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PHOTOPERIODISM IN CROPS

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Various aspects of photoperiodic control of growth and development in crops are reviewed. The mechanisms of photoperiodic signal perception, transduction and induction of further morphogenetic responses are described. Plant photoperiodic response provides the synchronization of their growth pattern with the seasonal events and, therefore, their better adaptation. At the same time high photoperiodic sensitivity can retard the dispersal of the important agricultural crops. These problems are solved with various breeding strategies.

Key words: agricultural crops, photoperiodism, adaptation, ontogenesis, productivity, plant breeding.

Abbreviations
GA: gibberellin(s)
LD: long day(s)
SD: short day(s)
LDP: long-day plant
SDP: short-day plant
DNP: day-neutral plant
LSDP: long-short-day plant
SLDP: short-long-day plant
CAM: Crassulacean acid metabolism

Introduction

Photoperiodism is a response of a living system to the length of day, one of the crucial environmental factors which from year to year gives the most reliable information about the passage of the seasons. In plants, it provides the synchronization of growth pattern with the seasonal events [105, 110]. Such a response can be used as a means of avoiding or preventing the adverse effects of an associated or subsequent unfavorable environment.

An ability to constrain plant life cycle to a seasonal climate is clearly important, and photoperiodic control of growth and development appears to be one of the principal

mechanisms for achieving this, and so avoid climatic extremes of winter cold and summer drought [5, 82]. Survival of the individual may be ensured by daylength-dependent physiological and morphological changes that increase resistance to unfavorable conditions. The day-length signal precedes these stress conditions and triggers switch on of the adaptive programs; various changes in plant growth habit and metabolism are adaptations to a particular environment.

Day-length controls many plant responses, flower initiation being the most important one. It may also affect flower development, sex expression, growth rate, cambial activity, dormancy, senescence, tuberization, etc. Several lists on photoperiodic behavior cover over 2000 species, and about 80 to 85 % of the studied plants are quoted as displaying photoperiodic behavior [56]. Photoperiodic response is of greatest importance for crops. Day-length influences many aspects of their behavior and has significant effect on plant distribution and on crop yield.

Plants precisely time the onset of flowering to ensure reproductive success. A major factor in seasonal control of flowering time is the photoperiod. The length of the daily light period is measured by the circadian clock in leaves, and a signal is conveyed to the shoot apex to initiate floral transition accordingly. There was a profound progress in the studies both on physiological and agronomical aspects of the process of photoperiodism during the last decades. Cutting-edge studies on the molecular mechanisms of photoperiodic timing in plant development have shown its leading position together with vernalization control among existing flowering pathways [67].

Mechanisms of photoperiodic response

1. Photoperiodic signal perception, transduction, and realization

In the photoperiodic control of flowering or tuberization, one could distinguish long-distance signaling with three successive steps: induction in leaves, commitment (evocation) to flowering or tuberization at the shoot apical meristem or at the stolon tip, and tuber initiation at the stolon tip or floral morphogenesis at the shoot apical meristem [97].

In photoperiodism, plants respond to the duration and timing of light and dark periods in daily cycles. The photoperiodic mechanism involves complex interaction of a photoreceptors with a timing system which is most probably a circadian rhythm [44, 48]. Day-length measurement involves the integration of temporal information, provided by circadian oscillator, with light/dark discrimination, provided by photoreceptors [35]. Phytochromes are involved in the phase setting of biological clock in time measuring [35, 62, 63], and the effect of blue light on floral initiation in Arabidopsis also suggests the involvement of blue light absorbing photoreceptors, cryptochromes, providing control mechanism crosstalk in photoreceptor signaling [35].

Circadian rhythms have been found in all eukaryotes and in some prokaryotes, they are believed to follow an internal biological oscillator, often known as biological clock. Circadian clocks integrate environmental signals internal cues to coordinate diverse physiological outputs so that they occur at the most appropriate season or time of day. Recent studies using system approaches have also begun to reveal the importance of the clock to key agricultural traits in crop species [47]. In the last two decades, the molecular players in the photoperiodic pathway have been identified in *Arabidopsis thaliana*. Moreover, the intricate connections between the circadian clockwork and components of the photo-

periodic pathway have been unraveled. In particular, the molecular basis of time-of-day-dependent sensitivity to floral stimuli, as predicted by Bünning and Pittendrigh, has been elucidated [51].

Photoperiodic induction takes place in leaves as response to photoinductive day and night cycles, while evocation occurs in the meristems in response to arrival of flowering stimulus and leads to floral morphogenesis. Among the plants with pronounced environmental requirements there are many examples of apparently alternative pathways to evocation [12, 13, 29, 93, 116]. Earlier, it was proposed that both stimulus and inhibitor appear to be produced in plant, and floral evocation depends on the balance between them [58]. Either the floral stimulus can be produced by a great number of alternative pathways, or these are the conditions under which an inhibitor is *not* produced, or a variety of conditions can lead to the particular interplay of influences at the shoot apex which is conductive to evocation.

