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
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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.

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

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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.

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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_2 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. Sjoseth (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 sub-tropical 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, adventious 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°), 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°N (Ethiopia) and 62-65°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°N) and Beaverlodge, Alberta (55°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 coworkers (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 disticchum) 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 researcher 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 primorda 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

intensity (irradiance) and temperature. They have cautioned that more experimentation is necessary to reconcile the results of field and growth chamber trials. Aspinall (3) has demonstrated that controlled environment studies are adequately reproducible. A complicating aspect of controlled environment and field trial (58) relationships is the built in rate of photoperiod change in the field which is generally not programmed into controlled environment experiments (13). There are limitations in both types of trials. Growth chambers can only approximate and never exactly equal field conditions, but field trials are compromised by not being able to thoroughly distinguish between the simultaneously varying factors of photoperiod and temperature (39). Changing photoperiods is a factor all plants must deal with in nature and greater testing is necessary to reconcile the results of controlled environment and field trials (22).

STATEMENT OF THE RESEARCH PROBLEM

The vegetative and reproductive development of cereal grains is governed by complex interactions of genetic and environmental characteristics. The major environmental factors affecting floral induction are photoperiod and temperature.

The experiments reported herein were designed to investigate some of these interactions for a population of barley varieties and lines, some of which are isogenic for earliness using plants grown in

growth chamber and field environments. Additionally, we tried to predict the ranking of spike emergence in a population of barley genotypes based on observation during more juvenile plant growth stages.

The specific questions to be answered by this research were: (1) Do the varieties selected for testing differ in the relationship between their rates of juvenile vegetative growth and their rates of spike emergence under moderate daylengths versus long daylengths; (2) Does the four leaf stage correspond to the attainment of the double ridge stage (upper ridge enlarging) which is reported in the literature to represent a non-reversible floral condition in the barley growing point; (3) How do the rankings of barley varieties heading dates differ between the growth chamber treatments and the field treatments; and (4) How do the barley varieties respond at two field locations possessing the same photoenvironment, but different temperature environments?

The conclusions reached in these investigations should enhance understanding of the complex interactions between plant genotype and photo and thermal environment or at least emphasize the research directions which must be taken to elucidate these relationships.

MATERIALS AND METHODS

Three experiments were conducted in an effort to answer the questions posed in the statement of the research problem; that is to investigate some of the phenological and developmental responses of barley to photoperiod manipulation.

Experiment One. Experiment one consisted of growing sixty-eight accessions (Table 1) of barley under two different photoperiod regimes, one a 14 hour 80°F day-10 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. Observations were made of germination, days to four-leaf stage and days to spike emergence (heading).

This experiment was conducted with two replications in time and five seeds of each species were planted in individual 4" X 4" pots. This experiment was designed to differentiate among those accessions which show a distinct daylength response in heading and those which exhibit a lesser daylength response. Analyses were made of the time intervals from seeding to attainment of each phenological stage observed to ascertain the relative sensitivity of heading to photoperiod manipulation among the varieties and lines and to determine whether the attainment of the four leaf stage adequately predicted the ranking of heading among a population of barley accessions.

TABLE I

LINES ISOGENIC FOR EARLINESS AND OTHER VARIETIES
USED IN THE PHOTOPERIOD STUDY

Betzes		C.I. 6625	74Inc38	Late Compana (erta)
Compana	B70Inc20	Edda	74Inc37	Spartan C.I.5027/684/B-53
Horsford		Olli	74Inc36	Bonus C.I. 8093/6032/Mon-56
Arimont	74AID16	Beecher	74Inc32	Utah B-5708 5513 B-56
Atlas 68	74AID19	Mars		Tammi C.I. 8345 55-6141
Athenais	74AID27	Titan early		Trisomic J-18-17
Steptoe	74AID22	Titan late		Early Carlsberg II
Galt	74AID21	Titan very late		Bonneville
Unitan	74AID23	Titan		Ingrid
Eskishier	74AID29	Titan early (Gateway)		Primus II
Eskishier	74AID28	Vantage		Tokak
Attilis	74AID25	Munsing		Dicktoo
Hector	74AID10	Hannchen		Frontier
Dekap	74AID9	Hannchen early		Cal. Mariout 1953 53-700
Glacier	Inc 10	Gigas		Kearney
Gateway	74Inc47	Early Freja		Tschermak
Erbet	74Inc45	Freja		Carlsberg II 1956
Prior	74Inc44	Early Betzes (Compana Dwarf)		Erbet
Briggs	74Inc43	Early Betzes (Hannchen Dwarf)		Atsel
Marie	74Inc42	Early Betzes (Orange Lemma)		Ubamer
Floya	74Inc40	Late Compana (ert d)		Late Compana
Radskorn	74Inc41	Late Compana (lb)		Kinai 5
Morroco	74Inc39	Late Compana (lb3)		

Experiment Two. Experiment two was carried out to determine whether or not the four leaf stage corresponded to the initiation of a floral condition in the barley growing point as had been reported by Bonnett (7). Ten barley varieties or lines representing a range of earliness to heading, as determined in the first experiment, were chosen from the original sixty-eight accessions. The varieties and lines selected were: Floya, Olli, Early Betzes (Compana dwarf), Titan, Prior, Steptoe, Marie, Dicktoo, Late Compana and Eskishier 29. Ten seeds of each accession were planted in 4" x 4" pots and thinned to five plants per pot (one for each sampling date). Each accession-pot was replicated six times in each photoperiod treatment.

The experimental treatments were in a completely randomized block design within each photoperiod treatment (growth chamber). Both photoperiods consisted of 14 hour, 80°F days and 10 hour, 60°F nights, but one treatment included the interruption of the dark period at its midpoint with one hour of low intensity fluorescent light. Though night period interruption is usually achieved with incandescent lights, we determined that fluorescent light was lower in energy, thereby reducing any potential photosynthetic influence, but almost twice as high in the ratio between red and far-red radiation, thereby enhancing the long day photoperiod effect.

The development of each accession was evaluated at 8, 12, 16, 20 and 24 days after planting. The samples were dug from the soil,

rinsed in water and placed in separate vials filled with 95 per cent ethanol to arrest growth and deformation and preserve the plant material. This prevented shrinkage of plant materials. The samples were removed from their vials to count the number of visible leaves. Then each sample was dissected to assess the condition of the apical growing point. Developmental morphology of the growing point was evaluated using a scale similar to that of Aspinall and Paleg (3,4) and consisted of (Fig. 1):

1. Presence of a single lateral ridge on the side of the apex (non-floral).
2. Condition as in #1, but with the apex elongating (non-floral).
3. Appearance of a double ridge on the side of the apex (reversibly floral),
4. Upper ridge (of double ridge) enlarging (floral).
5. Spikelet primordia visible as simple mounds on the side of the apex (floral),
6. Spikelet primordia beginning to differentiate into component floral structures (floral).
7. Spikelets well differentiated into component floral structures (floral).

