



Early vegetative and heading phenology of barley accessions grown in moderate and long daylengths in controlled environment chambers and field environments  
by Gregory Allen Brown

A thesis submitted, in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Agronomy  
Montana State University  
© Copyright by Gregory Allen Brown (1980)

**Abstract:**

The major environmental factors affecting floral induction are photoperiod and temperature. Three experiments were conducted to investigate photoperiod affects on vegetative and heading phenology in barley; One experiment consisted of growing 68 accessions of barley under two different photoperiod regimes, one a 14 hour 80°F day-8 hour 60°F night and the other identical to the first, but with the night period interrupted at its midpoint with one hour of low intensity fluorescent light. Days to four-leaf stage and heading were recorded. The second experiment was set up like the first (with only ten varieties), but was concerned with correlating leaf number with growing point morphology. The third experiment was conducted to evaluate heading dates for 112 varieties and lines grown in two different geographic locations (at the same latitude) seeded prior to and after the summer solstice.

Significant differences in days to heading under the two different photoperiods were detected in only five varieties. The accuracy of predicting heading phenology in a population of barleys based on their ranking of days to four-leaf stage is limited. Investigations of juvenile vegetative and floral phenology in ten barley accessions of varying maturity habits shows a consistent and significant correlation between leaf number and apical organogenesis in spring varieties. A significant similarity in heading date rankings between two geographic locations (for spring and post-summer-solstice) seedings was detected. Relative heading date rankings were significantly related between the growth chamber and field studies, but the correlation is low enough to advise caution in predicting field heading from growth chamber trials.

STATEMENT OF PERMISSION TO COPY

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at Montana State University, I agree that the Library shall make it freely available for inspection. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by my major professor, or, in his absence, by the Director of Libraries. It is understood that any copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Signature

Gregory A Brown

Date

Dec. 4, 1980

EARLY VEGETATIVE AND HEADING PHENOLOGY OF  
BARLEY ACCESSIONS GROWN IN MODERATE AND  
LONG DAYLENGTHS IN CONTROLLED ENVIRON-  
MENT CHAMBERS AND FIELD ENVIRONMENTS

by

GREGORY ALLEN BROWN

A thesis submitted in partial fulfillment  
of the requirements for the degree

of

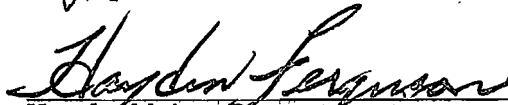
MASTER OF SCIENCE

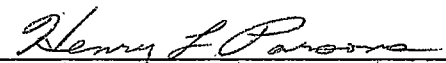
in

Agronomy

Approved:

  
Chairperson, Graduate Committee

  
Head, Major Department

  
Graduate Dean

MONTANA STATE UNIVERSITY  
Bozeman, Montana

December, 1980

N378  
B8136  
cp.2

TABLE OF CONTENTS

	PAGE
INTRODUCTION . . . . .	1
Literature Review . . . . .	1
An Introduction to Photoperiodism . . . . .	1
Plant Distribution and Latitude . . . . .	3
Critical Daylength Concept . . . . .	3
Temperature and Photoperiodism . . . . .	5
Irradiance Level and Photoperiodism . . . . .	5
Plant Maturity and Photoperiodism . . . . .	7
History of Photoperiodism Research . . . . .	9
Physiology of Induction . . . . .	11
General Review of Photoperiodism in Crop Plants. . . . .	12
Photoperiodism in Cereal Crops . . . . .	15
Photoperiodism in Barley . . . . .	18
Statement of the Research Problem. . . . .	23
MATERIALS AND METHODS . . . . .	25
RESULTS AND DISCUSSION . . . . .	33
SUMMARY . . . . .	59
LITERATURE CITED. . . . .	61

