THE EFFECT OF SOME ENVIRONMENTAL FACTORS
UPON THE CO$_2$ EXCHANGE AND THE EFFECT
OF PHOTOPERIOD UPON THE DEVELOPMENT OF
HORDEUM VULGARE L.

by

WILLIAM FREDERICK HUBBARD
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to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April, 1967
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Division of Plant Science

The University of British Columbia
Vancouver 8, Canada

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ABSTRACT

Experiments were conducted with a Blue M "Vapor-Temp" controlled environment apparatus to show the effect of temperature, light intensity, relative humidity and age upon the rate of CO₂ exchange for twelve barley varieties. All varieties showed an increase in CO₂ uptake with an increase in temperature to a certain optimum, varying with variety. When the temperature was raised above this point, the rate of CO₂ uptake decreased. In all varieties tested the rate of CO₂ uptake increased as light intensity was increased up to 2400 ft. candles. Three out of four varieties tested showed significant changes in rate of CO₂ uptake with changes in relative humidity. All varieties tested showed an initial decrease in rate of CO₂ uptake per unit leaf area as the plants aged from 15 to 30 days. Above this age there was little change in rate of CO₂ exchange.

Experiments were also conducted in photoperiod chambers to determine the developmental response of different barley varieties to different photoperiods. It was found that the varieties differed in overall response to photoperiod. Within a variety there was a difference in rate of development between plants subjected to different photoperiods. The optimal photoperiod for head differentiation and for head appearance was 21 or 24 hours for all varieties.
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INTRODUCTION

All plants are to some extent responsive to the surrounding environmental conditions, not only with respect to extremes but also within the limits favourable to growth (Leopold, 1964). In the present experiments twelve varieties of barley were examined for their carbon dioxide exchange rate under specific combinations of environmental conditions with the aid of a Blue M "Vapor Temp" apparatus (Ormrod and Woolley, 1966). The purpose of this examination was to determine if there are any significant differences between varieties with respect to response to temperature, light intensity, or humidity.

In addition the response of barley development to photoperiod was studied to determine if there were differences between varieties with respect to time to head differentiation and head appearance and if there were any differences in photoperiodic response within a given variety.
LITERATURE REVIEW

I Barley

Barley (Hordeum vulgare L.) is classed as one of the major crops in the world, accounting for over 10% of all grain produced (Cook, 1962). The acreage in the years 1950-1954 averaged approximately 121.18 million acres with a yield of 22.2 billion bushels (Leonard and Martin, 1963). It is grown in nearly all cultivated areas in temperate regions, and in many hot dry areas, such as Asia Minor and North Africa, as well as at higher altitudes in tropical latitudes (Leonard and Martin, 1963, Shands and Dickson, 1953). Barley is used primarily for human consumption in Europe and for livestock feeding in the Americas (Leonard and Martin, 1963). The principal producers are the U.S.S.R., China, the U.S.A., Canada, Turkey, India and Great Britain (Leonard and Martin, 1963). In Canada, barley is grown principally in Alberta, Saskatchewan and Manitoba with smaller amounts in British Columbia and Ontario (Wiebe and Reid, 1961).

Barley is recognized as the most ancient cultivated grain by some (Leonard and Martin, 1963) although others claim that einkorn wheat was cultivated first. Later this grain was ousted in favour of two and six-rowed barley and husked two-kernelled emmer wheat. About 3000 B.C. it is estimated that in Egypt barley constituted about 80% of the grain crop,
two-rowed barley accounting for 23% and six-rowed for about 57%, the remaining 20% being emmer wheat (Woolley, 1963). Certainly, at a very early stage it became the dominant crop and, as such, has been found to have been cultivated in Switzerland, Egypt, Mesopotamia and China before 2000 B.C. (Leonard and Martin, 1963, Woolley, 1963). In more recent times it has been to a great extent replaced in importance by wheat and rye, but still maintains its place in agriculture partially because of its malting properties (Shands and Dickson, 1953, Leonard and Martin, 1963).

Barley was brought to America by colonists as early as 1613. Before the middle of the seventeenth century it was probably cultivated widely by English settlers and was later carried westward by them in their migrations. In the eighteenth century it was introduced to the west coast of America by Spanish settlers. During the nineteenth and early twentieth centuries, new varieties of barley were brought to America from Europe, India and Asia in a definite barley improvement program (Leonard and Martin, 1963).

