apex with no visible flower bud present. For explanation see text p. 149.

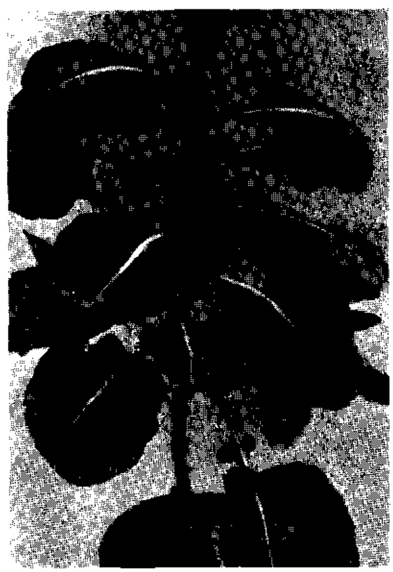

Fig. 19. The same plant as in figure 17 showing the side buds developing during bolting.

Fig. 20. Plants showing delay in bolting as a result of insufficient cold treatment.

Fig. 21. Fig. 22.
These figures show the same plant as in figure 20 in a later stage when they had reverted to leaf production and then produced more flower initials.
Figure 21 shows the right plant, figure 22 the left one.