The evidence confirming that photoperiod leads to the production of transmissable flowering signals results from grafting experiments. For different flower-promoting factors are perceived by different parts of the plant, this implies that these parts interact and that the fate of apical meristem of becoming vegetative or becoming reproductive is controlled by an array of various long-distance signals [14]. As early as in 1936, the comprehensive studies of flowering led M.Kh. Chailakhyan to the concept of florigen, a hormonal floral stimulus, and let him establish several characteristics of this stimulus. These studies set up for many years the main avenues for research into the processes that control plant flowering, and the notion of florigen became universally accepted by scientists worldwide. The present-day evidence of genetic control of plant flowering supports the idea that florigen participates in floral signal transduction. The recent study of Arabidopsis plants led the investigators to the conclusion that the immediate products of the gene *FLOWERING LOCUS T*, its mRNA and/or protein, move from an induced leaf into the shoot apex and evoke flowering therein [3, 25, 46].

Plants monitor changes in photoperiod and temperature to synchronize their flowering with seasonal changes to maximize fitness. In the Arabidopsis photoperiodic flowering pathway, the circadian clock-regulated components, such as FLAVIN-BINDING, KELCH REPEAT, F-BOX 1 and CONSTANS, both of which have light-controlled functions, are crucial to induce the day-length specific expression of the *FLOWERING LOCUS T (FT)* gene in leaves. Recent advances indicate that FT transcriptional regulation is central for integrating the information derived from other important internal and external factors, such as developmental age, amount of gibberellins, and the ambient temperature. These factors interactively regulate the expression of *FT*, the main component of florigen, in leaves [95].

In *Arabidopsis thaliana*, chromatin mechanisms play critical role in flowering time regulation through the expression control of key flowering-regulatory genes. Various conserved chromatin modifiers, plant-specific factors, and long noncoding RNAs are involved in chromatin regulation of *FLOWERING LOCUS C* (*FLC*, a potent floral repressor). The well-studied *FLC* regulation has provided a paradigm for chromatin-based control of other developmental genes. In addition, chromatin modification plays an important role in the regulation of *FT* which is widely conserved in angiosperm species. The chromatin mechanisms underlying *FT* regulation in *Arabidopsis* are likely involved in the regulation of *FT* relatives and, therefore, flowering-time control in other plants [45]. FT interacts with the basic leucine zipper domain (bZIP) transcription factor FD, and the resulting complex activates floral homeotic genes, such as *APETALA1* (*AP1*), to promote floral meristem identity and flower development [1].

The rice (*Oryza sativa*) *FT* homolog, *Hd3a*, interacts with the rice *FD* homolog, *OsFD1*, via a 14-3-3 protein. Formation of this tri-protein complex is essential for flowering promotion by *Hd3a* in rice. In addition, the multifunctionality of *FT* homologs, other than for flowering promotion, is an emerging concept [100].

Seasonal cues of day-length or winter cold trigger flowering of many species. Forward and reverse genetic approaches are revealing the mechanisms by which these responses are conferred. Homologues of the *Arabidopsis thaliana* FT protein are widely used to mediate seasonal responses to day length and act as graft-transmissible promoters or repressors of flowering. Winter cold in *A. thaliana* promotes flowering by repressing transcription of the MADS box gene *FLOWERING LOCUS C (FLC)*. The mechanism by which this occurs involves a complex interplay of different forms of long noncoding RNAs induced at the *FLC* locus during cold and changes in the chromatin of FLC. In perennial relatives of *A. thaliana*, flowering also requires the age-dependent down-regulation of miRNA156 before winter [84].

2. Juvenility and competence to photoperiodic induction

During the vegetative period the pre-inductive phase (juvenile or basic vegetative phase) is followed by inductive one. Post-inductive phase is not sensitive to photoperiod again.

Juvenility is the early period in plant life when it cannot respond to various stimuli by flowering. In herbaceous plants, it was classically believed that all meristems, young or old, are competent. In this case, juvenility seems unrelated to meristem incompetence but is due to physiological limitations in other plant parts. However, the situation appears to be not that simple: in pea, for example, length of juvenile phase is controlled by several genes [11]. In late varieties of *Pisum*, the juvenile stage can last up to 50 nodes, can be shortened by vernalization, and have interactions with day-length, earlier flowering being promoted in SD but not in LD [43].

After perceiving the floral stimulus, the apices of some species are permanently transformed, producing reproductive organs without a further environmental stimulus. Other species require repeated photoperiodic induction, reverting to vegetative habit in the absence of such signals [13].

Photoperiodic response groups

The classification of plants according to their photoperiodic responses traditionally was set up on the basis of flowering control, though other crucial processes (tuberization, dormancy, etc) are affected by day-length as well. The main photoperiodic groups are the following:

1. Short-day plants (SDP) only flower, or flower most rapidly, with fewer than a certain number of light hours in each 24 hour cycle.

2. Long-day plants (LDP) only flower, or flower most rapidly, with more than a certain number of light hours in each 24 hour cycle.

3. Day-neutral plants (DNP) indifferent to day-length and flower at the same time irrespectively of photoperiodic conditions.

Within these groups plants with absolute photoperiodic responses, where a particular day-length is essential for flowering, and quantitative photoperiodic responses, where particular day-length promotes but is not essential for flowering, could be found.

Critical day-length is defined as the day-length below which the flowering of SDP occurs, or above which the flowering of LDP occurs. The critical day-length often varies within ecotypes, especially in species with wide latitudinal or altitudinal dispersion. It is increasing with increased latitude or altitude providing plant adaptation to the shorter growing season in these habitats. Therefore, in photoperiodism the terms "long days" or "short days" refer to their relationship to the critical day-length rather than their absolute duration [104].

