ANNUAL GROWTH CYCLE IN TREE SPECIES

(a) Linear growth:

The diversity in height growth habit of trees is amongst the characteristics that has been studied most extensively. In some species, particularly the conifers, the tree adds to its annual height growth in a single spurt without any intervening rest period and then enters a dormant period, which lasts till the following spring when the growing conditions become favourable again. In some species extension growth stops by mid-July even though the conditions for growth are still favourable and continue as such for at least two more months. A single short spurt of growth, therefore, occurs in these plants. The individual shoots on the tree may, however, show periods
of active growth alternating with the periods of relative inactivity. This type of growth is known as 'recurrent or intermittent type of growth' and each growth period as 'growth flush'.

(i) Tropical tree species: Many tropical tree species show intermittent type of extension growth with several growth flushes during the growing season (Greenwood and Posnette, 1950). The shoot growth of Citrus occurs in a series of intermittent waves showing variable number of flushes depending upon the species (Cossmann, 1939; Randhawa and Dinsa, 1947; Sauer, 1951 and Cooper, 1957).

Koriba (1958) has classified tropical tree species into four main classes: (1) evergrowing trees with continuous leafing, a growing bud at the apex and with uniform leaf size and internodal length; (2) intermittently growing trees with seasonal contemporary or non-seasonal leafing with a growing bud at the apex of the shoot formed at the end of each growth period and with variable leaf size and internodal length; (3) trees with growth rhythms that arise in different parts and (4) deciduous trees.

Chowdhury (1958) described that in the broad leaved Indian trees the first growth flush occurred during the months of March to June, the second during July or August to September and the third during October to November and the fourth, if at all, during December to January.
In tea (*Camellia thea*) a vegetative shoot goes through cycles of alternation of growth, involving periods of unfolding of cataphylls and foliage leaves and of dormant 'banjlu' periods during which the growth in length is completed and lignification takes place, but no leaves unfold (Bond, 1942). About four flushes which appear to be independent of seasonal changes are completed in this species each year in Ceylon. The cyclic flushing pattern is sometimes modified to the extent that strong 'leader shoots' may grow more or less continually. Actually, the apical bud in tea has no real 'resting' period and primordia are produced continuously but with regularity of change in rate. The most intense activity is at the time of active flushing after the first scaly leaf of the current cycle has expanded. Thereafter activity decreases to a minimum. The rate of leaf growth is correlated with the rate of internodal growth (Bond, 1945).

According to Resende (1964) the annual rhythmic pattern of growth in tropical plants is not conditioned or is only partially and indirectly conditioned by seasonal variations. He presumes that these patterns of growth are controlled by some internal annual rhythms.

(ii) Temperate tree species: The shoot growth of temperate tree species is also variable and of an intermittent type (Kordy, 1937; Friesner, 1942, 1943a; Ow, 1957; Parke, 1959;
Petrenko, 1961; Kozlowski and Ward, 1961 and Kozlowski, 1962, 1964). Kramer (1943) showed that the apical growth in *Fraxinus americana*, *Juglans nigra* and *Quercus alba* occurred in recurrent waves. Farnsworth (1955) presented an interesting series of curves for apical elongation of a number of species during 1940 and 1942 growing seasons. These curves also show intermittency in growth rates within each year as well as variations between the years. He attributes yearly variations in the time of growth initiation to temperature differences.

(b) Bud dormancy:

Dormancy may be defined as a temporary suspension of visible growth. It was earlier considered that dormant condition in the plant originates autonomously in a certain season. Smolin (1943) linked dormancy with the theory that assumed that the potential of life activity gradually decreases during cycles of aging and rejuvenation. Unfavourable growth conditions cause aging for which dormancy provides the rejuvenation and partial recuperation. Klebs (1903, 1914, 1917) postulated that dormant condition in the plants is induced by a combination of external factors. On the basis of nature and possible causes of dormancy Chouard (1951) proposed the term 'correlated inhibition' when internal conditions of the bud causing rest, are the result of external factors.
When, however, these factors arise within the organ itself it may be termed as 'rest'. Samish (1954) termed cessation of visible growth caused by unfavourable environmental conditions as 'quiescence' and that caused by internal factors as 'rest'. Vegis (1964) termed the dormancy induced from unfavourable external factors as 'imposed dormancy' in contrast to physiological dormancy, that is caused by internal factors. He further recognised three phases of dormancy, pre-dormancy or early rest, middle rest and post-dormancy or late-rest. Smith and Kefferd (1964) supported the concept that bud dormancy involves a cycle of 3 separate phases of development, namely (1) dormancy development leading to the dormant state; (2) release from dormancy leading to the non-dormant state and (3) spring burst leading to spring development.

Considerable work has been done in recent years on different aspects of bud dormancy and excellent reviews on the subject have appeared from time to time (Samish, 1954; Vegis, 1964; Smith and Kefferd, 1964).

