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MORPHOLOGICAL, PHYSIOLOGICAL AND GENETICAL STUDIES OF EARLINESS IN CEREAL CROPS

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### THE UNIVERSITY OF ALBERTA

MORPHOLOGICAL, PHYSIOLOGICAL AND GENETICAL STUDIES OF EARLINESS IN CEREAL CROPS

### A DISSERTATION

SUBMITTED TO THE SCHOOL OF GRADUATE STUDIES IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

FACULTY OF AGRICULTURE

by

Aston Rupert Taylor

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### MORPHOLOGICAL, PHYSIOLOGICAL AND GENETICAL STUDIES OF EARLINESS IN CEREAL CROPS

A. R. Taylor

#### I. LITERATURE REVIEW

It is now commonly accepted that differences in earliness in plants are conditioned by a series of factors. However, a survey of available literature relating to cereal crops reveals that, while the physiology and genetics of earliness have received considerable study, the morphological aspect has been largely neglected.

The only publication on the morphology of earliness in cereal crops known to the writer is that of Suneson (29). He has shown that the effect of environment on earliness varies with the morphology of the plant.

In physiological studies Klebs (21) was able, by manipulating the light and temperature of the environment, to maintain continuous vegetative growth or to induce reproduction prematurely.

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He considered that both light and temperature could affect the balance between carbohydrates and soil nutrients, chiefly nitrogen. From a study of Sempervivum he observed that the process of flower formation proceeded in three separate phases -

- (1) onset of a ripe-to-flower condition,
- (2) formation of the flower primordia,
- (3) development of the flowering inflorescence.

He found that the initiation of each phase was dependent on the relative amounts of light intensity and temperature. A one-sided increase of one or the other would prolong phase (1) or (2) re-sulting in a delay in phase (3).

In 1934 Purvis (28) published data of his analysis on the influence of temperature and photoperiod during germination, on the subsequent development of winter rye. His study proved that length of day was interrelated with other conditions of germination in determining subsequent flower behaviour.

Harrington and Horner (13), working at the University of Saskatchewan, did a series of experiments on the reaction of wheat varieties to different dates of sowing. Theyfound that the interaction between varieties and dates was statistically significant.

Platt (26), working with wheat, showed the relationship between soil moisture and winter survival and established a correlation between earliness and a low survival index.

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<sup>\*</sup> This is the stage at which the growing point shows a differentiation into primordium and stem.

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Working with oats, Tincker and Jones (33) undertook a study of the influence of certain climatic factors upon the rate of growth. It was shown that the Unit Leaf Rate (measured on the "tops" of the plants only) was correlated with the previous rainfall and also with the temperature, during that period of growth in which the plants were forming new leaves and increasing their leaf area.

Jasny(18) investigated the variability in growing periods of several crops from latitude to latitude and found that variations in the total growing period of winter grains were caused primarily by the different lengths of the dormant period.

The investigations of Garner and Allard (10) on the influence of the relative length of day upon the rate of development of plants have shown that the time of flowering in some plants is controlled by the length of day. These workers (10) have reported one test on the effect of prolonging the illumination period of oats, wheat, barley, and rye, using a spring and a winter variety of each.

With each of these grains the forcing action of the electric light was much greater with the spring than with the winter variety. The authors state the following conclusion:

"It appears that the fundamental distinction between the winter and the spring types as such rests on the rapidity with which the latter respond to the increasing day length of spring".

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Eguchi (7) gives the results of experiments with shortday treatments. Some plants hitherto regarded as short-day types were tested under short-day conditions (9-hour day). The differentiation of the flower bud was accelerated and the flower opened early, but, if these plants were transferred to long-day conditions (24-hour day) further development took place rapidly and flowering occurred earlier. Eguchi concludes that there are two stages with different reactions to the photoperiod in the course of flowering, the first being the stage of bud differentiation, and the second the stage of blooming.

It is appropriate at this time to refer to the importance of micro-dissection of plants to determine the actual stage of flowering reached, as stressed in the work of Gregory and Purvis (11) and by Hammer (12) who states: "It would be helpful in much of the experimental work in this field if the investigators would examine all of their plants by micro-dissection to determine what stages of floral development are especially affected by the treatments used".

In a genetic study involving a cross between a spring and a winter variety of wheat, Aamodt (1) secured an  $F_2$  population which when spring-sown began to head with the spring parent and continued heading for a period of eight weeks. There were also some plants which like the winter parent, did not head. He recovered a homozygous family five weeks later than the spring parent.

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His results also indicated that the difference between the two varieties was due to a series of multiple factors.

Johnson (19) found, in crosses involving early by late varieties of barley, that the hybrid distributions were all skewed toward the "early" end. He suggested that this behaviour indicated dominance or partial dominance of earliness, and that from the degree of skewness partial dominance appeared to be the more likely. He observed that, from the particular lines studied, the inheritance of earliness might lie in a single-gene difference.

In a study of the nature and interaction of genes differentiating habit of growth in wheat, Powers (27) observed that the genotypes of the  $F_2$  suggested parents which were differentiated by three main factor pairs for habit of growth with modifying factors for earliness present. He believed that the environmental conditions were largely responsible for the reaction processes of the different genes.

Biffen (3), from his observations on an early Polish and a late Rivet wheat, concluded that earliness and lateness were inherited independently of other characters. Although the  $F_1$ ripened well toward the date of ripening of the Rivet parent he concluded from the  $F_2$ , which had a high percentage of early lines, that earliness was dominant. Fruwith, as cited by Florell (9), believed early maturity to be partially dominant in wheat as well as in rye and barley.

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Thompson, in a series of three articles (30, 31, 32) reports on an extensive study of early and late maturity in wheat. In the F, he found, in general, that ripening occurred at or near the date of ripening of the later parent. He thought that this behaviour was due to hybrid vigor causing added vegetative growth and not to the domiance of lateness. He found in the F2 that the great majority of hybrids were intermediate between the parents and in all types of crosses the distribution approached the normal curve of variation. No skewness toward either parental position was noted that could suggest dominance or simple segregation. On the basis of Mendelian segregation a multiple factor explanation was offered. While the multiple factor hypothesis held fairly well for individual crosses it could not be applied directly to the entire series. Thompson (32), however, points out that many factors in the hereditary constitution doubtless affect the rate of maturity, and many factors whose primary effects are on entirely different characteristics may have secondary effects on earliness. No linkage was found between earliness or lateness and other characters.

Bryan and Pressley (4) noted that in a Sonora x Turkey cross, the  $F_1$  progeny was exactly intermediate between the parents for date of first heading. The  $F_2$  showed an inclination toward the late parent but extended over a range slightly exceeding both parents. They were able to establish homozygous lines for early,

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intermediate and late heading in the F<sub>11</sub> generation.

In 1924 Florell (9) reported on crosses between Sunset (early) and Marquis (late). In the  $F_1$  the date of first ripening was slightly earlier than that of the Marquis parent. In the  $F_2$ there was a distinct segregation into a large early group and a small late group in a ratio of 3.07 early, 0.93 late, close to a 3:1 ratio. The indication was for one main allelomorphic pair of factors for earliness.

Studies on maturity were reported by Clark and Hooker (6) in 1926 on crosses of Marquis x Hard Federation. Three criteria of maturity were studied (1) the dates of heading, (2) the dates of ripening, and (3) the number of days between (1) and (2), or the fruiting period.

Partial dominance was shown by the  $F_2$  data and segregation in the  $F_3$  indicated that at least two genetic factors for early heading were involved. It was also noted that some  $F_2$ families were segregating in the  $F_3$  in a simple 3:1 ratio as found by Florell (9).

Among other characters studied in Kota x Hard Federation crosses Clark (5) reported in 1924 on maturity. He used as a criterion of earliness the date of heading and concluded that earliness was dominant over lateness. Few strains were found to be as uniform in the F3 as the parents.

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. . Since one might expect the inheritance of earliness in all plants to be similar, it is of interest to note what has been found in studies of earliness in other plants besides the cereal crops.

Mendel (24) reported that with garden peas the time of flowering of the  $F_1$  hybrids was almost exactly intermediate between those of the parents, but further results were not given. In other crosses of garden peas, Tschermak (34) secured  $F_1$  plants intermediate in earliness, and in the  $F_2$  families, plants varying from earlier than the early parent to later than the late parent. Some of the extremes bred true, but the intermediates gave offspring variable in time of flowering. His explanation was that two factors for earliness were involved.

In cotton, Leake (22), found the F<sub>1</sub> generation uniformly intermediate in time of flowering. In the F<sub>2</sub> populations there was variation in time of flowering with the mode and the mean nearer the late parent.

Keeble and Pellow (20) from a cross between early and late garden peas concluded that lateness was dominant. The  $F_1$ plants were earlier than the late parent but this was thought to be due to coupling (linkage) between thin stems, which were dominant to thick stems, and earliness.

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Veselovskii (35) working with interspecific crosses in potato found that in the  $F_1$  of the cross <u>S. andigenum x S. tuber-</u> <u>osum</u> the following characters were dominant: late maturity, fertility, ability to form tubers and a large number of tubers to the cluster. By back-crossing with early commercial varieties a combination of the following characters was obtained: early formation of tubers, short period of tuber development, early normal completion of the vegetative period and high productivity.

Emerson and East (8) in corn crosses secured  $F_1$  hybrids intermediate between the parents in earliness, and  $F_2$  populations which had a range exceeding both parents. In the  $F_3$  they had pure types practically as early as the early parent but none quite so late as the late parent.

Working with corn, Hayes and East (14) observed that the F<sub>1</sub> hybrids matured earlier than the average date of maturity of the parents. They believed that the increase in rate of maturity was due to hybrid vigor.

Hutcheson and Wolfe (17) compared, as to earliness, the  $F_1$  hybrids of six crosses of corn with the parent varieties. One cross was earlier in tasseling and silking than the early parent and had a higher percentage of mature corn. The others were intermediate in earliness but, except in the case of one cross, were more nearly like the early parents than the late.

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From a cross between two varieties of rice differing in earliness, Hoshina (16) recovered pure early races like the early parent in earliness. He favoured the multiple factor hypothesis and thought that in his cross the parents differed in three factors.

In his research on the influence of inbreeding upon the season of maturity, Pearson (25) compared inbred lines of cabbage with the hybrids between them and found that in crosses involving unrelated lines there was an increase in earliness. This difference was not observed in crosses of closely related lines. The yields showed similar relationships. He further observed that in some cases earliness was governed by definite genetic factors.

In crosses of tomatoes, Hayes and Jones (15) found early maturity associated with increase in production, and that crosses which did not show increase in earliness did not show increase in production.

