Physiology of Flowering and Fruit Setting

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PHYSIOLOGY OF FLOWERING AND FRUIT SETTING

CHAPTER 1

Theory of the Physiology of Flowering

From history of the experiment to theory

The physiology of flowering is about 100 years old. In between 1910 and 1920 the controlling influence of daylength on flowering in many plants was established, following by the controlling influence of low temperature, nutritional condition may also have a marked influence in some plants, carbohydrate / nitrogen ratio which overshadowed work on the effects of daylength and of low temperature vernalization. Nevertheless since then until now, the physiology of flowering still in the controlling of the following factors

1. Low temperature vernalization
2. Daylength control
3. The nutritional conditions
4. The carbohydrate / nitrogen ratio

Vernalization

Many biennial and winter annual plants prolonged exposure to low temperatures before they can flower. This prolong make them reach low temperature accumulation required for flowering in spring. This system known as ' vernalization '. To convent winter into spring wheat, nothing more is necessary than that the winter wheat should be allowed to germinate slightly in the fall or winter, but kept from vegetative by a low temperature or freezing, until it can be sown in the spring. This is usually done by soaking and sprouting the seed, and freezing it while in this stage and keeping it frozen until the season for spring sowing has arrived. Only two things seem requisite, germination and freezing. It is probable that winter wheat sown in the fall, so late as only to germination in the earth, without coming up, would produce a grain which would be a spring wheat, if sown in April instead of September. The experiment of converting winter wheat into wheat has met with great success. It retains many of its primitive winter wheat qualities, and produces at the rate of 28 bushels per acre. In rye, even spring rye did not have any 'chilling' requirement for flowering, winter rye would not flower unless it was held at low temperature for a prolonged period. Many winter cereals would flower only when vernalization was followed by exposure to long-day conditions. However, the effects of vernalization could, under some conditions, be reversed by subsequent high temperature, in the process of devernalization.

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The role of daylength

Many experiments all showed that flowering of several horticultural plants could be accelerate by extending natural daylengths with incandescent light. And the plants in short days grew most slowly, they flowered most rapidly. The successive plantings of certain varieties of soybeans made at short intervals through the spring and early summer all tended to flower at the same date. It was clear that a seasonal factor was involved. There were experiments that plants were growing in a warm greenhouse and were concluded that temperature could be excluded. However, it was lied in the fact that length of the day was dissociated from the factor of amount of solar radiation also light intensity as the operative factor after the critical daylength experiments were concluded.

The nutritional conditions

The nutritional conditions are usually related to water supply. Floral initiation in strawberry is strongly affected by nutrition. High rates of fertilizer application (NPK) are often used in strawberry plantings for rapid canopy establishment, but this may promote excessive runner formation and inhibit flower formation. The total number of inflorescences per plant can be increased if the dominant response to nutrients is the production of more crowns and therefore a greater number of flower sites. Restricting the water supply to strawberries, in addition to depressing vegetative growth, can promote flower induction under some circumstances. Nutrition has often been reported that plants in a vigorous growing condition with a great deal of foliage and new shoots fail to bloom. The vigorous growth is often caused by excessive fertilization, particularly with nitrogen, an element that promotes vegetative growth rather than flowering. To induce a plant under such conditions to bloom, decrease the rate of fertilization and water thoroughly to wash the excess nitrogen from the root area. Water infrequently from them on. It may require a year or two before the effect will be apparent on the trees or shrubs. Spring flowering bulbs reluctant to re-bloom in subsequent years. This frustration condition may be caused by lack of light or poor nutrition. If bulbs are receiving sufficient light but still not flowering well, poor nutrition could be the cause. An example of a current used technique to enhance growth and / or crop production of plants and of its limitations is as follows: Nitrogen added as a fertilizer or plant nutrient may be in the form of pentavalent (oxidized) nitrogen such as a nitrate or in the trivalent (reduce) form such as ammonia or urea. Assuming that the nitrogen applied to a plant is converted to a protein in which the nitrogen is trivalent, if the form of the nitrogen added is a nitrate it must be converted to the trivalent form which are requires a considerable expenditure of energy over and above what is required if the nitrogen is applied in the form

ammonia or urea. The energy required must come from tissues of the plant directly or through photosynthesis. This would indicate that the application of nitrogen as ammonia or urea would place less demand upon the plant.

The carbohydrate / nitrogen ratio

Component of proteins, enzymes, amino acids, nucleic acids, chlorophyll all are related to C/N ratio which can modulate the physiology in plant as follow

High C/N ratio- - - - - - - Reproduction

Low C/N ratio- - - - - - - Vegetative

Application of nitrogen wholly as ammonia or urea has or may have disadvantages such as:

1. A sudden drain of both carbon skeletons and energy.
2. As a result of the condition created in no. 1, a low carbohydrate / nitrogen ratio promoting vegetative but marginal reproductive growth.
3. Inhibition of photosynthetic electron transport by the ammonium ion.
4. Urea-mediated denaturation of proteins through disruption of sulfhydryl bonds.

Another approach is to add a carbohydrate, such as sugar, directly, for example by a foliar spray of a sucrose or other water soluble, assimilable form of carbohydrate. The sugar, when absorbed into the leaves, will provide a source of energy and also a source of carbon skeleton from which, for example, proteins can be synthesized by the plant. This can be, and often is, a very expensive way in which to apply a source of energy and carbon skeleton. Also if carbohydrate fraction, alone, are added to the plant, various various minerals would be needed to compensate for corresponding demands balance physiology. Under greenhouse conditions using daily, complete nutrient fertilizers (such as Hoagland's Solution) and a full rang of controlled climatic and other environment factors, the otherwise sudden physiological imbalances brought on by carbohydrate additions alone could be mollified. Resultingly, this would tend to be manifested in increased growth responses. Under actual field conditions, however, these same isolated additions of beneficial carbohydrates would tend to create offsetting physiological imbalances and would not manifest in full the potential benefits of these treatments. In accordance with the invention there is applied to plants by a suitable route, at suitable times during growth of plants or their crops and at suitable intervals and at suitable containing composition.

Other factors

Search of a hormone

It was believed that the leaves initially respond to daylength. The leaves may produce some substance, or stimulus, that is transported to the growing point. First, they concluded that this substance was ' florigen '. Support for the concept of a flowering hormone followed quickly from grafting experiments, in which it was known that receptor plants non-inductive conditions could be induced to flower by grafting them to donor plants of the same strain which had previously been kept under inductive daylength condition. Furthermore, this floral hormone was common to both long and short-day plants. But flower induction may well involve an interaction between inhibitors and stimuli whose production is controlled by the environment.

More darkness than light

From the experiment with *Xanthium* could summarized as following

1. *Xanthium* would flower only when the dark period was 81/2 hours or longer. With light-dark cycles both shorter and longer than 24 hours, they showed that it was not the relative length of the light and dark periods that controlled flowering, nor the length of the light period, but that it was the duration of the dark period, which had to exceed a critical length to be effective.
2. Exposure to light for one minute in the middle of a dark period of more than critical length render it ineffective.
3. Whereas, the temperature during the photoperiod had little effect, the temperature during the dark period had a marked effect on the flowering response.

'Hence, the plants should be refered to as short and long-night plants respectively'. The endogenous rhythms and that the flowering response depended on the time at which plants were exposed to light or darkness in relation to the oscillation of the rhythm.

Master pigments

The pigment was deduced to exist in two forms, one which an absorption peak in the red region of the spectrum (Pr) and the other, probably biologically active, form with peak absorption in the far red region (Pfr). It was also deduced that the Pfr form could revert in darkness to the inactive Pr form, at the rate depending on the temperature. Brief exposure to far red light at the end of the main light period reduced the length of the dark period needed for flowering, while exposure to red light increased it. The interpretation of these results was that the pigment was predominantly in the active Pfr form at the end of

the light period, and this had to revert to the Pr form before the dark reaction could begin. Exposure to far red light at the beginning of the dark period converted most of the pigment to the Pr form, and thereby shortened the length of the dark period required for flowering in *Xanthium*. Thus, dark reversion of the pigment was one component of time-measurement. Long-day plants were thought to need Pfr action during the night, while short-day plants had to await reversion to Pr before their dark reactions could begin.

Shoot apex response

The shoot apex is a tissue for the study of differentiation, because of its small size and inaccessibility, but experimental advantages of strict environmental control of the course and timing of differentiation may sometimes outweigh the disadvantages. Histochemistry, electron microscopy, autoradiography and other techniques are being used to elucidate the nature of the early changes at the shoot apex during flower induction. With this new techniques come new kind of experiments, whose involvement with the physiology of flowering may well after the whole framework of our approaches to the induction of flowering.

The central mystery

Flowering physiology have two terminal dogmas and a central mystery. The dogmas are that one pigment mediates the initial photoperiodic reactions in all plants, and one hormone, florigen, concludes them. The central mystery is how, with a common beginning and a common end, the intermediate reactions require darkness in short-day plants and light in long-day plants. Plant growth regulators such as auxin gibberellins abscisin are found to involved in flower induction. However, the reactions involved in flower induction remain a dark continent on biochemical maps, and we still have only the slightest of clues as to the nature of the terrain.

(a) Julien Tournois (1884–1914) of France.

(b) M. Chailahjan of U.S.S.R.

(c) H. A. Borthwick (left) with H. A. Allard (1880–1963) of U.S.A.

FIGURE 1 Some founders of flowering physiology

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CHAPTER 2

The effects of plant age on flowering

Successful fruit production requires flowering, pollination, and fertilization. However, some gardeners find that their plants do not bloom. This applies to fruit, landscape, indoor, and garden plants. The cause of failure to bloom is generally related to one or more of the following: **plant age**, temperature, light, and other environmental and cultural factors.

Many woody plants have a vegetative phase of growth called the juvenile stage in which the plant does not flower. This stage occurs early in the life of a plant and is sometimes characterized by leaf shapes different than those of other plant parts or leaves clinging to the branches in the fall. While the plant is in its juvenile stage, flowering is *prevented by an intricate chemical balance within the plant.* This juvenile phase may last 2-3 years on some flowering shrubs or 5-10 years on certain trees. Plants often experiencing a lack of flowering due to juvenility include century plant, crabapple flowering cherry, Wisteria, and tulip tree.

Many plants will respond to abundant fertilizer with abundant leafy growth the expense of flower formation. This is most often seen in tomatoes, though it can occur in landscape ornamentals also. A poorly selected planting site or improper planting can also interfere with flowering. Planting peony crowns or iris rhizomes too deep, for instance, will prevent flowering. Sun-loving plants planted in a shady spot may survive but produce only a few blossoms or none at all. Spring-flowering bulbs planted in poorly drained soil or too near a heated basement, where heat from the structure warms the soil and interferes with the bulbs' necessary cold treatment, will rot or simply fail to flower. Plants that are only marginally hardy. In our area may fail to flower most years. Many dogwood cultivars, for example, are spectacular farther south, but in Nebraska, their flower buds usually get frost nipped. Plants that are hardy may have flowers that are not – strawberries, for instance, and *peaches. Even forsythia, that old standby, may lose its flower buds in an especially cold* winter. Sometimes the buds above the level of a winter's insulating snow layer will be killed, while the ones below it will open as usually. Forsythia and other spring – flowering shrubs set flower buds in the fall on one year – old wood, so pruning them in the fall or during the winter removes the buds and so prevents flowering. Browsing deer and rabbits feeding on twig in winter can have the same effect. No buds, no flowers. The time to prune these plants is immediately after flowering, before they have a chance to produce the buds that

will open into next spring's floral display. It may take a little detective work to pinpoint the cause, but why a plant fail to flower usually isn't a major mystery. It usually has something to do with the plant's age, the planting site, nutrition or pruning, either by the garden or Mother Nature and her helpers. It's unusual to have to look much further.

Reducing the juvenile phase

Minimum node number to flower would seem to be a prerequisite measure before one can realistically compare advantages accruing to one or another technique for shortening the juvenile phase, but there are difficulties with the node number concept. The length of the juvenile phase is inversely correlated with the early seedling vigor (growth rate). There is no indication that chemical treatments are as yet generally useful in terminating the juvenile phase, although CEPA treatments force earlier flowering in mango and apple and some Gas markedly shorten the time to inflorescence formation in some coniferous species. There is little question that leaf number or area or some other aspect of plant size is important in determining the juvenile periods, i. e., the vigor factor which is rarely defined quantitative and confuses many physiologists. The best recommendation for the plant breeder working with trees is to force plants into as rapid growth as possible until flowering occurs. Greenhouse conditions are an excellent aid for forcing rapid growth but, since field studies are required to evaluate economic performance of a cv., seedlings must be transplanted to the field. Once the desired fruit quality and growth habit have been developed, grafting of adult wood onto selected rootstocks or rooting of adult cuttings is practical; the time – to – flowering of the new propagule is not determined by juvenile traits but by factors that determine the duration of the " transition period ". The transition period in woody species may be equivalent to " induction " in herbaceous species.

Extending the Juvenile Phase – Rejuvenation

Propagation of plants by rooting of stem cuttings is without question the easiest method of developing and maintaining uniform genotype (clones). For this reason much of the horticultural industry relies on cutting propagation and accounts for research interest on rooting and stem cuttings of valuable selections. Many adult trees are notoriously difficult to root from cuttings, whereas seedling shoots, or shoots from the base of old trees, root readily. The recent progress in rejuvenation by:

1. serial subculturing in vitro of adult lateral buds
2. serial grafting of adult buds onto juvenile rootstocks followed by in vitro propagation of the scion buds so that the clones from rooted cuttings can be developed. This has been accomplished with tissues taken from the largest *Sequoia sempervirens* known

(Figure 2) as well as from Douglas fir. During the rejuvenation process the growth rate of the scion – derived tissue gradually increases to that of juvenile tissue (Figure 2) and flower initiation is reduced or delayed considerable; thus, the scions are rejuvenated with respect to a number of morphological and physiological features that characterize the juvenile state. Using grafts to juvenile seedlings, rootable cutting of adult, difficult – to - root *Cupressus sempervirens* and *Eucalyptus grandis* have been obtained.

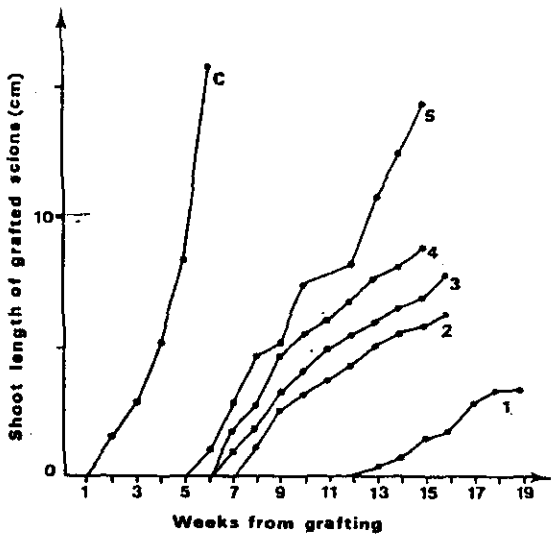

Figure 2. Growth curves of shoots issued from grafted buds collected on a 95-year-old tree of *Sequoia sempervirens*. 1 to 5 = 1st to 5th generation respectively. Each generation represents another graft generation; after bud has grown and produced a shoot, another bud is taken and grafted onto another 8-month seedling. C = control, an 8-month bud grafted on an 8-month stock. Terminal or axillary buds are used as scions. They are inserted in the terminal position of the decapitated seedlings (rootstocks). (From Franclet, A., *Ann. AFOCEL 1980*, 11, 1981. With permission.)

Alternate (Biennial) Bearing

Year - to – year cyclic fluctuations in fruit production, called alternate or biennial bearing, in perennial tree and vine crops have been thoroughly well known. Fruit development in many of these species occurs nearly simultaneously with flower initiation for the crop of the next year; thus the concept of nutrient competition between developing fruit and nearby meristematic sites for flower initiation should be considered. Even when the period of flower initiation is separated in the from that of major increases in fruit growth, as in olive and some *Citrus* species, emphasis is given to nutritional factors. Although some good correlations between storage carbohydrates and flower initiation have been uncovered, there are nevertheless clear indications of hormonal influences in all cases. There are pronounced influences of the developing fruit, particularly seeded fruit, on the bearing and

nonbearing spurs. Starch content in spurs bearing seeded fruit is much lower than in nonbearing spurs. For pear and apple, parthenocarpic cvs. are not as severely prone to biennial bearing. Apparently something diffusing from developing seed inhibit floral initiation in spurs, perhaps through its effect upon starch deposition and/or utilization. GA-induced inhibition of flower initiation in many deciduous fruit trees is well known. Hence, this class of regulators received special attention. There are now several studies showing diffusion of GA-like substances from seeded fruit. Growth retardant s, compounds that appear to inhibit GA biosynthesis or reduce GA activity, have been used commercially to increase flower initiation when fruit load is heavy. Most successful treatments have been with the growth retardant daminozide. However, it often depends on environmental factors that cannot be control.

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CHAPTER 3

Floral development and morphology of inflorescence

The development of the flower or inflorescence terminates the meristematic activity of the vegetative shoot apex. There are various changes that occur in shoot apices during floral evocation. Evoked apices normally develop into either a solitary flower or more often a cluster or flowers. The transition from vegetative to floral apex is often preceded by an elongation of the internodes and the early development of lateral buds below the shoot apex. The apex itself undergoes a marked increase in mitotic activity, accompanied by changes in dimensions and organization: the relatively small apex with a tunica-corpus type of organization becomes broad and domelike. The features of evocation seem fairly universal, there is on the contrary an extraordinary diversity of structural changes occurring during inflorescence and flower morphogenesis. All of these possible variations result in an enormous array of forms that make inflorescences and flower the beautiful objects they are. Inasmuch as the reproductive apex exhibits a determinate growth pattern, flowering in annuals indicates that the plant is approaching completion of its life cycle. By contrast, flowering in perennials may be repeated. Various environmental factors, including the length of the day and the temperature, are known to be involved in the induction of flowwering.