Klebs (1914) found that seedlings of *Fagus sylvatica* continue growing without forming terminal buds under the most favourable conditions. Under less favourable conditions they form terminal buds without scales which grow out immediately. Under more unfavourable conditions the terminal buds with scales are formed and these begin growth.
after a few weeks. But under the least favourable conditions
the terminal buds produced with numerous scales show a
long period of rest. Downs and Borthwick (1956) reported
that in oak and elder, onset of dormancy is evident first
by cessation of terminal elongation and leaf expansion and
then by the formation of a terminal bud, but in Ulmus americana
and Betula mandshurica, the formation of scaly leaf does
not take place and the leaves produced during dormancy
remain underdeveloped till the resumption of growth.
According to these workers dormancy can be due either to the
higher rate of elongation than the rate of initiation of
new structures or vice versa.

(c) Reproductive development:
The plant shifts from vegetative to reproductive
state with maturity. Klebs (1918) recognised three
ontogenic phases during this transformation and related
them with the photoperiod. Garner and Allard (1923)
brought out the importance of photoperiod in reproductive
development by their extensive studies on a number of
plants. Gassner (1918), on the other hand, related
reproductive development in plants to changes in temperature.
Considerable work has since been carried out on the factors
concerned in the transformation of the growing apex from
the vegetative to the reproductive state. Most of this
work, however, relates to flowering in annual plants.
This is particularly because the tree species undergo a period of juvenility before flowering can set in. In addition to this, in most of the tree species the flowering is indirect and a long period of dormancy intervenes between the initiation of floral buds and their opening into flowers. Grainger (1946) and Stanley (1958) have shown that the conditions necessary for the initiation of floral buds may differ greatly from those that favour their development into flowers. Not much work has been done on the physiology of flowering of trees. The available literature on this aspect has been dealt with in a subsequent section.

ENVIRONMENTAL FACTORS AND THE ANNUAL GROWTH CYCLE

The annual growth cycle of tree species is affected considerably by various environmental factors, such as photoperiod (Kramer, 1936; Zaring, 1956; Kitto, 1957; Olson et al., 1959; Donald, 1962; Vanda, 1963 and Vanda & Purohit, 1966); light intensity (Mitchell, 1936; Kozlowski, 1949 and Vanda & Purohit, 1966); temperature (Jarnsworth, 1965; Kramer, 1957 and Nikols, 1962) and physical properties of the soil (Steckeler, 1943; Cassell, 1949; Wanger, 1952; Cole and Schumacher, 1953 and Jameson, 1963).

(a) Photoperiod and annual growth cycle:
(b) Linear growth and bud dormancy: Garner and Allard (1923)
were the first to recognize the marked effect of photoperiod on the annual cycle of growth in plants and bud dormancy. The subject has since received considerable attention and a number of papers have appeared in recent years (Wareing, 1956, 1958, 1959; Allewelt, 1957; Nitsch, 1957, 1957a, 1959, Naylor, 1961 and Vegis, 1964).

It is apparent from a review of literature that response of tree species to photoperiod is not similar. In general, long days enhance and prolong the period through which extension growth continues and therefore, delay the onset of dormancy. Short days, on the other hand, decrease the rate of growth and hasten the onset of dormancy. Vegis (1953, 1956) showed that in Hydrocharis morsusranal dormancy can be induced in continuous darkness if plants are supplied with sucrose, indicating that the effect of dark period in causing the onset of dormancy may not be due to hampering of photosynthetic process. The importance of long dark period is also apparent from the fact that its interruption by a short light period causes the plant to show the same growth behaviour as that in continuous light. Reimers (1959) has, however, reported that in some plants long daily light period at high temperature leads to the cessation of growth and onset of dormancy, while short days cause continuous growth. Nitsch (1957b) listed a number of woody plants according to their reaction to photoperiod and divided them into four classes: (1) Plants in
which long days prevent the onset of dormancy and short
days cause it, as *Weigela* and *Acer rubrum*; (2) Those in
which long days cause periodic growth as *Quercus* and
*Rhododendron*; (3) Those in which short days do not cause
dormancy as *Juniperus* and *Thuja* and (4) Plants in which
long days do not prevent dormancy, as *Syringa* and *Buxus*.

Pauley and Perry (1954) and Vaartaza (1954, 1959)
found that the response of trees to a given photoperiod
varies with the geographical source of experimental plant
material. Leman (1948) and Wareing (1951, 1954) reported
that in most of the woody species which are characterised
by growth in rapid flushes, the growth periodicity is
maintained even when these are exposed to long days.
According to Bunning (1956) some endogenous yearly rhythms
within the plant contribute to the endogenous aging process,
apart from the influence of external environment. Wareing
(1950) and Nanda (1963) also reported that even under
constant photoperiodic conditions cessation of growth takes
place after a certain period. According to Wareing (1956)
in species with no critical day length requirement, growth
is determined primarily by the endogenous aging process and
is only modified by the environmental factors, including
the day length. Downs (1958) postulated that photoperiodic
reactions in plants where shoot elongation continues both
under short and long day conditions, other environmental
factors like temperature may directly operate the process
which ultimately governs the dormancy and active growth.