Some plants show dual photoperiodic requirements that change during ontogenesis. For example, in *Cestrum nocturnum* flowering occurs in SD only after plants have previously received a sufficient number of LD (long-short-day plants, LSDP) [86]. In *Scabiosa succisa*, flowering occurs in LD only in plants that have previously received SD (short-long-day plants, SLDP) [23]. In another SLDP, celery, vernalization during SD is required for transition to flowering. A few species have rather specialized day-length requirements. Some flower only when the day is neither too long, nor too short (intermediate-day plants); others flower rapidly in either SD or LD, at intermediate day-length their flowering is delayed (ambiphotoperiodic plants).

Eco-physiological background to photoperiodic response

1. Photoperiodism and plant reproductive strategies

Timing of flowering is the key to the reproductive success of many plants. In temperate climates, flowering is often coordinated with seasonal environmental cues such as temperature and photoperiod. It is clear that within a species the possession of an attribute such as photoperiodic behavior confers some competitive advantage over other species within the constraints of space (ecological niche, latitudinal limits) and of time (season of year) [82]. Plants rely on photoperiodic signals to trigger their seasonal responses - either to minimize or to avoid potentially lethal stress or to become fruitful and multiply under favorable conditions. For example, a long-day response in high latitudes can synchronize flowering with the high light integral of summer and thus to support the assimilate demand of seed production; alternatively, a short-day response may enable a woodland species to complete its reproductive cycle before the canopy closes [110]. In photoperiodically sensitive species, the onset of sexual or vegetative reproduction is governed by the relationship between the actual day-length and a critical or threshold day-length of genotype [105]. Plants in which flowering is accelerated by SD (SDP) generally flower in autumn before the adverse temperatures of winter; plants in which flowering is accelerated by LD (LDP) generally flower in favorable conditions of late spring or in the beginning of summer [35].

For an annual species, competitive advantage is expressed in seed number. One strategy of requirement for a delay in flowering is to produce a vegetative plant capable of supporting relatively large number of flowers and the complete development of resultant seeds. Another strategy could be observed in an ephemeral plant with a short life cycle and a low seed production; several generations within growing season give a large seed number spread in time. For perennials, the situation is more complex, and their periodicity could be controlled besides day-length by some additional signals such as temperature, water supply etc. Therefore, photoperiodic response that determines rhythm of growth and development in numerous species appears to be an important component of their regenerative strategies [38, 78].

2. Geographical origin of plants and photoperiodic response

The behavior of plants in the wild is closely related to their environment. So, information on the eco-physiological background to photoperiodic response in various species can be obtained after analysis of their geographical dispersal and rhythms of growth and development.

Day-length and irradiance change with season and latitude. In temperate climates, the growing season is centered around the spring and summer months when days are warm and long. Therefore, the vast majority of crop species that originate from the temperate latitudes are LDPs. Some are sensitive to low temperature and only respond to LD after they have experienced a cold period (after vernalization). This dual response prevent premature flowering in plants growing from seed, shed in summer and which will experience relatively LD before the start of cold season [83].

The timing (calendar-related) synchrony is less important in the tropics than in higher latitudes. However, the importance of seasonal timing of flowering is increasing in the moist tropics. Though the seasonal day-length change is much less here than at high latitudes, some local land races of rice, *e.g.,* show extremely high sensitivity to small changes of photoperiod [28, 76]. In more tropical climates the growing season is generally delimited by lack of rain. Crops become reproductive towards the end of the wet season, when day-lengths are shortening. So far all tropical and subtropical crops are SDP. DNP also occur both in temperate and tropical crops [83]. Major crop legumes fall into two major groups with respect to their flowering-time control: warm season crops such as soybean (*Glycine max*) and common bean (*Phaseolus vulgaris*), which require short days for flowering, and the temperate, cool-season crops such as pea (*Pisum sativum*), lentil (*Lens culinaris*), and chickpea (*Cicer arietinum*), which are long-day plants (72). While ancestors of many legume crops are geographically constrained by their photoperiod requirements, the isolation of variants with relaxed requirements has allowed cultivation across a much wider range and provided adaptation to a range of agronomic practices (114, 117).

A wide array of response types could be observed in perennial grasses and weeds. With kangaroo grass, *Themeda australis, e.g.,* genotypes from the northern, summer rainfall region of Australia are SDP, while those from the southern, winter rainfall areas are LDP, their requirement quite weak in the drier inland regions, but enhanced by vernalization requirement in the coldest regions. At intermediate latitudes some intermediate-day genotypes are found [32].

Various response types (both qualitative and quantitative) can be observed within widely adapted species of domesticated plants, as well [103]. The selection of cultivars for different latitudes had led to a wide range of sensitivities; for example, some cultivars of soybeans at the northern end of the species range can be successfully grown only within an 80 km band of latitude [41].

3. Interaction with temperature

The plant response to day-length may be profoundly modified by environmental or other factors, temperature and plant age being the most important ones. Their effect can induce both quantitative and qualitative changes in plant behavior. There is a variety of interactions between day-length, irradiance, and temperature in natural populations of different origin. Plants make use of temperature signals - either as precondition for a subsequent photoperiodic response, as in vernalization, or as a modifier of their photoperiodic response.

