Photoperiodism
A Biotechnological Perspective

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Photoperiodism: A Biotechnological Perspective

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2017

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Title: Photoperiodism: A Biotechnological Perspective

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Edition: First

Volume: I

ISBN: 978-93-86675-02-6

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Chapter 1: Definition of Photoperiodism

Photoperiodism is the physiological response of an organism to the duration of day or night. It is seen in plants, insects, fungi, animals and in humans. Photoperiodism can also be defined as the developmental reaction of organism to the comparative lengths of light and dark periods.

The response of an organism to the change in its photoperiod, especially as indicated by essential processes, for example, many plants exhibit photoperiodism by flowering only after being exposed to a certain amount of daylight, as by requiring either a long or short day to flower. Plant growth, seed germination, and fruiting are also dependent day length. Photoperiodic responses in plants are regulated by the pigments known as phytochromes.

In animals, migration, mating, amount of sleep, and other behaviors are also due to photoperiodism. In many animals, photoperiodism is synchronized by the hormone melatonin.

Many angiosperms are flowering at about the same season every year. This occurs despite the fact that they may have started growing at different times. Their flowering is a response to the change in length of day and night as the season progresses. The event is called photoperiodism. It is helpful in cross pollination.

The word originated from photoperiod in 1920. In 1920 two professionals of the U. S. Agriculture Department, W. W. Garner and H. A. Allard, discovered mutation in tobacco variety known as Maryland Mammoth that prevented the plant from flowering in the summer as normal tobacco plants. Maryland Mammoth would not bloom until the December.

Experiments with artificial lighting in winter and artificial darkening in summer, they found that Maryland Mammoth was affected by photoperiod. Because it would flower only when exposed to short periods of light, they called it a short-day plant. Some other short-day plants are:

- Chrysanthemums (bloom in the fall)
- Rice (*Oryza sativa*)
- Poinsettias

- Morning glory (*Pharbitis nil*)
- The cocklebur (*Xanthium*)

Some plants such as

- Spinach
- *Arabidopsis*
- Sugar beet and
- Radish

After exposure to long days these plants are flowered so known as long day plant.

In tomato plant the flowering is not regulated by photoperiod so it is day neutral. There are so many plants which are day natural.

Some plants are only grown in particular latitude that is also because of photoperiodism.

Spinach never flowers in tropics because it is a long day plant and it requires 14 hours of the days.

Ragweed, a short-day plant, fails to flourish in northern Maine because by the time the days become short enough to initiate flowering, a killing frost in appropriate to occur before reproduction and the formation of seeds is completed.

Photoperiodism in a Short-Day Plant

Experiments with the cocklebur have confirmed that the term short-day is something of a misleading fact; sufficient long night is required for cocklebur.

For the flowering of Cockleburs it requires a critical period of 8.5 hours dark.

Interruptions of an otherwise long night by light - red (660 nm) rays are particularly effective - prevents flowering. Unless, it is followed by irradiation with far-red (730 nm) light.

An intense exposure to far-red light at the start of the night reduces the dark requirement by 2 hours. These responses are mediated by phytochrome.

The knowledge of the season and day length is essential also to most of the animals. Many biological and behavioral changes are dependent on this knowledge. Together with temperature changes, photoperiod also controls changes in the color of fur and feathers, migration, entry into hibernation, sexual behavior, and even the size of sexual organs.

The singing frequency of birds such as the canary depends on the photoperiod. In the spring, when the photoperiod increases (more daylight), the male canary's testes grow. As the testes grow, more androgens are secreted and song frequency increases. During autumn, when the photoperiod decreases (less daylight), the male canary's testes regress and androgen levels drop dramatically, resulting in decreased singing frequency. Not only is singing frequency dependent on the photoperiod but the song repertoire is also. The long photoperiod of spring results in a greater song repertoire. Autumn's shorter photoperiod results in a reduction in song repertoire. These behavioral photoperiod changes in male canaries are caused by changes in the song centre of the brain. As the photoperiod increases, the high vocal centre (HVC) and the robust nucleus of the archistriatum (RA) increase in size. When the photoperiod decreases, these areas of the brain regress[1].

In mammals, day length is imprinted in the suprachiasmatic nucleus (SCN), which is informed by retinal light-sensitive ganglion cells, which are not involved in vision. The information moves through the retinohypothalamic tract (RHT). Some mammals are highly seasonal, while seasonality in humans' is largely because of evolution[2].

In the plant life cycle several responses controlled by photoperiod, like germination, flowering, and tuber formation, onset of bud dormancy, leaf abscission, and cambium activity.

Red light of wavelength of 660 nanometers is found to be the most effective to interrupt the dark period, and this effect can be reversed by a subsequent exposure to far-red light (730 nanometers). These observations led to the discovery of phytochrome, the pigment responsible for absorbing above wavelengths and apparently the light sensor in photoperiodism. It has been suggested that photoperiodism results from an interface between phytochrome and the biological clock plant, which measures the time between successive rich in red light and successive rich in far-red light. Under the appropriate conditions, these relations are thought to trigger the genes for flowering.

The flowering in plants is most commonly influenced response due to photoperiodism. Plants that flower only under certain day-length conditions are considered to be photoperiodic. There are three classifications of photoperiodic plants: short-day, long-day and day-neutral.

With regard to photoperiodicity, the critical length is the length of daylight a plant requires in order to produce flowers.

While plants don't have eyes to watch the amount of sunlight, they do have specialized cells. These photoreceptors are able to monitor the amount of light and help the plant determine the correct time to flower.

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2. Foster, Russell; Williams, Robyn (5 December 2009). "Extra-retinal photo receptors" (Interview). Science Show. ABC Radio National. Retrieved 2010-05-28. ...we have the evolutionary baggage of showing seasonality but we're not entirely sure what the mechanism is.

Chapter 2: Photoperiodism in Plants

It is always a mystery to the scientists that how a plant is responding to the seasonal variations. How it gets clues to initiate flowering and in precise season it flowers and these monitoring attracts the interest of scientists to study the phenomenon. The duration of day light changes with an expected pattern all along the year, providing a reliable environmental signal for the varying seasons. The ability to sense and respond to changes in day length is known as photoperiodism, and is a widespread phenomenon found in plants that allows these organisms to adapt to seasonal changes in their environment. The importance of day length in controlling seasonal responses was already proposed by Tournois and Klebs back in the early 1900’s independently suggested that the duration rather than the quantity of light is a major determinant in plant development[1, 2]. However, it was Garner and Allard (1920) using controlled photoperiodic conditions, showed for the first time that day length can determine the time of flowering, this is the first time photoperiodism phenomenon documented[3].

Studies on soybean and tobacco led to the proposal that flowering would only occur if the duration of the daily light period was sufficiently short. The plants were classified into three photoperiodic groups according to their flowering response to day length. In long day (LD) plants flowering is promoted by daily periods of light longer than a critical day length, whereas plants that accelerate flowering in response to day length below a critical threshold are called short day (SD) plants. Day-neutral (DN) plants flower at the same time irrespectively of the photoperiodic conditions.

Following the observations that established the central role of day length sensitivity in controlling plant development, several models have attempted to explain the basis of the photoperiodic responses. A first easy model proposed that the gradual accumulation of a substance is required to trigger a physiological response; the amount of this chemical can increase up to a threshold level only in photoperiodic inductive conditions.

Photoperiodism is one of the important environmental relations plants have so that the change of photoperiod throughout the year is made-up as a sign for seasonal change. One of the most reflective, and often beautiful, hallmarks of a plant’s response to seasonal change is the timely generation of flowers. The molecular measures that represent floral timing in response to inductive photoperiods are starting to be determined.

In many woody plants, photoperiod plays a prominent role in the rhythms of shoot growth[4-6].

Wood properties, in particular the early wood and late wood differentiation, have frequently been reported as being influenced by photoperiodism[7-9]. Typically, the production of early wood has been associated with treatments which promote shoot elongation, raising the question of whether early wood production is an immediate consequence of shoot extension rather than a direct effect of photoperiod.

Work on day length has concentrated on studying the response of plants to constant photoperiods, or where day length has been changed it has generally been changed abruptly. The few published studies using progressive increases and decreases in day length did not include any comparison with constant long and short photoperiods.

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Chapter 3: Seasonality and Photoperiodism in fungi

Very little is known about the seasonality and photoperiodism in fungi. By similarity, seasonality can also be a motivated process a straight outcome of environmental factors: day or night duration, temperature, and other climatic factors such as humidity and rainfall, or even triggered by other organisms in the form of food and, in the case of pathogens, host availability. Alternatively, seasonality can be a consequence of an active process, or rather of two "interrelated processes"[1]: (a) an organism that measures night length (rarely day length)[2, 3] and (b) some kind of memory that integrates the seasonal changes over time.

To study the likelihood of photoperiodism in fungi, the scientists have reviewed fungus photobiology, circadian systems, and seasonality of reproduction. Finally, the scientists have integrated the details of the *Neurospora* system into probable molecular and genetic research on photoperiodism in fungi.

Light reception is the essential factor of photoperiodism. Fungal reproduction, carotenoid formation and phototropism all are regulated by the intensity of light.

In *Saccharomyces cerevisiae* very little photoperiodism is observed. The growth rate is decreased due to increase illumination.

Another important aspect in photoperiodism is assessment of light which is well established fact in the plant and animals as circadian system.

Fungal circadian clocks can be delicately light sensitive, concerning both influence and duration. The *Pilobolus* clock requires no more than half a millisecond of light to be completely reset[4], and in Neurospora conidial banding is driven by light influences down to moonlight levels[5].

There are reports that the fungal reproduction is seasonal as in case of other organisms.

The most researches to prove photoperiodism is done on *Neurospora crassa.* It is very easy for biochemical, molecular, genetic, and physiological experiments, and it can without difficulty be grown in large quantities. The sequence of its haploid genome is complete
(http://wwwgenome.wi.mit.edu/annotation/fungi/neurospora/,http://www.mips.biochem.mpg. de/proj/neurospora/)

Neurospora is found at latitudes corresponding to regions where winter nights and summer days are as long as 16 h and the winter days and summer nights as short as 8 h.