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### II. OBJECT OF THE STUDY

This study is exploratory in nature with a threefold objective:

- (a) to observe the form and structure of various strains of barley - early, medium, and late - in order to determine the extent to which morphology may be used as a criterion of earliness,
- (b) to compare the rates of development of early, medium, and late lines under different photoperiods and temperatures,
- (c) to get more definite information concerning the genetic factors responsible for earliness and especially to determine if they are alike in their effects, and the number of factors involved in certain crosses.

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### III. MORPHOLOGICAL STUDY

1. Description of Varieties and Strains

The varieties or strains used are listed below; each one is given a number which is used to designate the variety or strain in the tables.

The seed was furnished by the Cereal Crops Division of the Plant Science Department, University of Alberta. Before the initiation of this study, all materials were tested for their purity for earliness.

#### Table 1

No.	Material	C.I. No.	Type Spring (S)	Season	Genus
1	Atsel	6250	S	Early	H. vulgare
2	Beecher	6566	S	Early	18
3	Tulare	000 ees	S	Early	18
4	н-ЦЦ-1		S Earl	Ly to mediur	n <sup>11</sup>
5	Titan	7055	S	Medium	18
6	Newal	6088	S	Medium	11
7	Montcalm	7149	S	Late	18
8	C.I. 7155		S	Late	T
9	C.I. 7248		S	Late	18

Varieties and Strains

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### 2. Experimental Methods

Crosses involving the individuals listed in Table 1 were made in the field. The F<sub>o</sub> materials together with the standard varieties were seeded in uniform soil in the greenhouse beds on August 22, 1949. All hybrids and varieties were sown in rows 8 inches apart, the seeds being seeded individually 4 inches apart.

Morphological observations made in the greenhouse study were again made under field conditions in the spring and summer of 1950 when the  $F_2$  generation was grown.

Since several crosses were studied, each was given a designation number for convenience in keeping the field records. These numbers are used in the tables, but the names of varieties or strains are indicated in the headings.

The crosses numbered lx to 16 x, inclusive, were made in the field in 1948 and 1949, and the  $F_1$  plants and parents grown in the greenhouse in the fall and winter of 1949-1950. All crosses were compared with the parents in earliness. A
# Table 2

Crosses	Studied
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Designation numbers	Varieties crossed	When grou Fl	m F2
lx	Atsel x Tulare	:49	• 50
2x	Montcalm x Tulare	11	tt
3x	Montcalm x Beecher	11	tt
Цх	Atsel x Beecher	11	11
5x	Titan x Newal	11	tt
6x	Montcalm x Atsel	11	11
7x	Montcalm x Titan	11	11
8x	Montcalm x Newal	11	tt
9x	Beecher x C.I. 7248	88	$\mathbf{H}_{\mathrm{s}0}$
10x	Titan x Tulare	11	tt
llx	Titan x C.I. 7248	11	tt
12x	Montcalm x C.I. 7155	11	ŦŤ
13x	Atsel x C.I. 7155	11	11
l4x	Atsel x C.I. 7248	11	11
15x	Montcalm x C.I. 7248	11	ŦŤ
16x	C.I. 7155 x C.I. 7248	89	11



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3. How Earliness was Determined

After examining the plants at different stages of development, earliness was based upon the date when the first plant began to head. The date for a particular plant was that on which the first spikelet of the earliest spike came through the flag leaf. During the time of heading, the plants were observed at the same hour each day and marked as they headed with dated string tags. There were only a few  $F_1$  plants of most crosses, but for the  $F_2$  populations all the seed was sown in four replications or dates of seeding on the rod-row plan.



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4. Observations on Leaf Emergence

For each variety or hybrid, notes were kept on the date of emergence of the first plant in each line. Emergence dates for the first appearance of a second leaf, third leaf, etc. up to the flag leaf were also taken. These observations were also made on a population basis. With the appearance of the third leaf, notes were taken showing the dates when 75% of the plants and the last plant in each line had acquired a third leaf. This was done for the fourth leaf, fifth leaf, and so on, up to the flag leaf. For complete data on dates of emergence see Tables 9 and 10.

It was observed that late varieties emerged later than early ones. <sup>T</sup>he emergence of the several leaves up to the flag leaf was consistently later for the later lines, but the average lag for each stage of emergence was only two days. Once the flag leaf was acquired there was a significant lag in the date of heading of the later varieties. <sup>T</sup>he correlation between the number of leaves and the dates of emergence for each of two varieties, one early and one late, and the  $F_1$  hybrid between them is shown in Fig. 1.

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Fig. 1

Correlation between dates of leaf emergence, varieties and F<sub>1</sub> hybrid, .

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The late variety, Montcalm, took longer to complete the various stages of leaf development than the early line, Atsel. The hybrid 6x was earlier in leaf emergence than Montcalm and was not intermediate but closer to the early Atsel. In the field the behaviour of these two lines was very similar but leaf emergence dates for the hybrid were closer to Atsel in the later stages of development preceding heading.

#### 5. Observations on Tiller Emergence

The appearance of tillers did not follow the pattern of leaf emergence. Except for the early variety Atsel, the three latest lines, Montcalm, C.I. 7155, and C.I. 7248, showed the emergence of a first tiller in advance of the early lines Beecher and Tulare and of the midseason varieties Newal and Titan. This behaviour seems to indicate that the date of tiller emergence bears a negative correlation to earliness.

In the  $F_1$  hybrids tiller emergence was very irregular when compared with the parental lines. From a cross between the two late lines C.I. 7155 and C.I. 7248, the first tiller emerged twelve days later than those for the parents while in the late

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Montcalm x C.I. 7155 the first tiller was intermediate in emergence to those of the parents. These wide differences in emergence appeared in the F<sub>1</sub> greenhouse study. In the field the F<sub>2</sub> material showed greater uniformity in tiller emergence. Here the hybrid behaviour was closer to the early parent and consistent throughout several crosses.

Not only did the later varieties require more days for tillering but when crossed with early varieties the hybrid tiller was always earlier than the late parent.

### 6. Observations on Growth Habit

Aberg and Wiebe (2) observed that in the early stages there were three distinct habits of growth both for spring and winter varieties of barley. They stress that the rosette habit was characteristic of the winter varieties, but that there was no sharp line of demarcation in this respect between certain of the winter and spring varieties.

In most varieties, winter or spring, the rosette-growth stage occurred between seeding and culm elongation, and a plant in this stage was characterized by having several tillers, very little elongation in stem internodes and a leafy appearance.



During the early stages of growth the leaves and tillers are held at various angles which may be described as prostrate, semiprostrate, and erect.

In the spring varieties used for this earliness study the three types of growth habit were evident when observations were taken at the six- to eight-leaf stage. The association between earliness and habit of growth is shown in Plate 1. Seeded in the field on June 1, 1950, the three varieties, Beecher, Titan, and Montcalm, headed on widely different dates. Beecher, the most erect in form with three tillers, headed on July 9. Titan was more spreading with five tillers and headed on July 13. Montcalm was semiprostrate to prostrate with eight tillers and headed on July 19. Other early, medium, and late lines observed showed a similar correlation between growth habit and earliness.

Suneson (29) studied the survival of four barley varieties in a mixture. He observed that the variety Atlas, though the least resistant to various leaf diseases, showed the largest survival value because of its erect, early growth, and weak tillering habit. His observation is supported by this phase of the study carried out in the greenhouse.

A count was taken of the total number of tillers in each variety and hybrid. The average for each population was used to establish a correlation between the number of tillers and days to heading. Table 3 gives a list of all the lines, varieties, and hybrids observed and the average number of tillers in each population.

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Plate 1. Barley growth types, seeded June 1, 1950
A - Montcalm, semiprostrate; B - Titan, semierect;
C - Beecher, erect.

## Table 3

Tillers Ob	serve	d
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No.	Variety or hybrid	Season	Av. no. of tillers (F <u>1</u> )
1	Atsel	Early	2
2	Beecher	Early	3
3	Tulare	Early	2
4	H-44-1	Early to medium	4
5	Titan	Medium	5
6	Newal	Medium	5
7	Montcalm	Late	6
8	C.I. 7155	Late	7
9	C.I. 7248	Late	6
lx	Atsel x Tulare		3
2x	Montcalm x Tulare		4.
3x	Montcalm x Beecher		4
4x	Atsel x Beecher		5
5x	Titan x Newal		5
6x	Montcalm x Atsel		4
7x	Montcalm x <sup>T</sup> itan		4
8x	Montcalm x Newal		5
9x	Beecher x C.I. 7248		5
10x	Titan x Tulare		6
llx	Titan x C.I. 721 <sub>1</sub> 8		4
12x	Montcalm x C.I. 7155	2	6
<b>1</b> 3x	Atsel x C.I. 7155		4
14x	Atsel x C.I. 7248		5
15x	Montcalm x C.I. 7248	3	5
16x	C.I. 7155 x C.I. 72	<u>+</u> 8	7



The  $F_2$  generation, grown in the field showed a marked segregation for earliness. The correlation between number of tillers and days to heading was however maintained. Fig. 2 illustrates the tiller-days-to-heading relation as studied from  $F_1$  greenhouse material.

The relationship between number of tillers and number of days to heading is shown in Table 4. It must be mentioned that under greenhouse conditions the varieties studied came to head an average of two weeks later than these same varieties did in the field. The greenhouse  $F_1$  hybrids showed similar behaviour to the pure lines but, with the  $F_2$  segregation for earliness in the field this difference can be explained.

#### Table 4

No.	Material	Tillers (F1 av.)	Season Early(E) Midseason.(M) Late(L)	Days to head
l	Atsel	2	Е	48
2	Beecher	3	E	52
3	Tulare	2	E	49
4	н-144-1	2 <sub>1</sub> -	E to M	54
5	Titan	5	Μ	71
6	Newal	5	M	73
7	Montcalm	6	L	74
8	C.I. 7155	7	L	108
9	C.I. 72/18	6	L	99

#### Tillers and Days to Heading





Fig. 2

The number of days to heading increases with the number of tillers.

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It was shown that under favourable growing conditions the form or habit of growth, in the early growth stage, could be used as a means of distinguishing between early, medium and late lines. This observation applies where spring varieties of barley are being considered.

Varieties are known to differ in certain leaf characters, such as blade, leaf sheath, auricle, ligule, colour, and size of leaf. These characters serve to separate a few varieties but were not observed to bear any definite relation to earliness. It was seen that, as a general rule, the leaves of early lines were shorter and narrower than the late varieties. Fig. 2 illustrates leaf-width differences which may be associated with earliness. The writer feels that environment may be a factor in determining the width of leaves. This character will not be advanced as a satisfactory criterion of earliness on the basis of the present study.