Physiology of floral evocation

In the normal course of their ontogeny, all plants pass through a certain amount of vegetative growth and attain the ripeness-to-flower state. Although there are no recognizable external characteristics that make the ripeness-to-flower state, upon completing this phase of development, most plants flower without any further treatment. In such plants, the events associated with floral evocation probably overlap with the final stages of vegetative maturation. In a few species, however, the ripeness-to-flower condition is followed by floral evocation, formation of flower primordia, and actual flowering only after the administration of proper environmental conditions. Among the environmental factors that have been found to trigger flowering in vegetatively mature plants, daylength and temperature are now recognized to be of primary importance. Under natural conditions, initiation of reproductive development in many plants is coordinated year after year by the reliable seasonal fluctuations in daylength and temperature that function as cues.

The induction of flower

The transition from vegetative apices to flower induction apices is one of the most important periods of ontogenesis. It requires the structural and physiological preparation of the entire plant and occurs at a definite time of the year and under definite conditions. Scanning electron microscopy (SEM) is a well established technique which has allowed a

advancement in studies on flower induction and floral morphogenesis. The induced apices of marigold (*Tagetes spp.*), chrysanthemum (*Chrysanthemum morifolium*), rose (*Rosa spp.*), ixora (*Ixora spp*), strawberry (*Fragaria ananassa* Duch.), grape (*Vities vinitera*) and rice (*Oryza sativa* L.) appeared as mounding of the apices. While the non induced apices were flatten. In the induced apices, the wilting of the leave primordia could be noticed in nearly every plant studied but the degree of the wilting was different. The mounding of the apex at the flower induction stage may result from a change in a biophysical boundary condition involving dome geometry. The plant vigor probably affects flower induction. However the effect of environment to control flower induction should be more investigated probably by using SEM technique. The stages of the development of the staminate inflorescence primodium of *Xanthium* showed in Figure 3.1

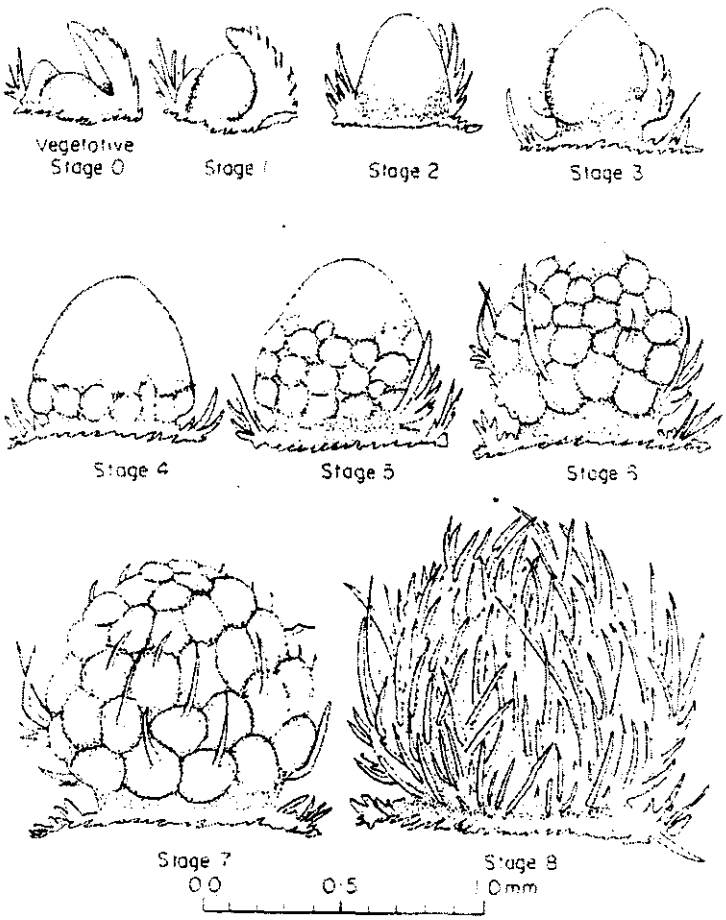

Figure 3.1 Stages of development of the staminate inflorescence primordium of Xanthium (From F. B. Salisbury, *Plant Physiol. 30, 327, 1955*)

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Some Case Descriptions Of the Morphogenesis Development of Flower

A Solitary Flower

Plant like Tulip (*Tulipa gesneriana*) produce a solitary flower at the top of the main axis. The apical meristem, from which next year's flower will develop, produces there to five foliage leaves, then increases in size and height and initiates in rapid sequence:

1. The three outer perianth member or tepals (Figure 3.2 A)
2. The three inner tepals
3. The outer whorl of three stamens, each located in the axil of an outer tepal (Figure 3.2B)
4. The inner whorl of three stamens, each located in the axil of an inner tepal and
5. The three carpels which alternate with the three inner stamens (Figure 3.2C)

With the more refined technique of scanning electron microscopy (SEM) has showed that tepals and stamens are initiated independently (Figure 3.2). The compound ovary then grows upward and produces a three-lobed stigma at its top (Figure 3.2D)

Solitary flowers may also found exclusively in axillary positions, e. g., in *Anagallis arvensis* and *Impatiens balsamina*. In conditions continuously favorable to flowering, these plants bear one flower in each leaf axil. This kind of floriferous stem is very similar to a raceme without a terminal flower, except for the presence of leaves instead of bracts. In other plants, like *Pharbitis nil*, both a terminal and several axillary flower are formed.

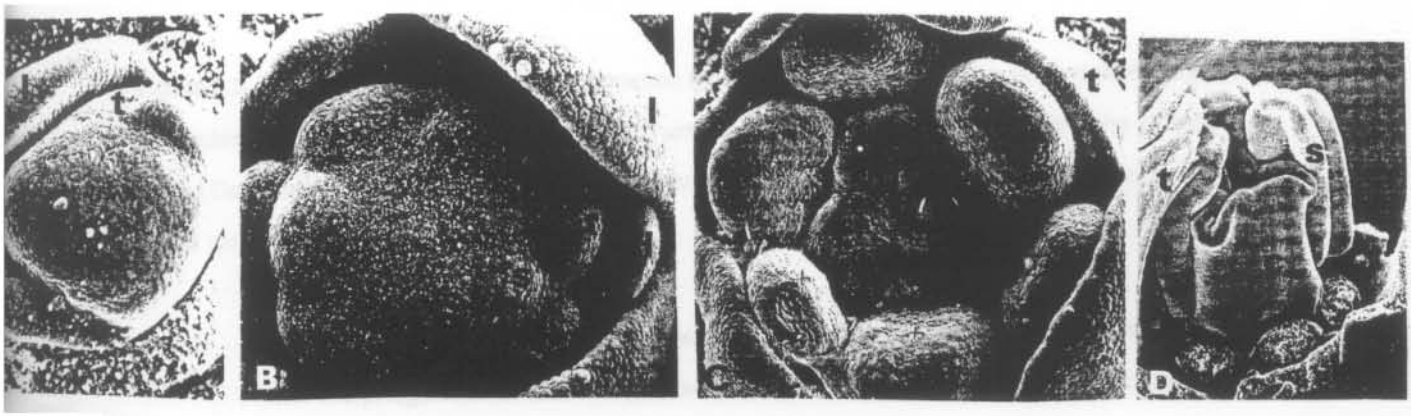


Figure 3.2 SEM micrographs of apical meristem of Tulipa gesneriana (tulip) . (A) At the stage of initiation of the three outer perinath members or tepals (t). The last leaf (l) primordium is visible. (B) At the stage of three stamens (s). Leaf primordia and the two sets of tepals are visible. (C) At the stage of initiation of the three carpels (c). (D) Young developing flower bud. Magnification in D is four times lower than in A, B and C. (From Shoub, J. and de Hertogh, A. A., *J. Am. Soc. Hortic. Sci.*, 100, 32, 1975. with permission.

B. *Racemose Type of Flower Groupings*

In the racemose inflorescences (Fig. 3.3A-H), the apical reproductive meristem produces flowers typically in an acropetal direction. The oldest flowers are thus at the base of these inflorescences and the youngest near their apex.

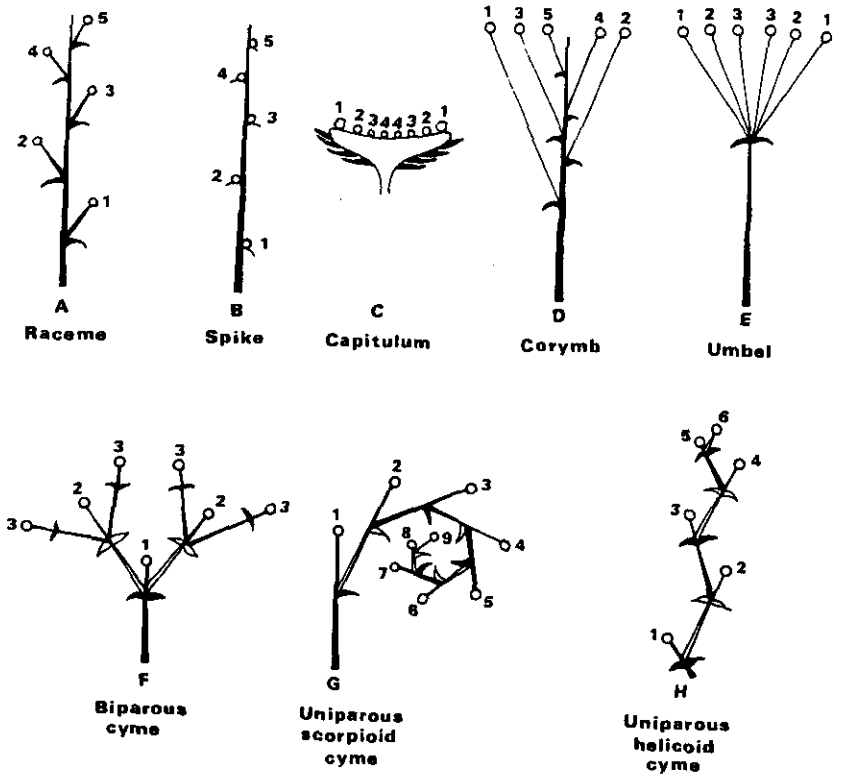


Figure 3.3 A-H Diagrams of some of the common types of inflorescences. Flowers are represented by circles and their order of initiation indicated numerical sequence with flower 1 being the oldest. (From Camefort, H. and Boue, H., *Reproduction et Biologie des Vegetaux Superieurs*, Doin, Paris, 1980. with permission.)

1. Raceme(Fig 3.3A) Cruciferae, like *Arabidopsis*, *Brassica* and *Sinapis*, typically racemes. Flower morphogenesis in Cruciferae follows a very characteristic pattern. The first part to differentiate from the nascent uniformly meristematic floral primordium is the pedicel. This occurs by cell vacuolation in the basal region of the protuberance. Then, the flower meristem initiates four sepals in such a rapid sequence. The four petals appear simultaneously in alternate positions relative to the sepals. The sepal and stamen primordia at initiation occupy a much smaller area of the periphery.
2. Spike (Fig 3.3B) like typical of some orchids. It is like raceme except that the flower are sessile. Like wheat (*Triticum aestivum*), rye (*Secale cereale*), barley (*Hordeum vulgare*),

and *Lolium* species, the lateral primordia from the reproductive meristem are not flowers but secondary spikes or "spikelets". In wheat, the first indication of spike (ear) formation is the appearce of "double ridges" at the apex, i. e., the formation of axillary meristems in the axils of the distichously arranged leaf primordia (Fig.3.4). These axillary meristems develop into spikelets.

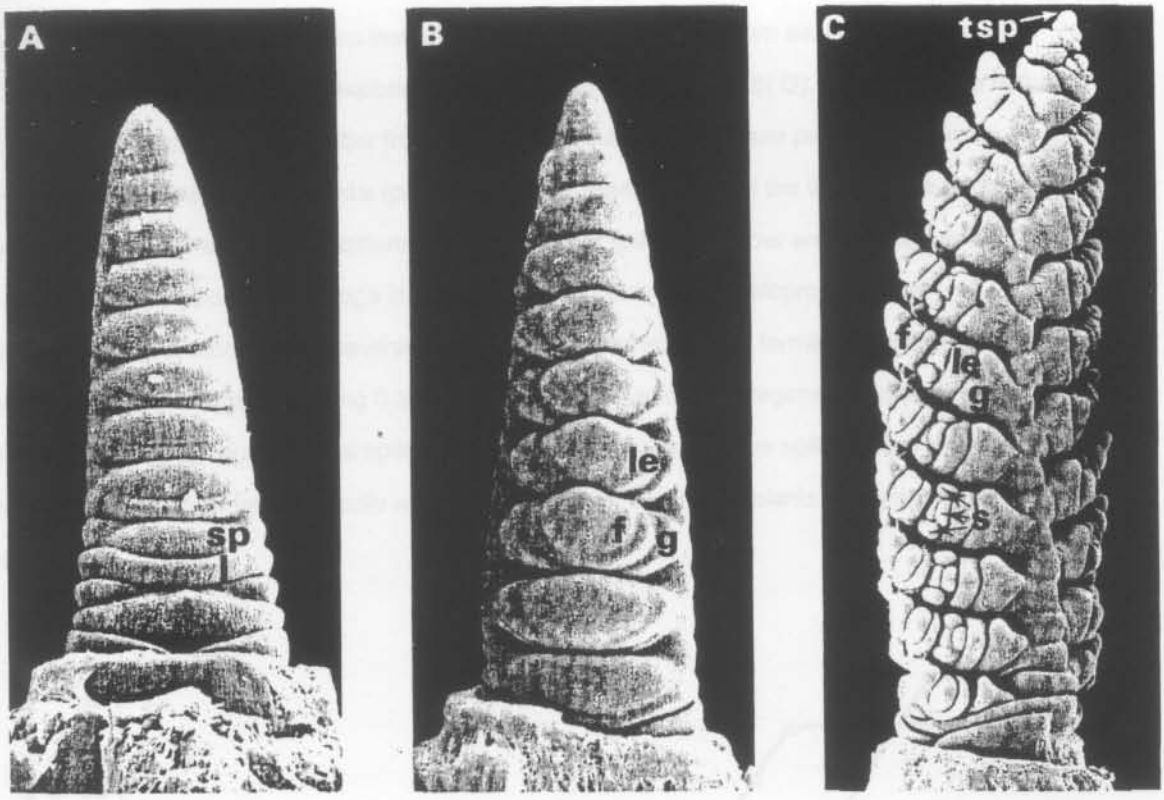


Figure 3.4 SEM micrographs of reproductive meristem of wheat (*Triticum aestivum*). (A) At the double-ridge stage. The lower ridge is the leaf (1) primordium and the upper ridge a spikelet (sp) primordium. Note that double ridges are most advanced about the middle of the elongated apex. (B) At the start of floret (f) initiation. Note the glumes (g), the first spikelet parts to differentiate, and the lemmas (le). At this stage the leaf primrodia are no longer visible. (C) At the stage of formation of the terminal spikelet (tsp). The three stamens (s) appear as swellings beneath the meristem of the floret. Magnification in C is half that in A and B. (From Moncur, M. W., *Floral Initiation in Field Crops. An Atlas of Scanning Electron Micrographs*, CSIRO, Canberra, 1981. with permission.)

Both the apical meristem of the spikelet and the floret meristem have the same histological organization as the apical meristem of the main axis, i. e., the meristem of the spike. Glume, lemma, palea, and lodicule primordia are all derived from periclinal divitions in the two most superficial cell layers, as are leaf primordia, and they also develop in the same ways as leaves. Stamens, on the

contrary, have a deeper origin since periclinal divisions associated with their initiation occur in the second and third cell layers but never in the epidermis.

The interaction between temperature and day length on flower induction

There is an interaction between temperature and day length on flower induction, initiation and flower development. Fig. 3.5 showed the interaction of cold requirment and long day (LD) on the spikelet primordia. It was concluded that after 12 weeks of wheat (*Triticum aestivum*) grown under 21/16 °C in 16 hr LD (seeds were exposed to cold – 2-4°C for 0 (0), 4( ), 8(O), or 12 ( ) weeks before planting) cold reduce spikelet number from 31 to 16 and that this decrease parallels that in the number of unexpanded leaf primordia (potential spikelet sites) present at the time double ridges first appear (indicated by arrows). The difference between final spikelet number and that present when spikelet initiation begins (double-ridge initiation) is due to continued development of the inflorescence apical meristem for several days until a terminal spikelet is formed. Thus, 10 to 12 days may elapse for the treatments lasting 0 and 4 weeks vs. 7 days for othe regimes, between first double-ridge formation and terminal spikelet initiation. In this time 12 more spikelets are initiated in plants receiving 0 and 4 weeks of cold whereas this number is only 8 in plants submitted to 8 and 12 weeks of cold.

