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8. Photoperiodism and Vernalization

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Abstract:

The fundamental mechanisms of photoperiodism and vernalization control when plants blossom in response to variations in day duration and temperature. The physiological and developmental reactions of plants to fluctuations in the length of light and darkness within a 24-hour cycle are referred to as photoperiodism. It is very important in deciding when flowers will bloom and other seasonal activities will occur in plants. Photoreceptor proteins that sense variations in light quality and quantity, such phytochromes and cryptochromes, mediate photoperiodic responses. On the other side, vernalization is the process through which plants gain the capacity to blossom following an extensive exposure to cold temperatures. It is crucial for plants that thrive in temperate climates, because winter temperatures prevent flowering and guarantee the plant's survival through unfavorable seasons. Vernalization includes intricate molecular processes that alter gene expression and activate flowering-related genes. Vernalization and photoperiodism are crucial adaptation processes that let plants time their reproductive activities with the best possible environmental circumstances. Numerous elements, including as genetic make-up, speciesspecific needs, and environmental signals, have an impact on these processes. Agriculture and horticulture stand to gain significantly by understanding the molecular processes underpinning photoperiodism and vernalization since it will be possible to manipulate crop blooming times, resulting in increased yields, seed generation, and overall plant productivity. This study provides an overview of current knowledge about photoperiodism and vernalization in plants. Specialized photoreceptor proteins, including phytochromes and cryptochromes, that perceive variations in light quality and quantity, are involved in the perception of photoperiodic stimuli. On the other hand, the vernalization process

involves the epigenetic control of flowering genes via the activity of certain proteins, including Polycomb group compounds, which alter chromatin states.

Keywords:

Photoperiodism, vernalization, phytochromes, cryptochromes, epigenetic

8.1 Introduction:

Workers in the early twentieth century held the belief that plant flowering was influenced by nutritional factors. In Kraus and Kraybill [1] conducted an experiment on tomato plants and found that providing an optimal supply of nitrates and carbohydrates resulted in accelerated vegetative growth. However, when the nitrate supply was inadequate, both reproduction and vegetative growth declined. In 1906, a new mutant variety of tobacco called Maryland mammoth emerged from a commercial variety called Maryland narrowleaved. These new plants exhibited vigorous vegetative growth in the summer but failed to produce seeds before the arrival of cold weather. Plant physiologists W. W. Garner and H.A. Allard took on the task of investigating the cause behind this phenomenon. Eventually, they discovered that these plants consistently bloomed during the short days of winter. By reducing the light period to seven hours a day, they were able to induce flowering even in the summer months. Garner and Allard [2] published their investigations, which led to the formulation of the concept of photoperiodism. Their studies focused on the flowering behavior of the Maryland mammoth variety, a single gene mutant of the tobacco plant. Unlike the wild type species, *Nicotiana sylvestris*, the Maryland mammoth variety did not blossom in the spring or summer seasons. After careful examination, Garner and Allard concluded that flowering in these plants was triggered by exposure to specific day lengths characterized by short periods of light and long periods of darkness. They observed that flowering occurred when the duration of light was less than 14 hours. This groundbreaking research established that day length, as an environmental factor, plays a significant role in controlling the flowering process. In tropical regions, where the day length remains relatively constant throughout the year and days and nights is of similar length, there is minimal variation in the flowering patterns of plants. However, in temperate regions, the duration of daylight changes from winter to summer, with longer days occurring during the warmer season. This alteration in day length has a profound impact on the flowering behavior of plants. When tropical plant species are introduced to temperate zones, they typically only flower when the days become shorter, as continued exposure to long days inhibits the formation of flower buds. In contrast, native temperate zone plants exhibit a diverse range of flowering habits. Some bloom during the moderate short days of spring, while others flower during the long days of summer. There are also those that produce flowers during the short days of late summer and early fall. This mechanism that enables plants to respond to day length so that they flower at a specific time of the year is known as photoperiodism. In other words, 'Photoperiodism' can be defined as a biological response to a change in the proportions of light and dark in a 24-hour daily cycle. Plant uses it to measure the season and to coordinate seasonal events such as flowering. The length of the daily period of light to which a plant is exposed is called photoperiod. The measurement of day length is believed to be achieved by the integration of the endogenous circadian rhythms with external light signals [3].