## LIST OF TABLES

TABLE		PAGE
1	Lines Isogenic for Earliness and Other Varieties Used in the Photoperiod Study . . . . .	26
2	Barley Varieties and Lines Seeded at Bozeman and Huntley . . . . .	31
3	Days Elapsed from Seeding to Appearance of the Fourth Leaf Under Moderate Daylength Conditions (14 Hours of Light) and Long Day Conditions (14 Hours Light Plus Dark Period Interruption). . . . .	34
4	Days Elapsed from Seeding to Heading Under Moderate Daylength Conditions (14 Hours of Light) and Long Day Conditions (14 Hours of Light Plus Night Interruption) . . . . .	35
5	t-test of Differences in Days to Heading Between the Two Photoperiods . . . . .	36
6	Linear and Quadratic Correlation Coefficients and Linear Slope for Early Floral and Vegetative Phenology of Ten Barley Accessions . . . . .	39
7	Differences in Rates of Development (Linear) for the Ten Varieties Under the Two Photoperiods . . . . .	40
8	Mean Days to Heading: Bozeman . . . . .	47
9	Mean Days to Heading: Huntley . . . . .	50
10	Relationship Between Heading Date Rankings for Early and Late Seedings: Bozeman and Huntley . . . . .	53
11	Relationship Between Heading Date Rankings at Bozeman and Huntley: Early and Late Seedings . . . . .	55

## LIST OF TABLES (continued)

TABLE		PAGE
12	Heading Dates for Varieties Paired in Growth Chamber and Field Trials. . . . .	56
13	Relationship Between Growth Chamber and Field Trial Heading Dates. . . . .	58

## LIST OF FIGURES

FIGURE		PAGE
1	Barley Growing Point Phenology (Developmental Morphology) . . . . .	29
2	Early Vegetative and Floral Phenology of Ten Barley Accessions . . . . .	41
3	Linear Relationship Between Vegetative Condition (Leaf Number), X-axis, and Floral Condition (Growing Point Rating), Y-axis . . . . .	44
4	Quadratic Relationship Between Vegetative Condition (Leaf Number), X-axis, and Floral Condition (Growing Point Rating), Y-axis . . . . .	45

## ABSTRACT

The major environmental factors affecting floral induction are photoperiod and temperature. Three experiments were conducted to investigate photoperiod effects on vegetative and heading phenology in barley. One experiment consisted of growing 68 accessions of barley under two different photoperiod regimes, one a 14 hour 80°F day-8 hour 60°F night and the other identical to the first, but with the night period interrupted at its midpoint with one hour of low intensity fluorescent light. Days to four-leaf stage and heading were recorded. The second experiment was set up like the first (with only ten varieties), but was concerned with correlating leaf number with growing point morphology. The third experiment was conducted to evaluate heading dates for 112 varieties and lines grown in two different geographic locations (at the same latitude) seeded prior to and after the summer solstice.

Significant differences in days to heading under the two different photoperiods were detected in only five varieties. The accuracy of predicting heading phenology in a population of barleys based on their ranking of days to four-leaf stage is limited. Investigations of juvenile vegetative and floral phenology in ten barley accessions of varying maturity habits shows a consistent and significant correlation between leaf number and apical organogenesis in spring varieties. A significant similarity in heading date rankings between two geographic locations (for spring and post-summer-solstice) seedings was detected. Relative heading date rankings were significantly related between the growth chamber and field studies, but the correlation is low enough to advise caution in predicting field heading from growth chamber trials.



## INTRODUCTION

### LITERATURE REVIEW

#### An Introduction to Photoperiodism

Photoperiod regulates diverse physiological and morphological attributes of plants and animals (12,61). Photoperiodism was first defined as the elicitation of a specific response by the length of the day and night periods by Garner and Allard in 1920 (28). They studied the flowering of tobacco and soybeans with controlled photoperiods. Photoperiodism is controlled by physical factors; directly by the length of the dark period and some times indirectly by temperature. Physiological, behavioral and morphological qualities which are subject to photoperiodism are said to be photoperiodically sensitive while those qualities and species which are not so controlled are said to be photoperiodically insensitive (12,61,38,71,35). The observable responses of photoperiodically controlled processes are photomorphogenic events (61).

Photoperiodic control of animals may trigger, at various stages in their life histories, reproductive behavior, migration and alteration of seasonal appearance. Some examples of these photoperiodic responses are: induction of estrus in goats, sheep and raccoons (2); stimulation of migration in water fowl, fish and mammals (61); and initiation of seasonal color changes in the plumage of yellow ptarmigan (2) and the pelage of snowshoe hare, ermine, raccoon and red fox (2).