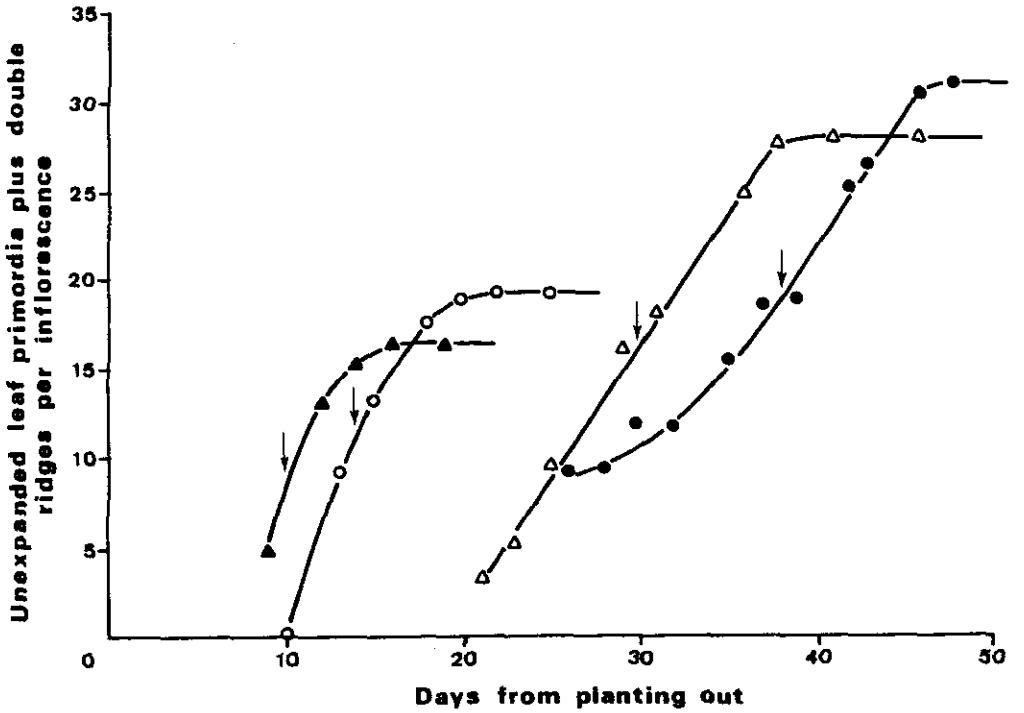


Figure 3.5 Spikelet primordia appearance on the main spike (ear) of the 'Late Mexico 120', a cold-requiring cv. Wheat (Triticum aestivum) grown at 12/160C in 16 hr LD after imbibed seeds had exposed to cold (2 to 40C) for 0( ), 4( ), 8( ), or 12 ( ) weeks before planting. (From Rawson, H. M., Aust. J. Boil. Sci., 23, 1, 1970. with permission.)

3. Capitulum Compositae, like *Chrysanthemum, Aster, Dahlia, Cosmos, and Xanthium*, typically produce "capitula" or "heads", in which all florets are insearted on the more or less flattened axis (receptacle) and are surrounded (involucre). The capitulum is a racemose inflorescence because the florests are initiated acropetally on this broadened axis (Fig 3.6).

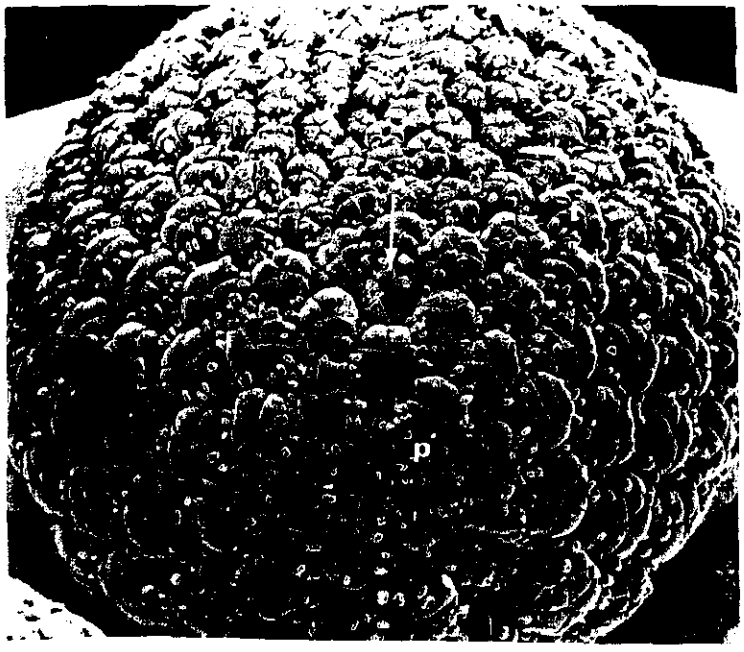


Figure 3.6 SEM micrograph of a developing capitulum of *Chrysanthemum morifolium* . At this stage the receptacle is entirely covered with well-developed florets. All visible florets are of the disc type. Marginal ray florets are invisible in this picture. The five petal lobes (p) of the corolla tube are evident on disc florets. Note that the most apical floret (arrow) is abnormal. (Reproduced by permission of the National Research Council Canada, from Vermeer, J. and Peterson, R. L., Can. J. Bot., 57, 705.1979)

4. Other Racemose inflorescences. The "coryp" is characteristically a racemes inflorescence in which the length of the various flower pedicels decreases acropetally in such a way that flowers are finally all at about the same level (Fig. 3.2D). In the "umbel", typical of Umbelliferae like carrot (*Daucus carota*), all flower pedicels arise from a common point, which as a rule is the top of the stem at the center of a whorl of bracts (Fig 3.2E)

5. Cymose Type of Flower Groupings. In the formation of the first flower of the cyme the apical the apical meristem is used up; growth of the primary axis ceases and is thus determinate. Continued growth of the inflorescence depens on precocious development immediately below the terminal flower of one or more axillary meristems which in turn from secondary branches each first terminated by a flower (Fig. 3.2F, G, H). Tertiary- and higher-order axes are each produced from new subterminal axillary meristems. Growth of cymose inflorescences is thus sympodial, whereas that of

racemose ones is monopodial. On an axis of any order in a cyme, flower formation follows a basipetal sequence, the reverse of that in racemose inflorescence. The case for *Nicotiana glutinosa*, illustrates the morphogenesis of a typical cyme (Fig. 3.7). The evoked meristem in this species is entirely transformed, after a typical prefloral stage, into the terminal flower, tf, of the inflorescence. At the same time a precocious axillary meristem, a_1 , is formed in the axil of the last leaf, l_n, produced before the floral transition (Fig. 3.7A). Very rapidly a_1 initiates successively two bracts, and , on the two opposite flanks. Then the axillary meristem a_1 is used up in the formation of the first axillary flower, f_1. A new axillary meristem, a_2, arises in the axil of (Fig. 3.7B) and follows the same morphogenetic course as $a_1$but in a perpendicular plane. The same process is repeated many times with successive axillary meristems being alternatively in two perpendicular planes. Thus flowers tf, 2, 4, etc. are all above each other on the same orthostichy, whereas flowers 1, 3, 5, etc. are on another orthostichy. On the other hand, the group of leaf l_n and bracts etc. and the group of the bracts etc. are both on two other orthostichies (Fig. 3.8)

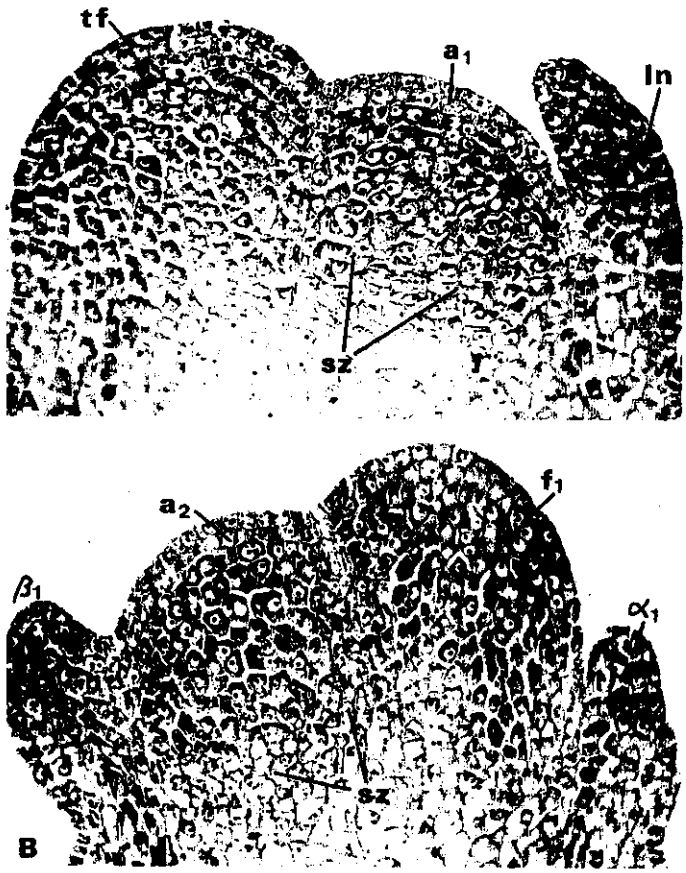


Figure 3.7 (A) Formation of the terminal flower (tf) of the cyme in *Nicotiana glutimosa*. The precocious axillary $a_1$is seem on the right in the axil of the last-formed leaf, l_n. (B) Production by meristem a_1 of the first axillary flower of the right. Bracts α_1 and β_1 and the new precocious axillary meristem a_2 on the left. The shell zone (SZ) at the base of a_1 and a_2 . (From Diomaiuto-Bonnand), J., Rev. Cytol. Biol. V'eg., 29, 1, 1966. with permission),

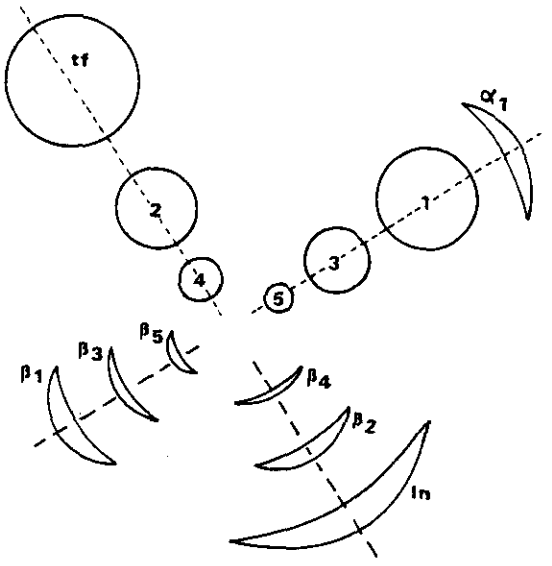


Figure 3.8 A top view of the uniparous scorpioid cyme *Nicotiana glutinosa* (circles), including the terminal one (tf), are on two orthostichies (doted lines) located on the same side of the inflorescence. The last leaf, I_n, formed before the floral transition and all bracts are on two other orthostichies (broken lines). (From Diomaiuto-Bonnand, J., Rev. Cytol. Biol. Veg.,29, 1, 1966. with permission.)

Plants such as tomato (*Lycopersicon esculentum*) etc. are sometimes believed to belong to this category too. However, the inflorescence meristem in tomato divides into almost equal parts (dichotomy): one differentiating into a flower primordium and the other giving rise to the meristem responsible for further inflorescence development (Fig. 3.9). This last meristem divides again in a similar manner and the process is repeated five to nine times.

D. Complex Inflorescences: Some flower clusters appear to be intermediate between the established types. For example, a short raceme with only a single terminal and two lateral flowers may resemble a dichasium. However, a precise study of early stages of inflorescence organization reveals the acropetal initiation of flowers, typical of racemes, and thus eliminates the confusion.

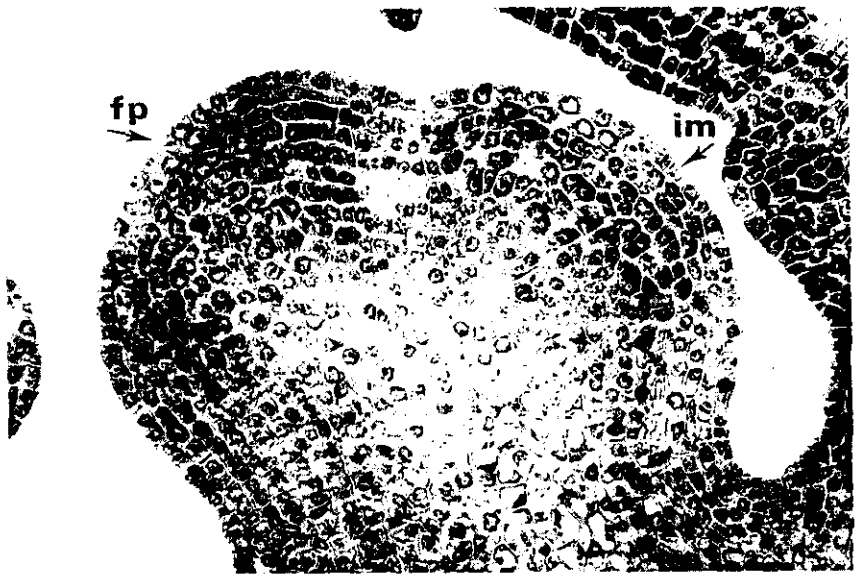


Figure 3.9 Inflorescence meristem of tomato (Lycopersicon esculentum). The meristem divides into two almost equal parts: one differentiating into a flower primordium (left part, ft), the other giving rise to the meristem responsible for further inflorescence development (right part, im). (Haematoxylin stain.)

Generalities on the morphogenesis of reproductive structures

A. Sequence of Initiation

The order of flower initiation in racemose and cymose inflorescences is, respectively, acropetal and basipetal, but cases are known in which the typical sequence is partly modified. The example is the spike of wheat in which, contrary to expectation, initiation of the upper bulges (spikelet primordia) of the double ridges does not proceed acropetally, but starts in the middle of the prospective inflorescence and then extends acro-and basipetally (Fig 3.4). However, the lower bulges (leaf primordia) were produced acropetally in advance of the upper bulges when the plant was still vegetative. *Cosmos bipinnatus* is the capitulum , after two thirds of the inflorescence apex is covered with disk florets, the single marginal row of ray florets is initiated below the already-formed disk florets, in a region of the apex that is elongating rapidly just above the involucral bracts (Fig. 3.10)

Generally, The various floral appendages are also initiated acropetally (centripetally) in the order: sepals, petals, stamens, carpels. However, there are plants in which the sequence for some of the members is perturbed, i. e. it is basipetal (centrifugal). Centrifugally initiated stamens are known in species of 32 families. In cacti, carpel primordia are initiated usually in advance of the first

the numerous stamens are initiated in basipetal sequence. The most impressive example of altered sequence is that of *Lithrum salicaria* as showed below:

Inner	Outer	Outer		Inner	
			Gynoecium		Petals
sepals	sepals	stamens		stamens	

The developing flower bud using SEM technique can conclusion the retarded development of small primordia of only a few cells.

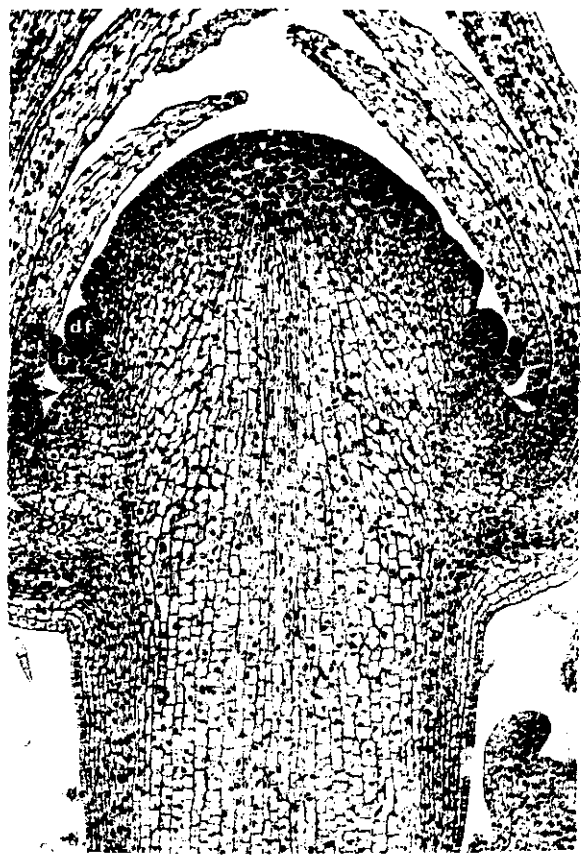


Figure 3.10 Inflorescence meristem of *Cosmos bipinnatus* showing initiation of disk floret (df) primordia and associated subjacent bracts (b). Arrows indicate sites of future ray floret initiations. (from Molder, M. and Owens, J. N., *Can. J. Bot.*, 51, 535, 1973)

B. Histogenetic Origin

Leaves originate from periclinal cell divisions in the subepidermal layer of the meristem flank (often also the epidermal layer in grasses), whereas buds arise by divisions in the third or fourth cell layer in the axil of young leaves. Flowers and inflorescence branches are invariably initiated by deep periclinal divisions and may thus be viewed as homologous to axillary buds. The sepals, petals, and carpels are very often borne from more superficial divisions in the manner of leaves. Stamens the situation is less clear since they are initiated from the subepidermis in some plants, e. g. *Chrysanthemum* , *Sinapis* and from the subjacent layer in other, e. g. Gramineae and tobacco. Thus,

whether stamens should be considered as foliar or cauline structures on the basis of their histogenicorigin remains unresolved.

C. Common Primordia

The meristem produces "common" or "double" primordia which at the later stage divide into two different parts. The production of common primrodia for flowers is associated bracts. The common protuberances bifurcate soon after initiation to form a flower meristem above and bract primordium below. Common primordia are not produced at the beginning and end of inflorescence formation. Common primordia occur only between these stages when the inflorescence meristem is presumably most active; they seem thus to result from *simultaneous initiation of the flower and its* axillant bract, a case of ultraprecocious initiation of axillary buds.