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Chapter 4: Photoperiodism: The Biological Calendar

To be promising and developed, organisms must grow, live and replicate. Fitness is determined by how many offspring stay till the end of their sexual life and ultimately produce offspring those survive and again reproduce. Resource invested in survival mechanisms depletes resources necessary for reproduction. Equally, reproduction requires major resources that may involve survival. Thus, strength reflects successful relationship between investments in the mechanisms underlying survival and reproduction that reflect life history strategies[1]. Natural selection has produced delightful adaptations that have allowed organisms to successfully survive and reproduce in astoundingly specific niches. Outside of the tropics, organisms have been selected to adapt to temporal niches, as well as spatial niches, because the yearly revolve of the Earth around the Sun oversee seasonal variation in several environmental factors that affect temperature, weather and food availability. Habitats may vary significantly from winter to summer and in some cases distinguishing sets of adaptations have evolved to cope with the often unique demands of winter and summer on survival and reproduction. For example, the winter set of adaptations may include a shift of energy allocations from non-essential functions such as growth and reproduction to those functions that are critical for immediate survival[2]. When the probabilities of successful reproduction are little, resources are shifted from reproduction and growth into survival mechanisms such as immune function, thermo-regulation, or cellular maintenance. Consequently, over evolutionary time, seasonal patterns in the expression of adaptations have emerged that allow relocation of energy resources to mediate tradeoffs between traits such as immune function and reproductive effort. During the winter, the dual challenges of limited food availability with the need for additional energy to support heat generation make reproductive efforts unlikely to be successful, especially among little vertebrate animals; thus, these animals often reduce their reproductive system activities[3]. In addition to reproduction, small non-tropical vertebrates also exhibit seasonal adjustments in body mass, adiposity, foraging, gut efficiency, pelage, sleep, growth, immune function, as well as cognitive and affective responses[4]. Because these seasonal adaptations often require significant time to develop, individuals depend upon an environmental signal to alter gene expression in order to produce the matching set of season-specific adaptations. Photoperiodism is the ability of plants and animals to measure environmental day length (photoperiod), a process called biological calendar[5]. The biological ability to measure day length permits organisms to ascertain the time of year and engage in seasonally appropriate adaptations. Although the specific mechanisms that underlie the ability to measure day length differ among taxa, individuals that respond to day length can precisely, and reliably, determine the time of year with just two things:

1. Length of the daily photoperiod and
2. Increasing or decreasing in Day lengths

For many species, the annual cycle of changing photoperiod provides the environmental switch between seasonal phenotypes. Changes in day length, while probably of little direct importance to most animals, provide the most error-free indication of time of year, and thus enable to anticipate seasonal conditions. Because the same photoperiod occurs twice a year (e.g., 21 March and 21 September), animals must be able to discriminate between these two dates; many photoperiodic vertebrates have solved this problem by developing an annual alteration between two physiological conditions[6]. Obviously, the environmental switch that controls the phenotypic trajectory is important in teasing out the interaction between environment and genes which drives phenotype. The objective of this discussion is to emphasis on the effect of photoperiod on phenotype, the distribution of energetically expensive processes across the year to maximize survival and fitness, and the stable effects of early life photoperiod on adult phenotype. Phenotype is the result of the interactions between genes and environment. In the wild, day length often determines the phenotype of newborn small vertebrates[7-9]. In mammals, photoperiodic information can even be passed to developing fetuses in uterus so that the summer or winter phenotype can begin to develop before the birth[10]. Thus, photoperiodic rodents born in the spring will grow to adult size, undergo puberty, and reproduce in 6–8 weeks, whereas a sibling born in the autumn will not grow or undergo puberty for 4–5 months[11, 12]. Day length can be used in the laboratory as a precise environmental factor to probe gene expression during phenotypic development.

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Chapter 5: Photobiology: The Science of Light and Life

Photobiology: the science of light and life is an exciting and challenging field. It involves scientific study of the effects of light on organisms and ecosystems. It is a vast, multi-disciplinary subject in which topics like photosynthesis, vision, photo-taxis, photoperiodism, photo-morphogenesis, bioluminescence, photo-medicine, environmental photo-biology, ultraviolet radiation effects, photo-technology, etc. are generally studied, and often using all of the methods of science.

Solar radiation is the only source of energy for almost all biological activity on Earth. Scientific knowledge of the outcome of solar radiation on different organisms and ecosystems has been the concern of many as it is essential to develop scientific understanding of the functioning of Nature, and further to develop alternate, more efficient light-mediated technologies for various human requirements. Researchers are able to develop molecular level understanding of several photo-biological processes. Such knowledge significantly influenced new discoveries in many areas of science and technology. Some of these include: Agriculture (e.g. efficient photosynthesis, aquaculture, plant genomic research), human health (photo-medicine, photo-immunology, light-activated drugs, cellular physiology, photodynamic therapy), electronics and communication (e.g. opto-electronic devices and photo-responsive bio-materials, bio-luminescence), energy (e.g. solar and related energy research), global climate and environmental changes (environmental photobiology, UV radiation effects, ozone depletion, ultraviolet radiation, carbon dioxide emission, and temperature), sensory biology (e.g. vision, non-visual photoreception, photo-movement, etc.) energy-transduction (e.g. ion-transport), etc. Certainly this subject has major effects on almost all disciplines of modern science and technology.

Chapter 6: Circadian Rhythms

Circadian rhythm is the term used to describe the physiological and behavioral twenty four hour cycle that most organisms experience. This, of course, includes the sleep/wake cycle, but includes many other factors, which vary as well (e.g., hormonal levels, eating, and drinking). In fact, in some ways our lives are simply rhythms within rhythms. There is a regular ninety minute cycle that characterizes the sleep of most humans, and, interestingly, there also appears to be a similar approximately ninety minute cycle that we go through during waking called the basic rest activity cycle. In terms of circadian rhythms, research with humans and other animals indicates that our bodies are tuned internally to cycle in this manner. However, it is also true that external indications can dramatically influence this cycle. The most obvious example of such external indications is light, which, for most of us, serves to "reset" this cycle each morning. The brain area that appears to play a central role in circadian rhythms is the suprachiasmatic nucleus (SCN) in the hypothalamus. The most direct evidence that supports this comes from animal studies in which the lesioning of this small nucleus completely disrupts the normal sleep wake cycle. Further, these lesions do not decrease the amount of sleep that an animal experiences, just the cycle. Lab animals with such lesions sleep at random times for varying lengths of time. The fact that light has been found to increase SCN activity is further evidence that this nucleus plays an important role in circadian rhythms. There is a direct pathway between the SCN and the retina in the eye. There is also a pathway between the lateral geniculate nucleus (LGN) in the thalamus and the SCN. The lateral geniculate nucleus is an important point in the main visual pathway that goes from the eyes to the primary visual cortex in the occipital lobe. Somewhat surprisingly, the pathway that connects the LGN and SCN appears to play a particularly important role in sensitivity to non-light circadian cues such as loud noises.

The rotation of the Earth causes predictable changes in light and temperature in our natural environment. Accordingly, natural selection has favored the evolution of circadian (from the Latin circa, meaning ‘about’, and dies, meaning ‘day’) clocks or biological clocks endogenous cellular mechanisms for keeping track of time. These clocks impart a survival advantage by enabling an organism to anticipate daily environmental changes and thus tailor its behavior and physiology to the appropriate time of the day. The clock is synchronized by the day–night cycle, allowing the organism to accommodate not only the daily cycles of light and dark attributable to the Earth’s rotation, but also the alteration in relative span of day and night caused by the tilting of the Earth’s axis relative to the Sun. Thus, a circadian timing mechanism that undergoes daily adjustment is useful as a seasonal timer as well.

Biological Rhythms

A biological rhythm is any cyclic change in the level of a body chemical or function. Biological rhythms can be:

Internal (endogenous)	- controlled by the internal biological clock e.g. body temperature cycle
External (exogenous)	- controlled by synchronizing internal cycles with external stimuli e.g. sleep/wakefulness and day/night. These stimuli are called *zeitgebers* -- from the German meaning "time givers". These stimuli include environmental time cues such as sunlight, food, noise, or social interaction. *Zeitgebers* help to reset the biological clock to a 24-hour day.

Biological Rhythms

Circadian rhythms	– endogenously generated rhythms with a period close to 24 hours.
Diurnal rhythms	– a circadian rhythm that is synchronized with the day/night cycle
Ultradian rhythms	– biological rhythms (e.g. feeding cycles) with a period much shorter (i.e., frequency much higher) than that of a circadian rhythm
Infradian rhythms	– biological rhythms with a cycle of more than 24 hours (e.g. the human menstrual cycle)

Circadian rhythms are defined by three fundamental parameters: periodicity, entrain ability, and temperature compensation. Although daily environmental changes drive diurnal rhythms, a true circadian rhythm persists in the absence of environmental time prompts with a free-running period of approximately 24 h. Environmental time information from the daily rotation of the Earth on its axis, such as light: dark and temperature cycles, entrains the oscillation to precisely 24 h. experimentally, one can entrain circadian oscillations to non-24 h periods with imposed environmental cycles. An intriguing characteristic of circadian rhythms is that the period of the rhythm is temperature compensated and remains relatively constant over a range of physiological temperatures, in sharp contrast to the temperature dependence of most biochemical processes.

The circadian system can be divided into three conceptual parts in plants: input pathways that entrain the clock, the central oscillator (clock), and output pathways to generate overt rhythms.

The most potent and best-characterized entraining stimulus in plants is light. Light perception in plants has been studied and reviewed in detail[1-5]. The Arabidopsis genome includes five phytochrome genes (PHYA-PHYE) and two cryptochrome genes (CRY1 and CRY2). There are other blue light receptors, including phototropin (NPH1) and possibly zeaxanthin, thought to be the stomatal blue light receptor[6].