Physiological and morphological responses to daylength are characteristic of many angiosperms (12,61). Floral initiation in such plants as big bluestem (1), barley (57,4,45), oats (62), wheat (17,72,42), soybean (36), sugar beet (1), radish (1,68), strawberry (1,68), coneflower and cucumber (1,68) is governed by photoperiod. Winter hardening in alfalfa (68), bulb formation in onion (68), tuber development in potatoes and yams (68) and stolon growth in strawberry (68) are also photoperiodically controlled. Still other plant functions so regulated include CO<sub>2</sub> fixation in Kalanchoe (67), cambium activity (77), bud swelling (12,76) and seed germination (1).

Seasonal changes in the length of diurnal radiation periods are a more reliable cue than temperature in prompting organisms to appropriate seasonal transformations (12). On a given calendar day the length of the light and dark periods are essentially identical from year to year. In environments like the ocean which are strongly buffered by mass against rapid temperature changes, temperature can be a reliable seasonal cue. In terrestrial environments, however, temperatures may vary greatly from year to year for a given calendar day. Plants which rely on temperature to initiate physiological changes would be at a selective disadvantage to plants which react to changes in the length of day and night to consistently key their seasonal functions (12).

### Plant Distribution and Latitude

Bunning (12) credits Henfrey in 1852 as the researcher to first mention daylength as a factor affecting the distribution of plants. Photoperiodism is an environmental parameter affecting niche exploitation and adaptation to changing niches (65) and has thus exerted selection pressure and contributed to plant evolution and speciation (46,42,11). The latitudes most subject to temperature extremes and which may experience wide deviations from one year to the next are the middle temperate latitudes (35-45°). Many photoperiodically sensitive plants originated in these middle temperate latitudes (12,65,13,55,54). Even within a single species, geographic races may vary in their photoperiod sensitivity along a latitude gradient (55).

Photoperiodism is not a hit or miss environmental cue; it is a very accurate biological means of time measurement. Bunning (12) reports that light and dark periods are measured accurately to within just a few minutes. This trait enables photoperiodism to operate even in near equatorial environments where only slight variations in the length of day and night occur throughout the year (53).

### Critical Daylength Concept

The triggering of responses by certain daylengths led to the concept of critical daylength. Garner and Allard (28) were the first to use the terminology long day, short day and day-neutral in

describing plant photoperiod responses. Plants which flower when exposed to a photoperiod longer than a critical minimum are long day plants while those flowering only when the light period is shorter than a critical maximum number of hours are short day plants (28). Day neutral plants are independent of photoperiod initiation of morphological or physiological changes, depending instead on achieving an appropriate level of physiological maturity controlled by other genetic and environmental parameters (61). Examples of long day plants are smooth bromegrass, oats and red clover (61). Short day plants include chrysanthemum, cocklebur and june bearing strawberry (61). Buckwheat, annual bluegrass and tomato are considered to be day neutral (61,20).

The critical daylength concept is somewhat misleading because the triggering affect of photoperiod is usually a matter of degree (quantitative) and not simply "on" or "off" (qualitative) (12,61,38,71,35,20). The rate of development of photomorphogenic characters is proportional to the extent by which the photoperiod surpasses the threshold level (41,45,17,16,62,70). Wareing (76) reported that the buds of beech trees remain dormant so long as daylength is less than twelve hours, but the more the light period exceeds twelve hours the more rapidly dormancy is broken. This is a quantitative rather than a qualitative response to daylength. Other plants are extremely specific in their photoperiod requirements. According to Bunning

(12), Cestrum nocturnum flowers only when exposed to photoperiods between eleven-and-a-half and twelve hours. Some varieties of sugar cane also have very specific photoperiod requirements (61).

#### Temperature and Photoperiodism

Plant processes immediately involved in perception of the light environment and signaling the pathways responsible for initiating the photomorphogenic event (induction, 38) are essentially temperature independent (32), having a  $Q_{10}$  of 1.02 (60). The ultimate manifestation of the induction (floral initiation, bud swelling, etcetera), however, may have a  $Q_{10}$  ranging from 1.5 to 2.5, indicative of more typical biochemical pathways (61). This may lead to the masking of the light perception-response induction system by the plant response to temperature (12). Photomorphogenic events then appear to be temperature dependent when in fact only the post inductive components of the response are influenced by temperature.