Common primordia for floral appendages are also seem, e. g. in *Cyclamen*, in which the flower meristems produce common primordia each differentiating into adaxial stamen primordia and abaxial petal primordia (Fig. 3.11). Stamens may be viewed as utraprecocious axillary buds of petals.

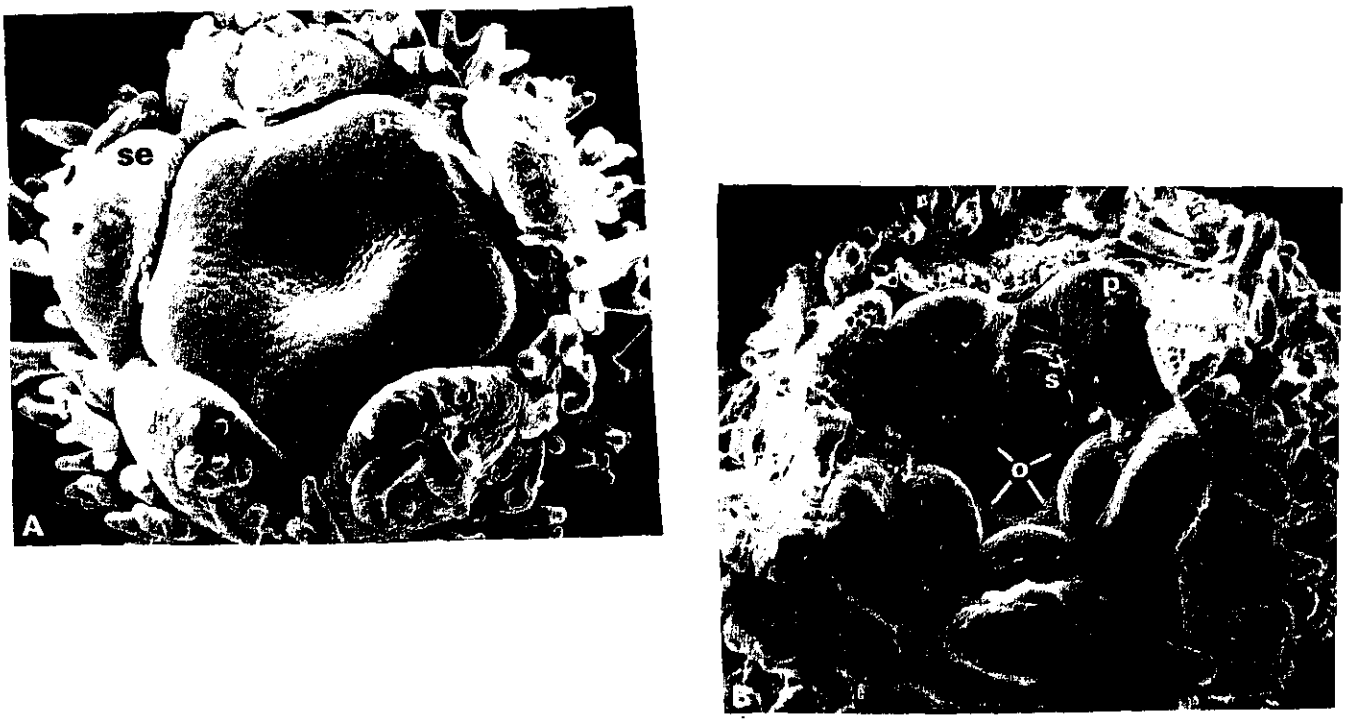


Figure 3.11 Production of petal-stamen common primordia by flower meristem of *Cyclamen orbiculatum.* (A) Initiation of common primordia (ps) alternating with sepal (se) primordia. (B) Common primordia have each differentiated into one abaxial petal (p) primordium and one adaxial stamen (s) primordium. Note initiation of ovary wall (o) in this older flower (sepals dissected). (From Sundberg, M. D., *Am. J. Bot.*, 69, 1707, 1982. with permission.)

D. Number of Floral Organs

The number for each type of appendages is fixed in the flower of many species. These flowers possess a small number of appendages of each sort, e. g., tulip, wheat, and tomato, but the flowers of other species normally have large and indefinite numbers of at least one class of appendages. For example, petal number varies from 57 to 184 in the glasshouse carnation and from 35 to 80 in 'Baccara' rose. The number of stamens in *Begonia*, carnation, etc. is also relatively high and is normally variable from flower to flower. These flowers are thus characterized by a relative lack of rigid control of flower morphogenesis compared to those having fixed numbers of parts. Petal number in flower plant e. g., carnation and rose, is important in determining flower quality.

The aberrant numbers of flower parts variations is certainly due to meristem misfunctioning and another part, perhaps more important, to transformations of appendages from one type to another. For conclusions, the morphogenetic pattern is never absolutely fixed and the control of these processes is not as perfect as one might think given the importance of floral appendage numbers for classification of some species. Because extra appendages necessarily arise in unusual places in aberrant flowers, the fate of a primordium cannot be entirely predicted from its site of initiation.

E. Changes in Phyllotaxis

Phyllotaxis (the arrangement of leaves on the plant) changes commonly occur just before or at the time of inflorescence or flower initiation in several species. With initiation of terminal flower, Silene coeli-rosa shifts from a decussate phyllotaxis(for leaf positioning) to spiral arrangement of floral appendages. In Figure 3.12A the first two sepals are already displaced from an ideal opposite arrangement: their divergence angle is 156° instead of 180°, typical of opposite primordia. The third sepal is displaced towards the first, whereas the fourth is formed on the opposite side of the meristem from the third, approximately midway between the first and second sepals. The fifth sepal is formed in the gap between the second and the third. All sepals appear in a spiral sequence which becomes obvious especially with initiation of the third one (Fig 3.12A). The divergence angles for the last three sepals average 141.7^{0}, a value which is close to the ideal angle for spiral phyllotaxis, 137.5^{0} (Fig 3.12B). Then, petals and stamens arise in such a quick succession that their exact order of appearance is sometimes difficult to determine. The five petals are initiated almost simultaneously and alternate with the sepals. The stamens are formed sequentially, first the five antesepalous (opposite to the sepals) stamens, and then the five antepetalous stamens (Fig 3.12C). Finally the carpels, seen as five flat areas on the meristem, appear to be initiated in a spiral sequence continuing the stamen sequence (Fig 3.12D). Divergence angles between petals, stamens, and carpels, while more variable than those between the last three sepals, are of the order of 141 to 148^{0}. A very large angle of 175^{0} separates the last stamen and the first carpel. The position and sequence of the last three sepals are determined by the older sepals, but the influence of an older primordium

seems to last for only two plastochrons. The phyllotaxis for useful leads concerning flower morphogenesis should be more examined.

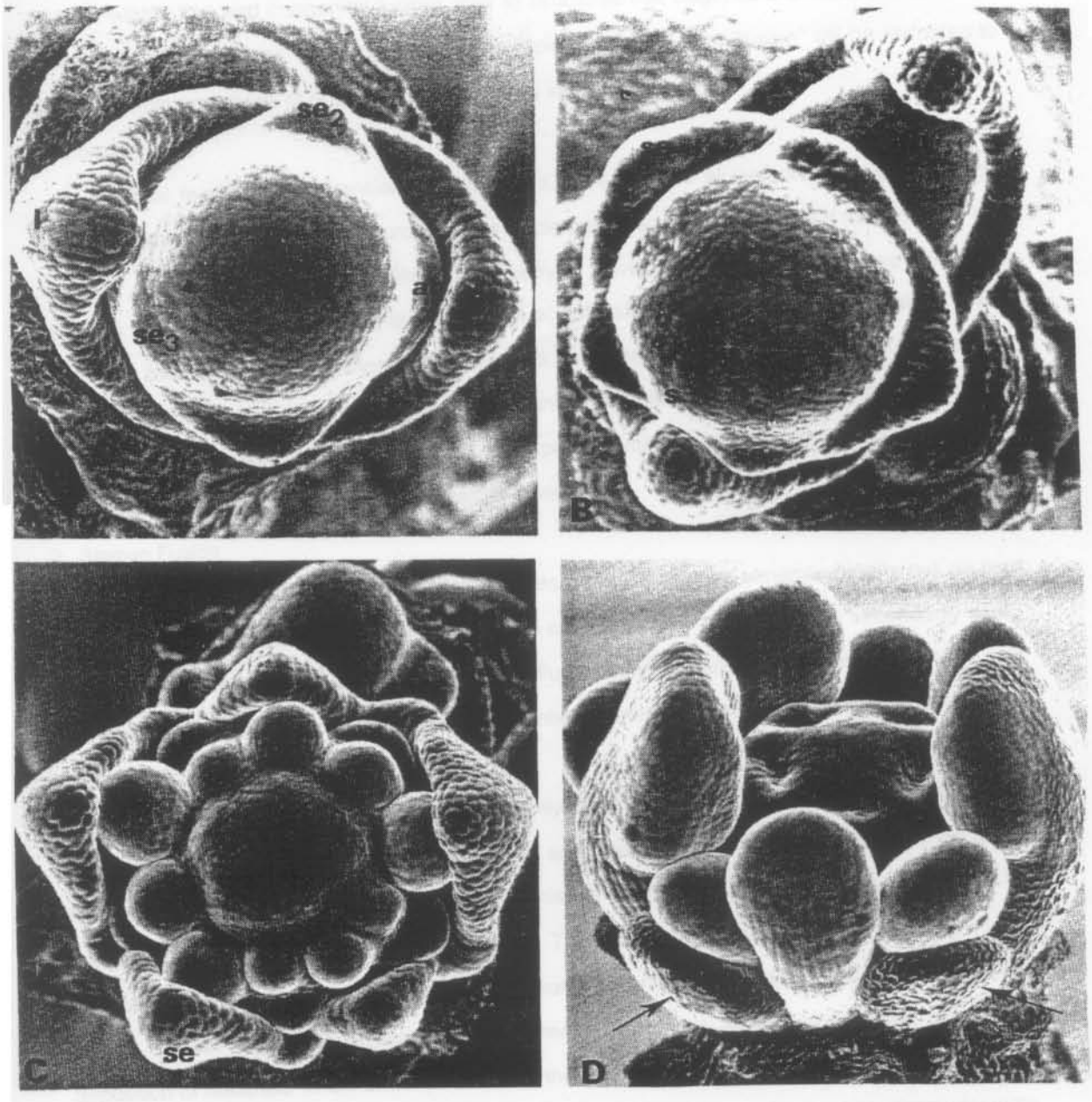


Figure 3.12 SEM micrographs of apical meristem of Silene coeli-rosa during formation of terminal flower. (A) At the stage of initiation of the 3rd sepal (se_3) I =leaf, ab=axillary bud. (B) Just at the start of the stamen (s) initiation. (C) Just after petal (p) and stamen initiation. (D) Carpels (c) have been initiated, two petals (arrows) are showed. (From Lyndon, R. F., Ann. Bot. (London), 42, 1343, 1978. With permission)

F. Fusion of Floral Organ

The fusion of flower parts is very importance for flower physiology. Morphologists usually contrast the "ontogenetic" with the "congenital" fusions. Ontogenetic fusions occur between parts that are initially free and congenital fusions refer to structures that begin as a unit but are believed, for phylogenetical reasons, to be composed of multiple parts. The term "fusion" will be restricted to the observable processes of ontogenetic fusions only in this case.

1. Corolla Tubes

Petal fusion can be transient or permanent. The process of temporary margin-to-margin fusion of petals was known. In this process, the epidermal layers of adjacent petal margins are "knit together" by interlocking of their cells so that early in development the corolla forms a hooded structure, enclosing the internal floral organs, but at anthesis the corolla breaks open along these temporary lines of union. Permanent petal fusion is a rare process, in Apocynaceae occurs when the corolla is about 400 to 500 um in height. The margins of adjacent petal lobes become apposed and then fuse very intimately. At later stages, the fused parts develop into the upper portion of the corolla tube, i. e., that portion above the level of stamen insertion.

2. Stamen Fusion

In Compositae, tomato, and other species, stamens arise as separate organs but, as they grow upward and differentiate into a filament and an anther, they become fused secondarily along their margins forming a tube encircling the style. Fusion may be more or less intimate involving only the merging of cuticles of contacting stamens, or interpenetration of elongated epidermal cells.

3. Carpel Fusion

Varied fusion processes are frequently encountered during gynoecium development differing in histological and cellular details as well as in the degree of intimacy attained by the united tissues. During fusion of carpel tips, there is an intense cytoplasmic activity in the regions where the walls of the epidermal cells become appressed. The plasmalemma is wavy, fusing in many places with vesicles originating from the numerous dictyosomes and rough endoplasmic reticulum present nearby. These organelles appear to be involved in a process of wall modification through the deposition of materials which effect adhesion of the contacting walls. After completion of fusion the fused cells have typically a wall of double thickness with "trapped" cuticles and no plasmodesmata. Also, secretory activity of the cytoplasmic organelles has ceased. The processes of ontogenetic fusions deserve further study because they raise significant questions concerning plant morphogenesis. The nature of the stimulus for fusion, which is certainly not random contact of epidermal layers, is still entirely unknown.

G. Zonal Growth and the Development of Perigynous and Epigynous Flowers

Corolla tubes in many species grow by a process called "zonal growth" after their inception. A complete ring of tissue below the level of attachment of the component parts is activated and by vertical growth produces a cylinder of tissue. The activity of the annular intercalary meristem may extend to the bases of successive whorls of floral organs producing more complex tubular structures, e.g., a corolla tube on which stamens are inserted. Processes of this kind are responsible for development of the peri-and epigynous conditions of flowers. Perigyny is characterized by the insertion of sepals, petals, and stamens on the margin of acup-like structure surrounding the gynoecium (superior ovary); the latter is at the bottom of the cup.

Anatomical evidence is in line with this ontogenetic description of the perigynous condition. The vascular bundles supplying traces to the floral members run upwards, with xylem and phloem normally oriented, then turn at a point about half-way to the apex, proceed downwards with vascular tissues inverted, and finally give off branches to the carpels at the base of the cup. Thus, *the cup in perigynous flowers is the result of an invagination of the floral receptacle* due to growth at the periphery of the receptacle exceeding that in the center.

H. Zygomorphic Flowers

Zygomorphic flower condition is established very early during flower ontogenesis, i.e., even before petal initiation. In pea, the order of appearance of the five sepal primordia is from the abaxial to the adaxial side of the flower meristem instead of the spiral sequence usually found in actinomorphic flowers. The five petals then appear in the following order: first the two keel abaxial petals and then almost simultaneously the last three petals comprising the standard and the two wings. The two keel petals grow independently for some time and then fuse along their common margin giving the false impression of a tetramerous corolla in the mature flower. In some cases, e.g., the corolla tube of ligulate ray florets in Compositae, postinitiation features alone seem responsible for zygomorphy since *these florets are indistinguishable from the tubular actinomorphic disc florets* during the early stages of ontogeny.

I. Incomplete and Unisexual Flowers

Floral appendages of one or another type may be normally missing in some flowers. In Gramineae and Compositae, all perianth members are absent, although structures like the lodicules and the pappus in these plants are sometimes viewed by morphologists as homologous to the missing parts. In monoecious cucurbits, like cucumber, the mature male (=staminate) flowers exhibit a three-lobed undeveloped pistillodium, whereas the female (=pistillate) flowers have three rudimentary staminodia. There are no anatomical differences between these two types of flowers during their early development. For instance, the rudimentary organs incorporate [^{3}H] thymidine into DNA during their early growth. Potentially male flower buds of cucumber, cultured in isolation, develop a normal pistil, whereas potentially female buds of squash show a greater development of

stamens in vitro than in vivo. Indicates that the rudimentary primordia of the missing sex are potentially capable of full development. In *Cucurbita pepo*, e.g., the axillary male flowers are restricted to lower nodes (Fig 3.13A)

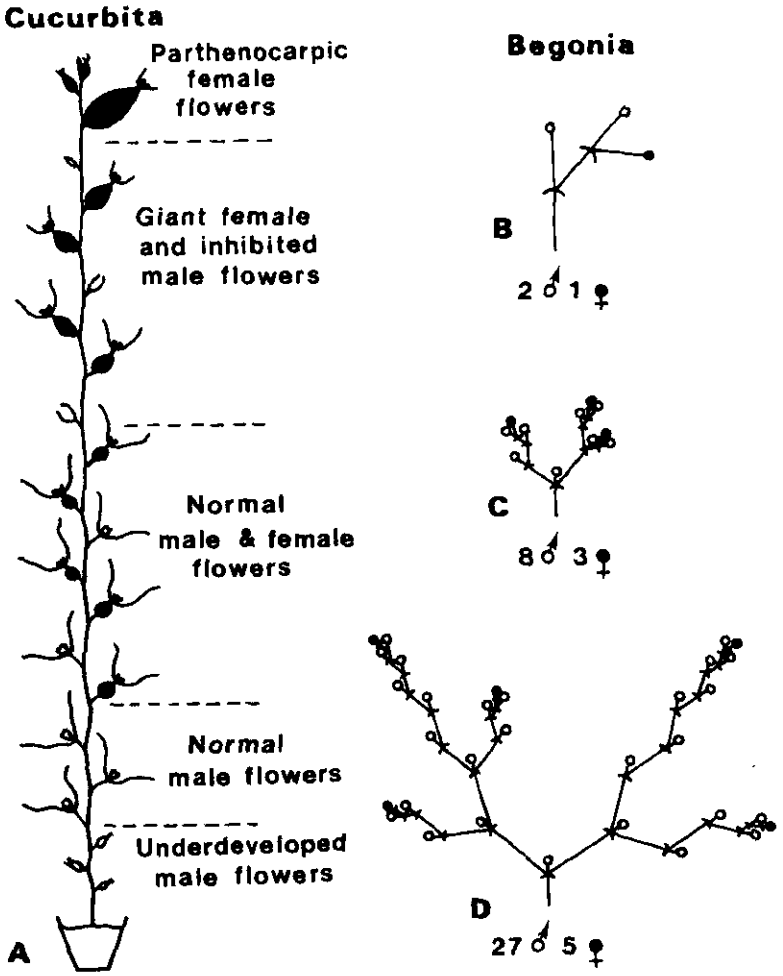


Figure 3.13A Schematic representation of the sequence of flower types in monoecious species. (A) *Cucurbita pepo* cv.'Acorn'. (B) *Begonia franconis*. (C,D) *Begonia semperflorens*. In all cases there is a shift from maleness to femaleness. In *cucrbita* (A), the male phase is restricted to the initial stage of plant development; the female phase extends over the greatest part of the life of the vine which continues to produce female flowers until death. In both Begonia species (B to D), the male zone extends over the greatest part of the cyme and the production of female flowers is exclusively associated with the final stage of inflorescence development. (From Nitsch, J. P., Kurtz, E. B. , Jr., Liverman, J. L., and Went, F. W., *Am. J. Bot.*, 39, 32, 1952 for *Cucurbita*; from Berghoeff, J. and Bruinsma, J., *Z. Pflanzenphsiol.*, 93, 303, 1979 for *Begonia franconis*; from Matzke, E. B., *Am J. Bot.*, 25, 465, 1983 for *B. semperflorens*. With pemission.)