(ii) Flowering: Some evidence is now available in literature to show that photoperiod may play a significant role in the initiation of flower primordia in some tree species as it does in many herbaceous plants. Thus long days are required for floral initiation in *Calluna vulgaris*, *Carvopteris mastacanthus*, *Ribes rubrum* and *Rosa* (Chouard, 1946, 1947), *Ulmus glabra* (Wareing, 1965). The flowering in these plants is suppressed under short days. On the other hand, Mirov (1956) worked on 35 exotic pine species and concluded that all were neutral in their 'flowering' response to photoperiod. Similarly, Downs and Piringer (1958) reported that the flowering response of five species of *Viburnum* was unaffected by photoperiod. Flowering of *Syringa vulgaris* is also not affected by day length (Chouard, 1947). There are contradictory reports on the photoperiodic effect on the flowering of *Gardenia* (Keyes, 1939 and Phillips, 1941).

The flowering mechanism in trees is complicated by the fact that a juvenile period of development must be completed before sexual maturity is reached. Comparatively little work has been done on the effect of photoperiod on the juvenility of woody plants. Moskov (1936) observed that juvenile period in *Ribes nigrum* and *Salix phylicesfolia* is reduced by two years if the plants are exposed to
continuous illumination. Nikitin (1949) also reported similar effect in the case of oaks. Scepotjev (1948) in Morus alba reported a long-term photoperiodic after-effect on flowering.

(b) Temperature and annual growth cycle:

(i) Linear growth and bud dormancy: Although temperature influences growth and distribution of plants, only a few reports are available in literature on the effect of temperature on conifers and these show that while temperature is a major factor in the initiation of growth in spring, it has very little effect on its cessation during winter (Reed, 1939; Friesner, 1943; Baldwin, 1956; Horton, 1958). Hellmers (1962) showed that recurrent flushes of growth are closely related to temperature. An increase in temperature causes an increase in the number of flushes.

It is well known that the normal growth of temperate woody plants occurs only when the high temperature of summer alternates with a period of low winter temperature. The response of plants to differing day and night temperatures, a phenomenon called thermoperiodism by Went (1948, 1953), also has an important effect on the growth of trees. Went (1953) considered that differences in the optimum day and night temperatures are more beneficial for the growth of plants than heat sums indicating close relationship between climate and plant growth. Kramer (1957) working with
loblolly pine found that growth was related more closely to the difference between day and night temperatures than to the actual temperature used within the range. He also observed that oak seedlings with very low night temperature grew eight times longer than those grown with equal day and night temperatures. Previously Pollock (1953) and Vegis (1956) also reported that high summer temperatures induce dormancy in buds. Hellmers (1962) reported that Pinus taeda grows taller under conditions with maximum day-night temperature differences. Perry (1962) found that day temperature required for optimum growth of Acer rubrum from different geographical sources was higher than the night temperature.

The temperature with low light intensity may counteract the favourable effects of the photoperiod and cause the onset of dormancy in A. rubrum. Nanda (1963) and Nanda & Purohit (1966) also consider that temperature modifies the effect of the photoperiod on extension growth indicating that it is probably the function of sum total of energy requirement rather than the effect of photoperiod alone and that this energy may be supplied within limits either in the photo or thermic form. It appears, that for the onset of secondary dormancy daily exposure of the plants to the high temperature for a few hours is sufficient (Vegis, 1948; Bennett, 1955).
(ii) **Flowering:** The marked effect of temperature on the flowering of annual plants is well recognised (Evans, 1960a; 1960b; Heslop-Harrison and Woods, 1959; Chouard, 1960; Purvis, 1961; Salisbury, 1963; and Zeervart, 1963) and it has also been shown that the temperature modifies the effect of photoperiod and may even cause a short day plant to flower under long day conditions at low temperature (Wellensiek, 1958; Nanda and Hamner, 1959). Studies on the effect of photoperiod and temperature on the flowering of wheat and other plants have lead to the postulation of the theory of photothermic quantum (Chinoy, 1956). Very little, however, is known on the effect of temperature on the flowering of tree species. In general, the time of flowering of many tree species seems to be controlled chiefly by temperature. The flower buds of many temperate species require a long period of low temperature to open into flowers (Goville, 1920; Chandler et al., 1937; Darrow, 1942; Crocker, 1948). Fraser (1956) has correlated meteorological data with anatomical studies of spruce and concluded that flower initiation is favoured by high summer temperatures.

**STUDY OF THE SHOOT APEX**

(a) **Structure:**

Wolff (1759) was the first to recognise shoot apex as
an undeveloped region from which growth of the plant proceeds. The position regarding the number, arrangement and activity of the initials in the apical meristem that are concerned with growth is still unsettled and many theories have been put forward from time to time.

