

16. TRANSMISSION OF STIMULUS - THEORIES OF FLOWERING.

Photoperiodic Induction

The influence of the length of day and night on the initiation of flowering is called *photoperiodic induction* or *photo induction*.

Plants may require one or more inductive cycle for flowering. An appropriate photoperiod in 24 hours cycle constitutes one inductive cycle. If a plant which has received sufficient inductive cycle is subsequently placed under unfavourable photoperiod, it will still flower.

Flowering will also occur if a plant receives inductive cycles after intervals of unfavourable photoperiods (i.e. discontinuous inductive cycle). This persistence of photoperiodic after effect is called as photoperiodic induction.

- An increase in the number of inductive cycles results in early flowering of the plant. For instance, xanthium (a short day plant) requires only one inductive cycle and normally flowers after about 64 days. It can be made to flower even after 13 days if it has received 4-8 inductive cycle. In such case number of flowers is also increased.
- Continuous inductive cycles promote early flowering than discontinuous inductive cycle.

Some of the examples of plants which requires more than one inductive cycle for subsequent flowering are,

Biloxi soybean (SDP) - 2 inductive cycles

Salvia (SDP) - 17 Inductive cycles

Plantago (LDP) - 25 Inductive cycles

Critical day length

Maryland mammoth tobacco and xanthium are short day plants, but the *Maryland mammoth* tobacco is induced to flower when the photoperiod is shorter than 12 hours (12L /12D) whereas, xanthium is induced to flower when the photoperiod is shorter than 15.5 hours (15.5L /8.5D). The photoperiod required to induce flowering is referred to as the *critical day length*. Hence, the critical day length for *Maryland mammoth* tobacco and

xanthium are 12 and 15.5 hours respectively. A short day plant is one that flowers on photoperiods shorter than the critical day length.

Long day plants, on the other hand, are induced to flower on photoperiods longer than critical day length. For example, the critical day length for *Hyoscyamus niger* is 11 hours (11L /13D) and it is induced to flower on photoperiods longer than 11 hours.

Suppose, xanthium and *Hyoscyamus niger* are exposed to a photoperiod of 14 hours of light and 10 hours of darkness (14L/10D), flowering will be induced in both plants. Xanthium, a short-day plant, will flower because 14L /10D photoperiod is shorter than critical day length of 15.5 hours. *Hyoscyamus*, a long-day plant, will flower because 14L/10D is longer than the critical day length of 11 hours.

Perception of photoperiodic stimulus and presence of a floral hormone

- Photoperiodic stimulus is perceived by the leaves and a floral hormone is produced in the leaves which are then translocated to the apical tip, subsequently causing initiation of floral primordia.
- Photoperiodic stimulus perceived by the leaves can be shown by a simple experiment on cocklebur (xanthium), a short day plant. Cocklebur plant will flower if it has previously been kept under short day conditions. If the plant is defoliated and kept under short day condition, it will not flower. Flowering will also occur if all the leaves of the plant except one leaf have been removed.
- If the cocklebur plant whether intact or defoliated is kept under long day condition it will not flower. But if even one of its leaves is exposed to short day condition and the rest are under long day condition, flowering will occur.
- The photoperiodic stimulus is transmitted from one branch of the plant to another branch. For example, if in a two branched cocklebur plant one branch is exposed to short day and the other to long day photoperiod, flowering occurs on both the branches.
- Flowering also occurs if one branch is kept under long day conditions and other branch from which all the leaves except one have been removed is exposed to short day condition. However, if one branch is exposed to long photoperiod and the other

has been defoliated, under short day conditions, flowering will not occur in any of the branches.

Flowering stimulus: Florigen

The flowering stimulus is produced in leaves and translocated to apical and lateral meristems where flower formation is initiated. Chailakhyan (1937) called the flowering stimulus or flowering hormone as *Florigen*.

Flowering stimulus is similar in long day plants and short day plants. This can be proved by a grafting experiment and can be translocated from one plant to another.

Maryland mammoth tobacco, a short day plant and *Hyoscyamus niger*, a long day plant, are grafted so that the leafy shoots of both the species are available for experiment. If the grafted plants are exposed to either long day or short day conditions, both partners flower. If grafting union is not formed, the flowering stimulus is not translocated from one partner to another partner.

Theories of Flowering

1. Bunning's hypothesis
2. Chailakhyan's hypothesis

Bunning's hypothesis:

Bunning (1958) assumes the presence of endogenous rhythms (Oscillator which consist of two half cycles. The first half cycle occurs in day and is called *photophilous phase*. During this, anabolic process predominates including flowering in plants. The other half cycle is dark, sensitive and is called *skotophilous phase*. In this, catabolic process (dehydration of starch) predominates.

SD plants have a critical day length of 9 hours. This period falls within the photophilous phase. Light during scotophil phase will inhibit photo process initiated during photophase. The L.D. plants have a critical day length of 15 hours and some light falls in the skoto philous phase. Under these conditions in L.D. plants will flower. In S.D. plants

oscillator is present close to skoto philous phase, while in L.D. plants it is close to *photo philous phase*.

Chilakhyan's hypothesis:

This hypothesis assumes that flowering hormone – florigen is a complex of two types of substances – gibberellin and anthesins. Gibberellin is essential for growth of the plant stems and anthesins are required for flower formation.

According to him, flowering in all annual seed plants requires two phases: (i) *Floral stem formation phase* (ii) *Flower formation phase*. First phase involves increased carbohydrate metabolism and respiration with increased content of GA in leaves. Second phase requires intensive nitrogen metabolism, higher content of anthesins in leaves and nucleic acid metabolites in stem buds.

Long day conditions favour the first phase while short day conditions favour second phase. In long day plants gibberellins are critical, while anthesins are critical in short day plants. However, anthesin is hypothetical; it has not been isolated as yet.