There are various theories concerning the place and line of descent of cultivated barley. Three areas have been postulated as most likely to have been the centre of origin. Abyssinia and Nepal, Sikkim, Tibet area are both characterized by an abundance of wild barley types (Shands and Dickson, 1953) and have both been widely accepted as centre of origin. Mesopotamia,
on the other hand, is no longer held by many workers to have been the place of origin (Leonard and Martin, 1963).

There are two theories concerning the line of origin of cultivated barley. The first theory assumed that *Hordeum spontaneum*, a wild two rowed species which crosses readily with cultivated varieties was the fore-runner (Shands and Dickson, 1953, Staudt, 1961). The other theory, more widely held now, postulated by Aberg in 1938, held that the modern barley arose from *Hordeum agricrithon*, a wild six rowed spring barley from Tibet (Leonard and Martin, 1963).

Barley is one of the most adaptable and widely distributed of all cereals, being found near the Arctic circle and within 17½ degrees of the equator (Shands and Dickson, 1953) and at high altitudes and desert lowlands (Bell and Lupton, 1962). Barley is one of the most dependable crops where drought, frost, and alkali are to be encountered (Shands and Dickson, 1953, Leonard and Martin, 1963). Optimum growth of barley occurs in a climate with a long, relatively cool growing and ripening season (Bell and Lupton, 1962). It will stand a hot dry climate but does not thrive in a hot humid climate, perhaps because of incidence of disease. It grows better at all temperatures with only moderate rainfall. Thirty-five inches per year is approximately the maximum in the U.S.A.
Some varieties of spring barley ripen in 60 to 70 days after sowing and in addition many of the varieties have good cold resistance, allowing them to flourish in the short growing seasons of high altitude and high latitude habitats. Winter varieties of barley are less hardy than winter rye or winter wheat varieties, and are unable to flourish where the average winter temperature is less than 30 degrees fahrenheit or the rainfall less than 25 inches per year. The growing period for these winter varieties may be about 180 days (Shands and Dickson, 1953, Leonard and Martin, 1963).

Barley is best adapted to very fertile soil with a pH of 7 to 8. Some varieties have a very high salt tolerance (Ayres, 1953). In general the barley plant is considered to be more tolerant to soil salinity and alkalinity but more sensitive to soil acidity than other cereals (Shands and Dickson, 1953, Leonard and Martin, 1963).

The minimum temperature for germination of barley lies between 37.4 and 39.2 degrees F, the optimum at approximately 68 degrees F and the maximum between 82.4 degrees F and 86 degrees F (Leonard and Martin, 1963). The optimum however varies between different varieties (Paris, 1965). High positive correlations have been found between the growth of barley and temperature (Gregory, 1926). Ten day old barley seedlings, when grown for a week at temperatures of 65 degrees F, 45 degrees F, and 35 degrees F were found to have developed from 9.1 nodes average to 31.9, 15.3, and 12.6 respectively, while five day old seedlings treated in the same way developed
from an average of 5 nodes to 14.7, 7.4 and 6.9 nodes respectively (Borthwick et al., 1941). Soil temperatures of 27 degrees C produced far less growth of barley than did soil temperatures of 9 degrees C and 18 degrees C (Mack, 1965). Barley is more readily damaged by spring frost than wheat. Six nights of frost with an average temperature of about -4 degrees C killed 13% of the leaves of OAC-21, 17% of the leaves of Vantage and 34% of the leaves of Montcalm barley varieties (Johnson et al., 1949). Montcalm barley varieties were killed at a rate of 23% after one night at -10 degrees C (Olson, 1946). It was shown that hardening against frost in some varieties decreases rate of development in cold rather than increases it (Chujo, 1961). The variety Trebi especially showed this (Dantuma and Andrews, 1960).