#### Irradiance Level and Photoperiodism

The photoinductive reactions are essentially independent of increases in irradiance levels above the threshold level (12, 38, 57). Obtratsov (54) reported less pronounced response to natural daylength reduction than to artificial daylength reduction. This may be partially explained by Paris and Jenner (59) who show that the threshold irradiance level for photoperiodic responses occurs when

the sun is several degrees below the horizon (at dawn and dusk). There are organisms which exhibit photoperiod sensitivity down to .1 lux (21), but moonlight (up to .5 lux) does not generally elicit a photoperiodic response.

Irradiance levels can affect photoperiodic response through photosynthesis controlled photosynthate availability. Jordan and Huffaker (41) studied the effect of light and dark periods on nitrate reductase activity and carbon dioxide fixation, finding that continuous light or flashing light increased the metabolic activity of seedlings, but that dark pretreatment decreased metabolic activity. Significant levels of plant metabolism are apparently dependent on the energy rooted in the carbon chain products of photosynthesis. Sjoeth (64) has reported that differing photoperiod effects can resemble variations in light intensity (irradiance levels) and that increased hardiness in meadow and pasture plants is probably associated with photosynthesis-photoperiod interactions as regulated by assimilate availability. Irradiance levels strongly influence photosynthetic rate and ultimately assimilate supply (61). Paleg and Aspinall (57) report that apical organogenesis in barley seedlings is not closely related to rate of assimilate supply. It therefore appears that the more closely associated the metabolic response is to the photoinductive reactions the smaller the photosynthetic influence. The light perception-induction system is intensity independent, but

light intensity can affect, via photosynthesis, the rate of the plant response to photoperiod.

#### Plant Maturity and Photoperiodism

Another factor affecting photoperiod sensitivity and response is plant maturity. Salisbury and Ross (61) report that not all plants respond to photoperiod treatments equally well. They cite the early German photoperiodism researcher Georg Krebs as the first investigator to use the term "ripeness to flower" to describe the condition a plant must attain before it will flower in response to environmental stimulus (61). The Japanese morning glory (Pharbitis nil) attains this ripeness at an early age, flowering in the cotyledonary stage and red goosefoot (Chenopodium rubrum) can flower even as a minute seedling when exposed to sufficiently short days (61). McKee and co-workers (50) have determined that flowering in crownvetch (Coronilla varia L.) is controlled by an interaction of plant maturity, photoinduction and thermoinduction. Younger plants of crownvetch require longer thermoinductive periods (less than or equal to 10°C) than older plants to flower when exposed to a critical fifteen hour photoperiod.

Related to the plant maturity requirement is the number of light-dark cycles necessary for photoinduction. Snyder (66) reports that plantain (Plantago lanceolata) will achieve 100 per cent

inflorescence formation after being exposed to twenty-five photoinductive cycles. The plant will not flower if first exposed to less than the twenty-five cycles and then returned to a non-inductive condition. Flowering will occur, though, when a total of twenty-five cycles has been completed after return to an inductive environment. Hillman (38) refers to this capability as fractional induction which is a fairly common trait among long day plants. Schwabe (63) determined that Glycine max (soybean), Chenopodium amaranticolor and Perilla ocymoides, all short day plants, will not flower if a non-inductive photoperiod is interposed between two inductive photoperiods. The non-inductive (long day) cycle apparently rendering the short days following it ineffectual (38). Carr (15) determined that at least some short day plants can be partially induced, thereby contradicting the reports of Snyder (66). His work suggests that the predisposition toward partial induction is species dependent and not confined to particular flowering types. The short-day plant cocklebur (Xanthium pennsylvanicum) and the long-day plant darnel (Lolium temulentum) (like some others of their flowering types) require only a single photoinductive cycle to initiate flowering (61).

Associated with the photoinductive cycle numerical requirement is the discrimination between increasing and decreasing photoperiods. The capacity to distinguish between lengthening and shortening days is a prerequisite in cueing the plant to the seasons, since each



individual light-dark combination occurs twice a year (12). Various combinations of short-long and long-short sequences can initiate flowering depending on the species (74). Vernalization requirements frequently work in conjunction with daylength sequences to control reproductive physiology (43,61).