(i) Theories on the structure of the growing apex: The apical cell theory was replaced by 'histogen concept' proposed for angiosperms by Hanstein (1868, 1870) who is considered as the founder investigator of the modern views on the apical meristem. According to this theory the main body of the plant arises, not from the superficial cells as was proposed by the apical cell theory, but from a mass of meristematic cells which are organised into three zones, the dermogen later giving rise to epidermis, the periblem which forms the cortex and the plerome which contributes to the entire inner mass of tissue of the plant axis. Another theory was proposed by Schmidt in 1924, according to which the apical meristem consists of two zones (1) the tunica, consisting of one or more layers periclinally dividing peripheral cells and (2) the corpus, consisting of a mass of cells enclosed by tunica end which divide in all planes.

Koch in 1891 described the occurrence of cytologically different zones in the shoot apex of certain conifers. The existence of such zones was later confirmed in Abies, Picea
and Pinus by Korody (1937). The zonate pattern of the shoot apex has since been described by Foster (1938) in other gymnosperms as Ginkgo and several members of the Cycads and by others in Pseudotsuga taxifolia and Torreyas californica (Johnson, 1939, 1944a, 1944b, 1950; Sterling, 1946; Allen, 1947; and Kemp, 1943). Extending this work to angiosperms, Gifford (1950, 1954) described four zones in the shoot apex: (1) Zone-1 consisting of outer layers of cells with varying degrees of cytological appearance and stability, (2) Zone-2 having a centrally located group of cells, often arranged in layers, more vacuolated and possessing other cytological details which differ from plant to plant and which is also called as metrameristem, (3) Zone-3 formed by a peripheral zone of generally small, highly meristematic cells derived from the flanks of Zone-2 and which participate in development of leaf and contribute to the procambium and cortex, and (4) Zone-4 including a central core of cells which function as rib meristem or flank meristem during the active period of shoot elongation and ultimately become the pith. The metrameristem is regarded as the seat of origin of all cells of primary body (Gifford, 1954). It maintains itself, contributes peripherally to the growth and organization of the apex, but exhibits little or no evidence to tissue segregation and emphasizes fundamental similarity between
angiosperms and gymnosperms (Johnson and Tolbert, 1960). The investigations of Helling and Gunckel (1950) on *Liriodendron tulipiflora*, Rouffa and Gunckel (1951b) on some members of Rosaceae and Johnson and Tolbert (1960) on *Bombax* show that the rib meristem grades into extensive files during rapid growth and shoot elongation. The files are, however, broken up by vertical division and lateral expansion during slow growth period to the onset of dormancy. The cytohistological zonate pattern of the growing apex has been reported in a number of plants from both gymnosperms and angiosperms (Foster, 1938, 1939, 1940, 1941, 1943; Johnson, 1939, 1944a, 1944b, 1950; Phillipson, 1947, 1949; Gifford, 1950, 1954, 1960, 1962; Stant, 1952; Senghas, 1956; Vaughan, 1952; Popham, 1958; Johnson and Tolbert, 1960 and Tolbert, 1961).

Buvat (1955) could not observe any mitotic figure at the summit of the apex of *Myosurus*, *Lupinus* and *Cheiranthus* during the vegetative phase. The cell division could be observed only in the flanks of the apex and in the central region below the tip. Based on the nature and location of cell divisions, the peripheral ring of tunica cells showing mitosis were called as *anneau initial*; the apical region without cell division as *meristème d'attente* and the central meristematic region as *meristème médullaire*. According to this theory the cells of the *anneau initial* and *meristème médullaire* stop dividing when the apex changes
from vegetative to reproductive state and the meristematic activity is then taken over by the meristeme d'attente, which is divided into two layers, the upper, _meristeme sperosine_ and the lower _meristeme receptaculaire_.

(b) **Seasonal variations in the structure of shoot apex:**

Although it is known that forest tree species exhibit periodicity in their annual growth (Cooper, 1957; Chowdhury, 1958; Parke, 1959; Petrenko, 1961; Kozlowski and Ward, 1961, Kozlowski, 1962 and 1964) very little is known about the changes that the shoot apex undergoes during the cycle of annual growth. Parke (1959) pointed out that annual growth cycle of _Abies concolor_ consists of three growth phases namely the rest phase, during which the apex remains dormant and which lasts from late September to early April, the first growth phase during which rapid shoot elongation and cataphyll formation occurs and which lasts from early April to mid June and the second growth phase from mid-June to September, during which shoot elongation is completed and an unelongated apex with many needle primordia is formed.

Kemp (1943) working with _Torreya californica_ and Sterling (1946) with _Pseudotsuga taxifolia_ showed that maximum size and cytological differentiation of the shoot apex occurs during the period of foliage leaf production. In _Ephedra_, on the other hand, it occurred during winter
months (Gifford, 1943). This difference was considered to be due to the differences in the growth habit of the plants. Marked periodic seasonal changes in the shoot apex of some woody Ranales have been reported by Gifford (1950). It was observed that the maximum width, the degree of stratification and cytohistological zonation in the two species of Drimys were correlated with the period of active appendage formation rather than the shoot elongation. Richards (1948) related the degree of changes in the volume of the vegetative apex during a plastochrone to the duration of plastochrone. Reeve (1943) reported the occurrence of heavy wall thickening and retarded mitotic activity of the inner cells in the inflorescence apex of Garrya at the end of growth. Tucker (1960) reported that in Michelia the rate of mitosis in the floral apex decreases and the apex thereby loses its convex form when growth is about to terminate. Tolbert (1961) observed that in Hibiscus syriacus L. there are no major seasonal changes in the structure of the apex during the yearly cycle and only the pith rib meristem displays marked seasonal variations.