Plants monitor changes in photoperiod and temperature to synchronize their flowering with seasonal changes to maximize fitness. Vernalization is an example of temperature influencing the timing of flowering and is defined as the process by which a prolonged exposure to the cold of winter results in competence to flower during the following spring. In cereals, three genes (*VERNALIZATION1 [VRN1], VRN2, and FLOWERING LOCUS T [FT]*) have been identified that influence the vernalization requirement and are thought to form a regulatory loop to control the timing of flowering [37]. It is important to recognize that a photoperiodic response could lead to confusion between spring and autumn, since the absolute day-lengths experienced at these times are the same [109]. Associated responses to low temperature conditions provide clear information about the season and synchronization of the plant life cycle with it. Cold-temperature vernalization ensures that winter annuals, biennials and some perennials respond only to day-length in spring. In some cold-requiring plants LD (or SD) may substitute for vernalization [70].

Warm temperature modifications of the photoperiodic response enables timing to be finely tuned so that flowering occur earlier or later if the season is warmer or cooler than usual [83]. High or low temperatures can modify plant critical day-length providing flower induction under relatively unfavorable photoperiod. In onions, high temperature decrease plant sensitivity to SD conditions in low latitudes, providing bulbing of tropical cultivars [18, 19, 26]. Lower temperature-dependent flowering regulation, has been characterized recently and temperature also regulates FT in leaves [95]. The effects of ambient temperature on flowering time are mediated in early and late flowering *Arabidopsis* mutants at the level of photoreceptor activity and also at the level of transcriptional regulation of *FT* [40], *FVE, FCA, FLC* [17], respectively. There are also indications that other genes could also participate in this response [8].

Photoperiodic control of sexual reproduction

1. Flower initiation

The great number of responses observed in plants are connected with the effect of day-length on their sexual reproduction. Photoperiodic control provides more or less synchronous flowering and subsequent successful outcrossing. Synchronization of flowering with favorable external conditions is another feature of the role of photoperiodism in the survival strategy of plant population. The timing of the transition from vegetative growth to flower formation is of great importance in agriculture, horticulture, and plant breeding.

1.1. Length of juvenile phase

Morphogenetic switch connected with the transition of shoot meristem from leaf production is investigated intensively in photoperiodic species. Before flower initiation some vegetative growth must have occurred. Juvenile plants cannot be induced to flowering by any treatment; only few exceptions refer to the stress responses. The length of juvenile phase is a component of the overall competitive strategy of the plant and is part of the cultivar genetic program [104]. Differences between early and late maturing cultivars, including DNP, are determined to a great extent by the variation in their juvenile phase length.

The failure of young plants to flower in response to photoperiodic induction can be determined either by the lack of the apex ability to respond to floral stimulus, or the failure of hormone production in leaves. Competence to photoperiodic induction with the subsequent

floral transition of meristems in annual herbaceous plants usually could be observed within several days or weeks after emergence. And in various woody perennials juvenile phase may last for years. However, application of plant growth substances in conifers, *e.g.,* was shown to be effective in the induction of their early flowering [78].

1.2. Multifactorial control of flowering

Appropriate timing of the shift from vegetative to reproductive growth is an important determinant of plant fitness. The time at which a plant flowers is determined through integration of signals reflecting extrinsic and intrinsic conditions, such as photoperiod, the duration of cold, plant health, and age [5]. Clearly, there are alternate pathways to flowering. Among the endogenous factors involved in the control of flowering, both nutrients and hormones are found, in line with the concept that this control is multifactorial and does not simply result from nutrient diversion [11, 14]. Genetic analyses in *Arabidopsis* have allowed identification of many genes involved in flowering time regulation [67, 93]. Several pathways regulate the expression of a few key genes known as flowering signal integrators whose main function is to regulate the expression of genes specifying flower meristem identity [8, 52]. Photoperiod pathway is one of the most important pathways regulating the timing of the floral transition [48]. Under long-day inductive conditions in *Arabidopsis*, photoperiod pathway components act to promote flowering by inducing *CONSTANS (CO)* and downstream genes. The floral integrator *FT* is a major target of multiple flowering pathways and the photoperiod pathway in particular. It is directly activated by *CO* [87]. Under LD conditions, the peak of *CO* expression is coincident with the presence of light, and *CO* activates *FT* expression in the leaf vascular system [120]. *FT* travels through the phloem to the shoot apex [25], where, together with *FLOWERING LOCUS D* [1, 118], it activates *APETALA1 (AP1)* and other floral meristem identity genes, starting the flowering process. Other flowering time pathways converge on *FT* and/or directly impact gene expression in the meristem. The changes in gene expression that accompany the floral transition must be rapid, robust, largely irreversible, and strictly controlled spatially. This is achieved through positive feed-forward and negative feedback loops involving multiple regulatory factors [53]. Members of the MADS-box family of regulatory factors are central players in the regulatory loops controlling the floral transition [94]. MADS-domain factors typically act in large multimeric complexes and are well suited for regulation that involves combinatorial action. During the floral transition, MADS-domain proteins can act either as repressors or activators. In Arabidopsis, important floral repressors include *SHORT VEGETATIVE PHASE (SVP)* and members of the *FLOWERING LOCUS C (FLC)*-like group, including *FLC, FLOWERING LOCUS M (FLM)/MADS AFFECTING FLOWERING1 (MAF1)*, and *MAF2* to *MAF5*. Promoters of flowering include such MADS-domain factors as *SUPPRESSOR OF CONSTANS1 (SOC1)* and *AGAMOUS-LIKE24 (AGL24)*. Together with non-MADS-box proteins FT and TWIN SISTER OF FT, SOC1 and AGL24 function as floral integrators. These operate downstream of the flowering time pathways but upstream of the meristem identity regulators such as *LEAFY (LFY)* and the MADS-domain factor AP1. The MADS-domain factors AGL15 and AGL18 also contribute to regulation of the floral transition in Arabidopsis. AGL15 and AGL18, along with SVP and AGL24, are necessary to block initiation of floral programs in vegetative organs [34].