Obviously photoperiodism is not a simple phenomenon. There are many factors acting in combination with the light and dark periods to control plant responses. The preceding review of photoperiodism observations and measurements provides a basis for investigating the details of the mechanisms of light perception and response induction.

#### History of Photoperiodism Research

Inquiries into the specific mechanisms of photoperiodism have become gradually more specific since the turn of the century. Hillman (38) and Murneek and Whyte (51) cite the accomplishments of several early workers in photoperiodism research, but point out that Garner and Allard (28) were the first to tie the previously isolated observations together. The discoveries of this research team came about inadvertently when investigating flowering in "Maryland Mammoth" tobacco (27). The mutant had arisen as a large leafed type in a field of tobacco plants. All other plants flowered as the season progressed; the mutant did not. Fearing the loss of this

mutant if unable to obtain seed, Garner and Allard transferred the plant to the greenhouse where it continued in a vegetative condition until mid-December. Flowering and seed set were then successfully completed and the seed was planted in the field the next growing season. The development pattern repeated itself and they set out to investigate the factors leading to this late flowering behavior. After testing many environmental parameters they eventually concluded that exposure to short days would cause flowering. Continued investigations determined that natural and artificial daylength reduction were both effective (28). Hamner and Bonner (35), working with cocklebur (Xanthium), established that the length of the dark period rather than the length of the light period was the critical factor in photoperiodism.

Not until the mid-fifties were the mechanisms of photoperiodic behavior elucidated. Then, Borthwick, Hendricks and Parker (8) established that a system of two at least partially reversible pigment states enabled plants to perceive the length of light and dark periods. They labeled this plant pigment "phytochrome." The action spectrum had two peaks, one pigment state having a maximum absorbance at 650 nm ( $P_{650}$ ) and the other at 740 nm ( $P_{740}$ ). Red light (650 nm) converted the  $P_{650}$  form to the  $P_{740}$  form while far-red light (740 nm) converted  $P_{740}$  to  $P_{650}$  in a thermally controlled dark reaction. Since white light is richer in red than far-red, the

$P_{740}$  phytochrome state was predominant at the end of white light periods. In turn, it was found that the  $P_{740}$  form inhibited the initiation of flowering in short-day plants, but enhanced initiation in long-day plants. They concluded that short-day plants require a dark period of sufficient length to allow conversion of  $P_{740}$  to  $P_{650}$ .

Bidwell (6) credits K. M. Hartmann with a modified theory of the phytochrome action system. The system is essentially like that described by Borthwick, Hendricks and Parker (8), but differs in that an inactive photomorphogenic-inducing precursor must combine with  $P_{740}$  to elicit the appropriate photoperiod response. Hartmann further concludes that the synthesis of the active derivative of  $P_{740}$  is probably dependent on the absolute quantity of  $P_{740}$  converted from  $P_{650}$  rather than the relative proportion of the two. The fact that some plants exhibit a requirement for a specific number of photoinductive cycles (38,66) perhaps supports this contention that an absolute quantity of the activated  $P_{740}$ , a level that could be incrementally increased by successive cycling, is necessary to trigger the photoperiod response.

#### Physiology of Induction

The mechanism linking photoperiodic induction with response initiation is still the subject of speculation (12,61,6,38), but several aspects of its operation have been characterized.

Phytochrome enables a plant to perceive the photoenvironment (8) and the formation of the biologically active pigment state (6) readies the plant for the physiological or morphogenic event. The dark reactions comprising the activation and readying process have been best evaluated in regards to flowering. A flowering hormone (florigen) has long been suspected as an important factor, but has never been identified. Evidence for its existence, however, is strong (61).

Leaves, having been shown to be the receptor site for photoperiodic induction (47), readily translocate a hormone to other plant parts (52). Exposure of a leaf to an inductive photoperiod causes floral initiation even if the bud is in a non-inductive environment (21,48). Non-induced plants will flower when induced plant parts are grafted to them (52,36). These findings correlate well with the established guidelines for hormone action (61,20) which state that a hormone is an organic substance synthesized in one part of an organism and translocated to another part where it controls or regulates a physiological response (61,20). It is evident that photoperiodism involves many aspects of plant metabolism.