Plants are grouped into three categories according to their response to day length:

- Short-Day Plants
- Long-Day Plants and
- Day-Neutral Plants

8.1.1 Short-Day Plants (SDP):

These plants flower when exposed to relatively shorter day light period (usually 8-10 hours) and a continuous dark period of about 14-16 hours or exposed to day lengths shorter than a certain criticalmaximum. The critical photoperiod, however, varies from species to species. If these plants are exposed to day lengths in excess of this critical point, they continue growing vegetatively. The Terms Long-Day and Short-Day Plants are actually misnomers. Earlier when the photoperiodism was discovered, the duration of the light period i.e. photoperiod was thought to be critical for flowering. However, later researches, noted that in short-day plants (SOP), when the long dark period was interrupted by a brief exposure to light, the plants failed to flower (Figure 1). From this observation, scientists concluded that what is critical or essential for these plants to flower is long and un-interrupted dark period rather than a short-day length. A brief interruption of the dark period with light nullified the effect of long night. So, to be more precise and appropriate, short-day plants may be regarded as long-night plants. They normally flower in the early spring or autumn.

Short-day plants are further classified as Qualitative SDP and Quantitative SDP. Qualitative SDP are plants where there is absolute requirement of short days for flowering. For e.g., Cotton, Soybean, Chrysanthemum etc. Quantitative SDP on the other hand are plants where shorter day accelerated flowering eg. Sugarcane, cotton, onion etc.

A. Photoperiod Regulation Techniques to Create Short Days:

Use of dense black polythene sheets generally with a thickness of 150 gauge is most suitable of complete blackouts [4]. Black tarpaulin also creates effective short-day conditions, generally done from 5 PM until 7 AM by putting the tarpaulin on iron frames. The shortday treatments that are mostly done from 5 PM to 9 AM are very effective in doubling the yield of flower in terms of cut stems, as there is increase in stem length and cut flower diameter [5].

8.1.2 Long-Day Plants (LDP):

These plants begin flowering when exposed to longer day light period (usually 14-16 hours) in a 24 hours cycle and shorter night. In other words, day lengths longer than a certain critical minimum. Below the critical photoperiod, these plants continue their vegetative growth (Figure 8.1). The critical photoperiod, in such plants also, varies from species to species. They normally flower in late spring or early summer. The long-day plants (LDP) respond to nights shorter than the critical dark period. Therefore, these plants are also called as short night plants. Curiously long day plants do not need an uninterrupted dark night. Further, LDP are classified as Qualitative LDP where there is absolute requirement of longdays for flowering example- Oats and Quantitative LDP where long-days accelerate the process of flowering example- Spinach, Barley, Wheat etc.

Photoperiod regulation techniques to create long days: The longs are mostly created during natural short-day conditions are present.

- Night interruption: long days can be created by providing artificial light sources at midnight so that the dark period gets interrupted.
- Day extension: in this a supplementary lighting is provided immediately after the sunset, so that the light period gets extended.
- Pre-dawn lighting: in this provide lighting from 2 am until sunrise, this will again increase the light period and interrupts the dark period.

8.1.3 Day-Neutral Plants (DNP)

These plants exhibit a flowering behavior that is independent of day length. Regardless of the duration of daylight or darkness, these plants undergo a period of vegetative growth before transitioning into the flowering stage. Their flowering process is not influenced by the length of day or night. Instead, it is driven by internal factors related to their developmental stage. These plants operate under an autonomous regulatory system, whereby they initiate flowering when specific internal developmental milestones are

reached. As a result, these plants have the ability to flower consistently throughout the year, irrespective of external photoperiodic cues. These plants have long flowering season. These plants are believed to be originated at equator as there is where we can find the day and night lengths equal and constant throughout the year. For example: Buckwheat, Pea, Tomato, Sunflower etc.