Under given production conditions temperature and daylength appear to be the most important environmental factors determining the time of heading of any cereal variety. The interaction between temperature and daylength is further complicated by genetic factors (Gregory, 1926). It was found, for example, that for a period in which the average day temperature was 20.9 degrees C and the daylength 14.4 hours that an Israeli barley variety took 16 days to reach head differentiation after sowing and 29 days to heading, while a similar variety given an average daylength of 10.5 hours and day temperature of 12.7 degrees C required 62 days to head differentiation and 88 days to heading (Pinthus, 1959). It has been noted that the development of spike primordia in early varieties of barley is influenced more
by photoperiod than by temperature, the effect of temperature being negligible under short day conditions, but more significant under long days (Johnson and Taylor, 1958). Others have noted different photoperiod responses to different temperatures (Roberts and Struckmeyer, 1958).

Long photoperiods hasten heading in barley (Carner and Allard, 1923; Downs et al., 1959; Ormrod, 1962); in other words barley is a long day plant. A 16 hour photoperiod was found optimal in wintex barley for producing most grain, but 16, 20, and 24 hour photoperiods were all approximately equal in their effects upon heading time (Berthwick et al., 1941). The barley variety Trebi was found to head in 85 days at a 12 hour photoperiod and in 66 days in a 16 hour photoperiod, both of these periods consisting of a majority of natural light supplemented by 100 ft. candle incandescent lights for 15 minutes and 4 hours and 15 minutes respectively (Downs et al., 1959). Olli and Montcalm varieties of barley showed a marked difference in their response to photoperiod with respect to head appearance but little difference from 9 hours to 24 hours illumination in time to head initiation (Ormrod, 1962). Short photoperiods were found to produce much vegetative growth and tillering with the plant tending to be prostrate and having little or no grain (Borthwick, 1941; Downs et al., 1959).

Montcalm barley, when given light intensities of 500 to 1500 foot candles at plant level and held at 73 to 76 degrees F with a photoperiod of 18 hours showed increasing yield with
higher light intensities, the number seeds per head being 21.7 at 500 foot candles and 31.7 at 1500 foot candles. The head number was the same in both cases (Gfeller and Goulden, 1954).

Barley grown in a controlled-environment with a light intensity of 1800 foot candles and a temperature of 20 degrees C for 18 hours and a temperature of 15 degrees C for the remaining time in each 24 hour cycle showed a constant assimilation rate for four weeks after which the rate dropped to half in the next four weeks (Thorne, 1960).

Barley generally responds to applications of nitrogen, potassium, and phosphorus (Leonard and Martin, 1963) although there is a differential response of barley varieties to different nutrient availabilities (Gregory and Crowther, 1931). Barley responds well to nitrogen although too much may lead to excessive vegetative growth (Leonard and Martin, 1963). Nitrogen added to Hannchen barley in Oregon produced significant increases in yields in normal seasons, but no increase in a dry season. About 50 to 100 lbs. of nitrogen per acre was most effective for both urea and ammonium nitrate, although it was found that ammonium nitrate gave a greater increase in yield than did urea (Foote and Datchelder, 1953). Nitrogen was found to be the limiting nutrient element when nine barley varieties were tested for response to nitrogen, potassium and phosphorus in Illinois.
Unfertilized soil gave an average of 30.5 bushels per acre, soil with 60 lb. of phosphorus and 60 lb. of potassium per acre gave 34.5 bushels per acre and soil fertilized with 60 lbs./acre of all three gave 45.6 bushels/acre. Varieties tested also varied in their response to fertilizer, the highest response being in Moore variety which gave 28.5 bushels/acre unfertilized and 54.5 bushels per acre fertilized, while the lowest response was in Montcalm which increased from 35.7 bushels per acre unfertilized to 47.5 bushels per acre completely fertilized (Pendleton et al., 1953). Betzes barley produced a significant increase in grain yield when fertilized with ammonium nitrate up to 150 lbs. per acre, although at this level the protein content of the grain was very high (Dubetz and Wells, 1965).