#### 7. Observations on Leaf-blade Curling

The barley leaf-blade is lanceolate-linear with a prominent middle nerve flanked by 10 or 12 parallel side nerves that are less strongly developed. The blades are rolled in the bud but there is no consistence in the direction of roll. 
It was observed that in the earlier growth stage up to the fifth or sixth leaf, the tendency for emergent leaves to remain partially rolled was stronger in the late varieties. This characteristic was first noted in the greenhouse study and was further verified in the field material. Fig. 3 shows typical third leaves taken from early, medium, and late varieties after all had acquired the sixth leaf. The earliest variety, Beecher, has a third leaf which is stiff in character with the rolling or curling almost completely lacking. The midseason variety, Newal, is rolled close to the tip while the late line, Montcalm, maintains the roll or curl throughout the length of the leaf. In Montcalm, except for the older leaves, the first and second also appeared curled.

The varieties Atsel and Tulare, both early, are similar in leaf-rolling characteristic to the early Beecher. Other late varieties studied, C.I. 7155 and C.I. 7248 had rolled leaves even during the later stages of growth though to a lesser extent than Montcalm. This leaf study points to the possibility of an association between stiffness of leaf-blade in the early growth stage and earliness. The hybrid material was less definite in this leaf characteristic, but early  $F_2$  segregates showed a strong tendency for leaf stiffness.

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## Fig. 3

Degree of leaf curling in three seasonal types of barley: I - Atsel, early; II - Newal, midseason; III - Montcalm, late. · .

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In the field the F<sub>2</sub> generation from the cross Montcalm x Tulare resulted in<sup>8</sup> wide variety of individuals. In earliness they ranged from plants earlier than the early Tulare to plants later than the late parent. A wide variation in morphology and leaf-blade character was also observed. Not only were the earlier heading plants more erect in habit of growth, but leaf-blade curling was significantly absent.

### 8. Study of Spike Characteristics

The spike characters of the barley plant are among the most useful in identifying varieties. Some of these characters are stable while others are affected by changes in environment. In some varieties the distance from flag leaf to spike varies from one locality to another as in Titan.

There are several varieties in which the spikes hardly emerge from the boot as in C.I. 7155 and C.I. 7248 and these cases can be easily distinguished from those in which the spike is fully exerted and the distance from flag leaf to spike is

. 6  great, as in Atsel and Tulare. The varieties Montcalm and Newal appear to fall in an intermediate group.

In this study there was no variation in the distance from flag leaf to spike in the varieties C.I. 7155 and C.I. 7248. With these two late lines the spike emerged half way up the height of the boot, and the distance of the neck was almost negligible. In these two varieties the flag leaf appeared at the uppermost half to completely above the spike after spike emergence was complete. About 5 per cent of the plants in the variety C.I. 7155 showed spikes which were only partly emerged from the sheaths. These heads contained several sterile spikelets.

Fig. 4 illustrates the spike-flag leaf relationship in the early variety, Atsel, and the late C.I. 7248.

In Atsel, the distance from flag leaf to spike is 1/3 the length of the spike. This character is typical of the early Atsel and variations in this distance are only slight. C.I. 7248 carries the flag leaf 2/3 the distance above from the base of the spike. The F<sub>2</sub> generation of Atsel x C.I. 7248 carries the spike in an intermediate position. Here there is a coincidence between base of flag leaf and base of spike.

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Fig. 4

Spike-flag leaf relation in the early Atsel, late C.I. 7248, and the  $F_2$  hybrid of cross, Atsel x C.I. 7248.

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The head of the F<sub>2</sub> hybrid is intermediate in size between the parents and the distance from last leaf to flag leaf, the boot, is greater than either parent. The neck is inconspicuous above the boot. Although Montcalm, a late variety, shows some variation in spike position, it is significant that 72 per cent of the plants studied carried the spike in the intermediate position while the rest varied from short neck to sub-flag leaf spike position.

On the basis of this study, it is evident that there is a correlation between size of spike, length of neck, and earliness. The varieties Beecher and Tulare, both early, are similar to Atsel in the spike-flag leaf relationship while the late Montcalm, with small variations, C.I. 7153 and C.I. 7248, have a typical short neck and low spike conformation. Table 5 gives data on heading dates of the early Atsel, late C.I. 7153 and C.I. 7248, and the  $F_2$  hybrids between early and late types all seeded in the field on June 1, 1950.

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#### Table 5

Heading Data on Early and Late Linesand F<sub>2</sub> Hybrids. Seeded June 1, 1950

Material	Season	Days to heading
Atsel	Early	36
C.I. 7155	Late	55
C.I. 7248	Late	50
Hybrids (F <sub>2</sub> ):		
Atsel x C.I. 7155		39
Atsel x C.I. 7248	800 800	42
C.I. 7155 x C.I. 724	.8	49

A comparison of Fig. 4 with data on heading dates in Table 5 serves to establish the correlation between the morphology of the barley head and earliness in terms of time of heading.

In connection with the morphology of earliness a study was made of node characters. It was observed that in the early varieties, Atsel, Tulare, and Beecher, and to a lesser extent H-44-1, the nodes were exposed to the sun's rays earlier than in the midseason lines, Newal or Titan, and the late varieties, Montcalm, C.I. 7155, and C.I. 7248.



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After two weeks of exposure to sunshine, the nodes took on a dark orange to purple colour due to the presence of anthocyanin. While the early node exposure in this study seems to be associated with earliness, the variation in node colour introduces a factor of uncertainty as to how much of the colour is due to environment and how much to inheritance. The unreliability of colour readings makes it difficult to use this character as a morphological expression of earliness.

A number of other plant characters were studied but were found, within the limits of this study, to be of little value in classifying varieties as to earliness. In some cases the varieties studied were so nearly alike that they could not be differentiated on the basis of these characters. In other cases the observations had to be abandoned because of variability obviously due to environment.

The lengths of spikes was studied but a great deal of variation was found between varieties and within the same variety.

In the greenhouse study no plant among the early lines Atsel, Beecher, and Tulare, was observed to carry more than 8 leaves on the main stem. The midseason variety Titan and the late Montcalm averaged 9 and 10 leaves respectively. This relationship did not hold completely in the field observation where Tulare again averaged 8 leaves per main stem but Atsel and Beecher carried 9 leaves on more than 60 per cent of the population. Here several Montcalm plants carried 11 leaves.

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The height of plant, that is, the distance from the ground to the base of the spike as used by Åberg and Wiebe (2) was found to be an unstable character, and could not be used in predicting earliness. The influence of environment on plant height within varieties will be dealt with in the report on the physiological study.

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#### IV. PHYSIOLOGICAL STUDY

- 35 -

1. Observations on Development of Barley

Both greenhouse and field studies indicate that there is a great deal of variation in the time of heading of barley. The rate of development and time of heading are influenced by weather and soil conditions and by soil differences. Ideal conditions for such a study would include uniform soil and unvarying conditions for growth throughout the growing season. In the field this ideal is practically unattainable.

The studies referred to on the influence of length of day on heading (10), (7), (11), and (12), are related to the present investigations of the factors influencing earliness in barley and other cereal crops. Photoperiodism is probably responsible for the irregular heading of the late varieties and for the failure of some plants, and of crosses with them, to head at all.

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#### 2. Materials and Methods

- 36 -

Seedlings of three seasonal groups of barley (early, midseason, and late) were grown in flats in three sections of the greenhouse at three different temperatures, 55°, 65° and 75°F. At each temperature a short and long day (13 and 17 hours) was simulated by light control - electric lamps and shading.

The varieties with date of seeding and dates of emergence under reasonably constant photoperiods and temperatures are given in Table 6.

### Table 6

Materials and Conditions of Photoperiodic Study in Greenhouse, with Days to Emergence from Seeding on November 15, 1949

Material	Season	Photo Days 75°F	Photoperiod 17-hr. Days to emergence 75°F 65°F 55°F			Photoperiod 13-hr Days to emergence 75°F 65°F 55°F			
Atsel	E	3	3	4	4	4	5		
Beecher	Е	4	4	5	4	5	6		
Tulare	Ε	3	4	4	4	4	5		
н-44-1	М	4	5	5	4	5	6		
Newa].	М	LF	5	5	5	6	6		
Titan	М	4	4	5	4	5	6		
C.I. 7155	L	6	6	7	5	6	7		
C.I. 72/18	L	5	5	6	5	6	7		
Montcalm	L	5	5	6	5	6	7		

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This Table shows that by adjusting factors in the environment, the developmental response, even in the early stages, can be increased or retarded. For example, the early variety Atsel showed an emergence range of three days when grown under photoperiods and temperatures differing by 4 hours and 20°F respectively. The latest line, C.I. 7155, showed a similar response under the same set of conditions, thus emphasizing the dependence of rate of development upon the quantity of light and temperature.

#### 3. Histological Observations

One seedling from each variety or hybrid and from each treatment was collected for histological study at different intervals. The following technique was employed for collecting and storing material:

Seedlings were carefully taken up in order to preserve the radicle and plumule. They were then washed and killed by emersing for a 48-hour period in Fharmer's mixture - 3 parts of 95 per cent ethanol to 1 part glacial acetic acid. The killing and fixing process was followed by washing and storage in 70 per cent ethanol. Collections at various intervals were identified by date tags.

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Photographs were made of three sets of plants, early Atsel, midseason Newal, and late Montcalm, taken up on the same date to show the difference in development of plants under specific photoperiods and temperatures. The correlation between rate of development, photoperiod, and temperature is shown in Figs. 5 and 6. The plants in both Figures were taken up on the same date, November 27, 1949. The labels A, B, and C, represent temperatures 75°, 65°, and 55°F. The varieties are grouped to show two photoperiods, 17 hours and 13 hours.

In both Figs. 5 and 6, the difference in development between plants A and B under each photoperiod is not very significant, though the size of the second leaf in each case indicates that in the early stages, a temperature of 75°F favours development. For each variety plant C is significantly later than A or B, though grown under the same photoperiod. It is evident that the temperature 55°F is below the ideal for maximum growth in the early stages.

When plant C is considered there appears to be no visible difference between the effects of the two photoperiods. Temperature appears to be the more important factor in development at this stage of growth. It would appear, further, that the ideal temperature lies between 75° and 65°F and closer to 75°F. Under a photoperiod of 17 hours plants A and B show an advance in development over A and B under a 13-hour day. The indication is that the effect of photoperiod upon rate of growth is largely dependent upon temperature.

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Fig. 5

Seven day old Atsel seedlings grown under two photoperiods, 17 hours and 13 hours, and three temperatures,  $A - 75^{\circ}F$ ;  $B - 65^{\circ}F$ ;  $C - 55^{\circ}F$ .

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## Fig. 6

Seven day old Montcalm seedlings grown under two photoperiods, 17 hours and 13 hours, and three temperatures, A - 75 F; B - 65 F; C - 55 F.

n  Earliness, having been based on the initiation, development, and final emergence of the primordia in the form of the head, all plants were dissected and measurements of leaves and internodes made. This was followed by examination and measurement of the primordia. If at one stage of development it could be established that the primordia was not present, and at a later growth stage it had been initiated, then the critical date in the primordia initiation could be used as significant of earliness.