These stages are photographically recorded in Figure 1 from selected samples which most clearly portrayed the morphological attributes of

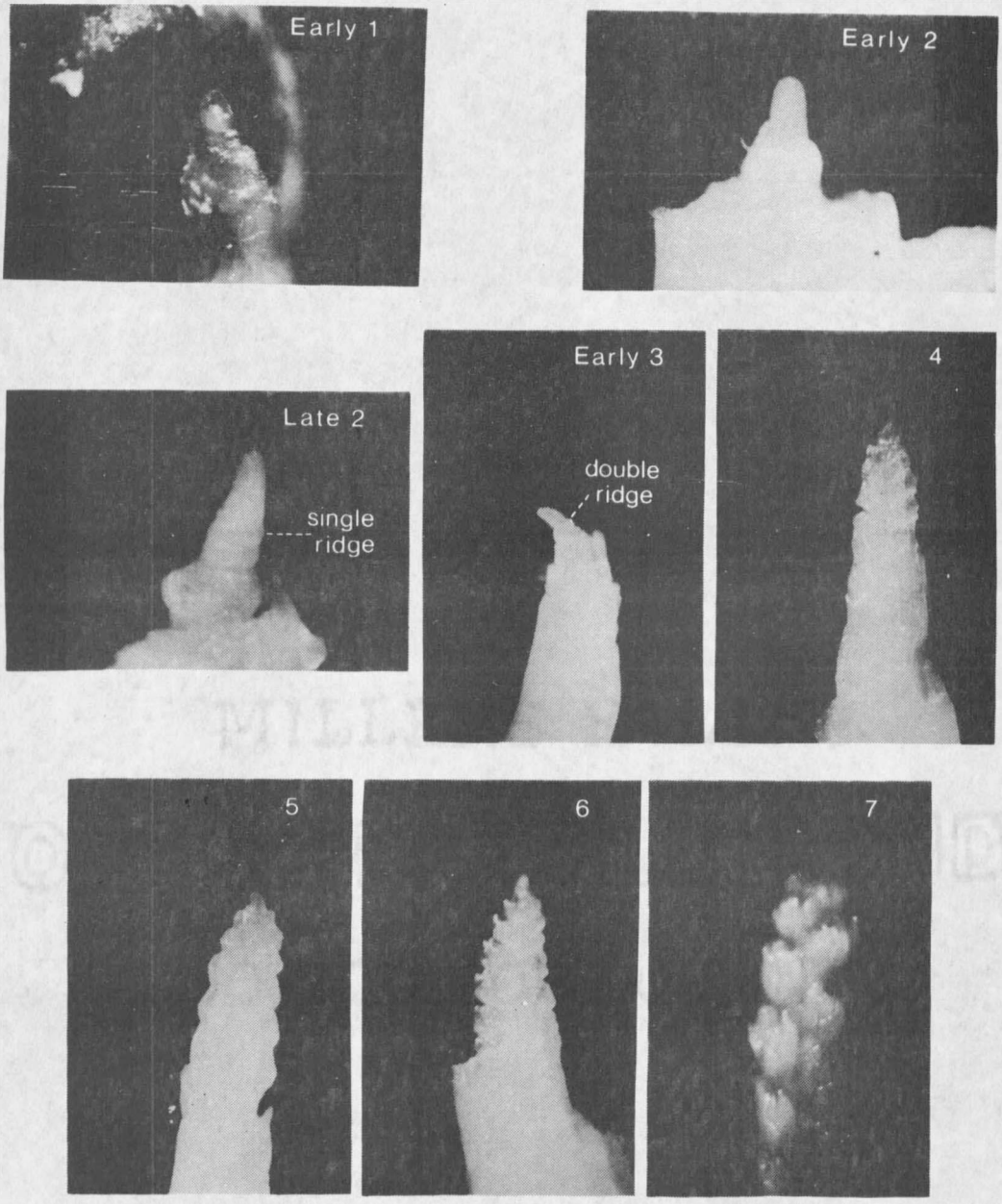

FIGURE 1

BARLEY GROWING POINT PHENOLOGY
(DEVELOPMENTAL MORPHOLOGY)

the growing point. Correlating leaf number with growing point condition enabled comparison of photoperiod effects on individual accessions and the population of accessions. It also allowed determination of what leaf number stage corresponded to an irreversibly floral growing point.

Experiment Three. The sixty-eight accessions evaluated in Experiment One, along with several sets of lines isogenic for earliness were combined to form a field trial of 112 accessions (Table 2). Each accession was planted in a ten foot row replicated twice. Two locations of the Montana Agricultural Experiment Station, Bozeman and Huntley, were used as different geographic environments. At each location the trial was planted at two different dates, once at an early spring planting date (April 28) and once at a date after the summer soltice (June 27) to determine the influence of long increasing versus longer decreasing daylength on the heading rankings of the populations of barley. Days to heading for 50 per cent of the population were recorded in each replication of each accession.

TABLE 2

BARLEY VARIETIES AND LINES SEEDED
AT BOZEMAN AND HUNTLEY

1	Compana
2	Horsford
3	Arimont
4	Atlas 68
5	Athenais
6	Steptoe
7	Galt
8	Unitan
9	Eskishier 1
10	Eskishier 2
11	Attilis
12	Hector
13	Dekap
14	Glacier
15	Gateway
16	Erbet
17	Prior
18	Briggs
19	Floya
20	Radskorn
21	Morocco
22	C.I. 6625
23	Edda
24	Olli
25	Beecher
26	Mars
27	Vantage
28	Carlsburg II
29	Carlsburg II - VVII
30	Carlsburg II - VVII
31	Carlsburg II - VVII
32	Carlsburg II - VVII
33	Carlsburg II - VVII
34	Carlsburg II - VVII, late
35	Carlsburg II - VVII, late
36	Carlsburg II - VVII
37	Freja
38	Vantage x 7 Freja
39	Vantage x 7 Freja
40	Vantage x 7 Freja
41	Vantage x 7 Freja
42	Vantage x 7 Freja
43	Vantage x 7 Freja
44	Vantage x 7 Freja
45	Munsing
46	Gigas
47	Early Betzes
48	Early Betzes
49	Late Compana (ert D)
50	Late Compana (1b)
51	Late Compana (1B3)
52	Late Compana (erta)
53	Spartan C.I. 5027
54	Utah B-5708
55	Tammi C.I. 8345
56	Trisomic J-18-17
57	Early Carlsburg II
58	Bonneville
59	Ingrid
60	Primus II
61	Tokak
62	Coast
63	Frontier
64	Cal. Mariout
65	CM67
66	Washonupana
67	Carlsburg II
68	Atsel
69	Ubamer
70	Piroline
71	Kinai 5
72	Klages
73	Summit
74	Titan
75	Titan early
76	Titan early

TABLE 2 (continued)

77	Titan derived
78	Titan derived
79	Titan derived
80	Titan med. late
81	Titan late
82	Titan very late
83	Albino lemma
84	Horsford
85	Albino lemma
86	Early Betzes
87	Marie
88	Bonus
89	Erbet
90	Betzes
91	Early Betzes
92	Early Betzes
93	Vantage
94	Hannchen
95	Titan
96	Titan
97	Titan
98	Hirsford
99	Titan
100	Titan
101	Titan
102	Titan
103	Betzes, early
104	Betzes late
105	RM Dwarf
106	F7 x F7 x 4 Betzes, early
107	Compana dwarf
108	Compana dwarf Betzes
109	Prior
110	Early Betzes
111	Shabet
112	Ershabet

RESULTS AND DISCUSSION

Experiment One. Only forty-one of the sixty-eight accessions planted in Experiment One germinated, survived and headed under both photoperiods with adequate replication to be included in the statistical analyses (Tables 3 and 4).