Winter barley produced an average of 8.3 bushels per acre increase from an annual application of 150 lbs. of superphosphate per acre in Missouri (Leonard and Martin, 1963). Betzes barley showed a significant increase both in weight of grain per plant and number of heads per plant when given 150 lbs. per acre of P₂O₅ (Dubetz and Wells, 1965). Aluminum in the soil decreased the effective uptake of phosphorus by barley seedlings (Clarkson, 1965). The effect of fertilizing with a complete N,P,K fertilizer varies with temperature and soil moisture (Mack, 1965). Betzes barley gave increased yields with increased soil moisture up to 3/4 field capacity (Dubetz and Wells, 1965).
Barley has a very high degree of salt tolerance although there is a great variability in this respect between varieties. In all cases, grain yield is reduced far less than plant growth by high salinity (Ayres et al., 1952). California Masiout variety is very tolerant. More than 50% of its seeds germinated and emerged within 10 days when the soil solution had an osmotic potential of approximately 19 atm., whereas there was no emergence of Arivat variety at this tension. Germination of O.A.C.-21 variety was inhibited by 15 atm. (Ayres, 1953).

Maximum yields of spring barley can be obtained when the crop is seeded as early as the land can be worked in the spring (Leonard and Martin, 1963). Seeding depth varies from 1 - 2 inches in humid regions but 2-- 3 inches in semi-arid regions (Leonard and Martin, 1963). The variety 01111, over a three year period produced an average annual yield of 51.4 bushels per acre with a 9 inch spacing between rows and 38.9 bushels per acre with 18 inch spacing, while Parkland variety gave 42.1 bushels/acre with 9 inch spacing and 50.1 bushels per acre with an 18 inch spacing (Faris, 1965).

II Photosynthesis

Photosynthesis is the process in which certain carbohydrates are synthesised from CO$_2$ and H$_2$O by chlorophyllous cells in the presence of light, O$_2$ being a by-product (Meyer et al., 1960).
Measurements of photosynthesis are complicated by the fact that certain other processes involving H₂O, O₂ and CO₂ are occurring in the cells at the same time. The process of respiration is continually in progress in all cells, resulting in an oxidation of part of the carbohydrates synthesized in photosynthesis. In many measurements of photosynthesis the other processes involving CO₂ are disregarded and the results obtained are designated as the apparent or net photosynthetic rate. For many purposes, particularly those concerning increase in plant dry weight, measurements of the rate of apparent photosynthesis have greater significance than the true rate (Meyer et al., 1960).

Chlorophyll has been known to be essential to photosynthesis for many years, but not until 1958 was it shown that the chloroplast is the complete structural and biochemical unit of photosynthesis in higher plants. This was shown by comparing the photosynthetic capabilities of various combinations of chloroplasts and their highly centrifuged components (Leopold, 1964). Blackman (1905) proposed two steps to photosynthesis, a light and a dark reaction. In 1958 it was shown by Trebst et al. that the light reactions of photosynthesis took place in the green grans of the chloroplast and the dark reaction in the surrounding stroma. Later it was shown that there occur in actuality two light reactions, mediated by slightly different wavelengths (Leopold, 1964). It has been shown that the light reactions provide high energy
compounds to supply the energy for the subsequent fixing of CO$_2$ in the dark, and also in certain schemes of photosynthesis, NADPH$_2$. CO$_2$ is reduced by a process of fixation of the carbon onto ribulose-1, 5-diphosphate. The first stable products of the fixation are two molecules of 3-phosphoglyceric acid, which then enter a maze of combining and counter-combining reactions, the Calvin cycle, leading finally to the formation of hexose and starch grains in the chloroplast. Some workers believe that the first stable product of photosynthesis is glycolic acid but this is not often subscribed to (Leopold, 1964).

Under field conditions, assimilation rates can be controlled by many external factors (Watson, 1947), some of which are intensity and quality of light, temperature, partial pressure of CO$_2$, amount of chlorophyll and amount of available water (Spoehr, 1926). Response to any of these factors can be altered by a variation in any one of them (Blackman, 1905).

Light is probably the principal factor involved in environmental effects on photosynthesis (Leopold, 1964). It has been found that many plants which grow in bright light required about 2500 ft. candles for maximum photosynthesis, while those that grow in shade required only about 1000 ft. candles. In fact, for the shade plants the rate fell off markedly at higher light intensities (Bohning and Burnside, 1956). At 30 degrees C Loblolly pine achieved maximum photosynthesis at a light intensity of about 10,000 ft. candles while red oak, white oak, and dogwood had maximum rates at about 3500 ft.
candles (Kramer and Decker, 1944). Duration of light increases photosynthesis of even day neutral plants such as tomato (Went, 1957; Leopold, 1964). However continuous illumination may bring about a decrease in net photosynthesis over a period of time (Bohning, 1949; Leopold, 1964). In some species continuous light causes chlorosis (Withrow and Withrow, 1949; Leopold, 1964) probably by a similar form of photo-oxidation as that produced by very high light intensity (Nielsen, 1952).