The seasonal changes in the activity of the shoot apex affect the growth pattern of the plant which may be sympodial where growth of the main axis terminates each year and is resumed in the successive years by subjacent axillary buds or monopodial or indeterminate where the main axis continues to grow indefinitely.
Changes in the shoot apex with reproductive development:

The most dramatic event in the growing apex of an angiosperm is its transformation from the vegetative to the reproductive state. The two fundamental problems relating to this transformation are (1) How do the various factors, whether environmental or genetic, become transformed into physiological signals which are transmitted to the growing apex and which determine whether the meristem will produce a floral or a vegetative bud? and (2) Whether this differential activity is correlated with any qualitative differences in the apical meristem? The former of these fundamental questions relates to the metabolic activities of the apical meristem which eventually lead it to reproduction and therefore, concerns with the mechanism involved in flowering and the latter to the ontogenetic changes that are histogenetic and morphological in nature that have baffled the minds of workers for a long time.

The present state of our knowledge on these two questions is as follows:

(1) Histogenetic changes: Plantefol (1947) claimed that the foliar helices and in flank meristems at a certain distance from the tip. This meristem was thought to perform the functions usually attributed to the classical initial cells and he claimed that there are no initial cells at the summit of the axis. This flank meristem was
termed 'anneau initial'. Its presence was later affirmed by a number of workers who also asserted that the central terminal cells of the axis have no histogenic function during vegetative growth and constitute a 'meristeme d'attente' or, waiting floral meristem, which becomes active only in the formation of a terminal flower or inflorescence (Buvat, 1952, 1953, 1955; Camefort, 1956; Catesson, 1953; Lance, 1952, 1954a, 1954b). In species without terminal flowers the inactive zone was called the 'zone apicale' or 'zone axiale'.

Many recent studies by French workers support this concept of the anneau initial and meristeme d'attente (Lance, 1957; Lance and Rondet, 1958; Rondet, 1958; Poux, 1960; Lance-Nougarecé, 1961a, 1961b; Vanden Born, 1963). The occurrence of mitotic figures at the summit of the apical meristem was, however, reported by a number of workers (Newman, 1956; Popham, 1958; Denne, 1959; Stein and Steffensen, 1959; Lance-Nougarecé and Loiseau, 1960; Gifford, 1960a, 1960b; Edgar, 1961; Crawford, 1961; Paolillo and Gifford, 1961; Gifford and Tepper, 1962b and Bowes, 1963). Ball (1960, 1962) working with the shoot apices of *Lupinus*, *Vicia* and *Asparagus* concluded that there was no quiescent meristene d'attente and that the concept of the anneau initial was not supported by his studies. The experiments with radioactive isotopes showed that DNA was synthesized in cells at the summit as well as
lower down in the apex (Partanen and Gifford, 1958; Clowes, 1959, 1961). The capacity and readiness of the cells of the zone apicale to divide under certain conditions has also been demonstrated by a number of workers including some of the French workers themselves (Doak, 1935; Wareing, 1953a; Loiseau, 1955, 1959; Camefort, 1955a, 1956b; Cutter, 1959; Moorby and Wareing, 1963). In addition to the effect of GA and gamma rays day length has a marked effect on mitosis in shoot apex. A considerable increase in mitosis in the apical meristem follows the inductive photoperiods (Lance, 1957; Wetmore, Gifford and Green, 1959; Gifford and Tepper, 1961, 1962b; Thomas, 1963). Mitotic rhythms in plants have already been shown by some workers (Gunning, 1952; Lance, 1952; Butler, 1965).

(ii) Morphological changes: Böke (1947, 1948) did not find any difference in the configuration of the two types of apices in Vinca, while on the other hand, Gifford (1950) and Tucker (1959) reported that the vegetative and reproductive apices of Drimys winteri were dissimilar. In Michelia fuscata the shoot apex was found to change in shape but not in configuration during its transformation to reproductive state (Tucker, 1960). Vaughan (1955) considers that the configuration of the growing apex is a reflection of growth habit of the plant. Gifford and Wetmore (1957) showed that in some gymnosperms
the pattern of zonation in both the vegetative and reproductive apices is similar. Soma (1958) observed more stratification and zonation in the vegetative than in the reproductive apex of *Ephorbia lathyris*.