The different numbers of perianth parts in male and female flowers of Begonia or the different morphologies of male and female inflorescences in Xanthium and Maize are called " secondary sex characteristics.

J. Polymorphic Flowers

Plants those have separate staminate and pistillate flowers borne either on the same plants or on separate plants (diclinous plants) are not the only species having more than one type of flower. Di-or trimorphism is also characteristic of heterostylous species in which the length of the style in relation to other parts of the flower, often the stamens, differs in the flowers of different plants. Other cases of dimorphic flowers are found in cleistogamous species which produce both open (or "chasmogamous") flowers. Despite all that flower morphology is basic to species identification and classification. But it is erroneous to believe that flower morphogenesis in a given species invariable.

K. Termination of Activity in Reproductive Meristems

In many racemose inflorescences the apical meristem is indeterminate. In those cases it aborts more or less rapidly thereby terminating growth without having formed a terminal flower. Less frequently, it may form spines or hairs. However, since in other species producing simple or complex racemes, e. g., lupin or tobacco, the reproductive meristem is finally used up in the formation flower. Racemes with or without a terminal flower are even found in the species, sometimes in the same individual, e. g., in *Primula malocoides*. In cereals some species produce a terminal spikelet (wheat, Fig. 3.4C), whereas others (barley) do not. The capitulum is a racemose inflorescence commonly believed to possess a terminal floret. A small axial area at the tip of the reproductive meristem in some Compositae, e. g., *Cosmos*, may remain free of florets. In other Compositae the most apical floret may sometimes exhibit anomalous features, e. g., it may be incomplete or devoid of a subtending bract (Fig. 3.6). Or the axial area may be occupied by a bract without an axillary floret. These abnormalities are probably related to insufficient residual meristematic material at the tip of the meristem for production of a complete floret and accompanying bract.

Growth and Development Patterns of Reproductive Structures

A. Sequence of Development

In racemose inflorescences the sequence of flower development follows the acropetal order of flower initiation with flowers opening first at the base. Similarly, in many capitula and umbels florets reach anthesis earlier at the periphery than in the center. In wheat the first-formed spikelet primordia , i. e., those located about the middle of the spike, are always morphologically the most advanced (Fig. 3.4). They initiate florets first, produce more florets and more grains, and give the heaviest grains.

In cymes, the first-formed (or terminal) flowers are generally the first to open, but lateral flowers may open in acropetal, basipetal, or other sequences. Thus, depending on the species and environmental conditions, the order of flower anthesis within the inflorescences may follow variable patterns.

For floral appendages, e.g., petals although initiated before stamens and carpels, may have a very retarded development compared to other flower parts. They may remain very small until shortly before anthesis at which time they then expand rapidly such as in Silene (Fig. 3.12A). Thus the order of development of floral members dose not necessarily follow the order of initiation.

B. Trend towards Synchronous Development

The reproductive development should be characterized by a trend towards synchronous initiation, differentiation, and growth of flowers or flower parts. Synchrony at the cell level has been found in relation to sexual reproduction. First, in the subapical tissues during bolting in rosette plants, second in the shoot apical meristem at evocation, and then during pollen and embryo sac formation in the anther and nucellus, respectively. There is a trend towards synchronization of development in the different spikelets of the same spike. Although spikelet 8 is initiated 8 days prior to the terminal spikelet, the latter starts floret production only 5 days after the former. Also, the different florets of a given spikelet tend to synchronize in their development despite being initiated in succession.

There are cases in which the anthers develop and ripen in advance of the pistil(s) of the same flower (protandry), e.g., carrot, onion, etc. Others, such as hemp and date palm are characterized by the reverse situation (protogyny). In **Annona hybrida**, e.g., the anthers ripen about 26 hr after the pistils become receptive. Such mechanisms, commonly assumed to prevent self pollination, require the closely controlled synchronous- but sequential- development of stamens and pistils.

C. Growth Rates

Growth measurements of inflorescences and flowers are very few studying because in such complex and changing structures are difficult and tedious. The whole bud and perianth members have a typical exponential growth from early ontogeny almost to anthesis. Growth of the anther is also exponential, but can divide into an early period of rapid increase in length and weight and a late period of slower growth. The ovary, on the contrary, dose not grow exponentially, but linearly with respect to the logarithm of bud length. In wheat, the early growth of each leaf during the vegetative phase is also exponential, but the relative growth rate, R, then rises to approximately twice that during the exponential phase before falling to zero. The only component of the wheat spike that exhibits such a growth pattern is the palea (Fig. 3.14). There is no evidence of an early phase of exponential growth in spikelet, glume, lemma, and ovule primordia. From the earliest growth stages the R values for these parts fall continuously with time.

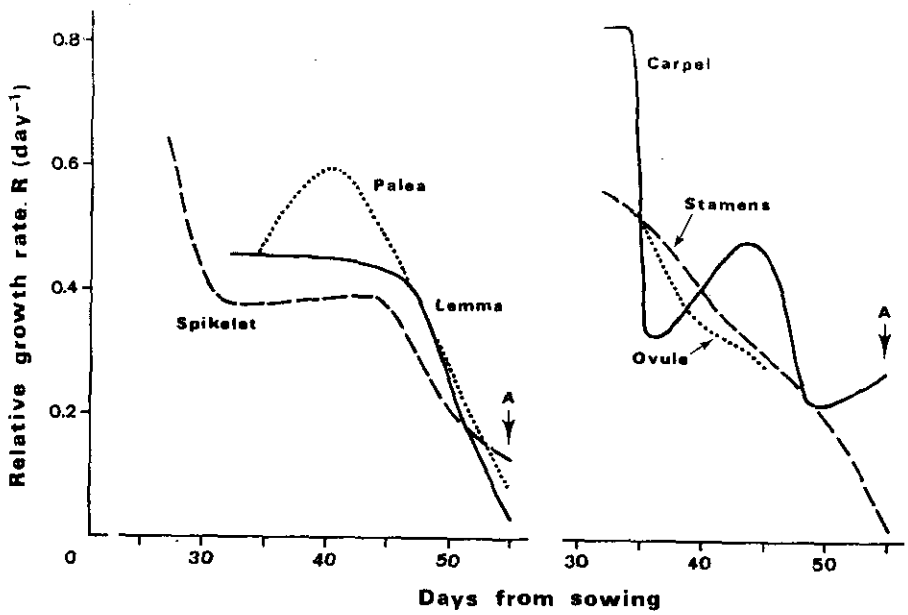


Figure 3.14 Relative growth rates for a spikelet and parts of its basal floret in wheat (Triticum aestivum). The time scale is different structures. A, time of anthesis. (From Williams, R. F., *Aust. J. Biol. Sci.*, 19, 949, 1966. with permission.)

In plant like in *Silene*, the primordia of all appendages have a higher relative growth rate than the reproductive (flower) meristem itself. Female strobili in *Pinus sylvestris* are formed first and on leading shoots, whereas male strobili are produced several years later on apparently less vigorous branches. Also in several annuals, e.g., *Xanthium*, hemp and spinach, development of female flowers requires stronger photoinduction than that of male flowers. In barley, wheat, and perhaps other cereals the onset of rachis internode elongation coincides with first floret initiation.

D. Secondary Displacement of Plants

The later processes of intercalary growth may become profoundly disturbed the spatial relationships between plant parts that are achieved at the time these parts are initiated. In many Solanaceae, like tomato, the last leaf and terminal reproductive axis of each sympodial until of the shoot are produced at about the same level. These two structures are secondarily displaced from each other by intercalary growth so that the inflorescence is finally inserted well below its corresponding leaf. This explains why in such cases the mature inflorescences appear in "abnormal" extraaxillary positions. Mature inflorescences in grapevine are also in extraaxillary positions and this again results from a process of secondary displacement due to intercalary growth.

Complications may also arise from secondary displacements of parts within the inflorescence. In *Nicotiana glutinosa*, e.g., the bract β_1 and axillary flower 1 which are closely

different levels in the mature cyme. This is due to one of these parts being displaced by intercalary growth into the next sympodial unit of the inflorescence, i.e., into the branch derived from the activity of meristem a_2.

E. Incomplete, Aborted, and Abnormal Development

Summaries of arrested or diverted development and examples are

1. Incompleteness and Abortion

The "curd" of cauliflower is an amplified prefloral inflorescence axis arrested in its development between the typical vegetative and reproductive stages. Tendrils in grapevine are aborted or incomplete inflorescence axes caused by exposure to unfavorable conditions to flowering. Thorn formation in Bougainvillea may be induced at many intermediate stages of inflorescence ontogeny, e.g., at bract or bracteole (showy bracts) formation or even after florets have been initiated.

Blindness in the rose results from the abortion of the apical meristem which occurs, depending on the cv. And/or growing conditions, at the vegetative stage or after sepal and petal initiation. As a consequence of abortion of the main meristem, an axillary meristem starts growing.

Reproductive meristems of many cultivated chrysanthemums grow slowly in unfavorable daylength conditions and generally fail to develop to anthesis. The stage at which development is arrested varies with cv. and environment conditions. In some cases an enlarged prefloral meristem bearing only involucral bracts is formed but no florets are initiated. In other cases florets (usually only ray florets) are produced, but cover only part of the meristem surface. Such incomplete capitula are known to horticulturists as "crown buds". Apical dominance is lost with the formation of these buds so that they are finally surrounded by shoots that function for a while vegetatively.

A spontaneous variant (mutation) of Aloe, also exhibits incompleteness: the inflorescence axis and normally initiated and show advanced development without floret initiation. This is incompleteness is of genetic origin. Abortion is apparently due to overproduction of reproductive structures in favorable conditions. Thus, in wheat, each spikelet produces six to eight florets but only two to four of these develop to anthesis. The other floret primordia normally abort. In barley the apical meristem of the spike and the last-initiated lateral spikelets abort usually before ear emergence, so that only about 20 spikelets remain for grain formation out of the 40 which are initiated. Similarly in many corn varieties only one of the florets of each spikelet is functional and many spikelets at the tip of the cob remain rudimentary. Generally, yield in corn is dependent upon the development of one or two cobs when the plant has primordia of potential cobs in all leaf axils. Soybean yield is only half of its real potential, partly because of high rate of flower abscission.

2. Abnormalities

Three types of reproductive anomalies can be distinguished.

2.1 Those relating to inflorescence structure, i.e., increase or decrease in the number of

bracts and/or branches, changes in receptacle shape in inflorescence internode length, etc.

2.2 Those relating to flower structure, i.e., changed numbers of parts, fusion of normally Free parts or independent growth (dialysis) of normally concrescent parts, abnormal Symmetry, virescence (development of one or several floral organs into leaf-like structures), etc.

2.3 Those in which a new axis, reproductive or vegetative, develops inside a flower, i.e., "proliferation": this new axis arises in place of a floral appendage or from its axil or it Is a continueation of the original flower axis; of special interest are the proliferations In which a vegetative bud continues the growth of the flower axis and results in the return to vegetative growth of the flower meristem, i.e., a "reversion".

Although many of these anomalous structure, e.g., virescent flowers or proliferations, are consistently observed in nature and can be produced at will in appropriate experimental conditions, they represent often an unpredictable proportion of the plant population and are very difficult to standardize. Consequently, most of the work in this area is a pure description of matures. Without better control over their production, a detailed study of how they arise is extremely difficult and their exact significance will remain unclear.

A system which seems better suited for environmental control is the cv. 'Buisson fleuri' of Impatiens balsamina, in which, contrary to the wild type, the shoot apical meristem is transformed under the influence of inductive SD into a terminal double flower. With as few as three SD there is a change from the alternate phyllotaxis of the vegetative shoot to the whorled phyllotaxis of the flower, but the lateral appendages formed by the apical meristem remain green leaves (Fig. 3.15 A). With four to six SD the shape of some appendages is intermediate between those of leaves and petal (virescent petals) (Fig 3.15 B, C, and D). Normal red petals, stamens, and gynoecium are produced after a minimum of 8, 12, and 20 SD, respectively (Fig 3.15 E, F, G,). In all cases because the SD treatment was transient, the floral appendages are followed by virescent petals and/or normal foliage leaves. In these virescent petals green patches committed to leaf development may occur side by side with red patches committed to petal development. Hence, the determination is expressed at the cell level rather than at the organ level (Fig. 3.15 B, C, D) and leaf and organs determination in ferns with a double nature, e. g., stamens bearing ovules, in teratological flowers.

F. Flower Bud Dormancy

Bulbous plants such as *Allium, Lilium,* and *Gladiolus*, have an annual rest period in their life history. This dormancy period occurs shortly after the formation of the storage organ and before the onset of stem, leaf and flower formation. But in *Tulipa, Hyacinthus*, and *Narcissus*, the dormancy period occurs after floral organ formation and is associated with flower maturation and elongation of the scape. Buds of many woody species also enter into a dormant state. Also in spring-flowering

woody plant, flowers are initiated within the differentiating resting bud before autumn and, often at an advanced stage of development, undergo dormancy. The apparent winter rest period generally includes a sequence of different physiological states: first, a correlative dormancy when the bud itself does not appear to be intrinsically dormant but is prevented from bursting by some stimulus arising elsewhere in the plant; second, an innate dormancy when bud burst is delayed as a result of conditions arising within the bud itself; and third, an imposed dormancy when bud burst is prevented by unfavorable environmental conditions. Flower bud dormancy also occurs in several alpine and tropical species. The developmental stage of the flower at the onset of dormancy is not the same for all species. Primordia of the inflorescence are present in the dormant of *Pyracantha coccinea lalandii*, but flower differentiation has not yet started.

Generally, growth is not completely stopped during the dormant state, but slowed. In peach buds indeed the floral cup enlarges continuously during the rest period when temperature does not fall below minimum growth requirements. Bulbs, too, are never physiologically at rest. This is an important fact both from a practical and a theoretical point of view as stressed.

Figure 3.15 Apical part of the shoot of plants of the cv. Buisson fleuri' of the SDP *impatiens balsamina* exposed to 3 (A), 4 (B), 6 (C, D), 8 (E), 10 (F), and 14 (G) inductive cycles and then returned to LD. Progressive formation of the terminal double flower is seen by production of whorled leaves (A); partial petalization of leaves as indicated by changes in blade shape and patches of red color on the margins (B to D, arrows); formation of normal petals followed by virescent petals and normal foliage leaves (E, F); and formation of normal petals and stamens followed by a progressive return to leaf production (G). Courtesy of L. Simon in The Physiology of Flowering VolumeIII.

Cellular and Molecular Changes

A. Cell Proliferation

In Silene *coeli-rosa* the cell- doubling time, this markedly decreases during the floral transition, lengthens during flower ontogeny from 17 hr in the evoked meristem to 27 to 28 hr in sepal and stamen primordia and 48 hr in the flower meristem distal to stamens. After the carpels are initiated the cell-doubling time increases to a week or so. This also occurs in other species e. g., Sinapis or Anagallis, where the mitotic index fall considerably after start of flower initiation.

B. Polarity of cell Growth and Division and the Genesis of Forms

The regeneration on a vegetative shoot by mature detached leaves of *Graptopetalum*, follow a model of organogenesis in higher plants that involves several critical polarity changes in the cells of the cells of the parent leaf epidermis as well as in those of the subsurface layers. This is since the formation of floral organs presumably embodies the same basic principles as that of their vegetative counterparts. Organ initiation put emphasis on the right-angle shift, from anticlinal, to periclinal, of the place of cell division in some cells of one subsurface layer (Fig 3.16). This shift in itself is insufficient to bring on a new direction of growth, and a second shift related to the growth direction of these cells, i. e., the orientation of cellulose microfibrils in their walls, is also necessary. These two 90^0 shifts are probably coupled and together they set up a new polarity in the core of the nascent primordium (Fig 3.16C). The epidermis continued anticlinal divisions following the growth of the interior rather than being the initiator of polarity changes. Although some epidermal cells continue to divide transversely anticlinally as before and also maintain their original cellulose orientation (cells 1 and 2 in Fig 3.16), there are others at the site of organ initiation which exhibit a 900 shift in their division direction. These cells, e.g., cell 3,4, and 5 in Fig. 3.16, now divide longitudinally anticlinally and the cellulose orientation in their walls is altered. Cells with polarities differing by up to 90^0 are in fact essential to give radial symmetry to a new surface. The polarity changes in the epidermis are great importance because this reorganization may proceed in the underlying cell layers. The morphogenetic role of the surface layer is at least as significant as, if not more important than, that of the interior layers. The coupling between division direction and cell growth polarity (cellulose "hoop" reinforcement in the wall) is facultative, not obligation. Some epidermal cells involved in organogenesis may exhibit a shift in their division direction not accompanied by a change in cellulose pattern. The cellulose alignments are altered on a cell-by-cell basis.