Table 7 shows data on leaf measurements in cm. of the first set of plants taken November 24, 1949. By dissection, the initiation of a third or a fourth leaf was observed in some plants, but in none was a primordia seen under the dissecting microscope. It was obviously too early a stage for the detection of differentiation of the growing point. Nodes and internodes were not discernible at this early growth stage.

Seedlings taken on November 27, 1949, samples of which are represented in Figs. 6 and 7, were dissected under the microscope. These were three days older than seedlings recorded in Table 7 and show in some cases the initiation of a fifth leaf and the presence of the primordia. Data on plants taken November 27, 1949, are given in Table 8.

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### Table 7

Measurement of Leaves in Cm. of Plants Seeded November 15, 1949

	المرحاني وفاحدهان والروادي	The sheet for the state			and the second secon		and the same of face of			-		
	A (75°F)					с (55 <sup>°</sup> ғ)						
Material	1	2	3	4	1	2	3	4	1	2	3	4
Period of	daily	expo	sure	- 17	hours							
Atsel	12.7	5.1	0.5	0.1	12.1	4.3	0.4	0.5	6.9	1.5	0.25	-
Beecher	11.7	4.1	0.5	1.15	13.3	3.9	0.3	0.05	4.7	0.9	0.2	60
Tulare	11.4	2.6	0.4	0.05	10.4	1.9	0.25	-	4.4	0.8	0.1	-
н-44-1	10.8	9.2	1.0	0.15	13.0	9.1	1.1	0.2	3.9	1.1	0.2	-
Newal	14.2	7.3	0.6	0.1	10.9	3.6	0.4	0.05	3.8	0.7	0.1	-
Titan	14.2	6.7	0.5	0.05	14.6	6.5	0.6	0.1	5.6	1.1	0.15	**
C.I.7155	11.5	3.4	0.45	0.05	11.7	1.95	0.45	0.05	4.2	0.5	0.05	-
c.I.7248	12.4	5.1	0.35	0.02	12.6	4.7	0.5	0.05	5.1	0.7	0.1	-
Montcalm	13.4	6.1	0.7	0.1	12.1	4.6	0.4	-	4.05	0.6	0.05	-
Period of	daily	expo	sure	<u>- 13</u>	hours							
Atsel	13.5	7.6	0.6	0.15	14.1	7.2	0.4	0.1	5.5	0.9	0.25	-
Beecher	14.8	4.2	0.4	0.1	14.2	5.5	0.2	0.05	5.8	0.7	0.15	•
Tulare	11.3	6.3	0.5	0.1	10.7	3.3	0.15	-	5.2	0.4	0.05	-
н-44-1	9.5	4.0	0.4	0.1	10.4	7.3	0.3	0.05	8.2	2.7	0.35	0.05
Newal	12.1	5.8	0.4	0.05	13.1	5.8	0.2	-	5.5	0.9	0.15	
Titan	14.6	5.3	0.35	0.05	11.4	4.8	0.25	-	6.2	0.95	0.15	-
C.I.7155	11.7	2.3	0.4	0.03	12.3	3.0	0.1	-	6.0	0.5	0.05	-
C.I.7248	12.2	5.8	0.3	0.05	12.0	4.6	0.2	-	5.6	0.85	0.1	-
Montcalm	11.3	7.4	0.5	0.05	14.0	5.2	0.3	0.05	5.7	1.0	0.15	

and Taken up November 24, 1949



# Table 8

Measurement of Leaves and Primordia in Cm. of Plants Taken up

November 27	', 1949
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		7	5°F		65°F				55 <sup>0</sup> F			
Material	1	3	5	Prim.	1	Jea 3	5	Prim.	ì	3	5	Prim
Period of	daily	expo	sure	- 17	hours							
Atsel	13.3	5.3	0.1	0.08	19.4	1.70	0.09	0.05	9.6	0.5	619	e#
Beecher	15.8	4.8	0.05	-	13.8	1.1	0.03		8.3	0.4		-
Tulare	13.4	1.5	0.05	0.04	14.7	1.4	0.07	0.03	9.1	0.3		-
н-44-1	12.1	3.4	0.02	**	13.4	4.8	0.1	60	7.2	0.25	-	-
Newal	13.1	1.4	0.05		13.7	3.0	0.1		8.0	0.2	-	
Titan	14.6	4.8	0.07	0.03	15.5	1.5	0.2	0.02	9•9	0.2		enti
C.I.7155	14.1	0.3	-		14.3	1.3	0.01	-	8.7	0.15	849	-
c.I.7248	13.1	1.0	0.02	-	13.6	0.8	0.02	-	8.4	0.25	-	-
Montcalm	14.3	1.7	0.04	0.05	16.7	1.3	0.03	0.02	9.8	0.2		ed
Period of	daily	expo	sure	<u>- 13 P</u>	nours							
Atsel	<b>1</b> 4.1	1.7	0.1	0.03	15.1	1.9	0.03	0.02	9.0	0.4		640
Beecher	13.9	1.4	0.05	0.02	15.3	1.4	0.01		9•9	0.3		
Tulare	13.5	0.7	0.02	-	13.9	1.5	0.01	-	7.9	0.2	-	
н-44-1	12.9	1.1	0.03		13.5	1.9	0.03	0.01	10.1	0.7	0.01	
Newal	13.3	0.5			13.7	1.2		-	8.3	0.25		88
Titan	13.4	0.7			14.7	1.3	0.02	88	8.1	0.2		
C.I.7155	14.9	0.25	-		14.1	1.2	-	-	7.1	0.15		
C.I.7248	14.5	0.35		-	13.9	1.0	0.01		6.8	0.15		-
Montcalm	15.2	1.45	0.03	0.02	14.6	1.1	0.05	-	6.2	0.8		

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From Table 8 it may be observed that under a photoperiod of 17 hours and temperatures 75° and 65°F, the primordia of the Atsel variety was initiated in 8 days after emergence. Under the same set of conditions (Table 7) it was not detected when the variety was 5 days old. Table 8 also indicates that primordia differentiation takes place only after the initiation of the fifth leaf.

The measurements for plants grown at  $65^{\circ}F$  show that this temperature is closer to the ideal for vegetative growth than  $75^{\circ}F$ , but the latter is more favourable to development. Under a temperature of  $55^{\circ}F$  there was a consistent lag in leaf emergence and primordia differentiation with all the varieties observed. The longer daily exposure did not favour development at  $55^{\circ}F$ .

Photomicrographs of growing points and primordia differentiation of plants in Figs. 5 and 6 are shown in Plates 2 and 3.

The top row of Plate 2, reading from left to right shows the enlarged growing points of the early variety Atsel grown under a photoperiod of 17 hours and temperatures of  $75^{\circ}$ ,  $65^{\circ}$ , and  $55^{\circ}$ F. The bottom row shows the late Montcalm grown under the same conditions. It may be observed that in both varieties, response to temperature, in terms of growing point elongation, is significantly higher for temperatures  $75^{\circ}$  and  $65^{\circ}$ F.

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Atsel



Montcalm



Plate 2. Effect of 17 hour photoperiod on primordia development of seven day old Atsel and Montcalm seedlings grown under three temperatures, A - 75°F; B - 65°F; C - 55°F.







A

В

С

Montcalm



Plate 3. Effect of 13 hour photoperiod on primordia development of seven day old Atsel and Montcalm seedlings grown under three temperatures, A - 75°F; B - 65°F; C - 55°F.

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In Plate 3 is shown the relative response of Atsel, in the top row, and Montcalm when plants are grown under a day length of 13 hours and different temperatures. As in Plate 1, development is more rapid under 65° and 75° than under 55°F. The day length of 17 hours (see Plate 2) shows a small increase in rate of development over the 13-hour daily exposure to light (Plate 3).

One sample from each variety grown under each of the six conditions previously mentioned was collected for primordia study on the following dates:

 November 2h, 1949

 November 27, 1949

 December 1, 1949

 December 7, 1949

 December 21, 1949

 December 21, 1949

 December 21, 1949

Each set of samples was studied in the same way as in the method described - microdissection followed by microphotography of the primordia. The fourth set of plants taken on December 7, 1949, and all later collections, were studied for leaf and primordia and in addition for tiller and internode development. It was established in the morphological study that the average number of tillers had a direct relation to earliness, and so the rate at which tillers developed should be correlated with the rate of primordia development.



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4. Photoperiodic Reaction with Advancing Age of Plant

It was observed that in the early growth stage the effect of a longer number of light hours per day was not significant. Development under the shorter period of light compared favourably with the longer, provided the temperature was the same. However, with an advance in the age of plants towards the 'ripe-to-flower' condition, the effect of photoperiod on growth and differentiation becomes more evident.

The results of differences in the daily illumination are given in Plate 4 with plants collected December 14, 1949.

The top row of Plate 4 shows early Atsel and late Montcalm plants grown under a 17-hour daylight and three temperatures- A,  $75^{\circ}$ , B,  $65^{\circ}$ , and C,  $55^{\circ}$ F. With both varieties,  $65^{\circ}$ F favoured leaf and stem elongation as well as primordia development (see Plate 5). At the lowest temperature,  $55^{\circ}$ F both varieties showed delayed or less profuse growth.

In the bottom row of the same figure are shown plants of the same two varieties of the same age and grown under the same temperatures but with 13-hour illumination. Under a 13-hour photoperiod the effect of higher temperatures on vegetative growth is less pronounced. The difference in plant structure at 75°F and 65°F is negligible in both the Atsel and Montcalm varieties. These contrasting behaviours at the present time appear to be dependent upon

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Plate 4. Twenty-five day old Atsel and Montcalm seedlings grown under 17 hour and 13 hour photoperiods and temperatures:  $A - 75^{\circ}F$ ;  $B - 65^{\circ}F$ ;  $C - 55^{\circ}F$ .


fundamental differences in the physiology of the two photoperiodic groups, and may be so regarded until further investigations have proved otherwise.

The measurements for leaves, tillers, internodes and primordia of plants collected on December 14, 1949, are reported in Table 9. It will be seen that the rate of development of the primordia is correlated with the length of the daily exposure. All plants under the 13-hour day length showed less development in this character than the corresponding varieties under the longer photoperiod.

The data on tillers (Table 9) indicate that the later varieties tend to have a more rapid growth and development of the tillers. The contrast in tiller growth under the two photoperiods shows that this character is also affected by length of exposure to light. The elongation of the internodes is similarly affected by exposure to light.

Photomicrographs showing stages of primordia development of plants in Plate 4 are given in Plates 5 and 6. Plate 5 shows primordia development under a 17-hour photoperiod and three temperatures. At temperatures  $75^{\circ}$  and  $65^{\circ}$ F the primordia show an increase in growth over the  $55^{\circ}$ F. The early Atsel and late Montcalm respond in a similar way to differences in temperature. In both varieties the primordia was smaller when the plant was grown under the same photoperiod of 17 hours and at a temperature of  $55^{\circ}$ F.