Photoperiod is the most important environmental variable to which plants couple their flowering [109], and gibberellins (GAs) are central nodes in networks connecting environmental inputs to growth and development [24]. The DELLA proteins act as repressors of GA signaling, and are destabilized by GA (GA–GID1–DELLA module) [42].

Although it is known that GA signaling integrates various endogenous and environmental signals, the molecular basis of their modulation of plant growth and development is only now beginning to be understood. The current suggestion is that the DELLA proteins act as one possible quantitative modulator of plant growth, achieved by integrating multiple environmental and hormonal signals via protein–protein interactions [119]. Besides, a DELLA-independent pathway is also involved in the regulation of GA responses.

1.3. The length of induction treatment

Various plant species, or plants within population, usually require different number of inductive day-night cycles before an irreversible commitment to form flowers, called floral evocation, is reached [11, 13]. In many species flower evocation (or apex induction) is particular sensitive to day-length, flower differentiation less so. The opposite situation is observed in *Papilionaceae* family, for example.

Inadequate time of induction (insufficient number of photo-inductive cycles or when the cycles are near to the critical day-length) may seriously affect further development of flowers, resulting in their complete or partial abortion. When the induction is minimal, flowers abort at an early stage; when the induction is stronger, flowers develop, but sporogenesis may be inhibited, microspore formation being more sensitive [109]. Both anther and carpel development may respond to photoperiodic conditions. Either male or female sterility may be affected in different species. Among economic plants effect of photoperiod on fertility was studied in soybeans [73], maize [66] and some other crops.

2. Effect of photoperiod on the formation of reproductive structures

Photoperiodic effects on flower initiation and development are known to be important determinants of yield in many of the major crop species [30, 98, 112]. Day-length is an important regulatory factor in the initiation and development of inflorescence in the cereal crops including both LDP (temperate cereal grains such as wheat and barley) and SDP (maize, sorghum, and rice). Day-length is also known to influence some components of yield, such as spikelet number in wheat [113] and grain weight and spikelet fertility in spring barley [55]. In grasses, the timing of the inflorescence meristem transition to floral meristems is critical to determine inflorescence architecture; *Arabidopsis LFY* and *TFL1* (promoting floral meristem identity or indeterminate state, respectively) homologs play a role in it [106]. As for the grain legumes, the photoperiodic requirements for flower development are more stringent than those for initiation [91]. The period of anthesis and seed set is a critical stage in their development, and a serious loss of buds, flowers, and immature pods usually occur under unfavorable day-length [41, 91].

3. Sex expression

Sex expression in various plant species is controlled by the day-length. Either femaleness or maleness may be enhanced by photoperiod. Within dioecious species, relative femaleness (higher proportion of female to male flowers) is promoted by SD in hemp and hops [107] and by LD in spinach [22]. High responsiveness is also observed in monoecious plants. SD promotes femaleness in SDPs maize [88], cucumber and other cucurbits [74]. This response must be taken into consideration during introduction of the cultivars and for better timing of the crops, especially in the greenhouse production of cucumbers.

Photoperiodic control of vegetative growth and reproduction

1. Vegetative growth and biomass accumulation

As it was mentioned above, numerous processes in plant besides flowering are sensitive to photoperiodic conditions, directly or indirectly. The principal responses are reviewed briefly below.

Effect of photoperiod on vegetative growth can be direct or indirect. The distribution of dry matter can be profoundly modified by day-length as it is clearly seen in the control of tuber and bulb formation. These changes in the growth habit can result partly from the changes in the assimilate partitioning due to the appearance of the new sinks. However, there is evidence of direct effect of photoperiod on the distribution of dry matter and growth habit in various life-forms, including changes in branching patterns [115]. In grasses, it is associated with greater tillering in SD than in LD (reduction of tillering in LD can be observed even in plants grown without vernalization, that is influence of a developing inflorescence as a sink was eliminated) [75, 85, 115].

Plant vegetative growth and biomass accumulation can be modified by photoperiodic conditions either being linked with determination of flowering or independently. In rosette LDPs, the stem elongation usually accompanies flower initiation [79]. Early induction of flowering decreases both biomass production and seed yield in early maturing varieties. In late maturing varieties, competence to photoperiodic induction appears in the life cycle later, resulting in increased branching, leaf area duration [18] and yield. In numerous vegetable salad crops, long juvenile phase (late competence to photoperiodic stimulus) is a desirable character providing their bolting resistance and, therefore, high quality of the yield. Thus, modern lettuce varieties are grown with artificial lighting under extremely long photoperiods without risk of bolting (highest lighting efficiency at photoperiod 20 h) [49].