Days to heading were significantly lower under long day conditions for the varieties Athenois, Morroco, Edda, Hannchen early and Kinai 5 (Table 5). Other varieties did not show significant changes in elapsed days to heading due to interruption of the dark period. The period from planting to the appearance of the fourth leaf was essentially identical for the population means under both moderate and long day conditions (Table 3). Even with similar means and low deviations from the population means (Table 3) the correlation coefficient, $r = .455$, indicates a variability ($p = .05$) in ranking for appearance of the fourth leaf between the two photoperiod treatments. Because the range of days to fourth leaf appearance is narrow, slight variations in ranking among the accessions would preclude the use of this phenological trait to accurately predict the ranking of later phenological events.

The correlation of days to appearance of the fourth leaf with days to spike emergence (heading) was not significant ($p = .05$). The two phenological events, appearance of the fourth leaf and emergence of the spike (heading), are not well correlated under the

TABLE 3

DAYS ELAPSED FROM SEEDING TO APPEARANCE OF THE FOURTH LEAF UNDER MODERATE DAYLENGTH CONDITION (14 HOURS OF LIGHT) AND LONG DAY CONDITION (14 HOURS LIGHT PLUS DARK PERIOD INTERRUPTION)

Variety	Mean Days to 4-Leaf	
	Long Day	Intermediate Day
Compana	19.9	16.2
Atlas 68	23.9	20.3
Athenais	17.8	19.3
Steptoe	21.4	19.8
Unitan	20.8	19.3
Eskishier 29	23.5	21.9
Attilis	17.8	19.6
Gateway	15.3	20.1
Erbet	17.2	18.3
Prior	18.1	17.4
Marie	19.7	16.5
Floya	14.8	17.8
Radskorn	14.5	16.2
Morroco	20.3	19.4
C.I. 6625	18.6	18.2
Edda	18.1	16.5
Olli	15.7	15.8
Beecher	18.9	20.7
Titan early	16.6	16.7
Titan	18.3	19.0
Titan early (Gateway)	16.7	16.9
Munsing	17.8	17.2
Hannchen early	18.3	17.7
Early Freja	17.2	16.3
Freja	20.6	17.9
Early Betzes (Compana dwarf)	17.3	18.4
Early Betzes (Hannchen dwarf)	17.6	19.1
Early Betzes (Orange lemma)	16.5	17.8
Late Compana	21.5	21.3
Spartan C.I. 5027	16.0	18.4
Utah B-570-8	17.8	18.9
Trisomic J-18-17	18.5	18.0
Early Carlsberg II	17.4	16.3
Bonneville	20.6	20.5
Primus II	18.3	16.5
Tokak	19.4	18.1
Cal. Mariout 1953	21.5	21.5
Erbet	19.8	17.9
Atsel	21.0	18.5
Ubamer	14.0	20.5
Kinai 5	18.9	17.2
Mean	18.5	18.4
Standard deviation of the means	1.62	2.26

Coefficient of linear correlation of the two populations: $r = .455$

TABLE 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)

Variety	Mean Days to Heading	
	Long Day	Intermediate Day
Compana	44.8	40.6
Atlas 68	57.8	48.3
Athenais	51.8	44.1
Steptoe	58.7	49.9
Unitan	55.0	47.0
Eskishier 29	54.0	48.7
Attilis	51.0	54.0
Gateway	52.7	46.6
Erbet	40.1	38.7
Prior	37.6	35.6
Marie	44.0	43.4
Floya	40.7	42.0
Radskorn	49.8	44.8
Morroco	50.6	37.8
C.I. 6625	38.5	36.0
Edda	67.0	47.0
Olli	50.0	44.8
Beecher	51.3	47.1
Titan early	47.8	49.7
Titan	42.2	45.0
Titan early (Gateway)	46.0	39.0
Munsing	45.0	43.9
Hannchen early	48.0	40.1
Early Freja	40.1	39.3
Freja	61.5	50.3
Early Betzes (Compana dwarf)	39.9	38.1
Early Betzes (Hannchen dwarf)	53.0	47.5
Early Betzes (Orange lemma)	40.7	37.5
Late Compana lb	54.5	43.0
Spartan C.I. 5027	47.5	46.9
Utah B-570-8	46.2	49.2
Trisomic J-18-7	42.0	34.0
Early Carlsberg II	44.2	41.7
Bonneville	51.8	43.9
Primus II	50.5	46.9
Tokak	52.0	48.4
Cal. Mariout 1953	45.3	43.0
Erbet	40.3	38.4
Atsel	41.8	34.8
Ubamer	56.3	47.5
Kinai 5	50.9	43.2
Mean	48.4	43.6
Standard deviation of the means	4.86	6.73

Coefficient of linear correlation of the two populations: r = .713

TABLE 5

T-TEST OF DIFFERENCES IN DAYS TO HEADING BETWEEN THE TWO PHOTOPERIODS

Variety	t
Compana	1.30
Atlas 68	2.57
Athenais	2.54*
Steptoe	2.04
Unitan	1.99
Eskishier 29	1.59
Attilis	-.63
Gateway	1.42
Erbet	.33
Prior	.68
Marie	.18
Floya	-.25
Radskorn	1.39
Morroco	3.50*
C.I. 6625	.66
Edda	4.54*
Olli	1.14
Beecher	1.21
Titan early	-.47
Titan	-.74
Titan early (Gateway)	2.27
Munsing	.36
Hannchen early	2.69*
Early Freja	.26
Freja	1.97
Early Betzes (Compana dwarf)	.61
Early Betzes (Hannchen dwarf)	1.92
Early Betzes (Orange lemma)	.67
Late campana lb	2.02
Spartan C.I. 5027	.12
Utah B-570-8	-.79
Trisomic J-18-17	1.68
Early Carlsberg II	.69
Bonneville	2.16
Primus II	.92
Tokak	1.17
Cal. Mariout 1953	.50
Erbet	.59
Atsel	1.59
Ubamer	1.54
Kinai 5	2.60*

*Significant at p = .05

long day conditions (r = .274) or the moderate daylengths (r = .263) for these forty-one barley varieties and lines. Evidently, juvenile phenological stages cannot be directly related to earliness of heading.

The ranking among accessions for days to heading shows a highly significant correlation between the moderate daylength treatment and the long day treatment (r = .713). Sensitivity to photoperiod, therefore, does not strongly influence the heading date of most varieties and lines. A t-test of the individual accessions shows only five of the forty-one varieties or lines displaying heading dates significantly earlier under long day conditions than under moderate daylength conditions (Table 5).

Experiment Two. The vegetative and floral phenology of the ten varieties investigated in the second study characterize their early development rates (Figs. 2, 3 and 4). Table 6 shows the linear and quadratic coefficients of correlation of all ten accessions under moderate and long day conditions.

All varieties except "Dicktoo" exhibit good correlations between vegetative development (leaf number) and reproductive development (condition of the growing point) under both photoperiods. "Dicktoo" is a winter variety requiring vernalization and provides a check against the other varieties (spring type barleys) which do not require vernalization. The shorter daylength condition which would

occur simultaneously with natural vernalization, results in a significantly higher correlation and positive rate of development for the variety "Dicktoo."

Apparently contradicting the expected increase in rate of floral development under long day conditions, several of the spring varieties develop more rapidly under moderate daylength conditions (as evidenced by a t-test of their slopes, Table 7). Figure 3 portrays the linear relationships of all accessions under both photoperiods and clearly depicts the more rapid rate of floral development under shorter daylength conditions.