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Table	9
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Measurements in Cm. of Plants Collected November 14, 1949

	75°F									650	F	55°F													
		I	eaf		Till	Ler	Inter	node		]	Leaf		Till	.er	Inte	rnode		]	Leaf		Til	ler	Inter	node	
Mater	ial	1	4	7	1	2	2	3	Prim	. 1	4	7	1	2	2	3	Prim		4	7	1	2	2	3	Prim.
Peri	riod of daily exposure - 17 hours																								
Atsel		11.4	26.7	2.7	<b>1.</b> 0	0.2	1.5	0.5	0.4	15.1	33.2	3.5	0.2	0.3	2.4	0.4	0.4	15.7	15.0	0.7	0.2	0.15	0.2	0.1	0.2
Beech	ler	15.2	37.2	1.1	9.1	0.7	0.3	0.15	0.3	13.2	29.8	0.1	0.15	0.1	0.2	0.1	0.2	11.1	10.9	0.15	0.1	0.5	0.15	-	0.15
Tular	e,	13.9	19.8	0.9	0.6	0.4	0.3	0.15	0.35	7•7	19.0	0.12	0.15	0.1	0.17	0.1	0.27	11.2	6.6	0.15	0.12	0.1	0.2	0.15	0.2
<u>H-]i]i</u> =	1	13.1	27.6	2.1	0.5	0.2	1.5	0.15	0.3	11.9	34•3	5.9	0.1	0.5	1.7	1.9	0.3	12.8	<b>1</b> 4•7	0.3	0.2	0.1	1.15	0.1	0.2
Newal	-	14.1	34.8	1.7	3.4	0.7	0.8	0.15	0.2	13.2	27•7	0.5	0.25	0.1	0.3	0.1	0.2	14.6	12.2	0.15	0.2	0.1	0.3	0.1	0.15
Titar	l	15.5	36.4	0.9	15.4	4.5	0.35	0.15	0.2	12.1	27.4	0.2	0.3	0.2	0.15	0.1	0.2	11.8	11.3	-	4.8	0.25	0.15	0.1	0.12
C.I.7	155	14.3	25.2	0.5	1.4	0.3	0.25	0.1	0.2	15.5	2.8	0.1	0.1	0.2	0.05	0.01	0.10	15.2	1.4	0.05	0.3	0.2	0.05	-	0.17
0.I.7	248	15.4	26.2	0.8	13.6	0.6	0.3	0.2	0.15	16.4	18.2	0.3	0.2	0.1	0.15	0.02	0.18	13.2	6.7	-	0.9	0.2	0.15	0.1	0.15
Monto	calm	14.7	28.7	0.6	10.0	2.6	0.15	0.1	0.15	13.8	36.5	0.7	0.15	0.1	0.1	0.07	0.25	15.2	15.1	0.15	0.1	0.5	0.17	0.1	0.16
Perio	od_0:	f dai j	ly ex	posu	re =	<u>13</u> h	ours																		

0.12 0.05 0.16 18.1 1.15 0.2 0.1 0.15 0.08 0.05 0.17 15.3 1.9 - 0.05 - 0.12 0.05 0.12 12.6 0.8 0.1 0.15 -Atsel 0.1 0.05 0.1 0.12 0.1 0.07 0.07 - 0.15 15.5 2.0 - 0.15 15.2 2.3 Beecher 16.9 6.5 -0.1 ----0.1 -0.1 0.05 0.08 -0.1 0.2 0.1 0.1 0.03 0.17 13.4 0.3 -0.1 0.05 0.15 0.1 0.12 6.4 2.2 -13.4 10.2 -Julare 0.08 -0.08 -0.15 0.1 0.07 0.05 0.02 0.14 15.2 0.6 -0.75 9.1 7.0 11.5 6.4 0.4 0.2 0.1 -----3-44-1 -0.08 0.05 0.05 0.02 0.12 13.2 0.6 0.05 0.1 0.4 0.3 0.12 0.1 0.2 0.1 0.1 0.05 0.15 15.6 1.8 -13.6 3.8 -Newal - 0.1 0.2 0.05 -0.12 15.2 4.0 0.1 0.1 0.05 0.08 0.02 0.1 13.3 1.2 0.1 16.0 10.1 0.1 0.15 0.1 0.15 litan 0.05 0.02 -0.05 0.02 0.05 - 0.02 19.3 1.07 -0.5 -0.1 - 0.1 12.7 0.49 -0.1.7155 14.4 1.1 -0.1 -0.15 0.2 0.02 0.08 -0.05 - 0.05 - 0.03 14.6 1.9 -0.05 - 0.15 15.4 1.7 -0.1.7248 14.3 0.6 -0.2 -Montcalm16.2 2.7 - 0.15 0.1 0.12 0.05 0.12 12.2 0.45 0.01 0.7 0.5 0.03 - 0.02 13.8 1.2 0.05 0.1 0.2 0.1 0.08

9 9 3 3 4 9 9 4 K 9 3 1 5 5 7 6 8 4 • • • • • • • • • • -7 A are g by prime R and a sum p . · · · · · · · · · · · · · · e a p p - a - d a p · · · · · · · · · · · · · • • • • • • • • • • • . 6... . . . • • • • • • •

In Plate 6 it may be observed that the highest temperature of  $75^{\circ}F$  and the lowest of  $55^{\circ}F$  does not make a significant difference in primordia size or development. The two contrasting varieties Atsel and Montcalm showed little variation in primordia size over the range of temperature  $75^{\circ}$  to  $55^{\circ}F$ . It is evident from Plate 5 that under the 17-hour day length the plants have approached the ripe-to-flower stage. Plate 6 shows that under the shorter day length of 13 hours this condition is not yet reached.

The contrasting behaviour of plants under the two photoperiods described above seems to indicate that in the late developmental stages a longer exposure to light is essential for early heading in barley. It may therefore be suggested that the plants have now reached a phase in which light becomes the decisive factor for earliness, accompanied by accessory factors such as temperature, humidity, etc.

# 5. Photoperiodism and Heading

Having discussed and illustrated the influence of photoperiodism and other accessory factors in the rate of development in the early and middle stages of growth, it will now be appropriate to give the observations made at the later and pre-inflorescence stage.

For this study of the physiology of earliness the last set of plants was  $\mu_{\pm}$  days old when collected. The comparative sizes

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a the set of . . . . . 

## Atsel



### Montcalm



Plate 5. Effect of 17-hour photoperiod on primordia development of twenty-five day old Atsel and Montcalm seedlings grown under three temperatures,  $A - 75^{\circ}F$ ;  $B - 65^{\circ}F$ ;  $C - 55^{\circ}F$ .

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#### Atsel



Montcalm



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Plate 6. Effect of 13-hour photoperiod on primordia development of twenty-five day old Atsel and Montcalm seedlings grown under three temperatures,  $A - 75^{\circ}F$ ;  $B - 65^{\circ}F$ ;  $C - 55^{\circ}F$ .

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attained by the two varieties Atsel and Montcalm under the various conditions of light exposure and temperature are shown in Plate 7.

The upper row, Plate 7, shows Atsel and Montcalm varieties grown under a light exposure of 17 hours per day and temperatures of 75°, 65°, and 55°F reading from left to right. Unlike the behaviour observed when the varieties were two weeks younger (see Plate 4) the two lines now give a greater differential response to temperatures  $75^{\circ}F$  and  $65^{\circ}F$ . The A plant  $(75^{\circ}F)$  of the late Montcalm variety has developed significantly beyond the B plant  $(65^{\circ}F)$  of the same variety. In the early Atsel line, the A plant has similarly advanced beyond the B which in both cases is much closer to the C plant  $(55^{\circ}F)$ .

A comparison of the A plant shows that Atsel has advanced towards heading beyond Montcalm, although both plants were the same age and grown under the same environment. On the basis of this observation, it must be assumed that some other factor or factors beyond the limits of present environmental control has influenced an earlier heading in the Atsel line.

The differences in growth between plants B and C in both the Atsel and Montcalm lines are not as significant as those between A and B. This would indicate that the critical temperature for earliness at this stage of vegetative growth in both varieties was between  $65^{\circ}$  and  $75^{\circ}$ F and closer to  $75^{\circ}$ F. Both varieties have shown greatest



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Plate 7. Forty-four day old Atsel and Montcalm seedlings grown under 17-hour and 13-hour photoperiods and temperatures:  $A - 75^{\circ}F$ ;  $B - 65^{\circ}F$ ;  $C - 55^{\circ}F$ .



response to the 17-hour photoperiod when the temperature is high  $(75^{\circ}F)$ . Atsel, however, has a greater capacity to react under higher temperatures and is therefore earlier than Montcalm grown under the same set of conditions.

An examination of the lower row of Plate 7 shows the effects of a shorter daily exposure (13 hours) on growth and development as the plants approach the ripe-to-flower condition. All the plants are characterized by spindly growth and are backward in leaf emergence and stem elongation. The differences in response between temperatures 75° and 65°F are not as clearly defined as under the 17-hour light exposure. Both Atsel and Montcalm show marked retardation at temperature 55°F. When the plants are compared by temperature figures the capacity of Atsel to react under higher temperatures is confirmed.

When the lower row (Plate 7) is contrasted with the upper, the importance of photoperiodism on the rate of development, or earliness, becomes apparent. The necessity for a longer daily exposure to light increases as the inflorescence stage approaches. This differential response to temperature and light was found in the other early, midseason, and late varieties observed. Measurements for the above and other varieties dissected are given in Table 10.