The cytoplasmic microtubules participate in the control of oriented cell growth and division. There is often a close coupling, in time and space, of the orientation of cortical microtubules and of cellulose microfibrils in the wall. Also, the orientation of the division plan is set, or at least anticipated, by a cortical preprophase band of microtubules.

Stresses do creates the altering the orientation of cell division and growth in a tissue by applied pressure. In a growing meristem internal stresses arise normally from the division and enlargement of component cells, and the stress pattern is a function of the overall shape of the meristem. In such a hydrostatic structure divided into many compartments by a continuous system of elastic cell walls, one may expect that the orientation of new walls (i.e., cell divisions) and cell growth is controlled by local stress pattern. Cell shape may be altered by stress and a polarity shift in cellulose reinforcement in the wall may occur when cell proportions are changed.

Polarity of cell growth and cell division happen according to these following steps.

1. Organ initiation occurs close to the tip of many vegetative and reproductive meristem.
2. A new radially symmetrical axis when initiation of dorsiventral organs might involve different principles (Fig. 3.16).
3. Organ initiation proceeds as well on conical-and dome-shaped meristems as on flat ones; it may even occur on concave meristems, as in epigynous flower.

The histologists believed that initiation involved periclinal divisions in one subsurface layer. However, the precise and localized changes in cell growth and division required for the genesis of the complex phyllotactic pattern recognized in the inflorescences and flowers. The influence of nearby primordia on the initiation site involves a physical (stretch) or chemical (production of a substance affecting the polarity of cell division) formative effect on adjacent tissues. Changes in gene expression are known to occur when the type of appendages produced by a meristem is changed, e.g., during transition from leaf to flower initiation or during flower ontogeny. During these transitions changes in gene expression (and the ensuing changes in metabolism) are integrated, in space and time, with changes in biophysical parameters. But how this happens and how it is controlled need to be studied.

C. RNA Content, Protein Complement, and Gene Expression

From stained sections of developing reproductive structures studied in several species showed that RNA content increases in cells involved in organogenesis (Fig 3.7 and 3.10). Also, using cytophotometry studied showing that there is a linear increase in RNA content during fertile floret development in wheat, but no increase at sites for sterile floret initiation. This temporal trend in RNA accumulation starts apparently at the earliest possible stage of ontogenesis, i.e., even before the periclinal cell divisions accompanying floret initiation. The protein complement of flowers and individual flower parts is specific and differs qualitatively and quantitatively from that found in the vegetative organs of the same species. Therefore, should be different sets of genes are active in different mature plant parts and during reproductive development there is a precise sequence of changes in gene expression in localized cell populations. However, the nature and function of the proteins specific to each class of flower members are generally unknown as is the proportion of proteins specific to each organ relative to the proteins common to all organs. The mechanisms

controlling changes in flow of genetic information during flower ontogeny have not received much attention. There were works on peroxydases which specific for stamens were also found in 26 out of 34 species of angiosperms and gymnosperms, including monoecious, dioecious and hermaphroditic species. Male and female flowers in some species also differ in their pattern of isoaccepting tRNAs and corresponding aminoacyl-tRNA synthetases. The female tRNAs for several amino acids are more numerous and/or more abundant and the corresponding synthetases are generally more active.

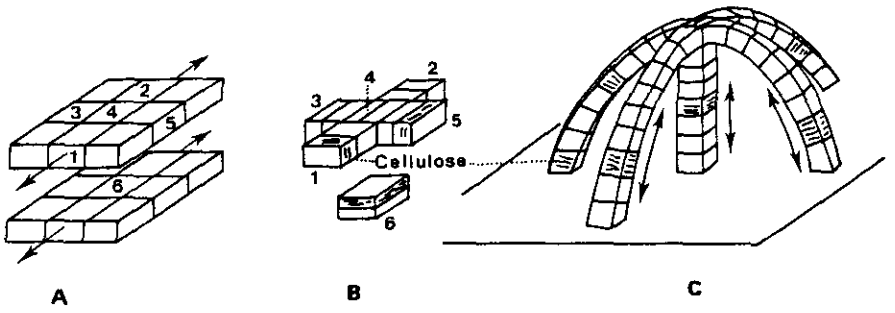


Figure 3.16 Showing polarity changes sufficient to convert important biophysical properties of the starting structure (A) to a skeleton from of a new lateral axis (C). (A) Two sheets of cells, all with parallel structural polarity as shown by arrows. Arrows pass through rings of cellulose in each cell. Only 6 of the 18 cells are involved in the new organ. At first, three kinds of decisions are made involving the 6 cells. Cells 1 and 2 divide transversely anticlinally and continue their original cellulose polarity. Cells 3, 4, 5 and 6 change their polarity. Three cells (3, 4, and 5) in the top layer divide in the longitudinal-anticlinal plane, and the cellulose polarity is also altered to be parallel to the new wall. Cell 6 in the lower layer also changes polarity by 90^0, but in adifference sense (periclinal division). Cellulose synthesis is also altered to conform. These changes lead to the configuration in B. A fourth decision is that all subsequent growth and division will be conservation, i.e., will maintain the existing polarities set up in B. Such activity will convert B to C. (Reproduced, with permission from Green, P. B., *Annu. Rev. Plant Physiol.*, 31, 51. 1980 by Annual Reviews Inc.)

Recently researches on physiology of flowering

There are many recently researches of physiology of flowering related to environmental factors, plant growth regulators and fertilizer using both stereomicroscopy and scanning electron microscopy (SEM) techniques done by the author. Some are presented as following title:

1. Scanning Electron Microscopy Study on Using Ethephon to Increase Pistillate / Staminate Flower Production in Cucumber.

2. Flowering Aspect in Strawberry by Light Microscopy and Electron Microscopy.
3. Inspection of the Increased Emergence of Jasmine Flower in Winter by SEM.
4. Change in Apices from vegetative to Flower Induction by SEM.
5. Application of SEM for Studying the Change in Apices of White Marigold (*Tagetes erecta* L.).
6. Application of SEM for Studying Physiology of Flowering in Rice (*Oryza sativa* L).
7. Using the Floral Status of Strawberry Plants, as Determined by Stereomicroscopy and Scanning Electron Microscopy, to Survey the Phenology of Commercial Crops.
8. Using Tissue Culture Technique to Produce Ready to Plant Strawberry Runners.
9. The Comparative Studies of the Changes in Apices of Some Kinds of Tropical Fruit and Temparate Fruit.
10. Change in Apices and Effect of Microclimate on Floral Initiation of Rambutan (*Nephelium Lappceam* L.).
11. Changes in Apices and Effect of Microclimate on Floral Initiation of Mangosteen (*Garcinia Mangostana* L.).

(Full paper and/or extended abstract of research title no.1-11 were attached in the appendix at the end of this chapter)

I found that apices without pronounced swelling were considered vegetative. The first evidence of flower initiation appeared as mounding of the apex. Signs of the start of sepal development on primary flower primordium were then seen. As sepals grew, petal initiation was noted. The sepals began to enclose the bud at about the time the stamens began to develop. Then the epidermal hairs developed and began to cover the flowers. At about this time pistil differentiation began. The SEM technique showed most detail; however, the stereo microscope technique was quicker and was more appropriate for determining flower initiation in plants grown in the field. Therefore, flower initiation of all the plants studied follow acropetal and basipetal sequence (Fig. 3.17).

The changes in apices from vegetative stage to flower induction stage in all plants studied are very importance and difficult to detected. However, this stage determined differentiation growth and development including fruit set of the plant. The changes in apices from vegetative stage to flower induction stage were studied by using SEM technique in Marigold (*Tagetes spp.*), Chrysanthemum (*Chrysanthemum morifolium*), Rose (*Rosa spp.*), Ixora (*Iora spp.*), Strawberry (*Fragaria ananassa* Duch.), Grape (*Vities vinitera*) and Rice (*Oryza sativa* L.). The apices without pronounced swelling or flatten were vegetative stages. The flower induction stages were found when the apices first forming round following with mounding apices (Fig 3.18). The wilting of the leave primordia could be noticed in nearly every plant studied but the degree of the wilting was different. The induction stage of flower happened when the mature plant got a complete factor for flower induction e.g.

daylenght, temperature, etc. and complete cycle for flower induction for each factor. The mounding of the apices at the flower induction stage may result from a change in a biophysical boundary condition involving dome geometry. The plant vigor probably affects flower induction. However the effect of environment to control flower induction should be more investigated by using SEM technique.

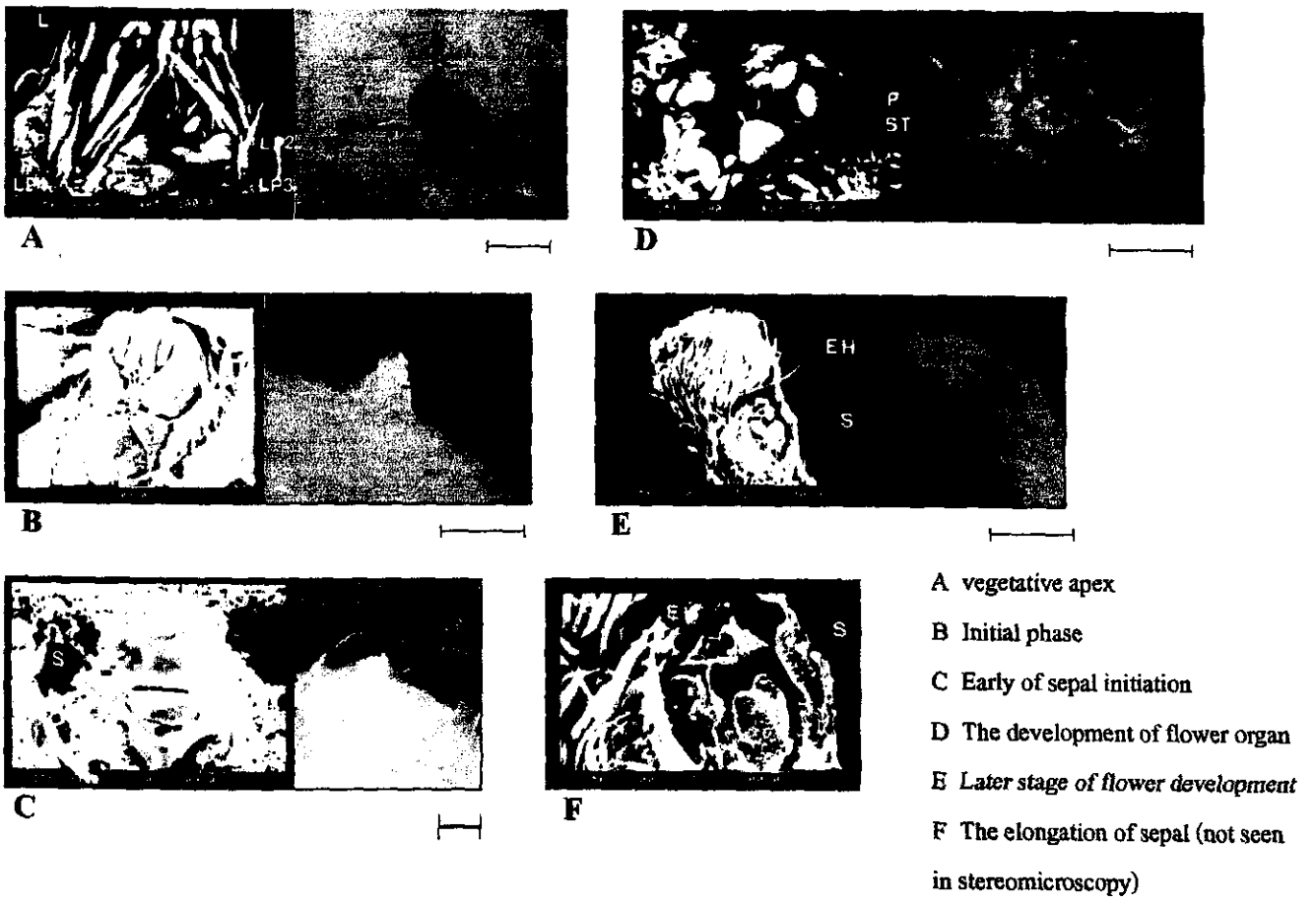


Figure 3.17 The ontogenies of flower development in strawberry observed using the SEM (left) and stereomicroscopy (right) techniques. From Y. Manakasem and P. Tuasange Proceding of the 8 th Asia-Pacific Conference on Electron Microscopy (8 APEM), 7-11 June 2004, Kanazawa, Japan

The plant age, the plant nutrition, plant growth regulators also growth retardant, the environmental factors such as temperature (minimum, maximum and average), daylength, relative humidity (RH), light intensity, soil moisture, soil temperature, soil fertility also fertilizer were all have effect on flower induction, flower initiation, flower development and flowering in overall.

Ethephon at the concentration of 200 ppm sprayed at 7 days interval, starting when the cucumber had 2-3 true leaves and continue until the cucumber started to flower can stimulate the pistillate flowers. While the cucumbers those were not sprayed with any concentration of ethephon the highest number of staminate flower (Fig. 3.19) and Table 3.1. Concentration and kinds of the

plant growth regulators and growth retardants treated to plants are very importance. From the literatures reviewed and preliminary tested, we had set experiment on jasmine (*Jasminum sambac* W. Ait) to increase the number of flower in winter. This is since jasmines flower very litter in winter, and those flowers are also very poor in quality. Despite this, its price is very high. There were attempts to increase the quality of jasmine in the cool season by using sucrose, fructose, GA_3 and NAA. However, the attempts to increase the number of flower of jasmine in winter need more study by using the others chemicals as well. The SEM technique was used to examine the morphogenesis of jasmine from vegetative stage to flowering stage as well. The result showed that treated Thiourea 1%, at the concentration of 2500 ppm to 1 year old jasmine on early winter at weekly intervals for 3 weeks, can increase the number of flowers of jasmine in winter. The morphology changes of apices from vegetative stage to flowering stage can clearly seen by SEM (Fig. 3.20) and Table 3.2 .

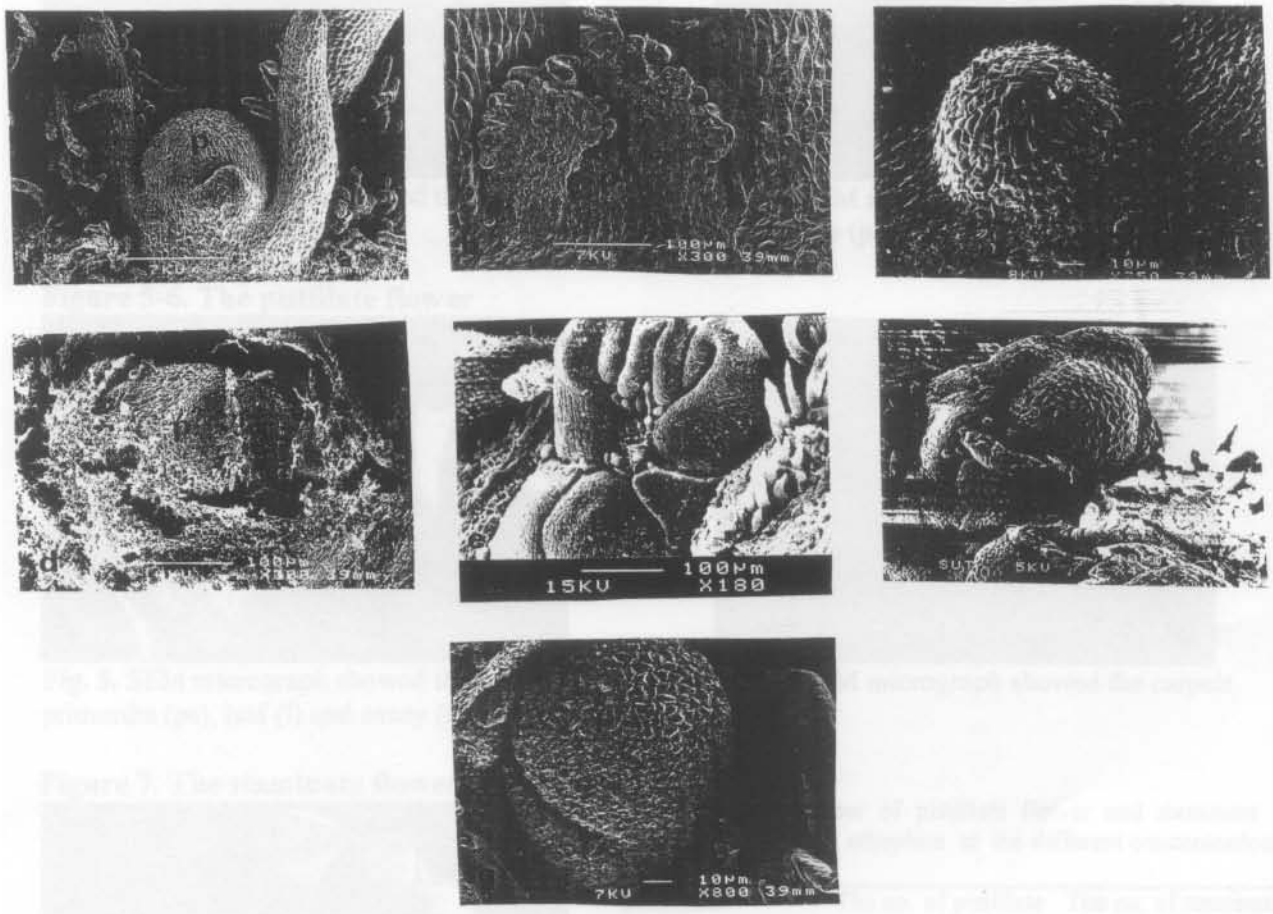


Figure 3.18 SEM of the flower induction apices of (a to g) showed as a mounding of the apices (p). (a) Marigold (*Tagetes spp.*), (b) Chrysanthemum (*Chrysanthemum morifolium*), (c) Rose (*Rosa spp.*), (d) Ixora (*Ixora spp.*), (e) Strawberry (*Fragaria ananassa* Duch.), (f) Grape (*Vities vinitera*), (g) Rice (*Oryza sativa* L.). From Manakasem, Y., 2002. Changes in Apices from Vegetative to Flower Induction by SEM. Proceeding of the 15 th International Congress on Electron Microscopy, 1-6 Sept 2002. Durban South Africa.