The use of quadratic curves to express the relationship between growing point floral condition and leaf number results in a better fit (higher correlation coefficient) than with a straight line (Table 6). The quadratic curves in Figure 4 therefore express the relationship between leaf number and growing point better than the straight lines in Figure 3. The rates of development depicted are more rapid at higher leaf numbers under long day conditions than moderate daylength conditions for most of the spring varieties, including "Floya," "Early Betzes" (Compana dwarf), "Titan," "Prior," "Steptoe," "Mari" and "Eskishier." It is also evident that with the exception of the winter type "Dicktoo" and the late isoline "Late Compana," the growing point attains an irreversibly floral condition prior to or during the fourth leaf stage. Dicktoo, being a winter

TABLE 6

LINEAR AND QUADRATIC CORRELATION COEFFICIENTS AND LINEAR SLOPE FOR EARLY FLORAL AND VEGETATIVE PHENOLOGY OF TEN BARLEY ACCESSIONS

	Long Daylength			Moderate Daylength		
	Linear r	Slope	Quadratic r	Linear r	Slope	Quadratic r
Floya	.900**	1.343	.904**	.875**	1.452	.875**
Olli	.794**	1.121	.826**	.870**	1.272	.872**
Early Betzes	.933**	1.166	.942**	.906**	1.534	.946**
Titan	.897**	1.449	.926**	.904**	1.395	.904**
Prior	.903**	1.375	.920**	.952**	1.551	.954**
Steptoe	.849**	1.304	.907**	.873**	1.119	.935**
Marie	.746*	.874	.788**	.953**	1.379	.958**
Dicktoo	.065NS	.013	.187NS	.640*	.207	.771**
Late Compana	.751*	.620	.794**	.698*	.811	.778**
Eskishier	.798**	1.071	.975**	.862**	1.037	.881**
Mean	.763	.903	.817	.853	1.176	.887
Overall (Individual variates)	.823	1.211	.847	.793	1.207	.795

*Significant at p = .05

**Significant at p = .01

TABLE 7

DIFFERENCES IN RATES OF DEVELOPMENT FOR THE TEN VARIETIES UNDER THE TWO PHOTOPERIODS

Variety	Difference in Slope	t
Floya	,009	-.117
Olli	.151	-1.958
Early Betzes	.368	-4.773**
Titan	.054	.700
Prior	.176	-2.283*
Steptoe	.185	2.399*
Marie	.505	-6.550**
Dicktoo	.194	-2.516*
Late Compana	.191	-2.477*
Eskishier	.034	.441

* t significant at p = .05

** t significant at p = .01

Legend: Left axis = growing point rating (floral):intermediate day o----o; long day o——o.
Right axis = number of leaves (vegetative):intermediate day Δ----Δ; long day Δ——Δ.
Bottom axis = days after seeding.

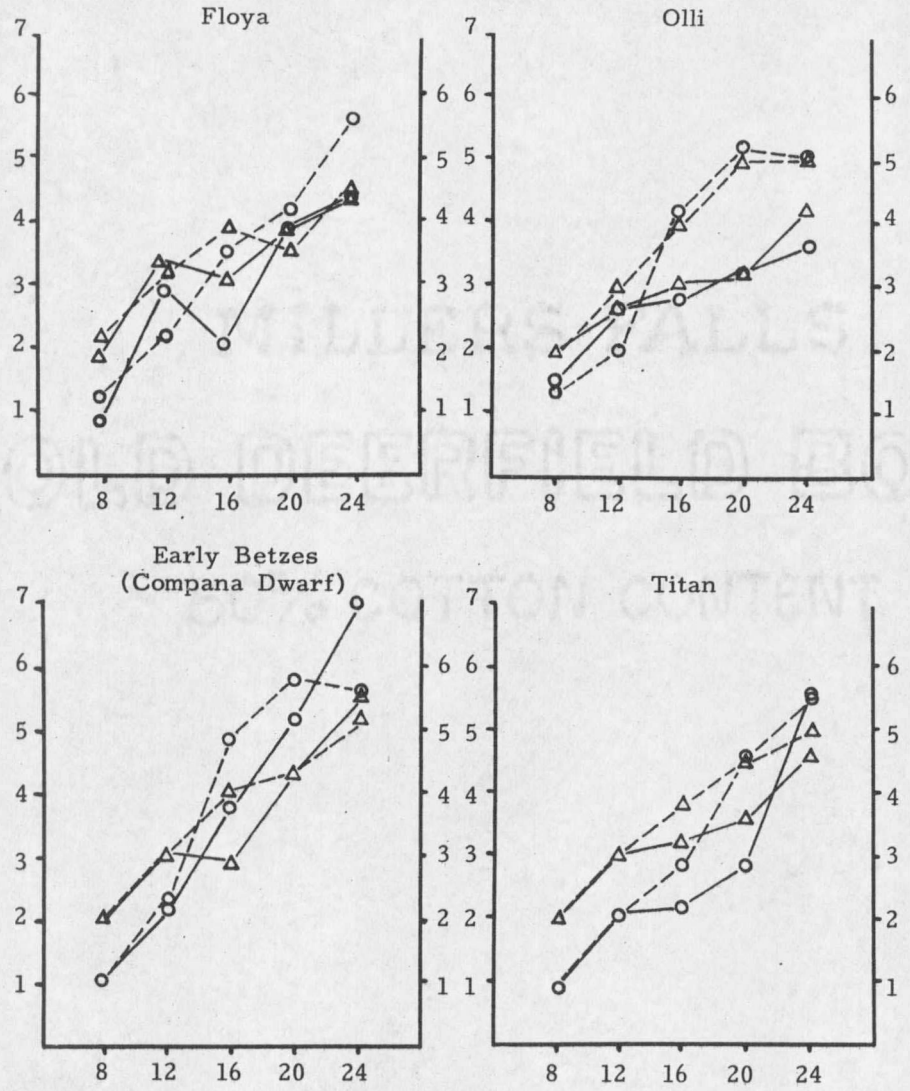

FIGURE 2

EARLY VEGETATIVE AND FLORAL PHENOLOGY
OF TEN BARLEY ACCESSIONS

Legend: Left axis = growing point rating (floral):intermediate day o----o; long day o——o.
Right axis = number of leaves (vegetative):intermediate day Δ----Δ; long day Δ——Δ.
Bottom axis = days after seeding.