#### General Review of Photoperiodism in Crop Plants

The economic traits of many agriculturally important plants (some of which have been previously mentioned) are photoperiodically.

regulated (61,45,42,20). Beets, normally biennial in their endemic range produced good roots the first year without flowering, but when taken from their native latitudes they became annual (19). They flowered and set seed, but produced poor roots, thus representing a long day biennial for which shorter days (at lower latitudes) replaced vernalization and promoted flowering instead of channeling the plant's metabolism into assimilate storage in the roots. Selection and breeding programs were necessary to widen the latitude adaptation of beets. In a reversed situation Garner and Allard found that a short-day tobacco mutant would not flower in the latitudes of the southern U.S. tobacco region, but would flower in the daylengths of subtropical latitudes (29). The economic potential persisted, but the reproductive potential was missing. Again, breeding was needed to widen the latitude adaptation for seed production.

Crop plants suited for global distribution would be poorly adapted in many areas if photoperiod sensitivity affected the development of their economically desirable traits. Homozygous, homogenous crop cultivars developed to efficiently utilize readily manipulatable environmental factors (fertility, irrigation, et cetera) often are poorly suited to non-manipulatable parameters (73). Plants which complete their life cycles independent of the influence of the length of day and night possess the best genetic background for varieties intended for international distribution (24). This is one reason that

evaluation of the photoperiod sensitivity of varieties in international breeding programs is important.

Another potential use of photoperiod sensitivity in crop plants is to develop varieties intended for very specific cropping situations. Francis (24) has speculated that when sufficient detailed varietal information is available to determine critical light intensities and critical or optimum daylengths it may be possible to use daylength as a cropping management tool. Planting and harvesting could be managed to achieve maximum economic yield per day. Breeding program goals may then be oriented to wide scale adaptation or toward very narrow application.

Sjoseth (64), as previously mentioned, evaluated the influence of photoperiodism on perennial meadow and pasture plants, finding that it did influence winter hardiness. Carlson (14) hypothesized that since axillary bud formation is photoperiodically controlled, adventitious stem initiation was likewise affected. He found, by studying alfalfa (Medicago sativa), crownvetch (Coronilla) and sheep sorrel (Rumex acetosella), that plants exhibiting long-day response produced more nodes, longer internodes and greater top weight, but fewer adventitious stems. Apparently apical dominance suppresses adventitious stem initiation through a balance of shoot produced auxin and root produced kinetin. McKee (50) determined that young crownvetch plants required longer cold exposure than older plants before

flowering in long days. Evidently, photoperiodism influences perennials at various stages of their life cycles,

Perhaps more work has been done to investigate photoperiodic phenomena in annuals where simpler life histories enhance evaluation.

#### Photoperiodism in Cereal Crops

Because cereals have been important primarily in the mid-latitudes (to  $60^{\circ}$ ), it is especially important to thoroughly evaluate physiological factors affecting wide scale adaptation, including photoperiod response, when developing varieties intended for distribution in more tropical environs (45). Kirby (45) cites the conclusions of Doroshenko and Rasumov who determined from plantings of wheat, barley and oats at  $5-10^{\circ}\text{N}$  (Ethiopia) and  $62-65^{\circ}\text{N}$  (USSR) that the higher the latitude of origin the greater the response to daylength. Carder (13) grew several varieties of spring wheat, oats barley, field peas and millet at two locations; Madison, Wisconsin ( $43^{\circ}\text{N}$ ) and Beaverlodge, Alberta ( $55^{\circ}\text{N}$ ). Despite lower effective heat units at the northern location the crops headed at the northern and southern locations at approximately the same time. Post heading development was slower at the more northerly location. The work of Guitard (31) does not support the concept of greater photoperiodic response for more northerly varieties. He has shown that varieties originating in Scandinavia, but adapted to Canada were less responsive to

photoperiod than more southerly varieties. It is generally accepted; however, that northerly strains or varieties are more subject to photoperiodic influence (55,62).