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Chapter 7: Chromosomal location of genes responsible for photoperiodic reaction

Photoperiod is very important to plants in temperate regions of the world as it allows them to track seasonal changes without relying solely on temperature, which can vary considerably between years, and initiate appropriate physiological responses. The plants ascertain the change in photoperiod by perceiving the length of day and night over a 24-hour period and integrating these signals with the internal circadian clock. So far, our knowledge on the molecular basis of plant response to photoperiod stems mainly from detailed studies of the model plant Arabidopsis. Genes involved in this response are commonly assigned to the photoperiod pathway and include light receptors, circadian clock genes and downstream targets of these genes. Light receptors such as the phytochromes (PHYA, PHYB, PHYC and PHYD) and the cryptochromes (CRY1, CRY2) and ZEITLUPE (ZTL) are used to capture different parts of the light spectrum, the former being most sensitive to red and far-red light and the latter more sensitive to blue light. These genes, together with integrating factors and other helper molecules, transfer the light signal to the circadian clock and light-regulated target genes. The circadian clock itself consists of a number of interconnected feedback loops that together create an internal rhythm of approximately 24 h length. Key genes here include the pseudo response regulators (*ARABIDOPSIS* PSEUDO RESPONSE REGULATOR 1-9, [APRR1, APRR3, APRR5, APRR7, APRR9]) and two genes with MYB domains (CIRCADIAN CLOCK ASSOCIATED 1, CCA1 and LATE ELONGATED HYPOCOTYL, LHY). In Arabidopsis, functional studies have also revealed that the genes GIGANTEA (GI), EARLY FLOWERING 3 (ELF3) and EARLY FLOWERING 4 (ELF4) are required to obtain a stable circadian clock, but their role is somewhat less well defined[1-3]. Finally, the signals from light receptors and the circadian clock (as well as other pathways) are integrated into several downstream genes such as CONSTANS (CO) and FLOWERING LOCUS T (FT) that either induce or repress flowering[4]. As data is accumulating from other species, it has become clear that many of the genes involved in photoperiodic response in model plants have a conserved function even in distantly related plant species, including gymnosperm species, like Norway spruce[5-6]. Further, studies of perennial plants suggest that the photoperiodic response and associated genetic pathways are not only involved in transition to flowering, but also in the control of annual growth, for instance the control of growth cessation in the autumn[7-8]. Therefore expect variation at these genes to be associated to variation in fitness. In population genetic studies aiming at describing the genetic variants underlying local adaptation, a first step has often been to identify genomic regions that display polymorphism deviating from expectations from the standard neutral model (SNM) of evolution. However, in most cases where multilocus data is available, it has become clear that the overall pattern of diversity does not fit the SNM and that ignoring this can lead to false inference of selection. A departure from the SNM has been reported in a number of European forest tree species, where inferences from multilocus sequence data suggest that the species went through severe and ancient bottleneck events followed by population expansion[9-11]. This likely reflects range expansion after periods of less suitable climate, when the trees were present in more restricted refugial areas.

Genes in the photoperiod pathway have been shown to be implicated in adaptation to local light conditions in several plant species. Forest tree species in temperate regions generally show strong latitudinal clines for growth cessation and bud set in response to photoperiod.

Plants have adopted unique developmental mechanisms that allow them to make the commitment to flowering in response to external signals. The key structure that provides this flexibility is the shoot apical meristem (SAM), which gives rise to the aerial structures of the plant, such as leaves, stems and, ultimately, flowers[12]. The principal functions of the SAM are: (1) to initiate the formation of lateral organs and structures, such as leaves and flowers; and (2) to perpetuate itself by maintaining a population of undifferentiated cells that remain uncommitted to a specific program. This ability of the cells in the SAM to remain uncommitted to flowering at a particular time endows the plant with a great deal of developmental flexibility. The transition from vegetative growth to flowering is a clear illustration of the importance of this. However, signals that originate outside the SAM are essential for directing the conversion to reproductive development. In this article, we describe recent progress in discerning the nature of the external signals that are responsible for the transition to flowering.

The life of higher plants is broadly divided into a vegetative phase and a reproductive phase. The SAM initiates structures such as leaves during vegetative growth and inflorescences and flowers during reproductive growth. The transition to flowering, when a plant switches from vegetative to reproductive growth, is a pivotal event in the life of a plant. Developmental signals that cause this transition to flowering originate outside the SAM, and so the SAM remains uncommitted to flowering prior to its perception of external signals. Floral induction causes a cascade of processes within the SAM that result in its restructuring, accompanied by changes in the rate and pattern of cell division, and the formation of floral structures instead of leaves[13].

Flowering time in Arabidopsis is accelerated significantly by exposure to long days. There are two components to this day-length response pathway – light quality and the circadian clock. The plant’s perceptions of these are mediated by phytochromes and cryptochromes[14–16]. Phytochrome regulation of flowering has been studied extensively, although it is only recently that components of the clock regulation of flowering have been identified. These include the cloning and characterization of the GIGANTEA gene, which provides a key link between the clock genes and the flowering genes[17-18]. It appears that the gene CONSTANS (CO) is the downstream target of both the light and the clock signals. CO encodes a zinc-finger transcription factor, and ectopic expression of CO causes early flowering under short days[19, 20]. The second pathway is the autonomous promotion pathway, which is required for flowering in response to internal developmental signals (e.g. the decision to flower after making a fixed number of leaves). Several genes in this pathway have been described and reviewed elsewhere. The autonomous promotion pathway can be substituted for by vernalization (the exposure of germinated seeds to low temperatures). It appears that the autonomous pathway and vernalization operate through the same downstream regulatory gene, FLF/FLC, which encodes a protein similar to the MADS-domain class of regulatory factors[21-22]. The third pathway that promotes flowering in Arabidopsis involves the phytohormone GA, which is required for early flowering in Arabidopsis but not in all plant species. It has been shown that no other flowering pathways operate in Arabidopsis by making a triple mutant in which genes from each of the three pathways have been knocked out: the resultant plants are completely unable to flower (G. Coupland, pers. commun.). An important regulator of the final stages of flowering is the LEAFY gene, which encodes a transcription factor[23]. LEAFY, which is itself a presumed target of the flowering-time regulators[24], acts at the SAM and surrounding leaf primordia to activate APETELA1 and floral homeotic genes required for flower development[25-26]. Expression studies suggest that LEAFY plays a central role in integrating external floral-inductive signals received at the SAM with the developmental events of flower formation.

A key flowering-time gene recently isolated from maize could provide the first clues about the molecular nature of floral inductive signals[27]. Maize plants that have mutations in the indeterminate gene (id1) are unable to undergo a normal transition to flowering; rather, the SAM of id1 mutants continues to initiate leaves long after normal plants have flowered. Eventually, id1 mutants do undergo the transition to flowering but they produce aberrant floral structures with vegetative characteristics[27,28]. The id1 gene was found to encode a putative transcriptional regulator[27], similar to what has been found in Arabidopsis, in which many of the late-flowering genes that have been isolated have possible regulatory functions.

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Chapter 8: Photoperiodism and Phototropism

Plants have a number of highly specialized uses for light that go far beyond their capability to perform only photosynthesis. Plants can differentiate and develop in response to light (known as photomorphogenesis), which allows plants to control their use of light and space. Plants use light to follow time, which is known as photoperiodism. They can track the time of day and time of year by sensing and using various wavelengths of sunlight. Light can also elicit a targeted response in plants that allows them to grow toward, or even away from, light; this is known as phototropism.

The sensing of light in the environment is essential to plants; it can be crucial for competition and survival. The response of plants to light is mediated by different photoreceptors: a protein covalently-bonded to a light-absorbing pigment called a chromophore; together, called a chromoprotein. The chromophore of the photoreceptor absorbs light in specific wavelengths, causing structural changes in the photoreceptor protein. The structural changes then elicit a cascade of signaling throughout the plant.

The red, far-red, and violet-blue regions of the visible light spectrum trigger structural development in plants. Sensory photoreceptors absorb light in these particular regions of the visible light spectrum because of the quality of light available in the daylight spectrum. In terrestrial habitats, light absorption by chlorophylls peaks in the blue and red regions of the spectrum. As light filters through the canopy and the blue and red wavelengths are absorbed, the spectrum shifts to the far-red end, shifting the plant community to those plants better adapted to respond to far-red light. Blue-light receptors allow plants to gauge the direction and abundance of sunlight, which is rich in blue-green emissions. Water absorbs red light, which makes the detection of blue light essential for algae and aquatic vegetations.

Chapter 9: Photoperiodism: Plant Hormones and Their Actions

There are five broad classes of hormones: auxins, cytokinins, gibberellins, ethylene, and abscisic acid.

Auxins

Auxin, indole-3-acetic acid (IAA), was the first plant hormone identified. It is synthesized in the shoot tips, in embryos, and in parts of developing flowers and seeds. Its transport from cell to cell through the parenchyma surrounding the vascular tissues needs the expenditure of ATP energy. IAA moves in one direction only, the movement is polar and downward. This downward movement in shoots is said to be basipetal movement, and in roots it is acropetal.

Auxins alone or in combination with other hormones are responsible for many facets of plant growth. IAA in particular:

Activates the differentiation of vascular tissue in the shoot apex and in calluses; initiates division of the vascular cambium in the spring; promotes growth of vascular tissue in healing of wounds. Activates cellular elongation by increasing the plasticity of the cell wall.

Maintains apical dominance indirectly by stimulating the production of ethylene, which directly inhibits lateral bud growth.

Activates a gene required for making a protein necessary for growth and other genes for the synthesis of wall materials made and secreted by dictyosomes.

Promotes initiation and growth of adventitious roots in cuttings.

Promotes the growth of many fruits (from auxin produced by the developing seeds).

Suppresses the abscission (separation from the plant) of fruits and leaves (lowered production of auxin in the leaf is correlated with formation of the abscission layer).

Inhibits most flowering (but promotes flowering of pineapples).

Activates tropic responses.

Controls aging and senescence, dormancy of seeds.

Synthetic auxins are extensively used as herbicides, the most widely known being 2,4-D and the notorious 2,4,5-T, which were used in a 1:1 combination as Agent Orange during the Vietnam War and sprayed over the Vietnam forests as a defoliant.

Cytokinins

Named so because of their role in cell division (cytokinesis), the cytokinins have a molecular structure similar to adenine. Naturally occurring zeatin, isolated first from corn (*Zea mays*), is the most active of the cytokinins. Cytokinins are found in sites of active cell division in plants for example, in root tips, seeds, fruits, and leaves. They are transported in the xylem and work in the presence of auxin to promote cell division. Differing cytokinin:auxin ratios change the nature of organogenesis. If kinetin is high and auxin low, shoots are formed; if kinetin is low and auxin high, roots are formed. Lateral bud development, which is retarded by auxin, is promoted by cytokinins. Cytokinins also delay the senescence of leaves and promote the expansion of cotyledons.

Gibberellins

The gibberellins are widespread throughout the plant kingdom, and more than 75 have been isolated. The compounds are numbered for example, GA1, GA2, and so on. Gibberellic acid three (GA3) is the most widespread and most thoroughly studied. The gibberellins are especially plentiful in seeds and young shoots where they control stem elongation by stimulating both cell division and elongation (auxin stimulates only cell elongation). The gibberellins are carried by the xylem and phloem. Numerous effects have been recorded that involve about 15 or fewer of the gibberellic acids. The greater number with no known effects apparently are precursors to the active ones.