In white clover there was significant increase in the rate of photosynthesis with increase in light intensity to 4200 ft. candles (Beinhart, 1962). In tomato there was a significant increase in photosynthesis with light intensities up to 1139 ft. candles (Porter, 1939). In Montcalm barley the rate of assimilation increased with an increase in light intensity through 500, 1000, and 1500 ft. candles (Gfeller and Goulden, 1954). In general, photosynthesis rates respond to light intensities on a two phase curve, being inhibited by intensities above an optimum which varies from species to species. These inhibitory effects of excessive intensities become accentuated with time of exposure (Meyer et al., 1960; Leopold, 1964).

Rice seedlings of 3½ and 5 weeks age were found to increase in amount of CO₂ uptake to 6000 ft. candles (Ormrod, 1961). Marquis variety wheat was found in a series of experiments to increase its rate of CO₂ uptake and its net growth as light intensity increased to 2200 ft. candles, the limit of the experiment (Friend et al., 1962; Friend, 1965). Leaves of
maize, sugar cane, and sorghum were all found not to be saturated by light at 7500 ft. candles with a CO₂ content in the air of 300 p.p.m. (Hesketh and Moss, 1963), and maize has not been found to be saturated at the equivalent of 10,000 ft. candles when the whole plant was tested (Hesketh, 1963).

Optimal CO₂ content of the air for photosynthesis is far above the usual ambient partial pressures. Lundegardh (1924) obtained increases in photosynthesis in wheat, cucumber, and tomatoes with increased CO₂, although the responses varied between species. Plants grown in areas of different CO₂ partial pressures did not vary in efficiency of CO₂ absorption (Decker, 1959). At higher light intensities plants can utilize greater quantities of CO₂ (Hoover et al., 1933; Leopold, 1964). 2.5% CO₂ can limit photosynthesis (Ballard, 1941) although others have found that inhibition does not occur until about 20% CO₂ is in the air (Livingstone and Franck, 1940).

The abundance of chlorophyll in the leaves has relatively little influence on photosynthesis in the field (Willstatter and Stoll, 1918; Leopold, 1964). Ash leaves with 10% normal chlorophyll were found to have only about a 15% lower rate of photosynthesis than normal leaves (Willstatter and Stoll, 1918).

The changes of net carbon dioxide exchange with temperature are complex (Leopold, 1964) since the rate
measured is actually the difference between two sets of enzymatically controlled reactions, photosynthesis and respiration, both of which vary with temperature. Plants are capable of photosynthesizing over a wide range of temperatures, *Opuntia* having a measurable photosynthesis at 55 degrees C and *Picea excelsia* at -35 degrees C. However long periods at these extreme temperatures have a drastic effect on the photosynthetic mechanism (Spoehr, 1926). Some have held that actual temperature has little effect on photosynthesis rate *per se*, but exerts all its influence on net photosynthesis through a temperature effect on respiration (Thomas and Hill, 1949). However others have held that the Q10 of photosynthesis itself is very high (Rabinowitch, 1956; Leopold, 1961). At a certain temperature net photosynthesis reaches a peak from which it drops again with further increase in temperature. This was shown with red pine which increased in photosynthesis from 20 degrees C to 30 degrees C but decreased by about 45% at 40 degrees C (Decker, 1944). This depression did not appear to be due to a thermal inactivation of the photosynthetic mechanism alone in *Pinus halepensis*, but rather to the interaction of three factors: a) the inactivation of the mechanism b) the thermal increase in respiration and c) an increased resistance to the CO2 uptake. The temperature at which photosynthesis started to decline was not found to depend upon light intensity (Whiteman and Koller, 1964).