Chinoy (17) determined that tiller production in wheat is significantly reduced under long day conditions, but is also reduced under extremely short days due to lack of assimilate. Tillering in oats, however, has not been shown to be similarly affected by photoperiod (45). Stevenson and Goodman (69) found that lower temperatures had a more profound influence on tiller increase than did shorter days.

Increases in main stem leaf number in corn are regulated more by photoperiod than temperature (69) and leaf emergence rate appears to also be controlled by daylength in wheat, barley and oats (45,16). Since leaves, like floral primordia (11), originate in the apex, the organogenesis of which has been shown to be affected by photoperiod (57), it logically follows that leaf development would also be affected.

According to Chinoy (16), alterations in developmental rate of change resulting from vernalization and photoperiod treatment change the whole pattern of plant growth. The change varies in the phases and components of growth which it affects (e.g., leaf dry weight; stem, leaf and tiller number; et cetera) in the different varieties (16).



The vegetative phase of wheat is most prolonged in the late flowering varieties (16).

Flowering in wheat responds quantitatively to photoperiod length (16,17), short days tending to retard heading (42). Variation among wheat cultivars to differing photoperiods is substantial and similar for both pre- and post-initiation stages, according to Halse (34). Oats respond similarly, heading earlier with longer photoperiods (62). Rice, unlike the other cereals, is a short day plant (61) and Suge (70) maintained rice in the vegetative phase with continuous illumination. When eight or more long nights were given to sixty day old plants, flowering occurred in another thirty days.

Vernalization can have strong influences in cereal floral development (45). Wheat varieties with strong vernalization requirements exhibited less pronounced response to short-cold days and photoperiod effects are more validly estimated on vernalized plants (34). Syme (72) determined that seventy-seven to ninety-four per cent of cultivar variation in time from sowing to ear emergence and to anthesis can be accounted for by the combination of vernalization and photoperiod.

The importance of photoperiodism to cereal crop breeding programs has led some researchers to investigate the genetics and inheritance of photoperiodic responses. Daylength insensitivity in wheat was found to not always be dominant over sensitivity (46). Crossing

studies did indicate that earliness (photoperiod insensitivity) tended toward dominance over the recessive lateness (photoperiod sensitivity). They concluded that the heading patterns could be explained by two major loci with three alleles at each locus. Chinoy (16) has suggested that the complex of genes controlling development in wheat also governs the extent and pattern of growth and that there may not be separate genes for the major growth processes. Keim (42) has concurred that a few major genes control photoperiodic response in wheat and indicated that minor genes governing earliness may mask the major gene vernalization and photoperiodism characteristics. Inbred and hybrid corn varieties were studied by Francis and co-workers (25) in growth chambers with 16 hour and 10 hour photoperiods. Genotypes differing more than six days in time from vegetative shoot apex to tassel development were considered to be sensitive; four to six days, intermediate sensitivity; and less than four days, insensitive.

Photoperiodic responses in barley (Hordeum vulgare and Hordeum distichum) have also been investigated.

#### Photoperiodism in Barley

The genus *Hordeum* (5,26), having originated in the eastern Mediterranean-central Asian region, had become established in Eurasia and North and South America by the Tertiary geologic period with

distinct speciation already evident (10). This migration into more hostile environments of the mid-latitudes undoubtedly enhanced development of the adaptive strategies of photoperiodism and vernalization (46). Ormrod (56) has reported that barley photoperiod sensitivity is not as great as that of wheat. Aspinall (3) cites evidence of several researchers describing barley photoperiod sensitivity as varying from insensitive to quantitatively sensitive to obligately sensitive. Varietal differences in barley photoperiod sensitivity do contribute to variation in heading date (56). Johnson and Gaul (40) state "The phenotypic expression of a quantitative character such as earliness may be considered as a result of two interacting factors, the genotype and the environment." Indeed, Chinoy's (16,17) work with wheat, showing that even very short days (six hours) would eventually bring a long day plant to flowering, suggests a strong quantitative response to photoperiod. Aspinall's (3) evaluation of several barley varieties also determined that no critical daylength was evident, but that a strong quantitative response existed. Photoperiod exerted a stronger influence on heading date than degree of spring habit or earliness in Ha and Yasuda's (33) investigation of 127 Korean land races. Ormrod (56), however, studying the varieties "Olli" and "Montcalm," found that differences in varietal development rates were due solely to varietal variation and not to photoperiod sensitivity.