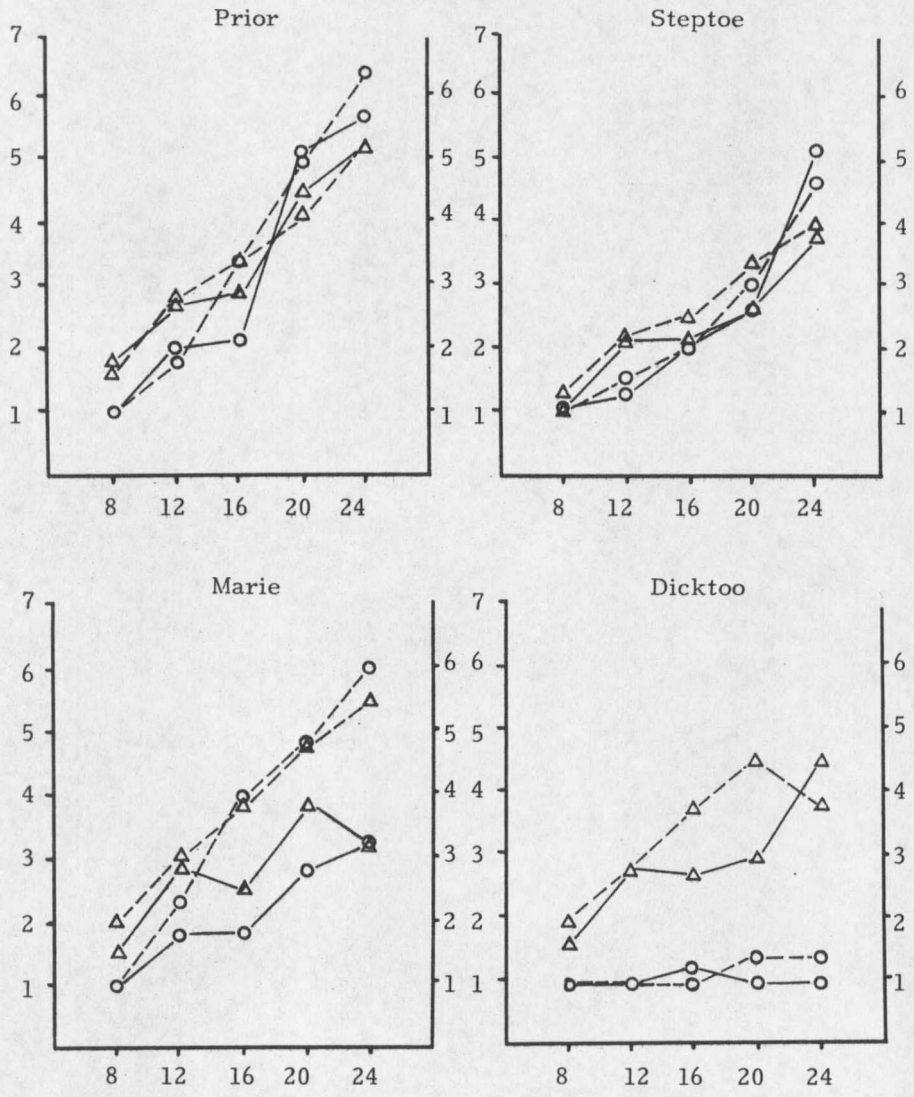

FIGURE 2 (continued)

Legend: Left axis = growing point rating (floral):intermediate day o----o; long day o——o.
Right axis = number of leaves (vegetative):intermediate day Δ----Δ; long day Δ——Δ.
Bottom axis = days after seeding.

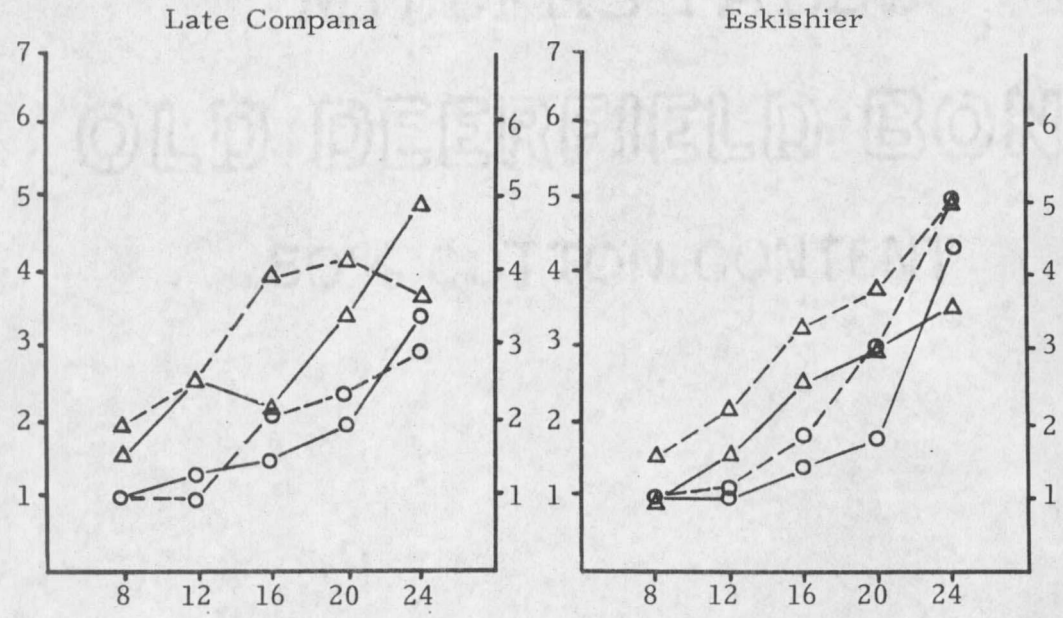

FIGURE 2 (continued)

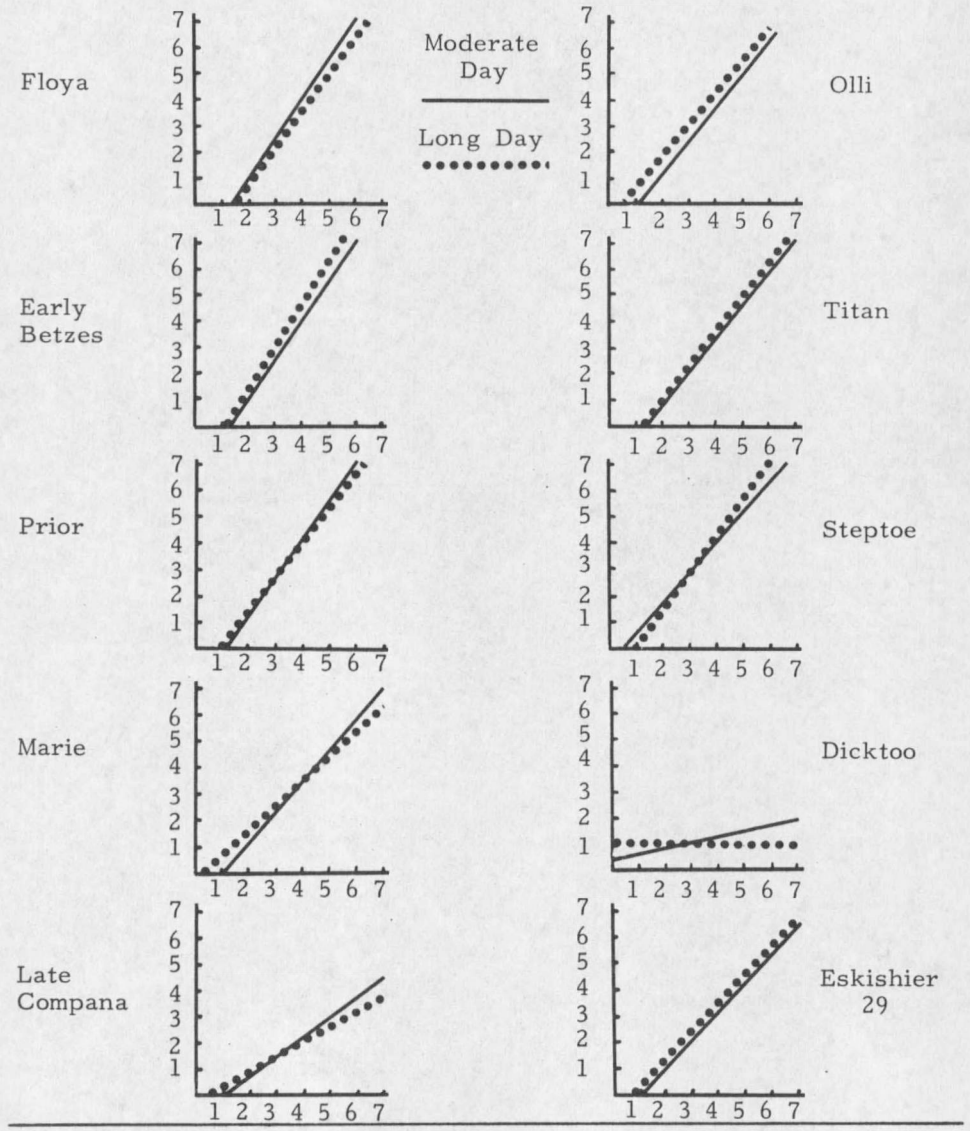

FIGURE 3

LINEAR RELATIONSHIP BETWEEN VEGETATIVE CONDITION (LEAF NUMBER), X-AXIS, AND FLORAL CONDITION (GROWING POINT RATING), Y-AXIS