Leaf growth and branching habit, stem elongation and rooting capacity are often under photoperiodic control, as well. In the succulent plants, the degree of succulence and leaf morphology can be influenced by the day-length, providing their better adaptiveness in the arid climate [89, 121]. Formation of the specific photosynthetic structures and dramatic adaptive changes in metabolism are observed in CAM plants in response to the increasing day-length before the period of drought [20]. Another example of seasonal dimorphism can be found in several chamaephytes of Mediterranean and desert vegetation. Large spring leaves are shed in early summer; they are changed by smaller summer ones, that results in reduction of plant transpiring mass when water stress is likely to occur. In autumn large leaves are produced again. These unique seasonal changes in growth habit are dependent upon day-length [10].

2. Photoperiodic control of dormancy

Dormancy is an example of adaptation to unfavorable environmental conditions to which the dormant plant or organ is more resistant than the non-dormant one (stress avoidance strategy). Dormancy may involve a suspension of growth without the production of special structures as in *Weigela florida* [109], but usually specialized resting organs are produced. Such processes are of great importance as the induction of dormancy, bulb and tuber formation in perennial plants are controlled by photoperiod.

Photoperiodic conditions can promote breaking of dormancy, as well. The control of the bud break time by day-length may be of special importance for the breaking of

dormancy in woody species in regions of warm winters [109]. Photoperiodic responses of grains to light, coupled with light intensity may have a very significant role in controlling germination of some grass seeds [92].

In the vast majority of woody plant species, the rate and duration of elongation growth or cambial activity is increased by LD, while in SD their growth rate is decreasing and the onset of dormancy is hastened. Resting structure formation, including resting buds, is induced by SD. Only few exceptions exist: dormancy in onions (formation of bulbs) or desert liverwort *Lunularia cruciata* [90] is induced by LD. In deciduous plants, dormancy is accompanied by the shedding of the leaves, leaf fall being directly influenced by photoperiodic conditions in many species [36]. This provides plant survival under water stress when water supply is dramatically reduced either due to low temperature blocking root activity or because of poor precipitation during the dry season. Bud dormancy is not induced by the short days of spring which follow immediately after dormancy had been broken by winter low temperatures; at this stage bud growth is usually insensitive to day-length which in autumn induces dormancy.

3. Photoperiodic control of storage organ formation

Vegetative storage organs are of special interest in some crop plants. Perennating storage organ formation is a result of lateral swelling in a number of plant tissues including stems (corms and tubers), roots (tuberous roots), and leaves (bulbs). Their development is usually followed by cessation of growth and senescence of the leaves and other plant parts. The change of plant morphogenetic pattern in some life-forms can be followed by the alteration in leaf morphology. Thus, bulb formation in *Alliums* induced by LD involves modifications of growth to form scales; the lamina is suppressed while leaf base lateral growth is increased.

The control of tuber and bulb formation have the same features as other photoperiodic phenomena. Phytochromes and cryptochromes appear to be the main photoreceptors, and the whole mechanism is very similar to that of the photoperiodic control of flowering. The perception of photoperiodic signal occurs in the leaves; stimuli originating there are translocated to the responsive organs and tissues. No unique tuber or bulb evoking stimulus has yet been identified. The concept of florigen, postulated in the early 1930s, has taken form after the identification of the FLOWERING LOCUS T (FT) protein as the flowering-inducing signal. Besides their role in flowering, *FT* genes were subsequently reported to play additional functions in other biological processes. This is particularly relevant in the nightshades, where the *FT* genes appear to have undergone considerable expansion at the functional level and gained a new role in the control of storage organ formation in potato (*Solanum tuberosum*). Neofunctionalization of FT homologs in the nightshades identifies these proteins as a new class of primary signaling components that modulate development and organogenesis in these agronomic relevant species [2]. Recent studies have led to the identification of members of the *FT* gene family as major component of the tuber-inducing signal and the characterization of circadian and photoperiodic components involved in the regulation of these genes. A relevant role of microRNAs in the control of storage organ formation has been established, and hormonal balance requirements similar to those controlling shoot branching were shown to be implicated in the activation of stolon meristem cells. Finding that *FT* controls branching through direct interaction with the TCP factors holds great promise for the identification of genes acting as *FT* signal integrators in the stolon [71].

As with flowering, the development of storage organs is an inductive process. However, bulbing is photoperiod-dependent right until maturity. Therefore, photoperiodic induction of bulbing seems to differ in this respect from photoperiodic induction of flowering which is truly inductive and requires photoperiodic stimulus for its initiation only [54].

Most photoperiodically induced storage organs are favored by exposure to SD, except bulbs in *Allium*. In onions, SD is unfavourable for bulbing and further response to inductive low temperature (vernalization) results in flower initiation; after that LD conditions usually accelerate flower-stalk emergence. Some tropical onion varieties have no vernalization requirement, and their transition to bulbing or flowering is determined exclusively by the day-length [101]. Besides onions, dual photoperiodic response can be observed in some other species. In potatoes, SD promotes tuber formation, and LD is favorable for flowering. As for Jerusalem artichoke, both tuberization and flowering are promoted by SD conditions.

There is considerable variation in the level of photoperiodic sensitivity within the species grown in a wide range of geographical localities. In potato, some cultivars have an absolute SD requirement for tuberization, but the great number of cultivars form tubers in LD as well, providing their disperse in the higher latitudes. Though in SD tuberization is accelerated, the final yield usually is higher in LD where vegetative growth is pro-longed [81].