Wetmore, Gifford and Green (1959) while working on short day (*Xanthium pensylvanicum, Chenopodium album* and *Glycine max*) and long day (*Papaver somniferum, Hyoscyamus niger*) plants reported a gradual elimination of the central zone with floral induction. The central zone is characteristic of the vegetative apex and its gradual disappearance with its transformation into reproductive state has also been reported by other workers (Phillipson, 1946, 1947a–c, 1948; Buvat, 1952, 1955; Popham and Chan, 1952; Lance, 1957; Tucker, 1959; Gifford and Zepper, 1961 and Marushige, 1965). Vaughan (1955), however, could not observe the disappearance of the central zone in the reproductive apices of *Capsella bursa-pastoris* and *Arabidopsis thaliana*.

Considerable changes in the dimension of the shoot apex during its transformation from vegetative to reproductive state have also been reported by a number of workers. Kerms, Collins and Kim (1936) have shown that in pineapple the terminal vegetative apex broadens greatly at the time of transition from leaf initiation to floral bract initiation. In *Calvcanthus, Ficus* and many Rosaceous genera, Rauh and Reznik (1951) reported an increase in
apical diameter during the initiation of flowers and their development. An increase in the size of the shoot apex with reproduction has also been reported by Tayal, Kaushik and Nanda (1961) and Tayal (1965) in *Avena sativa*. On the other hand, Stein and Stein (1960) and Jacobs and Raghavan (1962) could not observe any change in the size of the shoot apex during its transformation from vegetative to reproductive state.

Studies have also been made of the changes in the size of nuclei during the transformation of shoot apex. Buvat (1955) and Lance (1957) have shown that the size of the nuclei in 'meristeme d' attente' increases with floral induction. Gifford and Tepper (1961) while working with *Chenopodium album* also reported an increase in the size of the nuclei in all the zones of the apex after induction. The increase was found to be maximum in the cells of the peripheral zone and the inner corpus. The changes in the size of the nuclei at different ontogenic stages have also been reported by Marushige (1965) in *Pharbitis*.

**METABOLISM**

The limited information that is available on the metabolic changes that take place in the shoot apex during different phases of its growth has been obtained from
chromatography of extracts of shoot apices and other plant parts. Most of the work concerns with the metabolism of nitrogen and nucleic acids and changes in endogenous growth substances.

(a) Nitrogen metabolism:

Previously it was thought that it is the cells of the meristem proper that are concerned in active protein synthesis. Brown and Broadbent (1950) showed that in the case of roots protein synthesis takes place some what behind the tip. Steward et al. (1954, 1955) showed that the apices of the fern Adiantum pedatum have a lower total protein content than the apices of Lupinus albus and Syringa vulgaris and the content was more in younger than in mature tissues. They also reported that while arginine and lysine contents of the protein fraction were higher in leaf primordia than in more mature vacuolated cells, valine and alanine contents were lower in leaf primordia than in older leaves. The proteins of the growing cells were also found to be rich in serine content. Sunderland, Heyes and Brown (1956, 1957) compared growth and metabolism in three regions of Lupinus albus: (1) the apical dome itself, above the leaf primordia; (2) the individual leaf primordia; and (3) units of the embryonic axis corresponding to each leaf primordium, termed internodes. They found that the concentration of proteins in apical dome was higher than
that in the internode but lower than that in $P_i$. Protein content per cell, however, was higher in the internodes than in the primordia and least in the upper part of the apex. It was suggested that metabolites may be synthesised in the youngest internodes, which are characterised by a higher metabolic activity per unit protein, and then transferred to the leaf primordia.

Howlett (1925) reported a rapid accumulation of nitrogen in buds during their development into flowers and an intense breakdown of proteins in calyx and corolla when flowers open. The protein content of gynoecium, however, increased simultaneously (Comber, 1935), suggesting the translocation of the mobilized proteins from perianth to gynoecium. Gassner (1943) working with orchid flowers and Hsiang (1951) with Cattleya labiata flowers also reported such a concurrent change in nitrogen content of perianth and gynoecium with the onset of pollination. McKee and Urbach (1953) reported that while the amino acid content of flowers is higher than that of developing fruits there are no qualitative differences between them. Sen (1964) observed that proteins in induced buds are richer in methionine than the vegetative ones. Nitsch (1962) has correlated the photoperiodic sensitivity of Xanthium leaves of different ages with their protein content. Marushige (1962) working with the electrophoretic pattern of the extracts of vegetative and reproductive shoot apices
of *Pharbitis nil* could notice only a quantitative difference between them.

Exogenous application of amino acids and their analogues are also known to influence growth and development. Virtanen and Linkola (1953) observed that plants supplied with less than 0.2% DL-α-alanine in nutrient solution became bushy, branched and with tuft-like roots. Miettinen (1959) observed that DL-alanine was toxic to plant growth. Steinberg (1947, 1949) noticed that isoleucine and leucine at a concentration of 0.002 and 0.01% caused growth inhibition of stem branches and leaves in tobacco. However, the number of leaves was increased. A close correlation between amino acids and sugars and the resting buds of woody species has been reported by Bobrysheva and Oknina (1960) and Oknina and Pustovoitova (1960). Salisbury (1961) and Collins et al. (1963) showed that ethionine, which is an analogue of methionine, and some antimetabolites inhibit flowering. This may also be interpreted to imply an interrelationship between protein synthesis and flowering.