Both vegetative and floral development have been related to barley's photoperiod response (23,4,22).

Faris, Krahn and Guitard (23) determined that short days and high temperatures stimulated vegetative development more than apical development and that floral initiation was more delayed by short days in "Vantage" than in "Olli." Pre-inductive high temperatures extended the vegetative period, but post-inductive high temperatures decreased the interval from double ridge (apex) formation to arrival of the first node at ground level. Increases in temperature as day-lengths decreased resulted in the arrival of the first node at ground level at progressively earlier stages of apical organogenesis. Aspinall and Paleg (4) found that reductions in photoperiod and in light intensity delayed first tiller emergence. Long photoperiods and vernalization have been demonstrated by Mansuri (49) to reduce stem height and leaf numbers by altering the growth patterns of the shoot apex. Ormrod (56) determined that the rate of culm elongation in several barley varieties was apparently unaffected by photoperiod. It is evident that photoperiod and photoperiod-temperature interactions influence barley vegetative development.

In correlating vegetative with apical development Faris and co-workers (23) concluded that when a node arrives at ground level floral initiation has occurred. Arrival of the node at ground level

is not, however, predictive of an exact level of floral organogenesis under all conditions.

Guitard (30) evaluated the barley varieties "Olli" and "Vantage" for the influence of photoperiod on three specific growth stages; seeding to internode elongation, internode elongation to heading and heading to maturity. His results indicated that the number of days from seeding to internode elongation might provide an indication of earliness for certain varieties. Tiller number and duration of tillering also appeared to be indicative of earliness. Williams (78) has developed a maturity model for barley based on a biophotothermal equation which is adequately predictive for most of the barley growing areas of Canada. He also concluded that maturity is more difficult to predict in barley than in wheat.

Floral development of the barley apex is more strongly affected by photoperiod than temperature (39). In a given photoperiod temperature does have a marked influence on primordial morphogenesis, especially in the earlier varieties. Vernalization is essential for floral development of winter barleys as well as several spring barleys (43). Paleg and Aspinall (57) provided further evidence that light quality also influences apical primordia development. Increasing fluorescent light intensity did not affect primordia production, but the addition of incandescent light promoted increased production. The increased rate of response being more curved than linear has

suggested that the influence of incandescent light is a photomorphogenic response rather than a response due to increased assimilate supply.

Faris and Guitard (22) investigated the influence of photoperiod on primary culm yield components and concluded that seeds per head was most closely associated with yield. Short days applied to barley from seeding to internode elongation resulted in increases in fertile heads per plant, seeds per head and seed size. However, when the treatment was applied during the period between internode elongation and heading, decreases occurred in fertile primary heads per plant, seeds per head and seed size. Only seed size was decreased when short days were applied after heading. The insensitive variety "Olli" outyielded the sensitive variety "Vantage."

For plant breeders to take full advantage of opportunities to screen barley varieties for photoperiod sensitivity it is helpful to utilize both controlled environments (growth chambers and greenhouses) and field plantings. The results are not always comparable in the different situations (39,22). Tingle (75), evaluating the influence of light and temperature in controlled environments on floret number and fertility, determined that maximum seed production in barley occurred at 18°C and sixteen hours of the highest possible irradiance levels. Faris and Guitard (22) have shown that yield increases in controlled environments can be achieved by raising light

DA

& F " \$ H " , & # \$ "

- \$ & \$ \$

1 \$ ) , FAH " " \$

# " " & " \$ ) , \$ \$

\$ \$ " # " " FB?H

) " \$ " 1 \$

" \$ " # - F = A H ,

) & , 3 1 \$ ) \$

- " # - \$ & " \$ " / ) "

\$ " ) & ) ) & " )

& # & \$ " "

FA > H , " \$ "

" \$ & \$ \$

\$ " # " " FDDH ,

4 4 5 (

# # " " \$ # " # \$

# " ) & \$ - \$ \$ " #

\$ \$ \$ , . # \$ \$

" \$ " " ,

- " 1 " " #

\$ ) & #

/ 1 \$ \$







































































