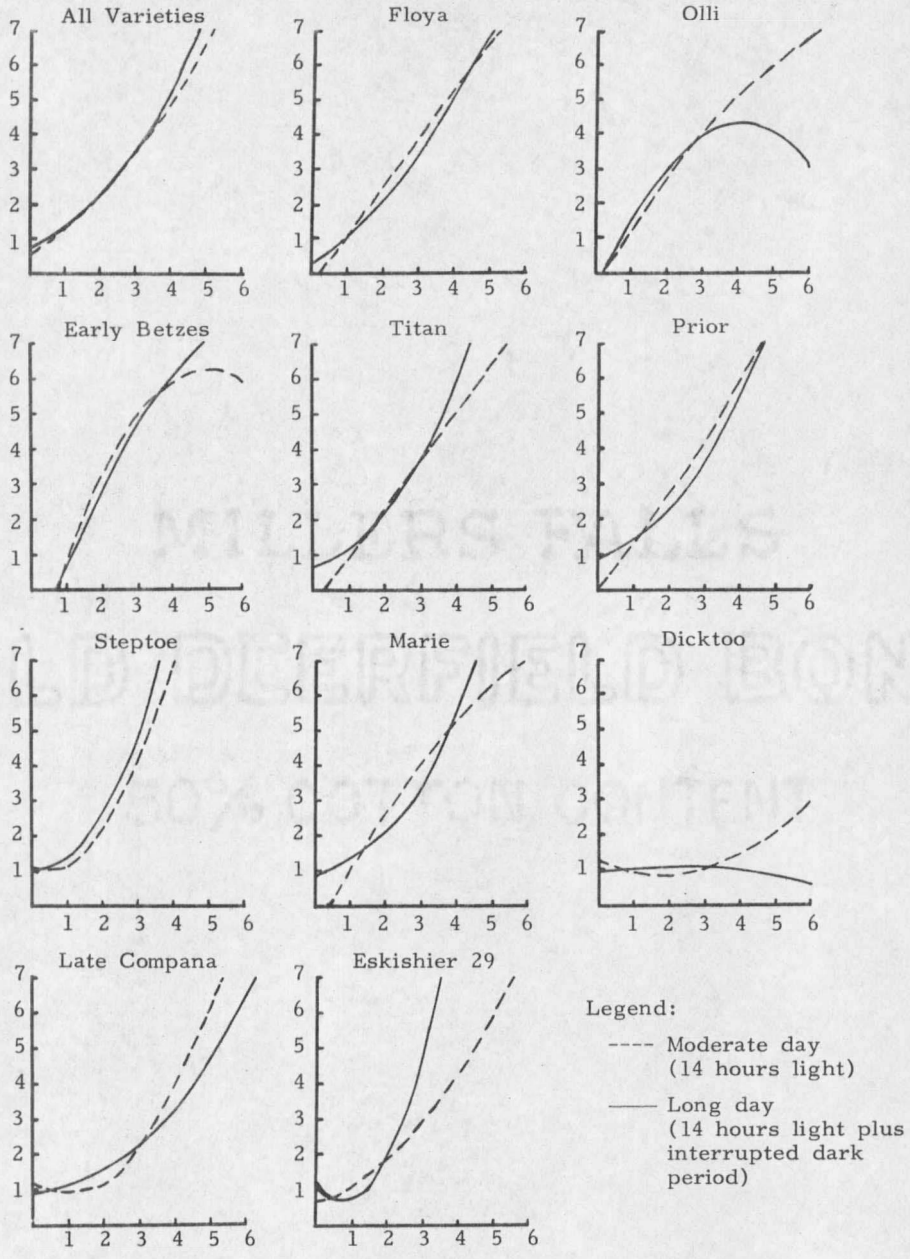

FIGURE 4

QUADRATIC RELATIONSHIP BETWEEN VEGETATIVE CONDITION (LEAF NUMBER), X-AXIS, AND FLORAL CONDITION (GROWING POINT RATING), Y-AXIS

type, exhibits a much higher correlation under the moderate day-length treatment even without vernalization than under the long day treatment.

Experiment Three. The field evaluation of heading dates conducted in Experiment Three at the Bozeman and Huntley Experiment Stations adds parameters not encountered in the controlled environments of the growth chamber, varying temperatures and photoperiods. The heading dates for both seeding dates are presented in Table 8 for Bozeman and Table 9 for Huntley.

The comparison of heading dates between the spring (early) and the post-summer-soltice (late) seedings is shown in Table 10. Though the mean of all accessions is considerably lower for the late seeding at Bozeman, the high significant correlation ($r = .815$) indicates a similarity in the ranking of days to heading among the accessions between the two seeding dates. The population means at Huntley are very similar for the early and late seedings. The correlation coefficient of $r = .711$, though significant, is lower than that for the Bozeman seedings and possibly indicates more variation in the ranking of days to heading among accessions for the two seedings at Huntley.

Photoperiod (seeding date) apparently does not change the rankings of the heading dates of the varieties and lines.

TABLE 8

MEAN DAYS TO HEADING: BOZEMAN

Variety	Early Seeding	Late Seeding
Compana	62.0	36.0
Horsford	61.5	45.5
Arimont	67.5	40.5
Atlas 68	57.0	36.5
Athenais	54.0	40.5
Steptoe	62.0	37.0
Galt	64.0	38.5
Unitan	62.5	36.0
Eskishier 1	63.5	38.0
Eskishier 2	71.0	no heading
Attilis	54.5	37.0
Hector	66.0	39.5
Dekap	62.5	39.0
Glacier	58.0	37.5
Gateway	56.5	32.5
Erbet	57.5	33.0
Prior	55.0	30.0
Briggs	57.0	38.0
Floya	56.0	32.0
Radskorn	55.0	30.5
Morocco	55.0	38.0
C.I. 6625	55.5	30.0
Edda	57.0	33.0
Olli	58.0	33.0
Beecher	55.0	36.5
Mars	61.0	37.0
Vantage	64.5	41.0
Carlsburg II	69.5	43.5
Carlsburg II - VVII	60.5	35.5
Carlsburg II - VVII	63.5	35.0
Carlsburg II - VVII	63.5	34.0
Carlsburg II - VVII	64.0	36.5
Carlsburg II - VVII	68.0	42.5
Carlsburg II - VVII, late	60.5	35.0
Carlsburg II - VVII, late	68.0	43.5
Carlsburg II - VVII	68.0	44.5
Freja	64.5	40.0

TABLE 8 (continued)