There are some other types of plants like Intermediate Day Plant, where flowering occurs when the days are neither too short nor too long e.g. *Chenopodium album.* Ambiphoperiodic plants are those plants where intermediate day length quantitatively inhibits the flowering process e.g., *Chenopodium rubrum.*

Figure 8.1: Lighting treatment of short-day plants and long day plants to the combination of light and dark periods of different lengths.

A. Critical Day Length:

It is defined as the duration of the photoperiod, or the length of the dark period that plays a crucial role in regulating both vegetative growth and flower production in plants. This duration varies from one plant species to another. For instance, Xanthium is classified as a short-day plant, meaning it requires a specific critical day length of 15.5 hours, consisting of 15.5 hours of light and 8.5 hours of darkness, in order to initiate flowering. If the plant receives less than 8.5 hours of uninterrupted darkness, it fails to flower and remains in its vegetative phase. The uninterrupted dark period is more critical than light period. As in SDP if the dark period is interrupted by a light period even for a fraction of time the plant will not flower. It will remain in its vegetative phase. However, in case of LDP if the day length exceeding the critical value is interrupted by dark period which is less than critical night period the flower will still produce.

B. Induction Period:

The induction period refers to the minimum duration of exposure to either a long or short day that is necessary to trigger the initiation of flowering in plants. Different plant species have distinct induction periods. For instance, Xanthium requires only one complete cycle of day and night to induce flowering, whereas many other plants typically require ten cycles for the same purpose.

Phototropism:

It is sometimes confused with photoperiodism. However, these two are different terms. Phototropism is defined as the differential growth of the plant in response to light stimuli. For example- the shoots bend towards the light while roots bend away from light. Phototropism has no correlation with the duration of light.

8.2 Photoreceptor:

Photoreceptor molecules play a crucial role in plants by detecting light and regulating various developmental responses. Photoperiod-induced flowering in plants is primarily governed by specific photoreceptors present within them [5]. These photoreceptors can be classified into two main groups: phytochromes and cryptochromes. Phytochromes, a family of chromoproteins, possess a linear tetrapyrrole chromophore, which is responsible for absorbing light. They exhibit sensitivity towards the red and far-red regions of the electromagnetic spectrum [6].

Phytochrome plays a crucial role in the regulation of flowering in short-day and long-day plants. It is found in various plant tissues such as roots, coleoptiles, stems, hypocotyls, cotyledons, petioles, leaf blades, vegetative buds, flower tissues, seeds, and developing fruits. This pigment exists in two distinct forms: Pr (red light-absorbing) and Pfr (far red light-absorbing). The interconversion between these forms is essential for controlling various physiological processes, including seed germination, leaf expansion, as well as flowering.

When exposed to red light (660-665 nm), the Pr form converts into the active Pfr form. Conversely, absorption of far-red light (730-735 nm) converts Pfr back into Pr form (Figure 2. This light-induced conversion alters the conformation and activity of the phytochrome protein. Pfr is the biologically active form that promotes physiological responses, while exposure to far red light inhibits phytochrome activity. In darkness, the Pfr gradually reverts to the Pr form. In short-day plants, the accumulation of Pfr during the day inhibits flowering, but during the critical dark period, the gradual conversion to Pr triggers flowering. Brief exposure to red light can reverse this process by converting Pr back to Pfr, thereby inhibiting flowering [7].

The inhibitory effect of red light can be reversed in short-day plants by subsequent exposure to far red light, which converts Pfr back to Pr. In long-day plants, prolonging the critical light period or interrupting the dark period with red light leads to increased accumulation of Pfr, stimulating flowering.