In onions, bulb formation is qualitatively dependent on exposure to LD conditions. However, there is considerable variation in critical day-length within cultivars. It is much lower in tropical genotypes, providing their proliferation in low latitudes. High temperature enhance bulbing; this response is of special importance for bulbing under SD conditions, as well. In the extremely LD bulb formation occurs sooner, and many tropical cultivars demonstrate ephemeroid rhythm of growth and development after introduction to higher latitudes. Only small bulbs can be produced here because of the decreased leaf area duration and early plant senescence [9, 18]. On the other hand, late competence to photoperiodic signal observed in some genotypes prevents rapid onset of bulbing providing emergence of the new leaves and further increase in photosynthetic capacity. This results in increased bulb yield under LD conditions. The same goals can be achieved in autumn-sown onions when plants are influenced by short photoperiod at the beginning of vegetation.

Besides formation of storage organs, photoperiodic conditions may affect growth of some other vegetative reproductive structures. The production of runners in strawberries, a SDP for flower initiation, is dependent on the exposure to LD, for example [39].

Genetics of photoperiodism

It is clear that genes are primarily responsible for the major differences that exist between LDP and SDP, or between the plants that have different length of juvenile phase, or need different number of inductive cycles [60].

In several major crops the genes for photoperiodic response have already been iden-tified. In wheat, *e.g.*, it was found that variation amongst chromosomes, particulary at the *Ppd* 1 and *Ppd* 2 loci are responsible for the close adaptation of the major groups to dif-ferent geographical regions. And the Green Revolution wheat species bred in Mexico owe their wide adaptability to an allele of *Ppd* 1 conferring insensitivity to day-length [60]. As a result, these cultivars were grown under the SD winter conditions in India and Pakistan successfully. The *Ppd* genes have effects on time to ear-emergence, plant height and plot yields [59].

Besides photoperiod, differences between winter and spring wheat in their response to temperature (vernalization) are determined by vernalization genes *Vrn*. It seems that in various wheat forms there is temporal specificity in the activation of *Ppd* and *Vrn* systems. [37].

One of the most extensively studied genetic systems for the photoperiodic control of flowering was described for pea [69]. There are several major loci that confer or modulate the plant ability to perceive and respond to day-length changes. Various genes control the formation of flowering inhibitor and photoperiodic response at law temperature, competence of meristem to floral stimulus and apex aging.

The evaluation of the genetic effect contribution to varietal performance under a range of conditions should lead to definitions of optimal genotypes for particular environments which would be of great value for plant breeders.

Under marginal photoperiodic conditions, the analysis of growing form and some quantitative characters within varietal populations of several vegetable crops, *e.g.*, shows significant variation in biotype developmental rhythms. Some of the genotype by environment interactions within various biotypes can be ascribed to the differences in the length of juvenile phase, critical day-length and civil twilight sensitivity [102]. These determinants of photoperiodic response must be taken into consideration for crop timing, breeding design and population screening.

Manipulation of photoperiodic response by selection and breeding

The adaptive advantage of photoperiodic response allows wild species to occupy successfully well-defined geographical locations and ecological niches. However, it presents agriculture with the problem of reversing evolutionary trends in order to increase the range for providing their crop species cultivation adaptiveness to the various geographical locations [27]. High photoperiodic sensitivity can retard the dispersal of certain genotypes. What may seem optimal for adaptation may not be so for the yield.

1. Modification of photoperiodic responses by selection

Modification of the photoperiodic response of domesticated plants by selection, much of it done unconsciously, has played a major role in adapting landraces and varieties to local conditions, permitting the spread of crops to new regions and environments, improving yield potential and reliability [31, 103]. Many successful crop plants share with weeds the property of adaptability to a wide range of environmental conditions [7]. The mechanism controlling their germination and flowering have been relaxed to some extent under selection. In many modern varieties of soybean, potatoes, wheat, and rice, for example, control of flowering by day-length is far less stringent than in related wild species [30]. With tropical crops grown under irrigation, such as rice, whereas previously it was advantageous for varieties to flower only at the end of the wet season, so that the grains grew on stored soil water and could be dried and harvested in sunny weather, now the emphasis is on using irrigation to grow several crops of rice per year, with the consequence that their flowering must be insensitive to day-length [31].

However, wild progenitors and crop plants, especially local landraces, are not consistently different in their sensitivity to photoperiodic conditions. Modern wheat cultivars from high latitudes often show an absolute requirement for LD, possibly to avoid frost injury to the young inflorescence [30]. And some tropical rice species, SDP, show

an extreme sensitivity to day-length [28, 76] that may also be adaptive. For example, floating rice must delay its flowering until the monsoon floods recede, or the grain cannot be harvested.

2. Modern strategies in plant breeding

When crop plants are considered, day-length responsiveness is a major factor to be taken into consideration in selection for improved productivity of wide geographical dispersal. Independence of day-length is specified as a desirable character in both Mexican wheat and IRRI rice breeding programs, to aid trans-world adaptation. The new varieties released were less sensitive to photoperiod and could therefore be planted more widely. Besides, shorter duration varieties were also important to increase productivity because they fit better in double or multiple cropping situations, were often less susceptible to drought and other stresses as well as insect and disease attacks because of shorter time in the field [80]. As a result, "history records no increase in food production that was remotely comparable in scale, speed, spread and duration" [61].