Experimentation with GA3 sprayed on genetically dwarf plants stimulates elongation of the dwarf plants to normal heights. Normal height plants sprayed with GA3 become large.

Ethylene

Ethylene is a simple gaseous hydrocarbon produced from an amino acid and appears in most plant tissues in large amounts when they are stressed. It diffuses from its site of origin into the air and affects surrounding plants as well. Large amounts ordinarily are produced by roots, senescing flowers, ripening fruits, and the apical meristem of shoots. Auxin increases ethylene production, as ethylene itself small amounts of ethylene initiate copious production of still more. Ethylene stimulates the ripening of fruit and initiates abscission of fruits and leaves. In monoecious plants (those with distinct male and female flowers on the same plant), gibberellins and ethylene concentrations determine the sex of the flowers: Flower buds exposed to high concentrations of ethylene produce carpellate flowers, while gibberellins induce staminate ones.

Abscisic acid

Abscisic acid (ABA), even though its name, does not initiate abscission. It is synthesized in plastids from carotenoids and diffuses in all directions through vascular tissues and parenchyma. Its major effect is inhibition of cell growth. ABA increases in developing seeds and promotes dormancy. If leaves experience water stress, ABA amounts increase immediately, causing the stomata to close.

Chapter 10: Photoperiodism: Crop Response to Light Duration

A broad review by Vergara (1978)[1] sheds more light on photoperiodism. Depending on the desired economic yield, the effects can be either advantageous or disadvantageous and vary with species and with variety.

The induction of flowering is the most studied aspect of crop growth relative to photoperiodism. It is perhaps the most important response of crops to photoperiod. This is so in most crops in which the economic product is the fruit or seed. But in sugarcane, tobacco, and forage crops, it is desirable if reproductive development is hindered to favor vegetative development.

Light hinders stem growth but promotes the enlargement of leaves. In lettuce and raddish, short days promote higher top: root ratio. This is desirable in lettuce because it is the top that is harvested but not in raddish in which the economic organ is the taproot.

In some varieties of potato, tuber formation is induced by short photoperiod but in others, it occurs only during long days with low temperature. A similar response is exhibited by different varieties of onion in terms of bulb formation.

Photoperiod is associated with abnormalities in sex ratio in cucurbits and other monoecious plants. Gherkins or cucumber (*Cucumis sativus*) have more staminate (male) flowers but lesser fruit-bearing flowers during long days.

The poinsettia (*Euphorbia pulcherrima*) naturally produces colourful flowers in December where day length period is short. According to aggie-horticulture.tamu.edu (n.d.), dark periods of 11 hours and 45 minutes will cause initiation in most cultivars, but initiation is most rapid at 14 to 14.5 hour dark periods at temperatures of 60-70 ^{o}F (15.56-21.11 ^{o}C) for 8 to 11 weeks in modern cultivars.

For chrysanthemum, short day length promotes flowering while long daylength favors vegetative growth. However, Kessler[2] (n.d.) explains that chrysanthemums have different critical photoperiods for floral initiation and for flower development. Further, the critical photoperiod can vary with cultivar and temperature.

Effect of Light Period

The relative length of the light and dark periods affects the production of carbohydrates by all crops (Edmond *et al*. 1978). In terms of flower initiation, the length of the light period has no effect on photoperiodism. However, it appears to have a quantitative influence on the number of flower primordia initiated. In the Biloxi soybean, it was found that a photocycle with a dark and light periods of 16 and 11 hours, respectively, produced maximum number of flower primordia. Light periods in excess or less than 11 hours produced smaller number of flower primordia (Devlin 1975)[3].

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Chapter 11: The Role of Photoperiodism

The phenomenon of Photo-periodism is very important for the survival of plants, insects, fungus and animals. The strategy of living organisms to cope with the change in seasons, the day length and dark length is imperative in the survival and reproduction of that organism. Some plants are only flowering in a particular season the delay in that season and early onset of that season affect the flowering of that plant and also from the human prospective the yield of the fruit from that plant will be vulnerable.

The energy source for the earth is Sun and all the organisms are directly or indirectly affected by the exposure to the solar energy.

Light also affects various aspects of animal's life. The growth, colouration of body, migration, reproduction and diapause are affected by light in most of the organisms. Many animals favour to remain in dark, while others fail to survive in absence of light.

While the plants act in response to light with the help of a number of pigment systems as chlorophyll and phytochrome, among the animals many kinds of photo-receptor systems exist. These include 'eyespots' with amylum granules in Protozoa; ocelli in jellyfish; pit in gastropods; vesicular eyes as in polychaetes, molluscs and some vertebrates; telescopic eyes in certain fishes; compound eyes in Crustacea and insects; simple eyes in other arthropods and dermal light receptors in other animals.

Light has also found to influence the development of these visual organs. Many animals of caves or deep sea generally have either vestigial eyes due to the absence of light in these surroundings. *Bathymicrops regis*, the deep sea fish (5000 metre sea depth) have no eyes. Some of the other important effects of light on animals are following:

Effects of Light on Animals

1. On protoplasm:

The bodies of the animals protected by body covering which save animal tissues from the deadly effects of solar radiations. But, sometimes sun rays penetrate the covering and cause excitation, activation, ionization and heating of protoplasm of different body cells. Ultraviolet rays are causing mutational changes in the DNA of the organisms.

2. On metabolism:

The metabolism of animals is significantly influenced by light. The bigger intensity of light results in an increase in enzyme activity, overall metabolic rate and solubility of salts and minerals in the protoplasm. Solubility of gases decreases at high intensity of light. Cave animals are found to be slow in their habits and to contain slow rate of metabolism.

3. On pigmentation:

Light effects pigmentation in animals. Cave animals are devoid of skin pigments. If they are kept in light for a long time, they regain skin pigmentation. The dark pigmentation of skin of the tropics also indicates the effect of sunlight on skin pigmentation. The skin pigmentation is reliant on the exposure to sunlight.

Light also determines the distinctive arrays of pigments of different animals which help the animals in sexual dimorphism and protective colouration. Animals that reside in the depths of the ocean where the environment is monotonous, though pigmentation do not show patterns in their colouration.

4. On animal movements:

Movements towards and away from a source of light is called phototaxis. Positively phototactic animals such as Euglena, Ranatra, etc., move towards the light, while negatively phototactic animals such as planarians, earthworms, slugs, copepodes, siphonophores, etc., move away from the light.

The light influenced growth mechanisms are called phototropisms which occur in sessile animals. Phototropisms also include responsive movement of bodyparts of some active animal to the light stimulus, such as the movement of flagellum of Euglena towards light and movements of polyps of many coelenterates.

The rapidity of the movement of some animals is also controlled by light. It has been observed that animals when responding to light decrease their velocity of movement and these movements which are non-directional are called Photokinesis. Photokinesis may be a change in linear velocity (Rheokinesis) or in the direction of turning (Klinokinesis).

During Photokinesis when only a part of the body of an animal turns always from the source of light, the reaction is termed photoklinokinesls. Larvae of *Musca domestic* show such movements. When animals are provoked with two lights of equal brightness they move towards or away to a position that is distance between the two lights.

This is termed phototropotaxis. Attraction of males towards the female is called telotaxis. Movement of animals at a constant angle towards the source of light is called light compass reaction or celestial orientation.

Some organisms, particularly arthropods, birds and fish, utilize their time sense as an aid to find their way from one area to another. To position themselves, the animals use the sun, moon, or stars as a compass. They utilize both their biological clock and observations on the azimuthal position of the sun in relation to an established direction. The azimuth is the angle between a fixed line on the earth’s surface and a projection of the sun’s direction on the surface.

Using the sun as a reference point comprises some problems for animals because the sun moves. The target angle changes throughout the day. But animals which use the sun as a reference, correct their orientation somehow. Such celestial orientation has been observed in fishes, turtles, lizards, most birds, and such invertebrates as ants, bees, wolf spiders and sand hoppers.

5. Photoperiodism and biological clocks:

Frequently occurring daily cycles of Light (day; and darkness (night) have been known to exert a profound influence on the behaviour and metabolism of many organisms. Underlying such environmental rhythms of light and darkness are the movements of the earth relative to the sun and the moon.

The earth's rotation on its axis results in alternation of night and day. The tilt of the earth's axis, along with the annual revolution around the sun produces the seasons. The response of different organisms to environmental rhythms of light and darkness is termed photoperiodism. Each daily cycle inclusive of a period of illumination followed by a period of darkness is called the photo- period.

The term photophase and scatophase are sometimes used to denote the period of light and the period of darkness respectively. Different animals have evolved different morphological, physiological, behavioural and ecological adaptations during the course of their evolution to varying photoperiods, which provide them with environmental information regarding the intensities of natural light.

(a) Daily responses:

Circadian rhythms:

Life evolved under the influence of daily and seasonal environmental changes, so it is natural that plants and animals would have some rhythms or pattern to their lives that would synchronize them with fluctuations in the environment. For years biologists have been intrigued over the means by which organisms kept their activities in rhythm with the 24 hours day, including such phenomena as the daily pattern of leaf and petal movement in plants, the sleep and wakefulness of animals and the emergence of insects from pupal cases.

At one time biologists thought that these rhythmicities were entirely exogenous, that is, the organisms responded only to external stimuli such as light intensity, humidity, temperature and tides. But now it is well investigated that most animals possess internal or endogenous rhythms in synchrony with the external or exogenous rhythms of the environment, due to which they remain able to measure the length of day.

The internal or endogenous rhythms are approximately of 24 hours duration, while the exogenous or environmental rhythms are exactly of 24 hours duration. The term circadian (from the Latin circa, about, and dies, daily) has been used to denote these daily rhythms. The period of circadian rhythm, the number of hours from the beginning of activity one day to the beginning of activity on the next, is called free running.

Photoperiod plays a role in providing time signals, for adjustments of the animals concerned to these daily rhythms. Circadian rhythms apparently are internally driven or endogenous, are affected little by temperature changes, are insensitive to a great variety of chemical inhibitors, and are innate, not learned from or imprinted upon the organisms by the environment.

The innate character of circadian rhythm is demonstrated by several animals. When Drosophila are kept under constant conditions from the larval stage on, they will still emerge from pupae with a regular circadian rhythm. Eggs of chicken and lizards kept under constant conditions produce animals that later show regular circadian cycles. The circadian rhythms have been observed in zooplanktons, polychaete annelids, many insects (*Lepidoptera*, *Diptera*, *Hymenoptera*, *Neuroptera*, *Coleopteta*, *Orthoptera*, *Odonata*, etc.), most birds, and certain mammals.