(b) Nucleic acid metabolism:

Considerable recent evidence implicates nucleic acid metabolism in the control of flowering. Gifford and Tepper (1961, 1962) found that in *Chenopodium album* after induction while starch grains tended to disappear from the apex, the nuclei of the cells on the flanks of apical
meristem and in the upper corpus enlarged and the concentration of RNA increased and became more uniformly distributed. Similar increase in RNA and size of the nuclei and nucleoli with inflorescence initiation has been reported in other short and long day plants (Lance, 1957; Poux, 1960; Gifford, 1964; Evans and Wardlaw, 1964 and Knox and Evans, 1966).

The experimental evidence based on the supply of various nucleic acid derivatives and their inhibitors to cultured apical buds is also available to show that flowering of SD plants is promoted by increased protein and nucleic acid metabolism (Chailakhyan, 1959; Chailakhyan et al., 1961; Chailakhyan and Khlopenkova, 1962 and Butenko & Chailakhyan, 1962). Derivatives of purine and pyrimidine have also been found to stimulate flowering in excised apices of Perilla. In Pharbitis nil cultured buds flowered even under LD when supplied with a mixture of RNA nucleosides and casein hydrolysate (Butenko and Chailakhyan, 1962). An increased flowering caused by treatment with uracil, xanthine, caffeine and guanine is also attributed to an enhancement of the synthesis of RNA and protein (Kessler et al., 1959 and Thompson, 1963). Madvedev and Zabolotskii (1960) found aspartic acid, methionine and leucine in noticeable amounts among the amino acids associated with RNA.

The inhibitors of RNA and DNA synthesis have been
reported to exert an inhibitory effect on flowering of
Xanthium and other plants (Heslop-Harrison, 1960; Salisbury
and Bonner, 1960; Hess, 1961; Marushige and Marushige, 1961;

**GROWTH REGULATORY SUBSTANCES**

The hormonal concept of growth and development has taken a firm hold on the thinking of plant physiologists. It is not necessary to review all the work with hormones, as excellent reviews on the subject are already available (Larsen, 1951; van Overbeek, 1952, 1956; Audus, 1953; Gordon, 1954; Leopold, 1955, 1958; Thimann and Leopold, 1955; Aberg, 1957; Galston and Purves, 1960; Fawcett, 1961 and Thimann, 1963). It may not, however, be out of place to discuss briefly different classes of regulatory substances:

(a) **Auxins**

These are the earliest known plant growth regulating substances, as defined by the Committee of the American Society of Plant Physiologists (Tukey et al., 1954). The presence of auxins and auxin-like substances has been reported by Czeja (1934) in a number of tree species, by Ogasawara (1960, 1961a, 1961b) in buds and needles of some species of Pinus, by Clark and Donga (1961, 1963) in Abies balsamea and by Bergen (1960) in apple. Denney (1942);
Kassem (1944) and Eggert (1949) showed that high concentration of auxin causes dormancy in buds and its gradual disappearance a resumption of growth.

Except in a few plants the evidence for the implication of auxins as factors affecting flowering is controversial and has received considerable discussion (Liverman, 1955; Salisbury, 1961; Hillman, 1962). Bergfeld (1960) observed a decrease in the content of growth substances at the beginning of inflorescence formation in the normal form of Antirrhinum majus. No such change occurred in mutant sterilis which failed to flower. In most instances, however, little is known about the mode of action of auxin on the apex itself. Moreover, as Fawcett (1961) pointed out there are only two reports so far of successful isolation and identification of IAA— one from maize kernel (Haagen-Smit et al., 1946) and other from cabbage leaves (Post, 1956). In precise chemical terms, therefore, very little is known about the flowering hormone and so far it has not been successfully extracted and isolated. Recently, however, Lincoln et al. (1961, 1962, 1964) have succeeded in inducing flowering in Xanthium treated with extracts of the flowering branch tips of Xanthium and Helianthus annuus and consider the extracts as florigen.

(b) Kinins:

This is another class of growth regulators (Miller et al., 1956, Miller, 1961) which are primarily concerned
with the process of cell division. Kinetin, a degradation product of nucleic acid, is a representative of this group. The most striking effect of this substance is on differentiation (Skoog and Miller, 1957), promotion of bud growth, thus modifying apical dominance (Thimann and Hickson, 1957), leaf enlargement (Kuraishi and Chumura, 1956, 1961 and Scott & Liverman, 1956), polarity and flowering (Sommer, 1961). These effects of kinins may be brought about through their effect on protein, DNA and RNA in the cells.

Kinin-like substances have been reported in coconut milk, banana and apple fruits, female gametophyte of Ginkgo and fruits of Aesculus (Steward and Shantz, 1959) among the tree species.