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Measurements in Cm. of Plants Collected November 28, 1949

	75 <sup>°</sup> F									65°F							55°F							
		Leaf		Til	ler	Inter	node		Le	af		<u>Till</u>	er	Inter	node			Leaf		Til	ler	Inter	node	
<u>aterial</u>	L	<u> </u>		<u> </u>	_2		4	Prim.	<u> </u>	4	(	<u> </u>			4	Prim	<u> </u>	4		<u> </u>	2	2		Prim
Period of	dai:	Ly_exp	osure	-	17 h	ours																		
Atsel	17.5	41.0	41.2	1.4	0.7	5.8	6.2	5.6	10.4	39.5	20.1	0.3	0.15	1.3	1.4	0.6	14.6	31.2	4.6	0.4	0.2	0.25	0.1	0.3
Beecher	16.4	48.1	3.1	19.2	0.8	1.4	0.1	0.4	12.8	39.1	18.6	0.2	0.4	5.8	0.4	0.35	15.6	44•7	5.6	0.38	0.2	4.1	-	0.25
Tulare	10.2	34•7	13.4	0.2	0.15	2.4	0.5	0.5	8.3	28.5	29•7	0.14	0.1	4.0	4.3	1.4	5.2	19.8	-	0.15	0.1	1.1	-	0.3
H-1;1;-1	5.1	20.1	1.1	0.2	0.1	0.9	0.1	0.3	10.9	34.8	9•7	0.60	0.2	2.1	3.0	0.3	6.4	21.5	-	0.15	0.1	0.5	-	0.15
Newal	14.0	39.1	3.2	0.4	1.1	2.1	0.15	0.35	14.1	37.4	4.7	0.15	0.2	1.3	0.4	0.45	13.2	20.4	1.4	0.17	-	0.2	0.2	0.2
Titan	10.0	34.6	6.1	0.4	0.3	0.7	0.1	0.3	12.3	40.1	9.0	0.15	0.12	3.5	-	0.25	14.1	35.2	0.9	0.5	0.2	0.3		0.15
c.I.7155	12.0	37•2	3.2	0.5	0.4	2.2	0.15	0.25	15.5	33.5	1.1.20	.13	0.14	0.4	-	0.13	16.8	11.3	-	0.15	0.1	0.2	-	0.13
C.I.7248	14.3	30.5	0.8	0.3	0.25	0.2	0.1	0.15	13.6	39.1	3.1	0.15	0.12	0.4	-	0.2	13.2	21.8	-	0.12	0.1	0.15	0.05	0.14
Montcalm	15.4	45.0	16.1	0.4	29.1	2.3	0.4	0.4	13.9	41.3	1.90	.15	0.1	0.7	0.1	0.25	10.4	40.3	1.40	0.15	0.2	0.5	0.1	0•2
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Period O	f dai	<u>ly ex</u>	posure	- 1	<u>n cı</u>	ours	- 1									0.70	0 0	10 L	o li	0.15		0.2		0 %5
Atsel	15.6	10.5	0.4	0•4	0.15	0.8	1.4	0.25	12.1	9•7	0.3	0.25	0.1	0.2	0.1	0.10	9.3	12•4	0.4	0.15	-	0.2	0.05	ريد. سر
Beecher	14.7	10.8	-	0.1	2 -	0.15	-	0.18	11.8	18.3	0.6	0.07	-	0.2	-	0.2	9.9	13.2	<b>*</b> 2	0=05	-	0.15	0.05	0.15
Tulare	11.3	1.6	-	0.1	-	0.15	-	0.13	14.4	17.1	0.8	0.05	0.02	2.6	0.2	0.3	9.5	2.4	-	0.06	-	0.15	-	0.18
E-111-1	9.2	24.6	0.2	0.1	3 0.1	0.4	-	0.16	12.3	26.5	-	0.08	-	1.4	0.2	0.2	15.0	13.9		0.1	0.12	0.15	-	0.14
Newal	10.2	25.1	0.2	5 0.1	7 0.1	0.3	0.1	0.14	14.1	18.6	0.25	5 <b>.</b> l	0%1	0.4	0.1	0.18	14.7	15.4	0.2	0.25	0.1	0.2	-	0.12
Titan	12.9	26.1	0.5	0.1	5 0.1	.2 .2	-	0.15	16.7	19.4	-	0.07	-	0.12	0.05	0.17	15.4	15.1	0.6	0.35	0.2	0.2	-	0.15
C.I.7155	16.3	5.8	-	0.1	0.1	0.14	0.04	0.13	14.2	1.6	-	0.12	0.1	0.12	-	0.1	18.6	0.8	-	0.08	0.12	0.13	-	0.1
0.1.7268	15.1	11.8	-	0.1	7 0.1	4 .12	0.1	0.12	16.5	10.7	0.2	0.13	0.1	0.14	-	0.13	12.2	2.5	-	0.13	0.15	0.12	-	0.12
Montcalm	15.0	6.6	_	0.1	2 0.2	2 0.15	0.15	12.3	8.6	0.2	0.04	0.15	0.15	0.02	-	0.12	14.2	2•6	-	0.12	0.1	0.4	-	0.13

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The data on primordia (Table 10) indicates that under shortday conditions development is retarded. It is further shown that temperature is effective in development only when the period of illumination is adequate. Although rates of growth and development differ under the two photoperiods studied, the three seasonal types of plants maintain their seasonal characteristics. Primordia sizes fall into three groups corresponding to the early, midseason, and late types utilized in the study.

Photomicrographs of the primordia formation of plants shown in Plate 7 are given in Plates 8 and 9.

The contrasting behaviour of the early Atsel and late Montcalm at the pre-inflorescence stage is evident when the upper and lower row of Plate 8 are compared. At 75°F and day-length of 17 hours, the awns and spikelet formations for Atsel are differentiated. With Montcalm, under the corresponding temperature, the spikelets are partially differentiated but awn structure has not yet appeared. The Atsel line has made more rapid utilization of the factors in the environment, and is therefore closer to heading.

The relation between temperature reaction at 65° and 55°F and development is obvious. The two varieties have shown response in proportion to temperature, but at each temperature the Atsel line is closer to heading.

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Montcalm



Plate 8. Effect of 17-hour photoperiod on primordia development of forty-four day old Atsel and Montcalm seedlings grown under three temperatures,  $A - 75^{\circ}F$ ;  $B - 65^{\circ}F$ ;  $C - 55^{\circ}F$ .

Atsel

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Plate 9. Effect of 13-hour photoperiod on primordia development of forty-four day old Atsel and Montcalm seedlings grown under three temperatures,  $A - 75^{\circ}F$ ;  $B - 65^{\circ}F$ ;  $C - 55^{\circ}F$ .

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Plate 9 shows primordia of the Atsel and Montcalm varieties which received a relatively shorter photoperiod (13 hours) each day. For these plants stems and leaves were shorter (see Table 10) and primordia correspondingly short. Differential response to temperature is not as clearly defined as in Plate 8.

Primordia size, under this short-day period, is observed to vary with temperature. Larger growth is seen for higher temperatures, but development towards flowering does not show a significant difference over a range of 55° to 75°F. The results are considered to show clearly that, as far as earliness is concerned, both Atsel and Montcalm are adapted to a relatively long day.

# 6. Observations on Heights of Plants

Height of plant, as used in this study, is the distance from the ground to the base of the spike and is measured in inches.

There was a great deal of variation in heights of varieties as observed in the field. Four replications or dates of seeding were employed. The study proved that height was not a stable character, even within the same variety, but that it was influenced by weather and soil conditions and by soil differences. Ideal conditions for a study of earliness would include uniform soil and unvarying conditions for growth throughout the growing season. This ideal, however, is practically unattainable in the field.

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The first seeding in the field was made on May 1, 1950, and consisted of certain varieties and the  $F_2$  hybrids between them. In addition, two varieties, not involved in crosses, were used for height observations. They were the early to midseason line H-44-1, and the variety Floya obtained in Norway specifically for earliness study at the University of Alberta. This variety, relative to other varieties, had a peculiar response in Norway where it originated. Under early, wet and cold spring conditions it was early, but was late in heading when grown under warm, long summer days. The variations in heights for the four replications and their relation to days to heading for varieties and  $F_2$  hybrids are given in Table 11.

An examination of Table 11 shows that with increasing length of day there is a corresponding increase in the mean height of plants. The plants of the first date of seeding are the shortest, and between the first and the second date of seeding there is an average gain in height of 2.25 inches.

Between the second and third date of seeding an average gain in height of 7.3 inches is represented. This is the most significant gain of the four replications, and is due to heavy rains on the  $14^{\pm}$  and  $15^{\pm}$  of July. Replication 3, seeded June 1, 1950, had then attained the early heading stage and still had active capacity for vegetative growth.

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## Table 11

# Relation Between Mean Plant Heights for Four Dates of Seeding

and Number of Days to Heading, 1950

Material	Mean ht.*	Days to head	Mean ht.*	Days to head	Mean ht.*	Days to head	Mean ht.*	Days to head
Atsel Beecher Tulare Newal Titan	17.8 18.0 16.5 19.3 20.0	49 51 59 55	18.5 18.8 17.7 22.3 20.3	36 43 42 50 48	22.5 21.8 19.3 30.0 30.3	35 38 37 48 42	26.8 24.8 23.0 32.3 30.7	36 38 47 45 43
C.I. 7155 C.I. 7248 Montcalm H-44-1 Floya	20.2 18.5 22.7 19.7 19.0	64 61 53 50	25.8 22.8 31.0 20.8 19.5	59 51 54 44 44	34.7 23.3 38.3 29.2 29.7	54 49 49 40	28.7 23.2 39.3 29.7 30.7	52 48 48 36 37
Atsel x Tulare Montcalm x Tulare Montcalm x Beecher Atsel x Beecher Titan x Newal	18.5 19.3 17.7 17.2 19.0	48 45 51 54 54	17.5 21.0 20.7 17.4 21.5	42 39 43 45 42	23.5 24.7 30.5 26.3 30.3	42 35 38 36 41	26.7 30.0 28.8 28.0 31.5	40 35 38 38 44
Montcalm x Atsel Montcalm x Titan Montcalm x Newal Beecher x C.I. 7248 Titan x Tulare	20.8 21.8 21.7 16.0 18.3	51 551 52 52	21.7 23.2 22.0 17.2 17.5	46 47 48 50	25.8 32.5 31.5 29.5 26.2	39 40 42 39 37	33.8 33.3 37.0 27.7	38 39 42 37
Titan x C.I. 7248 Montcalm x C.I. 7155 Atsel x C.I. 7155 Atsel x C.I. 7248 Montcalm x C.I. 7248	19.7 21.0 19.8 21.3 20.2	62 64 56 59	16.0 26.3 22.7 22.9 24.5	54 43 45 47	30.2 35.2 34.7 35.5 34.7	46 50 39 41 43	33.3 34.2 36.0	42 40 44
<b>C.I.</b> 7155 x C.I.7248	18.3	60	26.8	47	29.3	49	30.5	49

\* Mean height measured in inches.



The average gain in height between the third and fourth date of seeding is 2.1 inches. This figure represents the smallest increase although moisture supply was abundant during the growth period of the fourth replication.

The number of days to heading shows a significant decrease between the first and the third date of seeding. With the fourth date of seeding, the number of days to heading represents a levelling off in the downward trend. The range between the heading of the second and third replication represents the longest photoperiod. At the time of heading of the fourth date of seeding the days were again becoming shorter.

When the heights of plants for the first three dates of seeding are compared with the number of days to heading, a vegetative correlation between height and days to heading may be established (see Table 11). With progressive increase in height there is steady decrease in days to heading. These results indicate that with increasing photoperiod there is a corresponding increase in the rate at which the physiological processes operate. This increased activity leads to higher vegetative growth and at the same time speeds up the reproductive processes.

It is evident from the behaviour of the fourth date of seeding that the optimal condition for vegetative growth is reached. Some of the varieties such as C.I. 7155 and C.I. 7248 and some of the  $F_2$  hybrids show a decrease in height from the third replication.