Different species and varieties have been found to have different optimum temperatures for photosynthesis. Latitudinal
races of *Oxyria* were found to have clear differences in their maximum photosynthetic temperatures. Alaskan varieties had maxima of about 15 - 19 degrees C while California varieties had maxima of 30 - 34 degrees C. In addition the Alaska race was saturated with light at 3000 ft. candles while a Californian race reached saturation point at 5000 ft. candles (Mooney and Billings, 1960). Different races of *Solidago Vergaurea* were found to have significantly different maximum temperatures for photosynthesis (Bjorkman et al., 1960). Bermuda grass and seaside bent grass were found to have maxima of 35 degrees C and 25 degrees C respectively, corresponding to the climates in which they live (Miller, 1960). Varieties of *Lolium Perenne* were found to have the same maximum photosynthetic temperature, but to vary greatly in the amount of photosynthesis (Cooper, 1963).

Rice seedlings were found to increase the amount of CO2 taken up from 40 degrees F to 60 degrees F, but decreased when the temperature was increased to 80 degrees F (Ormrod, 1961). In a series of experiments Marquis wheat showed a maximum assimilation rate under temperatures of 20 to 25 degrees C, the two rates being approximately equal (D.J.C. Friend et al., 1962; D.J.C. Friend, 1965). Cotton, sorghum, and sunflower were all shown to increase the amount of CO2 taken up per dm.\(^2\) leaf area in 20 minute runs with 300 p.p.m. CO2, until a certain temperature, in all cases about 30 degrees C, had been reached. With further increase in temperature the rate dropped off dramatically (El-Sharkawy and Hesketh, 1964).
In blueberry leaf discs, an increase in O₂ output was noted with an increase in temperature from 13 degrees C to 29.5 degrees C.

In an experiment with Primula, at 24.5 degrees C, three atmospheric relative humidities of 70%, 40% and 10% were found to have no effect on photosynthetic rate (Mitchell, 1936).

The age of a plant was found to be reflected by a decline in its photosynthetic rate (Singh and Lal, 1935). In barley, grown at 20 degrees C with 1800 ft. candles for 18 hours, photosynthetic rate was found to remain constant for four weeks after which it dropped appreciably (Thorne, 1960).

An increase in CO₂ uptake was shown between 3 1/2 week old and 5 week old rice plants on a per-plant basis (Ormrod, 1961), but uptake was not correlated with area. In Marquis wheat, the assimilation rate dropped quickly with age immediately after emergence (Friend et al., 1962).

The highest rates of photosynthesis on a weight/surface area basis have been found in alpine plants in the Pamirs. Slower rates are found in temperate zone herbs and still lower rates in arctic and tropical plants. The lowest rates are found to be in mosses and lichens (Verduin, 1953).

III Photoperiodism

Photoperiodism may be defined as the development of plants as conditioned by the daily length of the light period (Meyer et al., 1960). The more precisely measured effect of
photoperiod is the action of light in interrupting the dark period. Another effect of light in photoperiodism is involved in the light period, one component of which is photosynthetic and the complete blocking of which blocks photoperiodic induction (Parker and Borthwick, 1940). However there appears to be some other function of day light obtainable at light intensities too low for photosynthesis (Leopold, 1964).

There are three main classes of response to photoperiodism and plants are classed according to whether they flower best in short or long days or whether they are not affected by photoperiod (Meyer et al., 1960). Barley has been found to flower more quickly under long days (Carner and Allard, 1923; Downs et al., 1959), therefore it is considered a long day plant.

Some workers have considered that there is an interaction of photoperiodism and temperature (Borthwick et al., 1940; Pinthus, 1959). Others consider this interaction to be negligible (Johnson and Taylor, 1958). Photoperiodic response is considered independent of light intensity and water status (Carner and Allard, 1920). Short photoperiods when given to long day plants result in a dominance of vegetative growth over reproductive growth with much tillering and a tendency to prostration (Tincker, 1929; Allard and Evans, 1941; Stuckey, 1942).
Wintex barley flowered best when treated with photoperiods of between 16 hours and 24 hours. With a 12 hour photoperiod the plants did not produce any reproductive spikes (Borthwick et al., 1940).
MATERIALS AND METHODS

Twelve varieties of barley: Asa, Huskey, OAC-21, Olli, Parkland, Pirrka, Stavropal, Trebi, Vantage, Vantmore, White Gatami and Wolfe, supplied by the Canada Department of Agriculture Research Station at Beaverlodge, Alberta, were observed to determine their response to various environmental conditions. Responses measured were not photosynthetic rate and photoperiodic sensitivity. The varieties were chosen to produce the greatest intervarietal diversity in genetic makeup.