Photoperiodism and Vernalization

Figure 8.2: Biologically inactive form of phytochrome (Pr) is converted to the biologically active form (Pfr) under illumination with red light and far-red light

8.2.1 Significance of Photoperiodism:

- The flowering time of a plant is determined by photoperiodism, which dictates the specific season in which it will bloom. Short-day plants, such as Dahlia and Xanthium, flower during the autumn to spring period, whereas long-day plants like Amaranthus produce flowers during the summer season.
- Besides its role in flowering response, photoperiod also plays a crucial part in other plant processes. It contributes to bud dormancy, the coordinated leaf shedding in deciduous trees, and the process of dark carbon fixation in CAM plants.
- Understanding the impact of photoperiodic effects is beneficial for managing plant growth stages. It allows for the control of certain plants, such as various vegetables, to remain in the vegetative phase. This helps in achieving a higher yield of tubers, rhizomes, and similar plant parts. Conversely, manipulating the photoperiod can also induce the reproductive phase, leading to increased flower and fruit production [8]. For instance, short-day conditions are known to promote tuber formation in potatoes. A plant can be made to flower throughout the year by providing favorable photoperiod i.e., offseason cultivation of crops is possible by controlling the photoperiod. Eg: cut flower production
- Apart from its involvement in regulating flowering, photoperiod also plays a role in other aspects of plant physiology. It contributes to the induction of bud dormancy, the synchronized leaf drops in deciduous trees, and the process of nocturnal carbon fixation in CAM plants.
- It provides valuable insights for plant breeders to manipulate the timing of flowering in different plant varieties, allowing for controlled hybridization. By manipulating the photoperiod, breeders can synchronize the flowering of different plants, ensuring successful pollination and facilitating the exchange of desired traits between parent plants.
- Short day conditions have been observed to promote a higher shoot growth in relation to their root development (high shoot-to-root ratio) in certain plants, such as lettuce.

This phenomenon can be seen as an adaptive response, as it allows lettuce plants to allocate more resources towards above-ground biomass production, including leaves and stems, while potentially limiting root growth.

8.3 Vernalization: Promoting Flowering with Cold:

Vernalization, a biological process crucial for certain plants, involves the necessity of a cold temperature period to initiate or expedite the flowering process. It is the process of accelerating the ability of flowering in plants by exposing them to cold temperatures. In this technique, cold treatment is given especially to flower buds, seeds or seedlings. We can also say that it is process whereby repression of flowering is alleviated by cold treatment given to hydrated seed or to growing plant. Extensive research in plant physiology has greatly enhanced our comprehension of plant adaptation and survival mechanisms through the study of this phenomenon. The exploration of vernalization dates back to the early 20th century, with notable contributions made by Trofim D. Lysenko (1898-1976), a Russian botanist and geneticist. Lysenko's investigations revealed that specific winter wheat varieties required prolonged exposure to cold temperatures in order to transition from the vegetative stage to the reproductive stage. His experiments effectively demonstrated that subjecting seeds or young plants to cold conditions could induce earlier and more synchronized flowering. Conversely, without exposure to cold, these plants would fail to flower when sown in spring [9].

Friedrich Laibach, a German plant scientist, carried several studies to investigate the genetic aspects of vernalization. Laibach found that the vernalization response could be transmitted by crossing different wheat types, supporting the idea that vernalization is a heritable attribute. This study opened the door for more research into the genetic regulation of blooming timing. This research paved the way for further investigations into the genetic control of flowering time. In the 1990s, the molecular mechanisms of vernalization were unraveled using Arabidopsis thaliana, a model plant species. Scientists discovered the pivotal role of the FLOWERING LOCUS C (FLC) gene in regulating the flowering response to vernalization [10]. In plants that have not undergone vernalization, FLC acts as a suppressor of flowering genes, impeding the transition to the reproductive phase. However, prolonged exposure to cold temperatures causes epigenetic changes that suppress FLC expression, allowing blooming to occur.

Vernalization is the process through which plants develop the capacity to bloom in the spring by being exposed to extended periods of low temperatures in the winter [11]. It involves subjecting growing plants or seeds that have been adequately hydrated to cold circumstances in order to hasten blossoming. The term "vernalization" originates from "jarovization," a term coined by Trofim Lysenko to describe this chilling process. It is often used to describe the requirement of certain non-woody plants, including various cereal crops like wheat, to undergo a period of cold dormancy to generate new shoots and leaves [12]. Vernalization is a crucial process for plants to transition from vegetative growth to flowering. It occurs when plants are exposed to cold temperatures, leading to the suppression of inhibitors that prevent flowering. The specific temperature range required for vernalization varies depending on the crop. For some crops, temperatures between 0ºC and 6ºC are optimal, while biennial plants like Henbane (*Hyoscyamus niger*) prefer a