Planktons of sea and lakes provides very interesting instance of circadian rhythms by showing diurnal changes in their vertical distribution. For example, numerous copepods and zooplanktons tend to swim toward the surface at night and to move downward to deeper layers during the day (see Clarke, 1954).

Reverse is true with the phytoplanktons. Phytoplanktons of Dal Lake, Shrinagar exhibit diurnal movement in reverse order: they are abundant in the surface layer during day time and at the depth of 2.5 metre at mid-night (Kant and Kachroo 1975).

The possession of a circadian rhythm that can be entertained to environmental rhythms provides plants and animals with a biological clock, which is an integral part of cellular structure and is a chemosensory system very receptive to the environmental stimuli. The biological clocks of different animals run or oscillate continuously and environment does not initiate or stop their function. At most certain environmental stimuli may serve to regulate the functions of biological clocks.

(b) Annual rhythms:

Circannual rhythms:

Solary day, lunar day, tidal rhythms, monthly and annual rhythms are also of common occurrence among animals. Endogenous annuals cycles or circannual rhythms have been known in many animals like ground squirrels, warblers and other birds, some crayfishes and slugs.

The circannual rhythms are of adaptive value for timing seasonal events and specify the levels of migratory activity that are just sufficient for the birds to reach the vicinity of their species—specific winter quarters. The circannual rhythms also affect gonadial activities, reproductive cycles, metamorphosis, and adaptations to cold (development of fur and feather coats of animals during winter), and so on.

The diapause in insects is directly related to photoperiod. The pupae of *Apatele rumicis* enter diapause at photoperiods less than 15 hours but skip this pause at 16 hour photoperiod. Likewise, experimental work with a number of species of birds has shown that the reproductive cycle is under the control of an exogenous seasonal rhythm of changing day lengths and an endogenous physiological response timed by a circadian rhythm.

After the breeding season the gonads of birds studied to date have been found to regress spontaneously. This is the refractory period, a time when light cannot induce gonadal activity, the duration of which is regulated by day length. Short days hasten the termination of the refractory period; long days prolong it. After the refractory period is completed the progressive phase begins in late fall and winter.

During this period the birds fatten, they migrate, and their reproductive .organs increase in size. This process can be speeded up by exposing the bird to a long day photoperiod. Completion of the progressive period brings the birds into the reproductive stage. A similar photoperiodic response exists in the cyprinid fish; the minnows (see Smith, 1977).

Seasonal cycles of photoperiodism influence the breeding cycles of many mammals such as white-tailed deer (Fig. 11.21) and flying squirrel. For example, flying-squirrel has two peaks of litter production, the first in early spring, usually April, in the Northeastern United States, and the second in late summer, usually August.

6. Effect of light on reproduction:

In many animals (e.g., birds) light is necessary for the activation of gonads and in initiating annual breeding activities. The gonads of birds are found to become active with increased illumination during summer and to regress during shorter periods of illumination in winter.

7. Effect of light on development:

Light in some cases (e.g., Salmon larvae) accelerates development, whereas, in other (e.g., *Mytilus* larvae) it retards it.

Further, occasionally the output of sunlight is increased by the development of sunspots. As a result of this excess energy is radiated to space and this naturally increases the output of solar energy near the earth. A direct consequence of this is the greater evaporation of water which results in cloud formation to prevent more exposure to sunshine and thus to equalize temperature and modifying climate.

Lunar periodicity:

It can be defined as a biological rhythm in which the maxima and minima appear once or twice in every lunar month at the same time; if the rhythm occurs once in 15 days

(14-77 days) it is called as semilunar; if it occurs once in 30 days, it is called lunar. The lunar cycle or periodicity controls many living activities. For example, marine algae, Dictyota, produces its garnets at the time of full-moon springtide. The spawning of fish, Leuresthes tenuis follows a semilunal cycle. Certain poly- chaete worms also exhibit lunar periodicity.

Chapter 12: Insect Photoperiodism

The dipterans are the model organisms to study the photoperiodism and circadian movement. *Drosophila melanogaster* is well studied organism for the photoperiodism. The animal photoperiodism is further cementing the fact of insect photoperiodism. Because of the commensalism in Drosophila the seasonal adaptations are not remarkably developed. Circadian and photoperiodic responses both are complementary to each other. Photoperiodic response in insects controls Diapause in the insects. Termination of diapause is also controlled by photoperiod in most of the insects.

In Dung beetle, it surprisingly takes their directions by targeting the milky wave in night but how it takes directions during the absence of moon it debatable topic.

Chapter 13: Photoperiod and Bedding Plants

Bedding plants are either long-day, short-day, or day neutral in response to photoperiod. Some long-day species are “obligate” (or “qualitative”) long-day plants meaning that they require day lengths longer than a certain critical length in order to flower. Other long-day species are “facultative” (or “qualitative”) long-day plants. These plants initiate flowers under any day length, but flower earlier with long-days. Snapdragon, sunflower, salvia, and petunia are some of the important long-day annual species. Like long-day species, short-day plants have either an obligate or a facultative response to photoperiod; the former type requires a day length shorter than a certain critical day length while the latter type flowers under any day length, but earlier with short days. African marigolds, cosmos, celosia, and zinnia are important short-day species. The flowering of day neutral species is not affected by photoperiod. Geranium, impatiens, and begonia are examples of day neutral species.

Chapter 14: Reproductive Cycle in Horses

The annual pattern of changes in monthly ovulation rate follows minimal, increasing, maximal, and decreasing day lengths. Changing day length is the primary controller of the follicle dynamics of seasonal reproductive rhythms. The effects of changes in day length on reproductive seasonality involve a neural pathway from eyes to pineal gland, with involvement of the hypothalamus and pituitary.

Chapter 15: Vernalization and Photoperiodism

Plants from temperate regions have developed complex mechanisms for the change from vegetative to reproductive growth in order to cope with the transition to occur when conditions for pollination and seed development are optimal. The control over the timing of flowering is achieved through intricate regulatory networks in tight connection with environmental signals. Many other plants from temperate regions, perennial ryegrass developed a dual requirement for the induction of flowering[1]. It requires a primary induction, represented by several weeks of low temperature (vernalization) accompanied by short days. This is followed by the secondary induction, which starts when the temperature and the day length increase.

The different flowering pathways interact and converge on a number of key regulators, forming a complex flowering induction regulatory network to ensure reproductive success. Environmental and endogenous signals are integrated by the floral induction pathways. The environment sensing pathways rely on external signals which contribute to the seasonal regulation of flowering. The photoperiod pathway relates floral induction to changes in the day length, in a tight interaction with components of the circadian clock. The vernalization pathway integrates temperature related signals to time the transition to flowering after winter. Although the mechanism shares some similarities, the components of the vernalization pathway differ between monocots and dicots[2]. The endogenous floral induction pathways integrate plant derived signals to mediate the transition to reproductive phase. The autonomous pathway integrates development related signals to promote flowering.

Probably the most important and most conserved of the flowering-time pathways is the photoperiod pathway that innerves signals coming from light quality and quantity to the ones coming from the circadian clock in order to promote flowering[3-4]. *Arabidopsis thaliana* is a small annual dicotyledonous species whose genome has been completely sequenced[5]. In photoperiod response it behaves as a facultative long-day plant because it would flower much earlier under long days (LD: 16h light, 8h dark) than under short days (SD: 10h light, 14h dark). Photoperiodic flowering depends on the gene CONSTANS so that mutations in this gene modify the response of the plant to day length. co mutants are inresponive to photoperiod because they flower constitutively late in inductive (LD) or repressing (SD) conditions. CO codifies for a protein exclusive to the plant kingdom with distinct amino acid domains that define a new class of transcription factors[6,7]. CO overexpression renders also plants insensitive to photoperiod but for the opposite reason: they flower much earlier than wild type plants either under LD or SD[8].

Plants are sessile organisms, therefore they cannot escape from the environmental phenomena that affect them like other mobile organisms do. Rather, they have adapted a very versatile regulatory network to detect and respond to these diverse, changing external conditions. The way they respond to environmental changes is by modifying their protein profile thanks to gene activation and posttranslational modifications of diverse nature. Thus they acquire new physiological and metabolic conditions that confer them an advantage when dealing with biotic (pathogens) or abiotic (drought, cold, salinity etc.) stress. Throughout evolution this characteristic has given plant and enormous physiological plasticity allowing them to adapt surprisingly quickly to changing external conditions[9]. So, the genomes of actual plants reflect probably an elaborate network of interconnected regulatory pathways that needs to be slowly and tenderly revealed. In this sense, there is a multidisciplinary effort involving laboratories from several countries, with help from the European Union Research Council, trying to elucidate these signals in *Arabidopsis*.

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Chapter 16: Photoperiodism in Insects and Other Animals

Some physiological and behavioural adjustments occur in direct response to environmental fluctuations that have an obvious and immediate adaptive function. For example, reduced food or water availability can inhibit breeding[1,2] (Nelson, 1987; Bronson, 1988). Such environmental factors have been termed the "ultimate factors" underlying seasonality[3] (Baker, 1938). Many animals need to forecast the optimal time to breed so that spermatogenesis, territorial defense, or any other time-consuming adaptations can be developed prior to the onset of the breeding season. Thus, seasonal breeding vertebrates often detect and respond to environmental cues that accurately signal, well in advance, the arrival or departure of seasons favouring reproductive success. The environmental cues used to anticipate environmental change may or may not have direct survival value. Such cues are called "proximate factors" (Baker, 1938)[3]. Photoperiod (day length) is the most notable example of a proximate factor. The annual changes in day length serve as a precise reference for the time of year. Under some circumstances, proximate and ultimate factors are identical (Nelson, 1987)[1]. For example, some individuals may not begin breeding until food cues are detected (Bronson, 1988)[2].