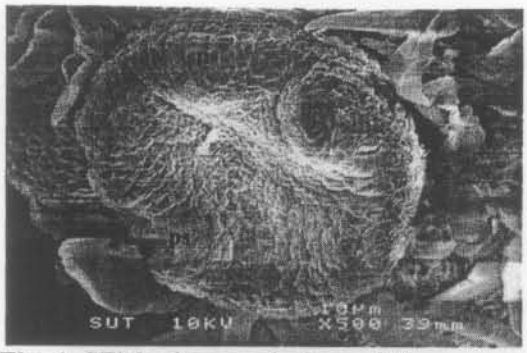


Fig. 1. SEM micrograph showed the common primordia (ps) of cucumber flower

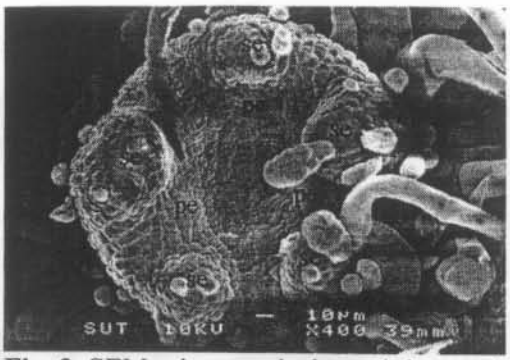


Fig. 2. SEM micrograph showed the sepals (se) and petals (pe) initiated

Fig. 3. SEM micrograph showed the sepals (se) and petals (pe) development

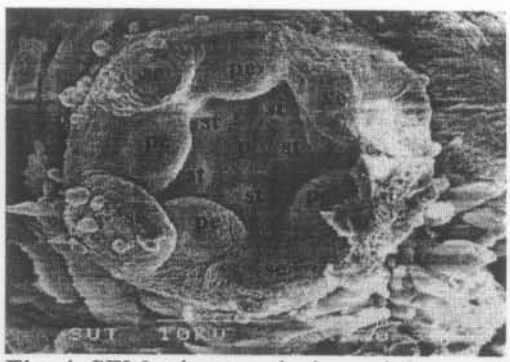


Fig. 4. SEM micrograph showed the sepals (se), petals (pe), stamens (st) and pistil (p)

Figure 5-6. The pistillate flower

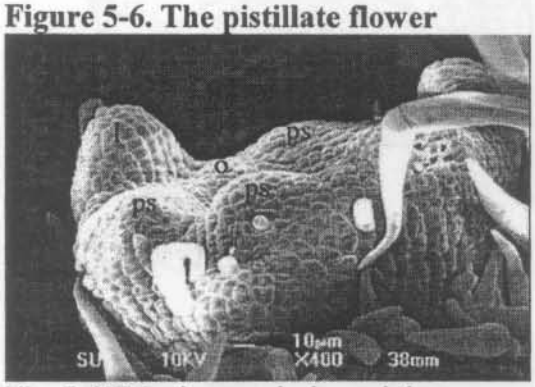


Fig. 5. SEM micrograph showed the common primordia (ps), leaf (l) and ovary (o)

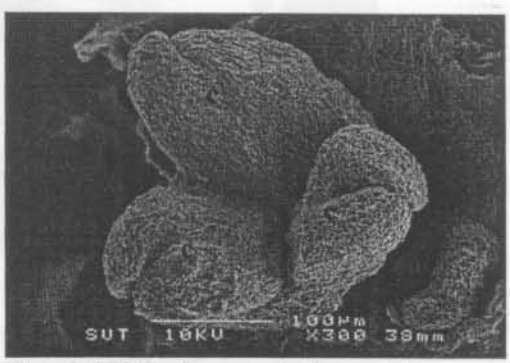


Fig. 6. SEM micrograph showed the carpels (c)

Figure 7. The staminate flower

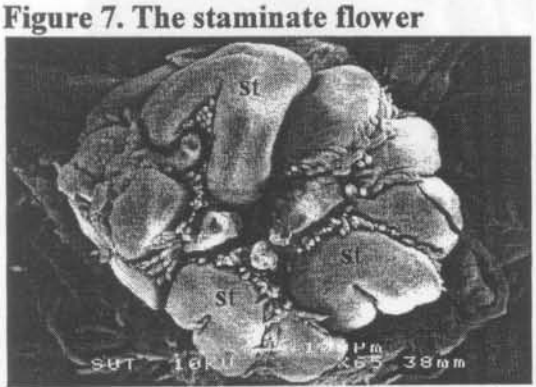


Fig. 7. SEM micrograph showed the staminate flower ; st = stamen

Table 1. The number of pistillate flower and staminate flower treated with ethephon at the different concentrations.

Treatment	The no. of pistillate flower/plant	The no. of staminate flower/plant
Control(distilled water)	53.29 ab[1]	3.71 c[1]
Ethephon 100 ppm	56.00 ab	3.00 bc
Ethephon 150 ppm	63.43 b	2.43 ab
Ethephon 200 ppm	87.29 c	1.57 a
Ethephon 250 ppm	50.29 a	1.57 a

[1]Mean values of variable followed by a common letter are not significantly at 5 % level by DMRT.

Figure 3.19 The flower development of cucumber (Cucumis sativus L.)

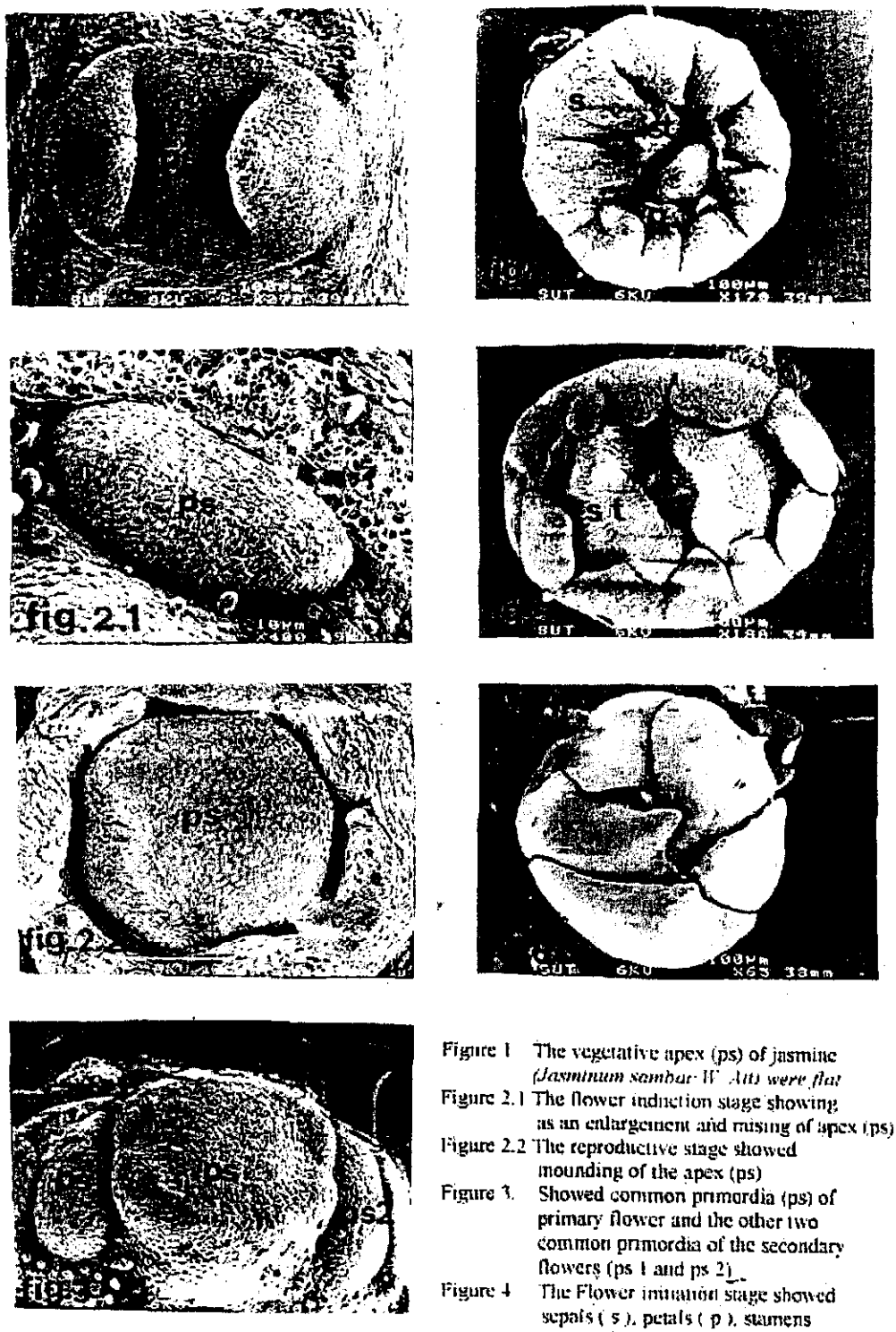


Figure 1 The vegetative apex (ps) of jasmine (*Jasminum sambac* W. Ait) were flat

Figure 2.1 The flower induction stage showing as an enlargement and rising of apex (ps)

Figure 2.2 The reproductive stage showed mounding of the apex (ps)

Figure 3. Showed common primordia (ps) of primary flower and the other two common primordia of the secondary flowers (ps 1 and ps 2)

Figure 4 The Flower initiation stage showed sepals (s), petals (p), stamens (st) and carpels (c)

Figure 5. The completely developed flower, stamens (st),and carpels (c)

Figure 6 The young flower of jasmine

Figure 3.20 The flower development of jasmine (*Jasminum sambae* W. Ait)

Table 3.2 The number of inflorescences produced per plant, the number of flowers produced per plant and width of the jasmine one month after treatment.

Treatment	The no. of inflorescences per plant	The no. of Flowers per plant	The width of the plant (cm)
Paclobutrazol 2500 ppm	5.50 a[1]	17.67 a[1]	24.83 a[1]
KNO_3 2.5%, 2500 ppm	8.33 a	24.83 a	26.13 a
Thiourea 1.0%, 2500 ppm	8.83 a	29.00 a	24.47 a
Ethylene 2500 ppm	1.83 b	5.17 b	17.03 b
Control	8.00 a	24.33 a	26.07 a

[1] Mean values of a variable followed by a common letter are not significantly different at 5% level by DMRT.

Changes in apices and effect of microclimate on floral initiation including phonological cycle of some tropical fruits such as mangosteen (*Garcinia mangostana* L.) and rambutan (*Nephelium lappaceum* L.) had been studied using stereomicroscopy (Fig. 3.21 and 3.22). The percent of apices induced to flower were correlated with microclimate factors. In mangosteen, among the microclimatic factors studied the minimum temperature was the most important factor which was highly correlated with the changes in apices followed by hours of sun shine and amount of rainfall (Fig. 3.33) and Table 3.3. The regression analysis showed that increased minimum temperature for 1^0C resulted in10.5% decrease of flower induction.

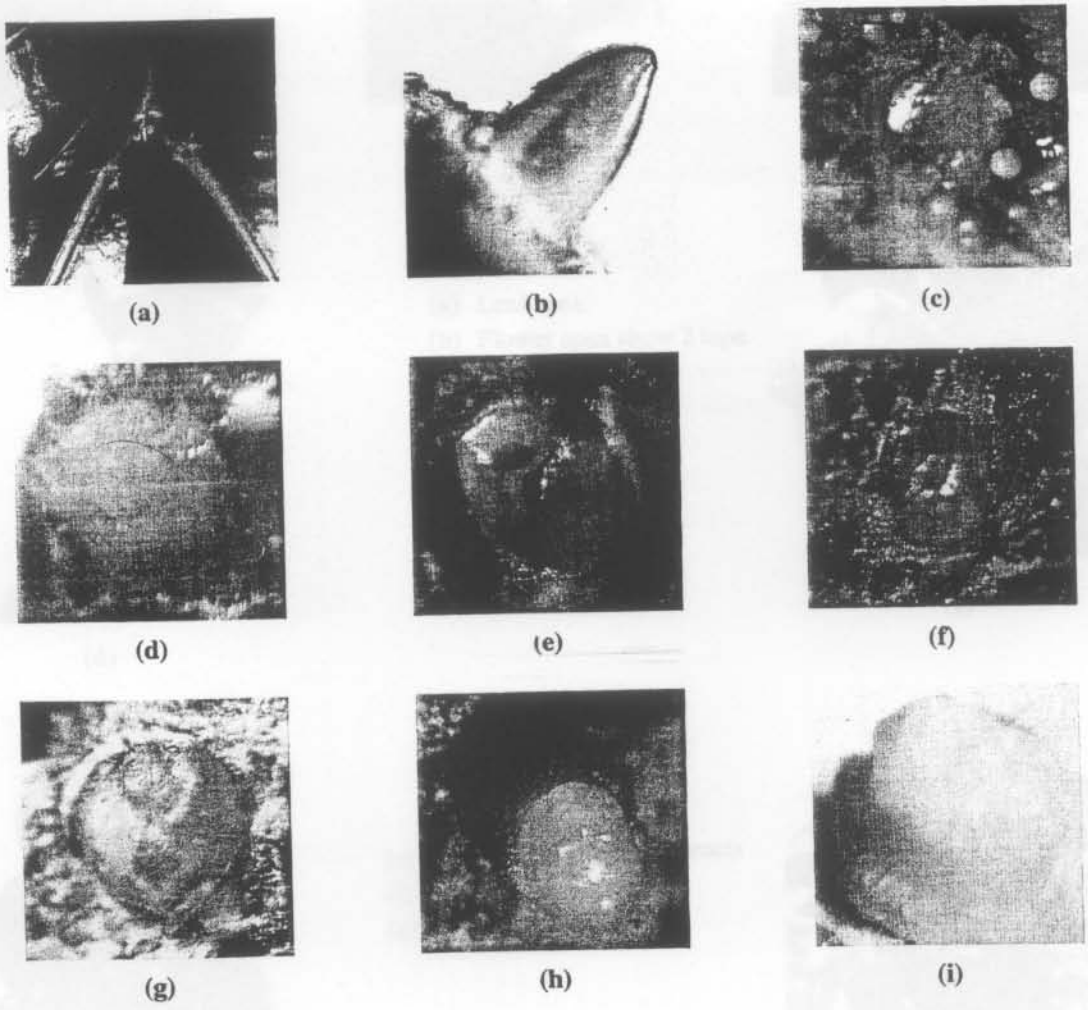
$$Y = 280.961 - 10.547^{*} \text{ min temp.} + 0.893^{ns} \text{ sun shine hr.} - 0.876^{ns} \text{ rainfall}$$

$$R^2 = 0.61^{**}$$

The study on the phenological cycle indicated that it would be effective to induce flower of mangosteen by such means as spraying chemical in mid to late September when the secondary leaves were fully expanded. However, the environmental condition from early November to mid December when minimum temperature was 21^0C could induce the changes in apices from vegetative to reproductive stage, which result in 90% initiation in mid December (Fig. 3.23 and 3.24). The same trend was found in rambutan. The increasing in minimum temperature for 1^0C resulted in 6.7% decrease of flower induction in rambutan. The study on the phonological cycle indicated that it would be effective to induce flower of rambutan by such means as spraying chemical in very late October when the secondary leaves were fully expanded. In addition the minimum temperature in late October which was around 23^0C could induce the changes in apices from vegetative to reproductive stage, resulted in 100% initiation in mid December to mid January. The watering should be controlled in mid to late December while the short raceme extended.