Variety	Early Seeding	Late Seeding
Vantage x 7 Freja	60.0	32.0
Vantage x 7 Freja	59.0	33.5
Vantage x 7 Freja	59.5	34.0
Vantage x 7 Freja	57.5	32.5
Vantage x 7 Freja	65.5	40.0
Vantage x 7 Freja	65.0	39.0
Vantage x 7 Freja	65.0	40.0
Munsing	60.0	35,5
Gigas	69.5	no heading
Early Betzes	57.5	32.0
Early Betzes	59,0	33.0
Late Compana (ert D)	69.5	43,0
Late Compana (lb)	68.0	40.0
Late Compana (1B3)	68.5	41.5
Late Compana (erta)	69,0	39.5
Spartan C.I. 5027	60,5	35,5
Utah B-5708	60,0	41.0
Tammi C.I. 8345	58.5	34.0
Trisomic J-18-17	58.0	32.5
Early Carlsburg II	61.0	35.5
Bonneville	68.0	42.0
Ingrid	68.5	42,5
Primus II	57.5	33.0
Tokak	61.0	36.5
Coast	63,5	41.0
Frontier	67.0	44.0
Cal. Mariout	55.5	35.0
CM 67	55.5	35.0
Washonupana	63.5	39.5
Carlsburg II	64.5	42.5
Atsel	54.5	30.5
Ubamer	61.0	36.0
Piroline	65.0	42.0
Kinai 5	61.5	36.0
Klages	67.0	42.0
Summit	67.5	42.0
Titan	64.0	37.5
Titan early	59.0	34.5
Titan early	59.5	34,0

TABLE 8 (continued)

Variety	Early Seeding	Late Seeding
Titan derived	61.5	36.5
Titan derived	63.5	36.0
Titan derived	63.0	38.0
Titan med. late	66.5	42.0
Titan late	67.5	43.0
Titan very late	69.0	45.0
Albino lemma	61.0	36.5
Horsford	61.5	no heading
Albino lemma	69.0	38.5
Early Betzes	59.0	33.0
Marie	58.0	34.0
Bonus	69.0	43.0
Erbet	59.0	33.0
Betzes	65.5	40.5
Early Betzes	58.5	33.0
Early Betzes	58.0	33.5
Vantage	64.5	39.0
Hannchen	63.0	37.5
Titan	59.5	34.0
Titan	59.0	34.5
Titan	60.5	36.0
Horsford	61.5	no heading
Titan	66.5	42.0
Titan	64.0	41.5
Titan	67.5	42.0
Titan	66.0	41.5
Betzes; early	58.5	35.0
Betzes, late	64.5	40.5
RM Dwarf	60.0	35.5
F7 x F7 x 4 Betzes; early	59.0	32.5
Compana dwarf	58.0	32.0
Compana dwarf Betzes	64.0	40.0
Prior	56.0	29.0
Early Betzes	61.5	37.0
Shabet	67.5	41.5
Ershabet	59.0	32.0

TABLE 9

MEAN DAYS TO HEADING: HUNTLEY

Variety	Early Seeding	Late Seeding
Compana	49.5	48.5
Horsford	51.5	--
Arimont	59.5	61.5
Atlas 68	46.0	51.0
Athenais	42.0	47.0
Steptoe	50.0	50.0
Galt	52.5	54.5
Unitan	50.5	49.5
Eskishier 1	61.5	51.5
Eskishier 2	63.0	--
Attilis	42.0	47.5
Hector	60.5	65.5
Dekap	53.0	53.0
Glacier	48.0	57.0
Gateway	49.0	45.0
Erbet	46.0	45.0
Prior	42.0	44.0
Briggs	46.0	48.0
Floya	49.5	49.0
Radskorn	46.5	46.5
Morocco	47.5	48.0
C.I. 6625	42.0	43.0
Edda	48.0	48.5
Olli	49.0	50.5
Beecher	43.0	49.0
Mars	51.0	51.5
Vantage	59.0	56.0
Carlsburg II	63.5	67.5
Carlsburg II - VVII	49.5	48.5
Carlsburg II - VVII	49.0	51.0
Carlsburg II - VVII	49.0	46.0
Carlsburg II - VVII	50.5	48.5
Carlsburg II - VVII	63.5	65.0
Carlsburg II - VVII, late	50.5	50.0
Carlsburg II - VVII, late	63.0	66.5
Carlsburg II - VVII	61.5	68.5
Freja	61.0	49.0

TABLE 9 (continued)

Variety	Early Seeding	Late Seeding
Vantage x 7 Freja	46.0	44.5
Vantage x 7 Freja	47.0	44.5
Vantage x 7 Freja	47.0	44.5
Vantage x 7 Freja	45.5	45.0
Vantage x 7 Freja	59.0	51.0
Vantage x 7 Freja	53.0	51.5
Vantage x 7 Freja	56.0	53.0
Munsing	49.0	46.0
Gigas	64.0	--
Early Betzes	46.0	45.0
Early Betzes	47.0	45.0
Late Compana (ert D)	64.0	58.0
Late Compana (lb)	61.5	56.0
Late Compana (1B3)	61.0	54.5
Late Compana (erta)	64.0	65.5
Spartan C.I. 5027	50.0	47.0
Utah B-5708	51.0	54.0
Tammi C.I. 8345	49.5	50.5
Trisomic J-18-17	46.5	44.0
Early Carlsburg II	49.5	48.0
Bonneville	61.5	53.5
Ingrid	58.0	57.0
Primus II	49.0	45.0
Tokak	49.5	45.5
Coast	51.5	64.0
Frontier	58.0	64.5
Cal. Mariout	43.0	44.5
CM 67	43.0	48.0
Washonupana	52.5	53.0
Carlsburg II	59.5	65.0
Atsel	42.0	43.0
Ubamber	51.0	51.5
Piroline	57.5	56.0
Kinai 5	49.0	44.5
Klages	60.0	65.5
Summit	60.5	62.5
Titan	51.0	55.0
Titan early	46.0	44.5
Titan early	47.0	45.0

TABLE 9 (continued)

Variety	Early Seeding	Late Seeding
Titan derived	51.5	49.0
Titan derived	51.0	50.5
Titan derived	51.5	52.5
Titan med. late	57.0	58.0
Titan late	57.0	58.5
Titan very late	61.5	62.5
Albino lemma	50.0	46.0
Horsford	51.5	--
Albino lemma	60.5	67.0
Early Betzes	48.0	45.0
Marie	47.0	45.0
Bonus	61.5	67.0
Erbet	49.0	45.0
Betzes	58.0	56.5
Early Betzes	47.0	45.5
Early Betzes	47.0	45.0
Vantage	55.0	50.0
Hannchen	50.5	50.5
Titan	48.0	44.0
Titan	47.0	45.0
Titan	50.5	50.0
Horsford	51.5	--
Titan	59.0	58.5
Titan	59.0	58.5
Titan	59.0	62.5
Titan	57.0	56.5
Betzes, early	47.0	45.5
Betzes, late	59.5	57.0
RM Dwarf	49.5	44.5
F7 x F7 x 4 Betzes, early	47.0	45.0
Compana dwarf	46.0	44.5
Compana dwarf Betzes	57.0	49.5
Prior	43.5	45.0
Early Betzes	50.0	48.5
Shabet	60.5	55.0
Ershabet	46.5	52.0

TABLE 10

RELATIONSHIP BETWEEN HEADING DATE RANKINGS FOR EARLY AND LATE SEEDINGS: BOZEMAN AND HUNTLEY

	Bozeman	
	Days to Heading	
	Early Seeding	Late Seeding
Mean	61.8	37.2
Standard deviation	4.3	3.9
	r = .815	

	Huntley	
	Days to Heading	
	Early Seeding	Late Seeding
Mean	52.0	51.7
Standard deviation	6.2	7.0
	r = .711	

Since the photoperiods for Bozeman and Huntley are nearly identical, differences in heading dates for a particular seeding must be ascribed to temperature or other environmental factors. The population mean at Huntley is lower than at Bozeman, 52.0 and 61.8 days respectively, for the early seeding, but the correlation, r = .932 (Table 11), indicates a high degree of similarity in heading date ranking among the accessions between the two locations. The late seeding resulted in a population mean heading date of 51.7 days at Huntley and 37.2 days at Bozeman (Tables 8 and 9). Again the high correlation, r = .830, indicates a similarity between the heading date rankings at Bozeman and Huntley. Temperature is apparently affecting all varieties and lines similarly.