In many species, substantial changes in both metabolism and food intake occur when animals are transferred from long "summer like" to short "winter like" days, leading to appreciable changes in body weight and total body fat. Although a wide variety of mammalian species undergo seasonal cycles of body fat, the vast majority of research on these seasonal responses has focused on Siberian hamsters (*Phodopus sungorus*) and Syrian hamsters (*Mesocricetus auratus*) (Wade and Bartness, 1984b[4]; Bartness *et al*., 2002[5]; Morgan *et al*., 2003[6]). For example, adult male Siberian hamsters housed in long days (16/8 h light–dark cycle [LD 16:8]) display relatively constant body masses; transfer to short days (LD 8:16), however, results in gradual and progressive loss in body weight (Wade and Bartness, 1984b[4]; Bartness *et al*., 2002[5]; Morgan *et al*., 2003[6]). Although some of this weight loss is driven by decreased testis and muscle mass, the majority of the weight loss occurs in the form of decreased adiposity (Mercer *et al*., 2001[7]). Approximately 30–40% of the initial long-day body fat is lost by approximately 12–16 weeks in short days. Indeed, if long-day Siberian hamsters are transferred to short days and subsequently food restricted during their progressive decline in body mass, then these animals lose a greater amount of body mass than do short-day animals fed ad libitum. When short-day food-restricted hamsters are allowed to refeed, they substantially increase their food intake to compensate for food restriction. Interestingly, however, these animals do not return to their pre-food restriction levels. Rather, they regain a stable body mass at the reduced level that is consistent with the progressive short-day–induced decrease in body mass (Steinlechner *et al*., 1983[8]). This and subsequent studies have confirmed the notion that body mass (and body fat) is a highly regulated, photoperiod-dependent, physiological response.

Seasonal variation is observed in most major classes of diseases among vertebrates (Nelson, 2004[9]). Although much of the seasonality, for instance, in infectious diseases is related to specific environmental conditions and life-history traits of pathogens and vectors, there are also prominent fluctuations in host immune function that can affect disease parameters. In common with other non-reproductive adaptations today length, changes in the immune system appear to be the result of "eavesdropping" on the neuroendocrine signals that tie photoperiod information to the reproductive system. Over evolutionary time adjusting immunological function in concert with changes in the reproductive system must have provided a competitive advantage. As the two systems are largely under the control of the pineal melatonin rhythm (Nelson and Demas, 1997[10]), marked adjustments in immunological function can be induced in the laboratory by altering day length.

Many animals have the ability to distinguish between daily cycles of light and darkness that differ in length. This photoperiodic process is clearly one of time measurement since, in effect, it involves the comparison of different intervals of time. The mechanism that controls it can therefore be regarded as a clock of a particular type, namely an interval timer. Although seasonal reactions to day length are common enough, information on the location and mode of operation of the clock is only available for a few groups, among which birds and arthropods are particularly prominent.

The annual reproductive cycle, pre-migratory fat deposition, migration, and other functions are often photo-periodically controlled in birds. The testicular response has been most closely studied, and refer briefly here to some of the salient features so that a comparison can be made with the arthropods.

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Chapter 17: Photoperiodiam: Regulation of Cerebral Blood Flow

Rotation of the Earth causes predictable changes in light and temperature, which provides exogenous cues of time that are implemented by a wide variety of organisms from cyanobacteria (Johnson *et al*., 1996[1]) to humans (Panda *et al*., 2002[2]). Biological timing is an important aspect for a number of physiological and behavioural processes. These biological cycles are precisely timed to coincide with favourable seasons for reproductive behaviour or to anticipate and prepare for the hardship of winter (Lincoln *et al*., 2003[3]). It is now well accepted that most cells and tissues in the body exhibit free running circadian oscillations, which can persist even in cultured conditions. However, by far the most important oscillator in mammals is the 'master biological clock' which resides in the suprachiasmatic nucleus (SCN) of the anterior hypothalamus (AH) (Dibner *et al*., 2010[4]). The SCN is responsible for synchronizing peripheral oscillators with the day-night cycle and in turn controls daily rhythms in behaviour (e.g. activity and sleep) and physiology (regulation of hormone release) (Kalsbeek *et al*., 2006[5]). Crucially, the SCN plays a key role in synchronizing the activity of the pineal gland (through a multi-synaptic pathway) as entrained by the light-dark cycle (Perreau-Lenz *et al*., 2004[6]). This results in the nocturnal secretion of melatonin, which provides an accurate internal representation of night length. Consequently, the duration of the melatonin signal provides a humoral indicator of the time of the year with long signal duration indicative of winter and a short duration signal indicative of summer.

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Chapter 18: Evolution of Animal Photoperiodism

To complete the life cycle of an organism it should wait for the favourable condition to come. Animals grow, reproduce and develop during the favourable season. The effect of seasonality and geographical condition greatly affect the life cycle of an animal. The season time controls whether the animal will go for reproduction and or will go for the dormancy so, that it will reproduce when the favourable condition comes it will again reproduce.

In most arthropods and in some vertebrates and for most deuterostomes, the timing of seasonal proceedings represents an interface between day length, circannual rhythmicity, and refractoriness. Circannual rhythms are endogenous (internal, self-sustained) physiological rhythms that persist under constant photoperiod and temperature. The period of this rhythm usually varies from 9–15 months and the rhythm can persist for several to as many as 10 years (Dawson 2002[1], Gwinner 1996[2]).

The interface of photoperiodism, circannual rhythmicity and refractoriness not only enhances the capability of animals to time their seasonal development at low latitudes, but also enables them to keep record of seasonal time with either fixed or quickly varying day lengths.

Photoperiodism has been reported in rotifers, annelids, molluscs, arthropods, echinoderms, bony fish, frogs, turtles, lizards, birds and mammals.

In annelids, rising day lengths start the seasonal reproductive cycle of *Nereis (Neanthes) limnicola* (Fong & Pease 1992[3]).

In the *Helix aspersa*, short days activate both dormancy and super cooling capability (Ansart *et al*. 2001[4]), and in the *Limax valentianus*, photoperiod is the necessary factor regulating both the commencement of reproduction and the rate of egg production (Hommay *et al*. 2001[5]).

In vertebrates, photoreception related to photoperiodism is fully retinal in mammals and involve retinal, pineal, or deep brain (mediobasal hypothalamus) photoreceptors in other vertebrates (Bj ¨ ornsson 1997[6], Borg *et al*. 2004[7], Bromage *et al*. 2001[8], Dawson *et al*. 2001[9], Dawson 2002[10], Tosini 1997[11], Tosini *et al*. 2001[12], V´ıgh *et al*. 2002[13]).

“Photoperiodic information has been shown to be the strongest synchronizer of seasonal functions in most species” of mammals (Hofman 2004, p. 63[14]).

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Chapter 19: Evolution of Plant Photoperiodism

There are two striking phenomenon of light and temperature in the biosphere: the daily measure caused by the rotation of the earth about its axis and the yearly seasonal measure caused by the rotation of the earth around the sun.

One of the most vital and first discovered types of photoperiodic responses involves the timing of the transition from a vegetative to a reproductive state in plants[1, 2].

Most of the short day plants have a dark dominant response, flowering is induced by the fixed duration of darkness, not considering of the relative duration of light, and that a short pulse of light during the dark phase can disturb the flowering response. Long day plants generally display a light dominant response, which means that a light pulse during the dark phase must be of significant length in order to bring a flowering response. The light dominant response involves sensitivity to light intensity during the day; red light during the first half of the day followed by a mixture of red and far-red light during the second half strongly promotes flowering[3].

The molecular biology of photoperiodism has been effusively studied in *Arabidopsis thaliana*. Much progress has been made in the mapping of interactions of the molecular components of the circadian clock, the endogenous pace maker, which constitutes an intrinsic part of the photoperiodic pathway.

Flowering at the particular season and age is crucial for reproductive successes of open flowers are particularly sensitive to unpleasant climatic conditions and seed maturation is costly in terms of energy and nutrient consumption. Furthermore, cross-pollination depends not only on coordinated flowering between individuals of the same species but sometimes also on the presence of appropriate pollinators. Management of the plant life cycle with the season depends on the recognition of environmental signals such as photoperiod and temperature, of which in particular the second requires incorporation over several weeks to provide strong information.

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Chapter 20: Plants Can Be Classified by Their Photoperiodic Responses

Photoperiodism: The phenomenon of photoperiodism was first discovered by Garner and Allard (1920). Relative length of day and night is called photoperiod. Flower requires a certain day length. Plants can be classified into three categories on the basis of photoperiod: Short day plant, long day plant, day neutral plant Photoperiod is very important phenomena which are described by Garner and Allard 1920. When they got the tobacco plant grown in long day it remains vegetative and non-reproductive, because tobacco plant is a short day plant. Short Day Plant (SDP)-These plants require a relatively short day light period (8-10 hours) and a continuous dark period of about 14-16 hours for subsequent flowering. Classification of Short Day Plants: Short Day Obligate Plants – Photoperiodic plants absolutely require a long night before flowering. Example – *Chrysanthemum*, *Poinsettia* Short Day Facultative Plants – Photoperiodic plants are more likely to flower under the appropriate light conditions, but will eventually flower regardless of night length. Example – Hamp (*Cannabis*), *Cosmos*, *Zinnia*.

Long Day Plant-These plants require a longer day light period (usually 14-16 hours) in a 24 hours cycle for subsequent flowering.

Long Day Obligate Plants – These plants absolutely require a short night before flowering. Example – Carnation, Bellflower (*Campanula*).

Long Day Facultative Plants – These plants are more likely to flower under the appropriate light conditions, but will eventually flower regardless of day length. Example – *Collinsia heterophylla*, *Phacelia tanacetifolia*.

Day Neutral Plant (DNP)-These plants flower in all photoperiods ranging from 6 to 24 hours continuous exposures. Example: Sunflower, Rose.

Chapter 21: Photoperiodism in Fishes

Fish are seasonally breeding animals, use environmental signals to coordinate and control their biological rhythms. Photoperiod represents an accurate indicator of time of day and season, and may be translated into a chemical body signal, melatonin, by the pineal gland. Pineal melatonin is released during night and the secretary pattern – which reflects the environmental light/dark cycle – may exhibit one of three known patterns. A daily and annual rhythmic production of melatonin may provide the fish with a physiological capacity to anticipate and prepare for upcoming seasonal changes. Manipulation of the photoperiodic control of pineal melatonin release has been successfully used to initiate biorhythms like spawning in cultured finfish species at mid and high latitudes.

In temperate species it is manifest that the duration of the solar day is the most important environmental prompt signaling the sexual periodicity. This has been utilized by use of manipulated photoperiods to induce out-of-season spawning (Bromage *et al*., 1992[1]; Migaud *et al*., 2010[2]). If fish farms in equatorial areas can utilize the same techniques, it can be an important progress for the aquaculture industry. Besides, by focusing on local endemic species the natural biodiversity will not be affected (Ross *et al*., 2008[3]; SPRN, 2008[4]). Among the indigenous fish species of Nepal, Katle (*Neolissocheilus hexagonolepis*), Mahseer (*Tor tor* and *Tor putitora*) and Snow trout (*Schizothorax sp*) have been identified as excellent food fish (Swar, 2002[5]). In addition are several induced exotic carp species like Common carp (*Cyprinus carpio*), Rohu (*Labeo rohita*), Silver carp (*Hypophthalmichthys molitrix*), Grass carp (*Ctenopharyngodon idella*) and Bighead carp (*Hypophthalmichthys nobilis*) proven to be of great use in fish cultivation and consumption (Shrestha, 1999[6]; Gurung, 2003[7]). All these species are herbivorous/omnivorous feeders which make them suitable for low energy input aquaculture (Shrestha, 1999[8]). However, little is known about these species reproduction physiology.