High photoperiodic sensitivity of a cultivar often can hamper its dispersal and limit the cropping area. It does not always follow, however, that the best approach is to breed for day neutrality. Though in selecting stable varieties - especially for the major cereal crops - significant gains have been achieved in adaptability and hardiness to stressful crop-growth conditions, the gains in stability selection may be compromised by selection for responsiveness, and vice-versa [6].

Therefore, photoperiodic control of flowering offers alternative strategies for the plant breeder. One strategy is to breed for responses that are tailored to make the best use of particular season conditions. Another strategy is to decrease day-length control so that autonomous induction occurs and flowering is no longer under strict control of environment [111].

Improving yield potential

1. Genetic background

According to the strategy of sustainable agriculture, among the factors that will influence the types of new agricultural technologies in the 21st century there will be a need for a greater specificity and, therefore, tailoring of genetic materials and agronomic practices for specific production locations [80]. The combination of improved biological potential of crops and intensive crop management has produced many benefits.

Adaptation to photoperiod can be an important component of high crop yields, and cultivars with developmental patterns tailored to make the best possible use of particular geographical and seasonal conditions offer an alternative strategy to the breeding of cultivars without day-length and temperature sensitivity [110]. Furthermore, there are some horticultural plants where a strong response to photoperiod enables their flowering time to be artificially manipulated and precisely controlled, providing the high yield of a good quality.

The manipulation of genotype flowering time to increase its yield potential may run counter to the changes involved in selecting for wider adaptation or greater yield stability [31]. Closer adaptation to local conditions and later flowering with more growth before it tend to enhance yield potential. The yield is often positively correlated with leaf number

and area and time to flowering under irrigated conditions. Changes over the last century among Philippine rice varieties illustrate some of the cross-currents and compensation factors [33]. The traditional local varieties were mostly sensitive to photoperiodic conditions, but varieties bred in the 1930s even more sensitive and the latest to flower in the field. As more rice was grown under irrigation, outside the wet season, varieties that were less strongly SD-requiring and that flower faster were selected. In the 1960s the trend towards day-length insensitivity became more pronounced but that towards faster flowering was reversed by the selection of varieties like IR 8 with a longer juvenile phase, associated with greater yield potential. And now, selection is focused on varieties with a shorter juvenile phase, so that more crops per year can be grown, but without a reduction in yield potential.

Another example of selecting plants to fit closely a given aspect of environment could be observed, *e.g.*, in sorghum. In West African genotypes of this plant, flowering has been selected to coincide with the average date of the end of rainy season (itself determined by latitude) so that grain loss by insect and fungal attack is minimized by dry conditions [68].

2. Adaptation of technologies

Some commodities and production technologies developed are inherently more sensitive to environmental factors than others. A common assertion is that crop-related technologies have more limited transfer potential than livestock technologies [77].

When a cultivar with appropriate level of photoperiodic sensitivity is chosen, precise timing of the crop can provide an effective use of its yield potential. In soybeans, at law latitudes plant is usually performed a month before the longest day, especially for early cultivars, so that plants are not stunted by premature photo-induction which may decrease yield [91]. In subtropical regions, sowing of onions in late summer will result in their bolting; for bulb production sowing is usually performed two months later.

3. Environmental manipulation of flowering.

Environmental manipulation to control the incidence, timing and quality of flowering is characteristic of modern horticulture. Control of day-length has long been applied to maintain year-round production of flowers in both SDP and LDP. In vegetable crop production, *e.g.,* day lengthening techniques is used to prevent bolting in celery grown in greenhouses during winter season.

As for the field crops, sugar cane is one of few examples of environmental manipulation of flowering. Its intermediate day-length response limits flower induction to a brief period each year, the first 20 days of September in Hawaii, and exposure to light breaks on at least 5 of these 20 nights prevents flowering and raises sugar yields [64]. It is an effective control system, although costly. An alternative is to stress the crop by withholding irrigation water for a month prior to induction.

Conclusions

The dual concerns of maintaining the resource base and increasing crop yields are connected with the progress towards formation of sustainability perspective into agricultural research that should be in the context of specific geographical areas, production systems, and resource concerns. All these issues are interrelated with the problem of photoperiodism in

plants. The advantages and disadvantages of responsiveness to photoperiod are considered for the field crops grown in natural environment and for glasshouse crops, where flowering time could be manipulated with artificial photoperiods. Day-length influences many aspects of plant behavior and has significant effect on plant distribution and plant yield. Therefore, photoperiodic response must be taken into consideration during technology transfer in plants and transfer of plant cultivars.

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ФОТОПЕРИОДИЗМ СЕЛЬСКОХОЗЯЙСТВЕННЫХ РАСТЕНИЙ

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В обзоре рассматриваются особенности фотопериодической регуляции роста и развития у сельскохозяйственных растений. Показаны механизмы, лежащие в основе восприятия фотопериодического сигнала и индукции морфогенетических процессов. Фотопериодическая реакция обеспечивает синхронизацию онтогенеза растений с ритмом сезонных изменений климата. Вместе с тем, высокая периодическая чувствительность может ограничивать ареал ценных сельскохозяйственных культур, сортов и гибридов. Эти проблемы решаются с помощью селекционных подходов.

Ключевые слова: сельскохозяйственные культуры, фотопериодизм, адаптация, онтогенез, продуктивность, селекция.

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