slightly broader range of 3ºC to 17ºC. However, vernalization effectiveness diminishes when temperatures fall below 0ºC or rise above 7ºC. In particular, temperatures around 12ºC to 14ºC are generally ineffective in inducing vernalization [13]. The period of cold treatment varies from few days to many weeks. After the cold treatment the seedlings are allowed to dry for some time and then sown. Vernalization prepares the plant for flowering. The cold stimulus usually perceived by the shoot apical meistems, but in some species all dividing cells of roots and leaves may be the potential sites of vernalization *eg. Leennario biennis*. Vernalization induces the plant to produce a hormone called vernalin which was discovered by Melcher (1936). The vernalization stimulus can be transmitted from one plant to another through grafting. 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 case of biennial variety of Hanbane (*Hyocyamus niger*), the plants will respond only when they are in rosette stage and have completed at least 10 days of growth. One of the important conditions required for vernalization is oxygen. The process is aerobic and requires metabolic energy. In the absence the cold treatment, it becomes completely ineffective. Sufficient amount of water is also essential as in dry seed it is not possible. A vernalization is often linked with particular photoperiod [14] The most common combination is requirement for cold treatment followed by a requirement for long days, a combination that leads to flowering in early summer. Vernalization can be lost as a result of exposure to devernalizing condition such as high temperature, but the longer exposure to the low temperature, the more permanent the vernalization effect.

Types of Vernalization:

- **Facultative Vernalization-** In this type the flowering appears earlier one exposed to low temperature. Example: Winter Annual Triticale.
- **Obligate Vernalization:** In this type the exposure to low temperature is must for a desired period of time. Example: Biennial plants (Cabbage)

Devernalization: The effect of vernalization can be removed by high temperature treatment. This reverse effect is called Devernalization. It occurs at more than 30 °C.

8.4 Mechanism of Vernalization:

Vernalization is the process by which flowering is accelerated by a delayed period of low temperatures, such as those seen in winter. There are two primary hypotheses for explaining the vernalization mechanism:

A. Phasic Development Theory:

Lysenko in 1934, put forth a theory concerning the growth and development of annual seed plants. According to this theory, the advancement of these plants follows a sequential pattern, where each stage relies on the completion of the preceding phase. Each step necessitates specific external conditions, such as temperature and light, for its fulfilment. This theory outlines two primary stages within this process. These are:

Thermostage: The thermostage of plant growth is influenced by temperature, and vernalization acts to expedite this phase. The thermostage represents the vegetative stage, which thrives under cool temperatures (around 0.14°C), adequate humidity, and proper air circulation. The duration of this phase varies depending on the plant species and environmental conditions. For instance, winter wheat completes its life cycle most efficiently when exposed to short days and low temperatures during the thermostage [15].

Photostage: During the photo stage of plant growth, higher temperatures are necessary. In this stage, the presence of vernalin promotes the production of florigen, a hormone that induces flowering. Winter wheat exhibits an accelerated life cycle when exposed to longer daylight periods and higher temperatures during the photo stage.

B. Hormonal Theory:

In 1939, Melcher proposed a theory stating that the exposure to cold temperatures triggers the production of a floral hormone called vernalin, which induces flowering. According to this hypothesis, the vernalin hormone is transmitted to dividing cells in different parts of the plant through phloem. Melcher demonstrated this transmission of the vernalization stimulus across graft unions in hyoscymus by grafting a vernalized plant with an unvernalized plant. Interestingly, the unvernalized plant also started flowering as a result. The vernalin hormone diffused from the vernalized plant to the unvernalized plant, stimulating the process of flowering.

8.5 Phase of Vernalization Process:

The vernalization process is completed in the three stages indicated.

Setting the FLC expression level before cold exposure: During sexual reproduction and embryogenesis, the expression level of the FLOWERING LOCUS C (FLC) gene is established. The initial level of FLC expression is determined by a number of regulators. The RNA polymerase-associated factor 1 complex (Paf1C) is responsible for the increase of FLC transcription. The FRI protein is important in increasing FLC transcription. Furthermore, full FLC activation necessitates the activity of particular H3K4 and H3K36 methylases.