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Chapter 22: Photomorphogenesis and Photoperiodism

In developmental biology, photomorphogenesis is a light-mediated development, where plant growth patterns respond to the light range. This is a completely distinct process from photosynthesis where light is used as a source of energy. Phytochromes, cryptochromes, and phototropins are photochromic sensory receptors that restrict the photomorphogenic effect of light to the UV-A, UV-B, blue, and red portions of the electromagnetic spectrum[1].

The photomorphogenesis of plants is often studied by using tightly frequency-controlled light sources to grow the plants. There are at least three stages of plant development where photomorphogenesis occurs: seed germination, seedling development, and the shift from the vegetative to the flowering stage (photoperiodism)[2].

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Chapter 23: Photoperiodism in Rice

It is very important to study the effect of photoperiodism and its significance on rice. The rice is a very important crop for the humans and to some animals, rodents and snakes. Lot will depend on the production of rice. Rice is a one of the imperative staple food all across the world. The yield of the rice crop is depending on the photoperiod.

There are so many rice varieties cultivated across the globe and different varieties behave differently in their photoperiodic response.

Generally wild species of the *Oryza* and many of the primitive cultivated rices (*O. sativa* L.) are photoperiod sensitive and may be classified as short-day plants.

Photoperiod influences a number of facets of plant development. Some of its effects on rice have been studied by Best[1], Gwinner[2], Katayama[3], Morinaga[4], Sircar[5], and Wagenaar[6].

The growth of the rice plant can be divided into three stages:

1) The vegetative growth phase, from germination to panicle initiation;

2) The reproductive phase, from panicle initiation to flowering; and

3) The ripening phase, from flowering to fully developed grain.

In the tropics, the reproductive phase is about 35 d while the ripening phase ranges from 30 to 35 d. Both phases are relatively constant, although low temperatures have been known to prolong them and high temperatures to shorten them. The ripening phase may be prolonged to as much as 60 d. However, it is the vegetative growth phase whose duration generally varies greatly and which largely determines the growth duration of a cultivar, especially in the tropics.

The vegetative growth phase can be further divided into the basic vegetative phase (BVP) and the photoperiod-sensitive phase (PSP). The BVP refers to the juvenile growth stage of the plant, which is not affected by photoperiod. It is only after the BVP has been completed that the plant is able to show its response to the photoperiodic stimulus for flowering — this is the PSP of the plant.

The optimum photoperiod differs with cultivars although many workers have observed it to be 8-10 h.

Farmers have complained that their rice plants did not flower regularly because of the electric lights installed along their fields[7].

Suge[8] showed that different numbers of photo-inductive cycles produced different amounts of floral stimulus. He also found that Gibberellin A3 reduced the minimum number of photo-inductive cycles necessary to induce flowering. However, gibberellin alone did not induce flowering under non-inductive photoperiods.

The phytochrome pigment interacts with photoperiod or with different light qualities, such as red, far-red, and blue. Such pigment has been studied in rice coleoptile by Pjon and Furuya[9, 10].

Most studies on the photoperiodism of the rice plant have been considered from two standpoints, namely, classification of the cultivar into photoperiod-sensitive and photoperiod-insensitive types and measurement of the degree of sensitivity. The classification may be relatively easy, but the measurement is rather complex[11].

The flowering of the rice plant is mainly controlled by two ecological factors: day length and temperature, which are often interrelated. The plant may respond to temperature and photoperiod simultaneously, but the degree would vary according to the cultivar.

Rice can be grown over a wide range of environmental conditions, from the equator to about 53° N latitude, leading to the differentiation and establishment of various ecotypes and forms. The great diversity in photoperiod sensitivity from one latitude to another or within a latitude probably indicates that the rice cultivars predominantly cultivated in each area are those that have been selected on the basis of local adaptability (that is, adaptability to the temperature of the rice-growing season, day length, and duration of the growing season) to assure the full development of the plant and the best possible balance between vegetative and reproductive growth[12, 13].

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Chapter 24: Mammalian Photoperiodic System

To cope with seasonal fluctuations in environmental conditions, particularly temperature and food availability, most long-lived species of mammal exhibit seasonal cycles of physiological functions and morphological changes (Goldman, 2001)[1].

The use of photoperiod as an analytical indication was first confirmed in mammal by Baker and Ranson (1932)[2].

The response to photoperiod in mammals is not based solely on absolute day length, but also on photoperiodic history of the animals. In the ewe, 13 h of light per day cause a stimulation of luteinizing hormone (LH) secretion if animals have been exposed previously to 16 h of light. In contrast, 13 h of light per day inhibit LH secretion if animals had been exposed previously to 10 h of light. Thus, exposure to a same photoperiod may produce opposite effects depending on the photoperiodic history of the animals (Robinson and Karsch, 1988)[3]. Similar results have been obtained in several other species, and the importance of photoperiodic history appears to be a general characteristic of photoperiodic responses (Gorman and Zucker, 1998[4]; Goldman, 2001)[1].

The importance of the pineal gland was demonstrated by numerous experiments showing that the effect of photoperiod on seasonal functions is profoundly altered in pinealectomized animals.

Pineal melatonin secretion is regulated by light through a multistep nervous pathway connecting the retina to the pineal gland, including the suprachiasmatic nuclei as a major step (Schwartz *et al*., 2001)[5].

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Chapter 25: Lemna Photoperiodism

Lemnaceae (duckweeds) are one of the pilot systems to investigate the physiological basis of flowering. Most of the different photoperiodic reaction types are found within these tiny water-plants, which can be held in axenic culture in the laboratory.

Lemnaceae, or duckweeds, are very productive water-plants (HILLMAN 1961)[1].

During summer-time lakes and other places with standing water may be covered by a duckweed mat within a few weeks.

Photoperiodism is the most popular photoregulation process in flower physiology, but covers only a part of the whole story of light mediated flower induction. In plants light set in motion several physiological processes simultaneously and — in principle — all of them may have an influence on flower initiation.

Since BÜNNINGS[2] pioneer work it has been well established that daylength measurement by plants and animals uses physiological clocks (BÜNNiNG 1977)[2]. This holds true also for Lemnaceae. The late W. S. HILLMAN, one of the best scientists in phytochrome, photoperiodism and Lemna physiology, has worked out this in great detail.

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Chapter 26: Photoperiodic Regulation of Insect and Molluscan Hormones

Photoperiod is the primary environmental signal that regulates the timing of reproduction (Goldman, 2001)[1].

In comparison to the vertebrate central nervous system, that of mollusks is relatively simple and could provide an avenue for revealing the cell physiological responses to environmental signals.

Molluskan model systems have also been successfully used to understand the second-messenger pathways activated by synaptic transmission and modulatory peptides (Conn and Kaczmarek, 1989)[2].

Although there is a relatively limited literature on physiological mechanisms underlying environmental regulation of reproduction in mollusks, three species in which this topic has been studied are the giant garden slug *Limax maximus*, the freshwater pond snail *Lymnaea stagnalis*, and the marine snail *Aplysia californica*. All three species are hermaphrodites, containing both male and female gonads.

Limax maximus is a common garden slug, which undergoes reproductive maturation from mid-May through late July and reaches full reproductive competence in August. Sokolove and colleagues demonstrated that maturation of the Limax reproductive system is dependent on photoperiodic signals (Sokolove *et al*., 1984)[3].

Slugs raised in the laboratory on short photoperiods remain immature indefinitely. Exposure to long day-lengths stimulates growth and development of the gonad, penis, albumen gland, various female accessory sex organs, and maturation of sperm.

Further work demonstrated that in response to long days, both the cerebral ganglion and blood contain a male gonadotropic factor that stimulates proliferation of spermatogonia in recipient slugs maintained on inhibitory short days.

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Chapter 27: Flowering and Photoperiodism

Plants have adapted flowering time for their natural habitats and, therefore, the onset of flowering varies widely among different species and ecotypes. Temperature and day length are the principal environmental signals for plants to track the seasons of the year, which allow flowering to be synchronized for maximum reproductive success. Since the discovery of photoperiodism in soybean and Maryland Mammoth tobacco plants by Garner and Allard (1920)[1], numerous experimental approaches in different plant species have been undertaken in order to study the day-length dependent flowering in a large variety of photoperiodic plants (Thomas and Vince-Prue 1997)[2]. These classical studies, however, were limited in their ability to identify the underlying molecular nature for flowering time control in long- and short-day plants.

In recent years, quick progress has been made in understanding the molecular mechanisms of floral induction in *Arabidopsis thaliana*, a facultative long-day plant and, more recently, in rice (*Oryza sativa*), a short-day plant (reviewed in Searle and Coupland 2004)[3]. In *Arabidopsis* four main pathways that control flowering time have been defined genetically. The photoperiod and the vernalisation pathways are involved in the perception of environmental signals, whereas the autonomous pathway acts independently of environmental signals (Koornneef *et al*. 1998[4]; Mouradov *et al*. 2002[5]; Simpson and Dean 2002[6]). Gibberellins (GAs) are limiting for flowering in Arabidopsis (Wilson *et al*. 1992[7]) and by genetic analysis of double mutant combinations of GA and late-flowering mutants the promotion of flowering by GAs has been shown to be mediated by a fourth independent pathway (Reeves and Coupland 2001[8]). These flowering time pathways converge on pathway integrators, such as LEAFY (LFY) (Blazquez and Weigel 2000[9]), FT (Kardailsky *et al*. 1999[10]; Kobayashi *et al*. 1999[11]) and the MADS box protein SOC1 (Borner *et al*. 2000[12]; Lee *et al*. 2000[13]; Samach *et al*. 2000[14]). CONSTANS (CO) encodes a zinc finger protein that is a central regulator for flowering time control in *Arabidopsis* by long days. CO is expressed in the vasculature where it directly activates FT transcription (An *et al*. 2004[15]). The FT protein has been shown to be transported to apical meristems (Corbesier *et al*. 2007[16]; Tamaki *et al*. 2007[17]), where it interacts with FD (Abe *et al*. 2005[18]; Wigge *et al*. 2005[19]) to activate SOC1 expression (Searle *et al*. 2006[20]), which finally leads to the activation of floral meristem identity genes and the formation of flowers.