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Shorter photoperiods have also led to longer periods to heading as seen in the varieties Atsel, Tulare and <sup>T</sup>itan and the hybrids Atsel x Beecher, Atsel x C.I. 7155, and Montcalm x C.I. 7248. Other varieties, such as Beecher and hybrids such as Montcalm x Tulare, Titan x Newal, and Montcalm x Newal, did not show a significant change in the number of days to heading for the later dates of seeding.

It appears, from the observations on primordia development and plant heights under different conditions of growth, that earliness is largely influenced by the plants response to photoperiod and not by the amount of vegetative growth.

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#### V. GENETICAL STUDY

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1. Materials, Methods and Observations

The crosses numbered lx to 16 x inclusive (see Table 2) were made in the field in 1948 and 1949, and the F<sub>1</sub> plants and parents grown in the greenhouse in the winter of 1949-1950. The F<sub>2</sub> generations of these crosses were grown in the field in the spring and summer of 1950. All crosses were compared with the parents in earliness.

### 2. Relation of Time of Heading to Length of Heading Period

It was observed both from the greenhouse and field study that the later varieties headed over a longer period than the earlier ones. The correlation between the time of heading and the length of the heading period is shown in Tables 12, 13, and 14. As a rule, not only did the later varieties require more days to complete their heading, but when the same varieties were seeded at different dates the later planted lots headed as a rule over a longer period. This is shown in Table 15. As the rate of heading is influenced by other factors besides the length of day, the behaviour observed in this study may not always apply.


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Correlation Between Mean Date of Heading of Parent Varieties and Number of Days in Heading, 1949. (Greenhouse)

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#### Table 13

Correlation Between Mean Date of Heading of Parent Varieties

and Number of Days in Heading, 1950 (Field)

						Days	req	uire	d to	hea	ıd				
Date	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
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July 1 2 3		1	1 - -	1	-		- 1 -	8	1 1 1					1 3	1 1 1
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7 8 9			-		1		2	- 1 -	8		- 1			1	1 1
10 11 12			1 1		1 2 -		- 2		-						1 1
13,14 15			1		- 1			-						-	-
16 17 18								1 - -						-	- 1
19,20 21			- 1					-						-	
22 23 214								- - 1						-1	

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### Table 14

Correlation Between Mean Date of Heading of Parent Varieties

- 70 -

and Number of Days in Heading, 1950 (Field)

Dete			-7	8		10		Days re	quir	ed to head	7.8	10	20	21	- 22
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# Table 15

Influence of the Time of Planting and of Heading Upon the

	No. 1	No. 2	No. 5	No. 6	No.7	No. 9
Dlonted	Atsel 1950	Beecher 1950	Titan 1950	Newal 1950	Montcalm 1950	C.I.7248 1950
June 19 20 21 22 23 24 25 26 27 28 29 30	2 5 6 7 10 11 5 4 2 1	$ \begin{array}{c} 2 \\ 7 \\ 10 \\ 12 \\ 16 \\ 10 \\ 8 \\ 1 \\ 5 \\ 1 \\ 5 \\ 1 \\ 2 \end{array} $				
July 1 2 3456 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31	277824417221	1 3 , 2 1	5 17 10 4 1 1 10 4 1 1 1 1 1 1 1 1 1 1 1 1 1	10-40-42	2599897322 4671160921 10921 21 1	443375161

Number of Days Required to Head



#### 3. Experimental Results

#### (a) The Fl Generations

The dates of heading of the F<sub>1</sub> plants and the parental varieties are given in Table 16. While the conditions in the greenhouse were favourable there was a lack of uniformity in temperature in different parts of the bed and this doubtless affected the rate of development of certain lines. In the greenhouse most of the varieties headed over longer periods than they did under field conditions, the only exception being the last field planting made June 15, 1950.

It is considered that these data show only roughly the relative earliness of the  $F_1$  generations with respect to the parents. In most of the crosses, however, it was significant that the hybrids varied from an intermediate to a heading date nearer to the early parents. In the apparent exceptions, such as Atsel x Beecher, Montcalm x C.I. 7248, and C.I. 7155 x C.I. 7248, while the differences between the mean dates of heading of the parents were large, the differences of the means of the  $F_1$  populations and the means of the early parents were comparatively small.

Previous mention was made of the fact that Hayes and East (14) believed the increase in rate of development in  $F_1$  crosses



Dates of Heading of F1 Plants and Parents in Greenhouse, 1949. Seeded August 22, 1949

				Dates o	f heading		
		Pistilla	te parent	Stamina	te parent	F <sub>1</sub> p	arents
	Material	Range	Mean	Range	Mean	Range	Mean
lx	Atsel x Tulare	10/10 - 25/10	17/10.50 ± .24	10/10 26/10	18/10.71 ± 1.12	11/10 - 25/10	18/10.22 ± 1.35
2x	Montcalm x Tulare	2/11 - 19/11	10/11.88 ± 1.32	10/10 - 26/10	18/10.71 ± 1.12	18/10 - 6/11	27/10.33 ± 1.00
3x	Montcalm x Beecher	2/11 - 19/11	10/11.88 ± 1.32	14/10 - 22/10	18/10.75 ± 1.66	18/10 - 9/11	29/10.50 ± .72
4.x	Atsel x Beecher	10/10 - 25/10	17/10.50 ± .24	14/10 - 22/10	18/10.75 ± 1.66	20/10 - 9/11	31/10.90 ± .82
5x	Titan x Newal	38/10 - 20/11	8/11.14 ± 1.29	5/11 - 16/11	10/11.50 ± .24	1/11 - 19/11	10/11.67 ± 2.41
6x	Montcalm x Atsel	2/11 - 19/11	10/11.88 ± 1.32	10/10 - 25/10	17/10.50 ± .24	20/10 - 14/11	1/11.25 ± 1.06
7x	Montcalm x Titan	2/11 - 19/11	10/11.88 ± 1.32	28/10 - 20/11	8/11.14 ± 1.29	28/10 - 20/11	8/11.79 ± 1.45
8x	Montcalm x Newal	2/11 <b>-</b> 19/11	10/11.88 ± 1.32	5/11 - 16/11	10/11.50 ± .24	3/11 - 29/11	16/11.80 ± 2.94
9x	Beecher x C.I. 7248	14/10 - 22/10	18/10.75 ± 1.66	16/11 - 18/12	1/12.17 ± 2.57	14/10 - 20/11	1/11.33 ± 1.00
10x	Titan x Tulare	28/10 - 20/11	8/11.14 ± 1.29	10/10 - 20/10	18/10.71 ± 1.12	16/10 - 18/11	2/11.25 ± 1.06
llx	Titan x C.I. 7248	28/10 - 20/11	8/11.14 ± 1.29	16/11 - 18/12	1/12.17 ± 2.57	7/11 - 26/12	1/12.50 ± 1.12
12x	Montcalm x C.I. 7155	2/11 - 19/11	10/11.88 ± 1.32	18/11 - 12/12	30/11.79 ± 1.45	9/11 - 18/12	29/11.12 ± 1.29
13z	Atsel x C.I. 7155	10/10 - 25/10	17/10.50 <u>+</u> .24	18/11 - 12/12	30/11.79 ± 1.45	28/10 - 18/12	22/11.83 ± .87
147	Atsel x C.I. 7248	10/10 - 25/10	17/10.50 <u>+</u> .24	16/11 - 18/12	1/12.17 ± 2.57	25/10 - 10/12	17/11.14 ± 1.32
15x	Montcalm x C.I. 7248	2/11 - 19/11	10/11.88 ± 1.32	16/11 - 18/12	1/12 <b>.</b> 17 ± 2.57	27/11 - 14/12	6/12.75 ± 1.66
16x	C.I. 7155 x C.I.7248	18/11 - 12/12	30/11.79 ± 1.45	16/11 - 18/12	1/12.17 ± 2.57	21/11 - 20/12	5/12.07 ± .34

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of corn to be caused by hybrid vigour. It is possible that, in these  $F_1$  barley hyrbids, hybrid vigour induced somewhat more rapid development and earlier heading, but the data secured in the  $F_2$  generations indicate that this does not adequately explain the increase in earliness.

# (b) The F<sub>2</sub> Generations

In the  $F_1$  plants heading coincided with the early parents, was earlier than the early parents or was intermediate between the early and late with some skewness towards the early end. From this behaviour it might have been expected that the  $F_2$  generations would range in time of heading from the early parent to the late parent or from earlier than the early parent to later than the late parent. In either case, the majority of the plants would have been expected to be early.

Four dates of seeding of the  $F_2$  generations of 16 crosses and the parents involved were grown in the field. Fig. 7 shows a sectional view of the second field replication seeded on the 15th of May, 1950. Between the two paper markers at the ends of rod row No. 50, may be seen three sections of plants separated by white pegs. The middle section represents the  $F_2$  generation of the cross Montcalm x C.I. 7248 while the Montcalm parent occupies the foreground and the parent C.I. 7248 is in the rear of row No. 50. .

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### Fig. 7

Sectional view of second field replication seeded May 15, 1950 and showing parental types towards ends of rows with F<sub>2</sub> hybrids between them. •

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The most noticeable fact is that the majority of the  $F_2$  families (see Fig. 7, middle section of rows) began to head earlier than the early parents. It was observed in these crosses that the earliest plants ranged from 2 to 10 days earlier than the earliest plants of the respective early parents. This behaviour was, in general, true for the other three replications.

In Fig. 8 is seen, on the left of the white stake, the pistillate parent and on the right the  $F_2$  generation of the cross Montcalm x Tulare, both sections being seeded on the 1st of June, 1950, in replication 3. The early Tulare and late Montcalm parents differed by 12 days in time of heading, whereas the earliest plant of the  $F_2$  hybrid was 3 days earlier than the earliest Tulare.

Dates of seeding for the four field replications differed by 15 days, the first seeding being made on May 1, 1950. The heading periods of the  $F_2$  generations in comparison with those of the parents are given in Tables 17 to 20.

The heading in  $F_1$  and  $F_2$  of the 16 crosses studied may be summarized as follows:

In 7 crosses the  $F_1$  plants headed earlier than the early parents or a little later (in crosses 5x, 6x, and 16x), and the  $F_2$  families began heading earlier than the early parent.

In 3 crosses the F<sub>l</sub> plants headed with the early parents, and the F<sub>2</sub> families began to head earlier than the early parents.

In 2 crosses the F<sub>l</sub> plants headed after the early parent, but the F<sub>2</sub> families began to head earlier than the early parent.

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# Fig. 8

Left, pistillate parent; right, F<sub>2</sub> hybrid of a cross Montcalm x Tulare, both sections seeded June 1, 1950.