VERNALISATION

The cold treatment given to plant buds, seeds or seedlings for promoting early flowering is known as *Vernalisation*. In short, the chilling treatment for induction of early flowering is called Vernalisation.

Besides an appropriate photoperiod, certain plants require a low temperature treatment during their early stages of the life for subsequent flowering in the later stages. This low temperature treatment requirement was termed vernalization by Lysenko (1928). Due to vernalization, the vegetative period of the plant is cut short resulting in an early flowering. In nature, vernalisation takes place in the seed stage in annuals like winter rye (*Secale cereale*). The biennials and many perennials respond to cold treatment at a very late stage. E.g. Henbane, apples etc.

Perception of cold stimulus and presence of floral hormone

The cold stimulus is perceived by the apical meristems. The perception of the cold stimulus results in the formation of a floral hormone which is transmitted to other parts of the plant. In certain cases, the cold stimulus may even be transmitted to another plant across a graft union.

For instance, if a vernalized henbane plant is grafted to an unvernallized henbane plant, the later also flowers. This is due to the induction of the plant to produce a hormone named as *Vernalin* by Melchers (1939).

Conditions necessary for vernalization

1. Age of the plant

The age of the plant is an important factor in determining the responsiveness of the plant to the cold stimulus and it differs in different species. In cereals like winter wheat, the vernalization is effective only if the germinating seeds have received cold temperature treatment for sufficient time.

While in the case of biennial variety of henbane (*Hyoscyamus niger*), the plant will respond to the cold treatment, only if they are at rosette stage and completed at least 10 days of growth.

2. Appropriate low temperature and duration of the exposure

Most suitable temperature for vernalizing the plants ranges between 1-6°C. The effectiveness of low temperature treatment decreases from 0 to 4°C. Low temperature at about -6°C is completely ineffective. Similarly at high temperatures from 7°C onwards, the response of the plants is decreased. Temperature of about 12-14°C is almost effective in vernalizing the plant. Besides an appropriate low temperature, a suitable duration of the cold treatment is essential for vernalization. Depending upon the degree of temperature and in different species this period may vary, but usually the duration of the chilling treatment is about one and half months or more.

3. Oxygen

The vernalization is an aerobic process and requires metabolic energy. In the absence of O₂, cold treatment becomes completely ineffective.

4. Water

Sufficient amount of water is also essential for vernalization. Vernalization of the dry seed is not possible.

Mechanism of Vernalization

There are two main theories to explain the mechanism of vernalisation.

1. Phasic developmental theory

This theory was proposed by Lysenko (1934) as follows.

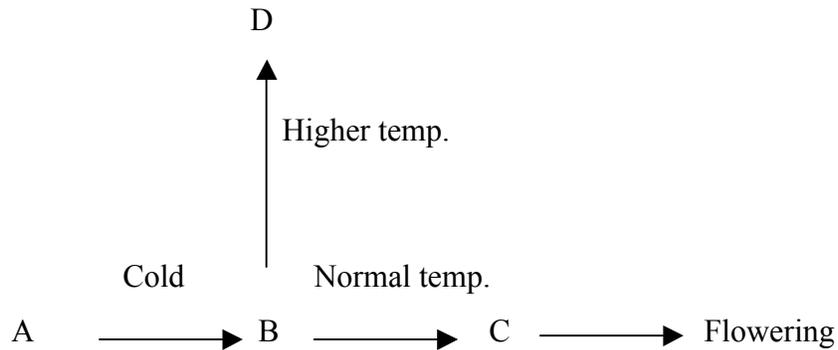
- (i) The growth (increase in size) and development (i.e. progressive change in the characteristic of the new organs) are two distinct phenomena.
- (ii) According to this theory, the process of the development of an annual seed plant consists of a series of phases which must occur in some predetermined sequence.
- (iii) Commencement of any of these phases will take place only when the preceding phase has been completed.
- (iv) The phases require different external conditions for the completion such as light and temperature.
- (v) Vernalization accelerates the thermo phase i.e. that phase of development which is dependent upon temperature.

Thus, in winter wheat, low temperature is required for the completion of first thermo phase. After this, the next phase that is dependent upon light (photo phase) starts. Vernalization of winter wheat accelerates the first thermo phase so that there is an early swing from vegetative to reproductive phase or flowering.

2. Hormonal theories

It has already been described that vernalization probably involves the formation of a floral hormone called as *vernalinalin*. Based on this fact, many hypothetical schemes have been

proposed by different workers from time to time. The first hormonal theory proposed by Long and Melchers (1947) is schematically shown below.



According to this scheme, the precursor A is converted into a thermo labile compound B during cold treatment. Under normal conditions B changes into C which ultimately causes flowering. But at higher temperature B is converted into D and flowering does not take place (devernalization).

Devernalization

The positive effect of the low temperature treatment on the vernalization of the plant can be counteracted by subsequent high temperature. This is called devernalization. The devernalized plant can again be vernalized by subsequent low temperature treatment.

Vernalization and Gibberellins

The gibberellins are known to replace the low temperature requirement in certain biennial plants such as henbane, where the plant normally remains vegetative and retains its rosette habit during the first growing season and after passing through the winter period flowers in the next season. The gibberellins cause such plants to flower even during the first year.

Significance of vernalization

1. Vernalization shortens the vegetative period of the plant
2. It increases cold resistance of the plants
3. Vernalization increases the resistance of plants to fungal diseases.
4. It is a physiological process that substitutes or compensates the effect of thermo phase.
5. In biennials, vernalisation induces early flowering and early fruit setting.
6. A non vernalised shoot apex can be induced to flower by grafting the plant with a vernalised plant.