Cold-induced FLC silence: It occurs when plants are subjected to cold temperatures, resulting in a fast decrease in FLC transcription. This down-regulation is aided by COOLAIR, a non-coding antisense transcript. Cold temperatures also cause the FLC locus to accumulate Polycomb-based epigenetic-silencing complexes and histone alterations. With longer periods of cold exposure, trimethylation of histone H3 lysine 27 (H3K27me3) accumulates at the FLC locus nucleation site [15].

Epigenetic Silencing: When plants are returned to warm temperatures after extended cold exposure, a considerable and relatively rapid shift occurs at the FLC locus, resulting in epigenetic silencing [16]. This silencing process is independent of vernalization and can occur even during mitosis. The VRN1 gene, which codes for unique DNA-binding domains, is implicated in chromatin control at the FLC locus [17].

8.6 Factors Affecting Vernalization:

Factors that influence vernalization include the following:

- **A. Location of vernalization**: The apical meristem's metabolic activity is responsible for sensing temperature and commencing flowering. Younger leaves are more vulnerable to vernalization than older ones.
- **B. Plant age:** The age of the plant is critical in determining its reactivity to cold treatment, and this differs between species. Vernalization can occur in germinating seeds or even at the embryonic stage within the mother plant in cereals such as winter wheat. Vernalization occurs in biennial plants after at least ten days of vegetative growth, during the rosette stage. When the plants have 6-8 leaves, they are most sensitive to low temperatures.
- **C. Optimal low temperature range:** The optimal temperature for vernalization is usually between 1-6°C. Vernalization efficiency falls below 0°C and becomes ineffective at roughly -4°C. Similarly, temperatures above 7°C reduce the plant's reaction to vernalization, and temperatures between 12 and 14°C are mainly useless [18].
- **D. Duration of exposure**: The duration of cold treatment, in addition to an appropriate low temperature, is critical for successful vernalization and differs between plant species. The cooling period often lasts at least one and a half months, if not long.
- **E. Oxygen requirement**: Vernalization is a metabolically driven aerobic process. The cold therapy for vernalization becomes completely ineffective in the absence of oxygen [15].
- **F. Moisture**: Vernalization requires a sufficient amount of moisture. Dry seeds do not respond to vernalization and must be moist for the process to take place.

8.6.1 Some Important Features of Vernalization:

- It is an active metabolic process.
- Site of perception of cold treatment in seed-Embryo is the most receptive tissue and in Plant- Shoot apical meristem.
- Effective temperature: Below freezing point to 10^oC, optimum temperature 1-7^oC.
- Vernalisation results in competence.
- It is negative regulator of flowering i.e., epigenetically represses the FLC. However, the range of species in which these repressors can affect flowering has not been explored in detail vernalization alone cannot induce flowering [19].
- After vernalization correct photoperiod is required. Example: Henbane plants can recall their previous vernalization (i.e., they acquire flowering competence), but they do not flower until the photoperiod need is reached.
- Economic important of vernalization: There are numerous instances where vernalization is economically significant. A substantial vernalization need inhibits flowering in the first growing season in many crops where the vegetative portions of the plant are the commodity, such as cabbage, beets, or carrots. Cold weather in the spring can occasionally cause blooming and damage crops like these. Winter cereals' vernalization need allows them to be planted and grown in the fall season [20].

8.7 Conclusion:

Vernalization and photoperiodism are crucial processes that influence the life cycles and adaptations of a wide range of plant species. Critical processes including blooming, dormancy, and development are influenced by photoperiodism, which controls how plants react to changes in day duration. Depending on their particular light needs, plants can be classified as short-day, long-day, or day-neutral. By synchronising their reproductive cycles with the ideal environmental circumstances, plants may successfully reproduce. These events demonstrate how plants are remarkably resilient and adaptable, allowing them to thrive in response to shifting environmental conditions. Vernalization and photoperiodism work together to help plants survive and adapt to their environment.

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