(c) Gibberellins:

These constitute a group of growth regulators which cause marked stimulation of stem growth. Excellent reviews on the chemistry and physiological action of these substances are available (Lone, 1957; Stone and Yamaki, 1957, 1959; Stodola, 1958; Brien, 1959, 1964 and Palmer, 1965).

Although so far 13 gibberellins have been reported from herbaceous plants, these have not been reported from any tree species.

(d) Growth factors of coconut milk and corn milk:

A number of growth promoting substances have been isolated from coconut and corn milk and other plant extracts
(Steward and Shantz, 1959). The growth activity of these extracts is considered to be due to a complex of growth promoting substances which interact with one another.

(e) **Inhibitors:**

The concept of inhibitors as endogenous growth regulators has been applied to explain many growth processes. Their presence in trees during rest periods has been shown by a number of workers (Mitsch, 1957; Jones et al., 1957; Tyree, 1957; Hemmert, 1959; Powaz, 1960, 1961; Allen, 1960; Lerner & Eveneri, 1961 and Giertych & Forward, 1964).

Their synergistic effects on the one hand (Shiner & Bonner, 1949; Mitsch & Mitsch, 1961, 1962; and Henderson & Mitsch, 1962) and antagonizing effects on the other (Kohler and Lang, 1957) is indicative of the diversity of physiological mechanism in which they participate.

Recently Pyles and Haring (1963) demonstrated that bud dormancy is induced when an extract of birch leaves is applied to a leaf of actively growing birch seedling and it resumed growth when subsequently treated with GA. It is suggested that the bud dormancy may be regulated by the balance between such growth inhibitors and endogenous gibberellins.

(f) **Vitamins:**

Some of the vitamins of D complex group are known...
to be essential for regulating the growth of excised roots in culture (Bonner and Bonner, 1948) and can be classified as hormones as these are synthesized in leaves and are translocated to cause active root growth. Ascorbic acid, amongst the water soluble vitamins, is now known to possess growth regulating properties (Reid, 1937, 1938, 1941, 1941a, 1941b; Venkataramani, 1950; Chinoy, Nanda and Garg, 1957, 1958; Tonzig and Marre, 1961; Shkl'nik & Abdurashtov, 1962; Chinoy, 1962, 1964 and Tayal, 1965). These workers have shown that AA, whether exogenously applied or endogenously produced, accelerates growth and development. Milan School of workers, on the other hand, have reported that exogenously applied AA inhibits growth in many annuals. Tonzig and Marre (1961) considered that the inhibitory effect of increased AA in a tissue is essentially through a concomitant increase in DHA. Key (1962) has shown that inhibited leaf growth is associated with a decrease in AA content. Barks (1964) showed that there was an increase in the concentration of AA with the development of lemon leaves. A fall in the level was observed after the leaf had reached maturity. Extensive work on endogenous drifts of ascorbic acid and indole acetic acid in the growing apices of many plants has shown that there is an upsurge in the AA content of the growing apex with its transformation into the reproductive state (Venkataramani, 1950; Garg, 1960; Chinoy, 1962, 1964; Tayal, 1965). The presence of AA and
its effectiveness in growth of some of the tree species has also been reported by some workers (Sugawara, 1941; Dregateva, 1952; Asaoka, 1957; Hulan & Qi, 1961 and Berk, 1964).

INTERACTION OF GROWTH REGULATORS

The most important development in the regulatory mechanisms is the concept of interaction between the growth regulators and their antagonists. The interactions of auxins and anti-auxins (Burstrom, 1951; Aberg, 1951, 1952; Audus & Chilton, 1959; Hollis and Bonner, 1957; Hitzch and Hitzch, 1959; and Brian, 1957) and auxins and kinetin (Miller, 1956; Skoog and Miller, 1957; Strong, 1958 and Hiscron & Chirn, 1960) have been demonstrated and are almost firmly established. Recent studies have shown that there is an interrelationship between ascorbic acid and IAA content (Chinoy, Grover and Zirati, 1957; Chinoy and Vanda, 1959; Jr., 1962). It has been shown that lower auxin content synchronizes with high AA concentration and also with its high level of utilization (Chinoy, 1962), with the change of the growing apex from vegetative to reproductive. On the basis of these evidences Chinoy (1962, 1964) postulated the 'Ascorbic acid-nucleic acid-protein metabolism' concept of growth and development in plants. According to this concept "the formation and utilization of ascorbic acid in
the shoot apex of a plant stimulates the production of nucleic acids which are known to participate in the synthesis of proteins. With increased production of proteins protoplasm increases and growth activity results in the form of laying down of organizer centres, cell division and enlargement. Under suitable environmental conditions the formation and utilization of ascorbic acid is greatly accelerated and as a consequence of which nucleic acid-protein metabolism is also considerably stimulated resulting in a tremendous upsurge in the rate of formation of organizer centres, cell division and cell enlargement. This brings about a profound change in the differentiation of the shoot apex. Ultimately the cellular activity is accelerated to such an extent in some cells that the chromosome material does not get sufficient time to grow and divide normally and thus meiosis results.