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Chapter 28: Photoperiodism and Phytochrome

Plants can react very particularly to any changes in day duration. This purposeful action is called *photoperiodism*. In the northern hemisphere, some plants flower at the same time each spring, despite of the temperature. There are shrubs with small yellow flowers called *forsythia*. On March 20th, day and night are equal lengths. After that day, the day length increases the period of darkness at night and getting longer until about June 20th. The forsythia reacts to this enhance in day length and flower, always at the same time every year, the last week in March, because the day length at that time triggers their flowering response. These plants are called long-day (or short-night) plants. There are other plants that are called short-day (or long-night) plants. They flower when the day length gone below a definite level. In the northern hemisphere, these plants flower in the winter. In the forest in central Pennsylvania in the fall, there are trees that have small yellow flowers on it, these are *witch hazel trees*. At this time, many of the trees have lost their leaves so these trees are easily seen. These trees flower in the winter, responding to this shortening in day length. Some plants are day-neutral plants. Day length has no effect on these types of plants. Snapdragons are day neutral plants because the length of the day has no effect on the flowering.

What is the mechanism by which plant knows what the day length is? This is a highly evolved and complicated thing for a plant to be able to sense, the comparative length of light and darkness during the day. Experiments were conducted to know how this machinery functioning and to see if this machinery could be revealed. These were done in a laboratory, where the plant is exposed to light in a controlled surrounding. This was done for both a long-day plant and a short-day plant. When the plants were exposed to longer day length, about 16 hours, the long-day plant flowered and the short-day plant not flowers. Also, when exposed to shorter day length, about 8 hours, the long-day plant did not flower and the short-day plant flower. What would happen if the period of darkness were interrupted by a flash of light? When this was done under the conditions that caused the short-day plant to flower (a long night), interrupting that night, and the long-day plants reacted as though it was a short night and flowered, while the short-day plants did not flower. How could this one spark of light so intensely affect these plants?

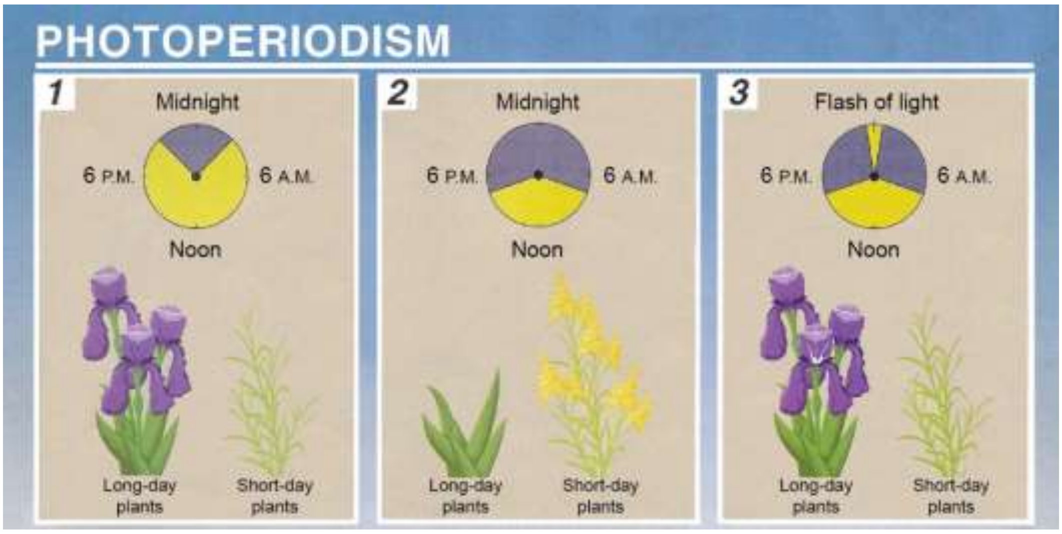

Figure. The Effect of Light on the Flowering of Long-day and Short-day Plants

This process is controlled and done by a pigment. Pigments absorb light, just as the pigments in retina absorb light allowing animals and humans to see. The pigment involved in photoperiodism is *phytochrome*. There are two forms of this pigment: P_r is the stationary form and P_{fr} is the active form. It is the P_{fr} form that triggers the plant response. When this P_{fr} form is present, it triggers flowering or triggers a seed to germinate. It was known that abscisic acid can help seeds to go dormant. One of the triggers that the seeds use to come out of dormancy is the amount of light that the plant is exposed in the spring as the light levels increase during the day. A spark of red light converts the inactive form, P_r, to the active form. P_{fr}. In these type of plants that were exposed to that spark of light during the dark period, that flash converted the inactive form to the active form. This signals to the short-day plants that there is too much light, so they will not flower. However, it signals to the long-day plants that there is enough light, so they flower even though the actual day length is too short to trigger that response.

This reaction happens because the two forms of phytochrome respond to different wavelengths of red light. P_r is converted to P_{fr} by red light in the visible spectrum, about 660 nm. Under normal conditions with no flash of light during the dark period, the P_{fr} will gradually convert back to P_r. However that spark during the night reconverts all of the P_r to P_{fr}, making the plant respond as if it were under long-day conditions. P_{fr} also can be converted to P_r by far-red light, about 730 nm, at the end of the visible spectrum. This finding was very exciting because it was the first time that we realized that a pigment can be used to control a plant's behaviour towards photoperiodism and the time at which it flowers. The plants are using these pigments to sense surrounding conditions, day length.

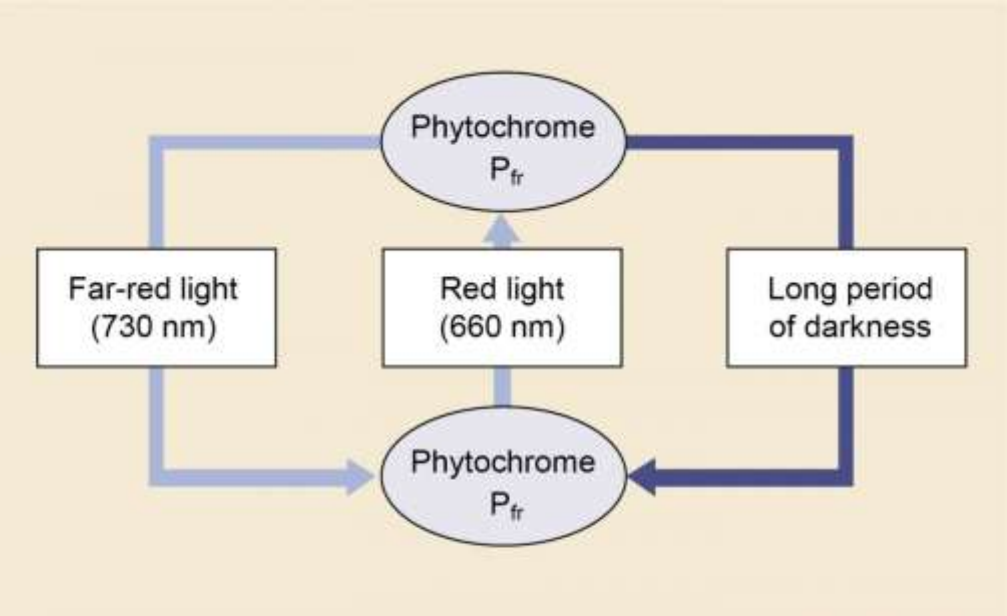

Figure. The Relationship between the two Forms of Phytochrome

Chapter 29: The Genetic Basis of Photoperiodism

Identifying the genetic mechanisms underlying the adaptation and divergence of natural populations remains a fundamental evolutionary problem. Divergence is a product of mutation, genetic drift, natural selection, and dispersal, factors that can interact in complex ways to affect the evolution of quantitative characters. In Wright's (1977)[1] shifting-balance theory, local adaptation and genetic divergence of populations depend on the interactive effects of drift and selection on genetic variation in quantitative traits. However, the roles that the different components of genetic variation play in this process remain indefinable. While it has long been recognized that allelic and genic interactions (i.e., dominance and epistasis) may have important fitness consequences (Fisher 1958[2]; Wright 1968[3], 1977[1]), how these non-additive genetic variation forms affect adaptation and divergence is poorly understood. In the absence of sufficient genetic drift, the divergence of populations for traits with low additive genetic variance must involve the conversion of non-additive to additive genetic variance, at least over the short term (Wade and McCauley 1984[4]; Bryant *et al*. 1986b[5]).

The relationship between genetic variation and population differentiation is frequently hindered by a lack of knowledge about the evolutionary ecology of the organism in question. Two bits of information, critical to the interpretation of this evolutionary relationship, are often unavailable. First, in many cases the characters under examination have unknown effects on fitness. Second, the evolutionary trajectory for a species (its major pattern of dispersal, colonization, and differentiation through time) is often unknown. As a result, little empirical work is available that relates potential evolutionary pathways of adaptation to actual patterns of differentiation.

Flowering time has been investigated extensively at the molecular and developmental levels in the model species *A. thaliana*[6–8] and some crop species[9]. In *Arabidopsis*, the flowering time gene network consists of more than 60 genes[6], which are regulated by four pathways: photoperiod, autonomous, vernalization and gibberellin[6, 7].

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Chapter 30: Period Gene

Strong confirmation against the crucial role of *period gene* in photoperiodism originates from the study on periodic mutants of *D. melanogaster*.

PER3 is a Period family of genes and is expressed in a circadian pattern in the suprachiasmatic nucleus, the primary circadian pacemaker in the mammalian brain. Genes in this family encode components required for circadian rhythms of locomotor activity, metabolism, and behavior. This is up-regulated by CLOCK/ARNTL heterodimers but then represses this up-regulation in a feedback loop using PER/CRY heterodimers to interact with CLOCK/ARNTL. Polymorphisms in this gene have direct link to sleep disorders. Multiple transcript variants encoding different isoforms have been found for this gene.

Circadian clock genes are remarkably conserved between eucoelomates. Although *Drosophila* has one copy of each major component, vertebrates have two or (in the case of the *Period* genes) three paralogs (*Per1*-*3*).

Drosophila per was the first animal clock gene to be identified through its mutants and named, and recognized as a core oscillating component of the circadian clock.

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ISBN:978-93-86675-02-6