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Adjusted Frequency Distributions for Parental and F, Plants, Classified for Days to Heading, 1950

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Adjusted Frequency Distributions for Parental and Fo Plants, Classified for Days to Heading, 1950

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Table 17 (Continued)

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1950 Adjusted Frequency Distributions for Parental and F2 Plants, Classified for Days to Heading,

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el x C.I. 7155 Atsel C.I. 7155 F2		3	6	24	3 10	5 2	Ч Г	n m	ţţ	2		ьt	50	s s	Ъ	3	01	2027 2027
el x C.I. 7248 Atsel C.I. 7248 F2	Ч	Ś	р ч	24 2	л0 Л0	n u	Ч Г	a ru	9	tw	лч	50	6 M	00 <b>N</b>	6	2		240 240
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tcalm x Beecher Montcalm F2				NM	-700	0 M	5-0	<b>м</b> н	2010	5 mt	19	17	10	5 4	<u>н</u> н	2		20 M 10 0 10

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Table 18 (Continued)

Adjusted Frequency Distributions for Parental and F2 Plants, Classified for Days to Heading, 1950

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Table 18 (Continued)

Adjusted Frequency Distributions for Parental and F2 Plants, Classified for Days to Heading, 1950

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Adjusted Frequency Distributions for Parental and F2 Plants, Classified for Days to Heading, 1950

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Table 19 (Continued)

Adjusted Frequency Distributions for Parental and F, Plants, Classified for Days to Heading, 1950

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Table 19 (Continued)

Adjusted Frequency Distributions for Parental and  $F_2$  Plants, Classified for Days to Heading, 1950

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Adjusted Frequency Distributions for Parental and F2 Plants, Classified for Days to Heading, 1950

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In 4 crosses the  $F_1$  plants were later than the early parents and the  $F_2$  generations were later than the early parents but earlier than the late parent by 2 to 4 days.

This summary is based on the results of the first three dates of seeding. The last replication, seeded on June 15, 1950, shows a great deal of fluctuating variation in time of heading both in the F<sub>2</sub> generations as well as in the parental lines (see Table 20).

## (c) Observations on Variation

It was observed that even in the pure lines the individuals varied somewhat in time of heading. The results presented in Tables 17 to 20 confirm this observation. Even in the early lines, such as Atsel and Tulare, there was a much wider range in the heading periods for the third and fourth dates of seeding. These differences are presumably due to environmental conditions which are very difficult to equalize exactly.

In all 16 crosses studied, there were two noteworthy facts about the  $F_1$ : first, that the mean in each case was approximately intermediate between that of the two parents (see Table 16); and second, that the variability in the  $F_1$  was about as low as that of the parents. In the  $F_2$  populations the behaviour was quite different. The means were close to those of the  $F_1$ , but, due to segretation in the  $F_2$  populations, variability had been greatly increased.

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# Fig. 9

 $F_2$  generation of a late by early cross Montcalm x Tulare showing segregation for both parental types.



The  $F_2$  families showed a range in heading dates comprising the  $F_1$  range with other plants approaching the early and late extremities of the  $P_1$  parents. Fig. 9 shows a section of the  $F_2$ family of the cross 2x, Montcalm x Tulare.

Montcalm is a late, semiprostrate variety and Tulare an early erect line. In the  $F_2$  population (see Fig. 9) are plants intermediate in type and plants varying towards the parental extremes. Early heading is evidenced in the more erect types while some plants in the same family are yet in a state of vegetative growth resulting in late heading.

There were indications in the field study that there were soil differences in the area on which the barley was grown. These evidently affected the time of heading, though the land comprised an area of only 18.5 feet by 128 feet and seemed uniform.

## 4. Interpretation of F<sub>2</sub> Results

#### (a) The Hypothesis

The results obtained from these crosses indicate that earliness is dominant or partially dominant to lateness. In all the large  $F_2$  populations, the distribution according to time of heading gives a skew curve having the mode near the beginning of heading period.

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Both the  $F_1$  and the  $F_2$  data give evidence in support of the hypothesis that the time of heading is dependent upon multiple factors which together produce a cumulative effect. These conclusions are supported further by the fact that  $F_2$ segregates earlier than the early parents were secured in eight different crosses:

Atsel x Tulare- Table 17Montcalm x Tulare- Tables 17, 18, 19, and 20Titan x Newal- Tables 17 and 20Montcalm x Newal- Tables 17, 18, 19, and 20Montcalm x Titan- Tables 17, 18, and 20Montcalm x C.I. 7248- Tables 17, 18, 19, and 20Montcalm x C.I. 7155- Tables 17, 18, 19, and 20Montcalm x C.I. 7248- Tables 17, 18, 19, and 20

In some crosses there was also transgressive F<sub>2</sub> segregation for lateness as in:

Atsel x C.I. 7155	-	Table 17
Montcalm x Newal	-	Tables 17, 18, and 20
Montcalm x Titan	-	Tables 17 and 18
Montcalm x C.I. 7155	-	Table 17
Montcalm x Beecher	-	Table 18
Titan x Newal		Table 19
C.I. 7155 x C.I. 7248	-	Table 17

Fourteen out of the 16  $F_2$  populations showed an approximate l-in-16 ratio for grandparental recovery. This would suggest a dihybrid inheritance for earliness. The other two  $F_2$  families, Beecher x C.I. 7248 and C.I. 7155 x C.I. 7248, tend to support a condition of monohybridity or single-gene difference.

The occurrence of transgressive segregation in 12 out of 16  $F_2$  populations is further evidence that at least two factor pairs are responsible for earliness. If this holds true generally, then two varieties of barley or other cereal may differ genetically for earliness in one of two ways, such as:

(A) One or more dominants may be found in one parent while the other has the recessive allelomorphs. The genotype of one parent may thus be represented as AABB and the other as aabb. Such parents when crossed would give an  $F_1$  population like the early parent in time of heading and an  $F_2$  population with heading ranging from the early to the late parent.

Such a relationship of parents seems to have existed in crosses 2x, 3x, 7x, and 9x. (See Table 16 for  $F_1$  heading and Tables 17 to 20 for the heading in  $F_2$ ).

(B) One or more dominants may be present in each parent while lacking in the other. Thus if the genotype of one parent is represented as AABBcc, the other would appear as aabbCC. A cross involving the two types of parents should

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give an  $F_1$  population earlier than either parent and an  $F_2$  ranging in heading from earlier than either parent to later than either. This relationship was evident in cross lx. (See Table 16 for  $F_1$  and Tables 17 to 20 for  $F_2$  heading).

It seems likely that in some of the crosses included in this study, there may be one or more factors causing unlike rate of development under different conditions. For example in cross l4x the parents headed 52 days apart in the greenhouse (see Table 16) but only 16 days apart in the field (see Table 19).

### (b) The Quantitative Effect of the Genes

One object of the present study was to determine the quantitative effect of the factors. The influence of the factors upon time of heading was shown to vary with different dates of seeding. Because of the variability in heading from early to late seedings, it was not satisfactorily proved that the factors are the same in their effect.

When the  $F_2$  populations are compared with the early parents it appears that the factors may have approximately the same effect and that each caused an average difference of one and one-half to two days in time of heading. Transgressive

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segregation in the F<sub>2</sub> strongly suggests a quantitative inheritance for earliness. This effect is presented in Fig. 10 which shows the F<sub>2</sub> and parental types of the cross 2x, Montcalm x Tulare.

The Montcalm parent appears on the left and the Tulare parent on the right of the  $F_2$  hybrids. The cumulative effect of the factors for earliness is seen in the heading of the  $F_2$  population which is earlier than the early Tulare parent.

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## Fig. 10

Upper: Montcalm parent, left and  $F_2$  generation, right. Lower:  $F_2$  generation left and Tulare parent, right. Transgressive segregation is seen in the hybrid population.



#### VI. GENERAL DISCUSSION AND CONCLUSIONS

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The experimental results of the three aspects of earliness studied have been analyzed, and with respect to the more specific points, more or less fully discussed in the sections devoted to the respective experiments.

In discussing the scope of the present study and the results secured, it must be recognized that the general and exploratory nature of the work does not permit final and conclusive observations. Certain points related to the work as a whole should however be discussed, particularly those regarding the physiology and nature of the inheritance of earliness.

It was shown that there was a negative correlation between the number of tillers and the number of days to heading, The later varieties, as a rule, carried more tillers than the early or midseason lines. With a reduced number of tillers, a morphological characteristic, it is probable that there is more rapid assimilation and utilization of soil nutrients promoting speedy growth and development. The association established in the morphological study between leaf curling and earliness may also be based on the rate at which the various physiological stages are acquired. The relation of flag leaf to spike seems to hold definite promise as a morphological character in the study of earliness.



Evidence has been presented to show that exposure to high temperature does not induce development unless accompanied by an adequate photoperiodic treatment. The results of microdissection, referred to by Hamner (12), have proven that the rate of development of the primordia is influenced by the number of hours of daily exposure. This phase of the work on the relation of photoperiod to earliness, substantiates the physiological theory of "phasic development" postulated by Klebs (21) and Lysenko (23).

The study on the relation of height of plant to earliness did not yield any definite results. There was a great deal of fluctuating variation in height even within the pure lines. The average height for the third and fourth dates of seeding was the same, but the third was earlier than the fourth date of seeding by an average of 1.5 days. Thus, the height attained by the plant may be considered as having no direct relation to the number of days to heading.

The acceptability of the genetic analysis rests in the assumption that parents might be alike in time of heading and contain different dominant factors for earliness. Most of the crosses included in this study seemed to have such a relation-ship of parents for in several of them the  $F_1$  as well as the  $F_2$  began heading earlier than the early parent.

In some crosses in which the F<sub>2</sub> began heading earlier than the early parent, there were no plants later than the late

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parents. However, the expected proportion of the population later than the late parents in such crosses would be small. This behaviour further supports the assumption that the genotype of one parent may be AABB and the other aabb.

The limitations imposed by small F<sub>2</sub> populations made it difficult to conclude at this stage of the study which crosses would result in early lines as the segregation of all possible intermediate and extreme types could not be accounted for with the small families used.

In order to establish conclusively the mode of inheritance of earliness it is necessary that homozygous races be recovered. This would require the growing of  $F_4$  generations from selected  $F_3$  families. However, the scope of the present study serves to indicate the trend, that is, the time of heading is dependent upon multiple factors having a cumulative effect.

There were indications of soil differences in the area on which the  $F_2$  generations and parental plants were grown which affected the time of heading. In order to facilitate accuracy in the results, soil differences could be carefully marked on the planting plans so that it be known on which soil type each row is located. The hybrid generations and parent varieties could then be planted in duplicate on each soil type.

Present data do not prove conclusively that the genes or factors have the same effect, but the results point to a strong

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possibility, and that each factor caused an average difference in earliness of from one and one-half to two days.

It is hoped that some crosses initiated later between the varieties now involved, as well as between races and varieties with wider date-of-heading differentials will prove to be monohybrid crosses. In this way the quantitative effects of some factors could be determined with greater certainty and genetic analyses facilitated.

#### ACKNOWLEDGEMENTS

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