In breeding programs and physiology research problems it is frequently useful to study as many plant generations as possible. To do so it is important to understand how the plants behave in different environments, including field, greenhouse and growth chamber, so that studies conducted in different environments may be related to one another.

Thirty-three of the varieties and lines studied in the first experiment were common to the Bozeman and Huntley field trials and successfully completed heading in both environments (Table 12). The relationship between the heading dates of the early Bozeman seeding and the moderate daylength growth chamber study exhibits a

TABLE 11

RELATIONSHIP BETWEEN HEADING DATE RANKINGS AT BOZEMAN AND HUNTLEY: EARLY AND LATE SEEDINGS

	Early Seeding	
	Days to Heading	
	Huntley	Bozeman
Mean	52.0	61.8
Standard deviation	6.2	4.3
	r = .932	

	Late Seeding	
	Days to Heading	
	Huntley	Bozeman
Mean	51.7	37.2
Standard deviation	7.0	3.9
	r = .830	

TABLE 12

HEADING DATES FOR VARIETIES PAIRED IN GROWTH CHAMBER AND FIELD TRIALS

Variety	Moderate Day			Long Day		
	G.C.*	Boz. E.	Hun. E.	G.C.	Boz. L.	Hun. L.
Compana	44.0	62.0	49.5	38.5	36.0	48.5
Atlas 68	60.5	57.0	46.0	40.5	36.5	51.0
Athenais	47.5	54.0	42.0	40.5	40.5	47.0
Steptoe	58.5	62.0	50.0	47.5	37.0	50.0
Unitan	52.0	62.5	50.5	42.5	36.0	49.5
Eskishier 29	46.5	63.5	61.5	44.0	38.0	51.5
Attilis	49.5	54.5	42.0	51.5	37.0	47.5
Gateway	51.5	56.5	49.0	44.5	32.5	45.0
Erbet	37.0	57.5	46.0	37.0	33.0	45.0
Prior	35.0	55.0	42.0	34.5	30.0	44.0
Marie	45.0	58.0	47.0	40.5	34.0	45.0
Floya	40.5	56.0	49.5	39.0	32.0	49.0
Radskorn	42.5	55.0	46.5	42.5	30.5	46.5
Morocco	44.0	55.0	47.5	37.0	38.0	48.0
C.I. 6625	37.0	55.5	42.0	35.0	30.0	43.0
Edda	62.0	57.0	48.0	44.5	33.0	48.5
Beecher	44.0	55.0	43.0	40.5	36.5	49.0
Titan early (gateway)	47.5	59.0	46.0	37.0	34.5	44.5
Munsing	42.5	60.0	49.0	42.5	35.5	46.0
Hannchen early	42.0	59.0	47.0	35.0	34.5	45.0
Early Freja	40.5	59.0	47.0	33.5	33.5	44.5
Early Betzes (Compana dwarf)	37.0	57.5	46.0	37.0	32.0	45.0
Early Betzes (Hannchen dwarf)	50.5	59.0	47.0	44.5	33.0	45.0
Early Betzes (Orange lemma)	39.0	58.5	47.0	41.0	33.0	45.5
Late Compana lb	59.5	68.0	61.5	42.5	40.0	56.0
Utah B-570-8	52.5	60.0	51.0	48.0	41.0	54.0
Early Carlsburg II	42.5	61.0	49.5	38.5	35.5	48.0
Bonneville	51.0	68.0	61.5	42.5	42.0	53.5
Tokak	49.5	61.0	49.5	46.0	36.5	45.5
Cal. Mariout 1953	44.0	55.5	43.0	40.5	35.0	44.5
Erbet	37.0	59.0	49.0	35.5	33.0	45.0
Atsel	42.5	54.5	42.0	32.5	30.5	43.0
Kinai 5	44.5	61.5	49.0	40.5	36.0	44.5

*Heading dates in growth chamber study are for the first plant in a pot, not for the mean of the pot as presented in Experiment One.

correlation coefficient of only .367 (Table 13). Thus, the growth chamber does not seem to predict very accurately the ranking of heading dates in the early spring Bozeman seeding. The order of heading among accessions in the late Bozeman planting is more accurately portrayed by the long day growth chamber treatment (r = .489) but the predictive power is still fairly low (Table 13).

The relationship between the early Huntley seeding and the growth chamber moderate daylength treatment is equal (r = .387) to the previously discussed Bozeman relationship. The Huntley late seeding exhibits a slightly closer relationship with the long day growth chamber treatment (r = .500) (Table 13).

Though none of these correlations is especially strong all are significant at the p = .05 level or better. Though caution should be taken in interpreting the closeness of the relationship between the order of heading in the field and the appropriate growth chamber treatment, the relationships are statistically significant.

TABLE 13

RELATIONSHIP BETWEEN GROWTH CHAMBER AND FIELD TRIAL HEADING DATES

	Growth Chamber Long Day	Bozeman Late Seeding	Coefficient of Linear Correlation (r)
Mean	40.5	35.0	.489**
Standard deviation	4.44	3.14	
	Growth Chamber Intermediate Day	Bozeman Early Seeding	
Mean	46.0	58.7	.367*
Standard deviation	7.13	3.57	
	Growth Chamber Long Day	Huntley Late Seeding	
Mean	40.5	47.2	.500**
Standard deviation	4.44	3.25	
	Growth Chamber Intermediate Day	Huntley Early Seeding	
Mean	46.0	48.1	.387*
Standard deviation	7.13	5.10	

*Significant at p = .05

**Significant at p = .01

SUMMARY

The evaluation of sixty-eight accessions of barley, including varieties and lines representing a wide range of earliness to heading, in growth chamber photoperiods of fourteen hours (moderate day-length) and fourteen hours with a broken dark period (long day-length) detected significant reactions to photoperiod for days to heading in only five accessions. More variability was evident in juvenile vegetative phenology than in heading phenology and the accuracy of predicting the ranking of heading in a population of barley accessions is thereby limited.

The investigation of vegetative and floral phenology in ten barley accessions of varying maturity habits shows a consistent and significant correlation between leaf number and apical floral organogenesis in all of the spring varieties. The winter variety studied was not vernalized and did not, therefore, attain a floral condition. Differences in rate of development were more accurately depicted by a quadratic than a linear function. Except for the winter barley and a late spring isoline all varieties attained an irreversible floral condition prior to or during the fourth leaf stage.

The field evaluation of 112 barley varieties and isolines showed a significant similarity in heading date rankings between two geographic locations and for spring and post-summer-soltice seedings. The reaction of the population at two different geographic locations

to differing photoenvironments indicates that the accessions behave similarly (in respect to the population means) to both daylength and temperature. Paired plot comparisons between field trials and growth chamber treatments resulted in low, but significant correlations in days to heading for both environments. Relative heading date rankings were significantly related between the field and growth chamber studies, but the statistical relationships indicated that caution should be exercised in interpretation of the heading date rankings in making predictions from one environment to another.

More detailed specific varietal analyses would probably be useful in clarifying the exact predictive relationships for heading date rankings in different environments.

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