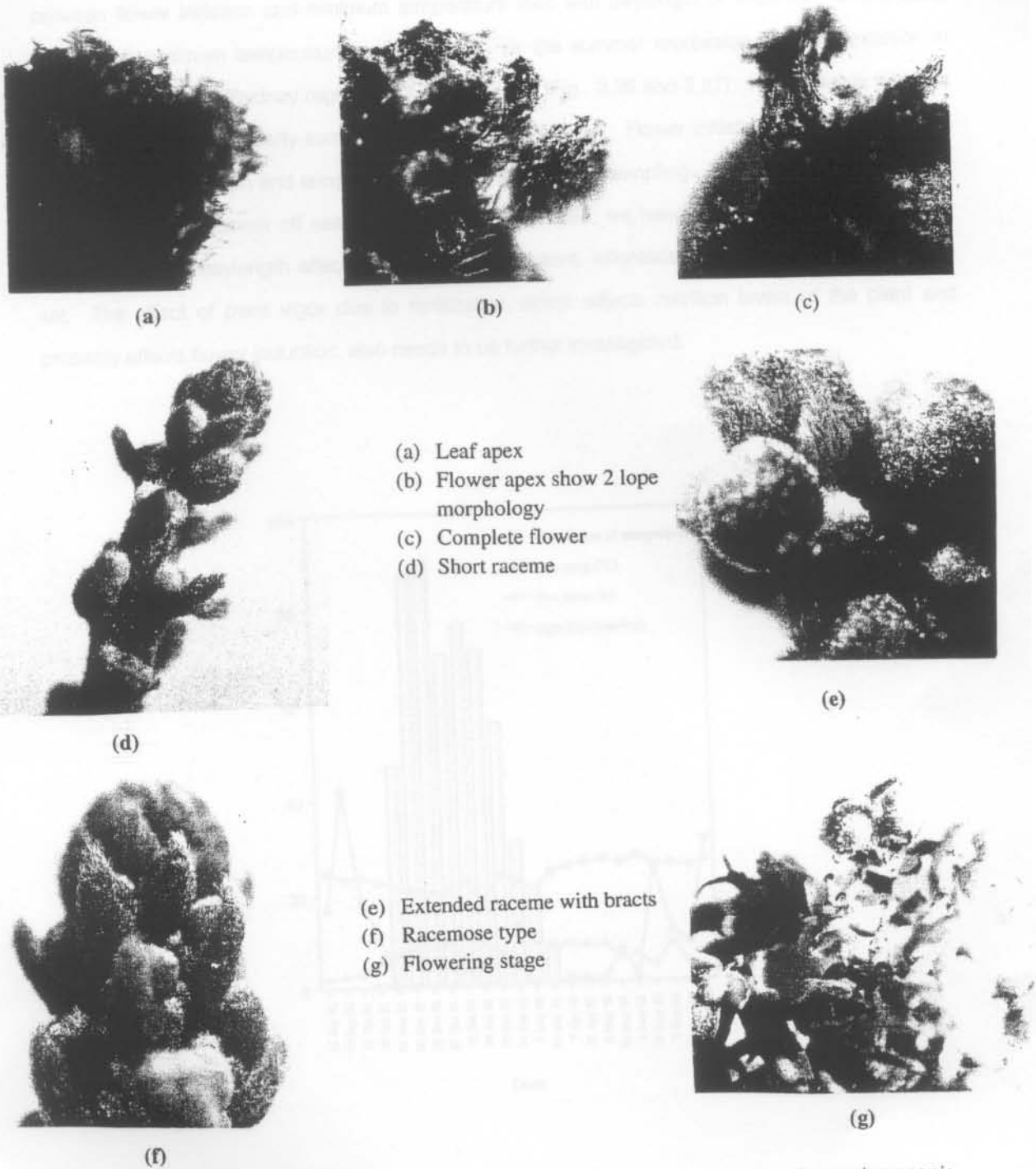
The comparative studies of the changes in apices of some kinds of tropical fruit and temperate fruit have conducted. The conclusions were the morphology of vegetative apices of all crop studied were soft and flat. The first evidence of flower initiation was an enlargement and raising

of the apices. Then the sequence of flower initiation followed acropetal and basipetal. That is sepal, petal, stamen and pistil developing in ordering.



(a) Bud sample **(b) Shoot pit** **(c) Flattening apex**
(d) Four round parts of apex **(e) Leaf bud initiation** **(f) Flower bud intiation**
(g) Flower development **(h) Complete flower development** **(i) Core of blossom flower**

Figure 3.21 Changes in apices of mangosteen (*Garcinia mangoatana*) under stereomicroscopic magnification 10 to 64 times.



(a) Leaf apex
(b) Flower apex show 2 lope morphology
(c) Complete flower
(d) Short raceme
(e) Extended raceme with bracts
(f) Racemose type
(g) Flowering stage

Figure 3.22 Changes in apices of rambutan (*Nephelium Lappaceum* L.) under stereomicroscopic magnification 10 to 64 times.

Using the floral status of strawberry plants, as determined by stereomicroscopy and scanning electron microscopy to survey the phenology of commercial crops in short day variety (Torrey) and day neutral variety (Aptos) of strawberry showed flower initiation is very responsive to temperature, daylength and also their interactions (Fig. 3.25). However, the correlation was stronger

between flower initiation and minimum temperature than with daylength or maximum temperature. The critical minimum temperature and daylength for the summer repression of flower initiation in 'Torrey' growth in the Sydney region is 13.8^{0}C at 14.9 h (Fig. 3.26 and 3.27). Hence flower initiation of this cultivar stops in early summer and resumes in mid-fall. Flower initiation in 'Aptos' occurred regardless of daylength and temperature during the period of sampling. To recommend production procedures for maximum off season production in the field, we need a precise knowledge of the temperature and daylength effects on flower development, inflorescence emergence and also fruit set. The effect of plant vigor due to fertilization, which affects nutrition levels of the plant and probably affects flower induction, also needs to be further investigated.

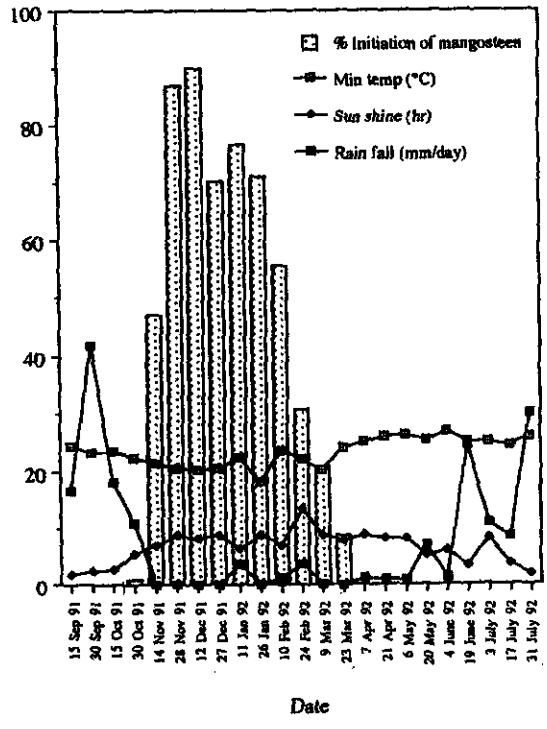


Figure 3.23 Microclimatic data and percent initiation of mangosteen.

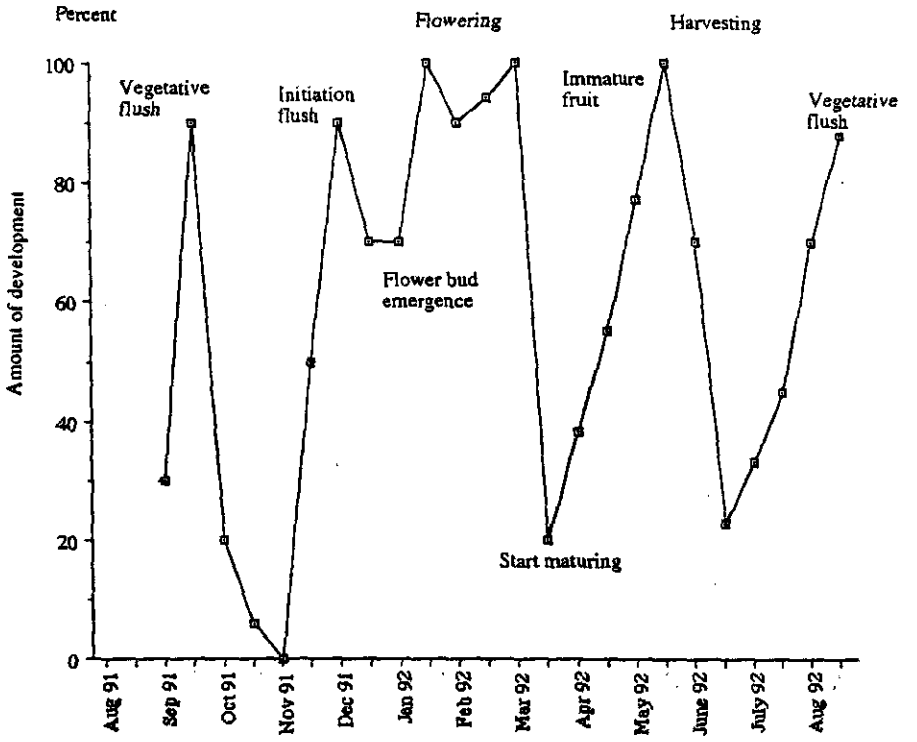


Figure 3.24 Mangosteen phenological cycle.

Table 3.3 The correlation between percentage induced to flower of mangosteen (Garcinia mangostana L.) and maximum and minimum temperature (^{0}C), sunshine hour (hr), rainfall (mm/day), maximum and minimum relative humidity (%) and soil temperature at the depth of 100cm.

Climatic data (everage every fortnight)	**Percentage induced to flower**
Maximum temperature	0.271ns
Minimum temperature	- 0.780**
Sun-shine-hr	0.458*
Rainfall	- 0.472*
Maximum relative humidity	- 0.296^{ns}
Minimum relative humidity	- 0.075^{ns}
Soil temperature	- 0.326^{ns}

*ns, *, ** = not significant, significant at 0.05 and 0.01 levels of probability, respectively.*

Figure 3.25 Flower development in strawberry observed using scanning electron microscopy. (A) Vegetative apex showing the last trifoliolate (L), nonswelling apex (primordium) (P), and 2/5 spiral arrangement of leaf primordia (LP). (B) Initial phase of change from vegetative to reproductive stage showing mounding of the apex and last young trifoliolate leaf (L). (C) Early stage of sepal (S) development showing the start of sepal initiation. (D) The development of sepals (S), petals (PE), and stamen (ST). This is about the time of pistil differentiation. (E-F) later stage of flower development showing the elongation of sepals (S) and epidermal hairs (EH).

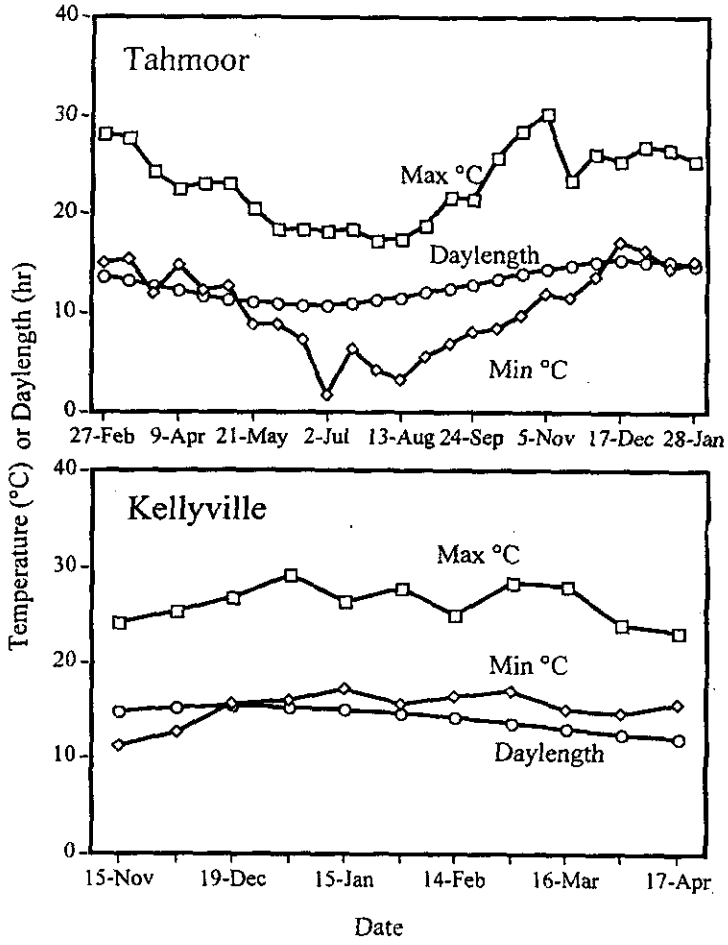


Figure 3.26 *The mean daily maximum and minimum temperatures and daylength at fortnightly intervals from* 14 Feb. 1988 to 11 Feb. 1989 at Tahmoor, and from 1 Nov. 1989 to 2 May 1990 recorded in the field at Kellyville. The date is the starting date of the fortnight.

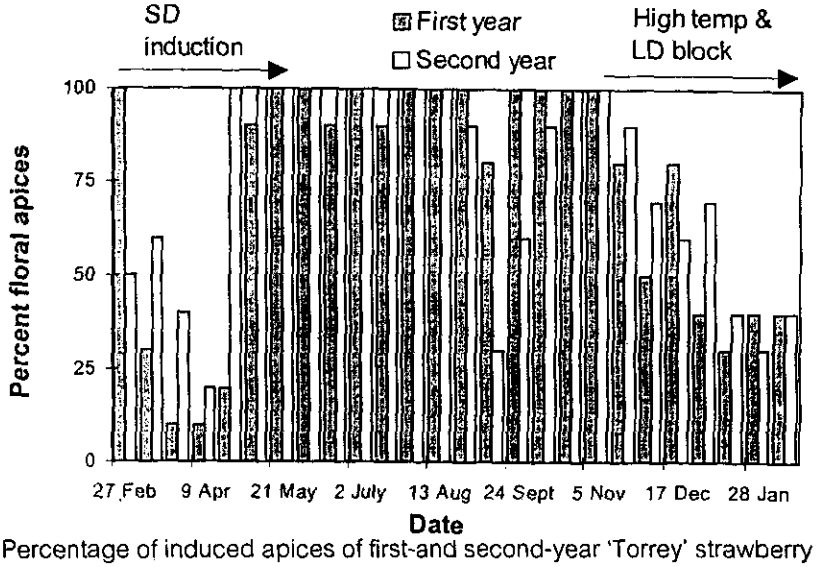


Figure 3.27 Percentage of induced apices of first-and second-year 'Torrey' strawberry plants grown in the field at Tahmoor, Australia, and dissected each fortnight.

To produce ready to plant strawberry runners by using tissue culture technique was set at Doi Tung Royal Villa, Mae Fah Luang district, Changrai province, from 1994 to 1988. After getting the plantlets from tissue culture, the plantlets were then transplanted into the nursery and were grown with a special fertilizer programme for another 4 months. The plants were dissected to investigate of flower initiation under stereomicroscopy (10 to 64 times) to check flower initiation. Figure 3.28 showed flower development of strawberry as seen using stereomicroscope as mentioned.

Determination of the flower or vegetative status by stereo-microscopy and SEM in strawberry found that the SEM technique showed most detail, however, the stereomicroscope technique was quicker and was more appropriate for determining flower initiation in strawberry plants grown in the field.

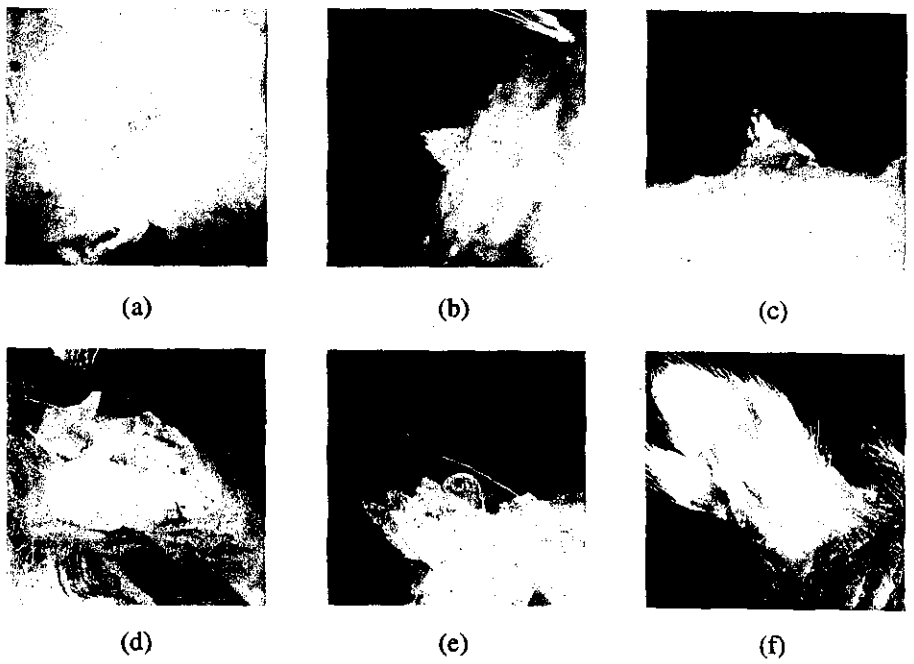


Figure 3.28 Flower development of strawberry as seen using stereomicroscope magnification 10 to 64 times. (a) vegetative apex (b) early stage of floral initiation showing the enlargement and raising of the apex (c) early stages of sepal development (d) petal initiation and development (e) later stages of flower development (this is about the time the pistil differentiation) (f) final stage of floral development showing the elongation of sepal to enclose the bud, and the development of epidermal hairs.

Physiological process of induction, initiation and development of flowers are very importance for crop production. The effects of environment on flowering and fruit set should be studied in details. The use of hormonal and chemical control for flowering and fruit setting have to be aware and very carefully. Before treated anything to plant should study and consider physiology of those plants very well.

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