The information available concerning the barley varieties used is summarized in table 1.

The object of these experiments was to determine accurately the photosynthetic capabilities of each variety and to determine the usefulness of a Blue M Vapor-Temp Controlled Relative Humidity Chamber (Ormrod and Wooley, 1966), as a selection tool for determining adaptation of barley varieties. With this instrument, temperature may be controlled automatically from 0-degrees C to 75 degrees C with an accuracy of within .5 degrees C for dry bulb temperature. Relative humidity can be controlled to within 1% between 30% and 98%. The rate of air circulation within the glass chamber may also be varied. The environmental conditions were maintained within this cylindrical glass chamber of 40.6 cm. diameter and 34.6 cm. height. Prior to usage the entire chamber
was sealed with grease and silicon rubber, the chamber not having been sealed by the manufacturer. Any condensation was allowed to drain into a water trap. Illumination was supplied by six V.H.O. reflector cool white tubes mounted 2 inches apart and 4 inches above the chamber. These lights gave an illumination of about 2400 ft. candles measured by a Weston Model 756 Illumination Meter at the level of the bottom of the chamber and did not measurably raise the temperature within the chamber. For these experiments this unit was placed in a closed system with a Beckman Model 15A infra-red gas analyzer (Ormrod and Wooley, 1966).

In the first experiment, that dealing with the effect of temperature upon net CO₂ exchange, a Drierite absorber, Model 1 Thiberg Aerator, flowmeter and needle valve were placed in series before the analyzer. The air stream moved through this sequence at the rate of 1 liter per minute and then returned to the glass chamber. The infra-red analyzer continuously recorded the CO₂ content of the air stream with a ca. 20 second lag between the chamber and the analyzer. In subsequent experiments the Drierite absorber was dispensed with because it had negligible effect upon the readings on the analyzer. The total volume of the system in the first experiment was 55 liters. In subsequent experiments the volume was increased to 65 liters by the increase in the height
Table 1. Origins, present ranges of agronomic usage, and relative maturities of nine of the barley varieties used in this study.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Origin</th>
<th>Present Range</th>
<th>Relative Maturity</th>
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<td>Husky</td>
<td>-bred in Canada -Sask., Man., and Alta. -late</td>
<td>-late</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-Peatland x Regal 2 x OAC-21 x Newal</td>
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<td></td>
</tr>
<tr>
<td>OAC-21</td>
<td>-Manchuria -selected in Ontario</td>
<td>-Prairies and northern States</td>
<td>midseason</td>
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<tr>
<td>Olli</td>
<td>-Finland -selected in Canada</td>
<td>-Canadian Prairies</td>
<td>-very early</td>
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<tr>
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<tr>
<td></td>
<td>-Newal x Peatland x OAC-21 x Montcalm</td>
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<tr>
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<td>-introduced from Ukraine earlier North Africa</td>
<td>-Kansas and Oklahoma -midseason</td>
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<tr>
<td>Trebi</td>
<td>-selected in Idaho, Oregon and Minnesota from Nebraska. Some in seed from North Canada</td>
<td>-midseason</td>
<td></td>
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<tr>
<td>Vantage</td>
<td>-bred in Canada -Canadian Prairies</td>
<td>-Canadian Prairies</td>
<td>-midseason</td>
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<td></td>
<td>-Newal x Peatland 2 x Plush</td>
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<tr>
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<td>-midseason</td>
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<tr>
<td></td>
<td>-Titan x Vantage</td>
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<td></td>
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<tr>
<td>Wolfe</td>
<td>-bred in Canada -Canadian Prairies</td>
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<td></td>
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<tr>
<td></td>
<td>-Sanalta x Titan x Montcalm x Olli</td>
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</table>

(Wiebe and Reid, 1961)

Information on the origin and adaption of the varieties Asa, Pirrka and White Gatami is not readily available.
of the chamber from 34.6 cm. to 42.2 cm. by the addition of an extra base ring.

The factor measured in these experiments was the CO₂ concentration in the air surrounding the plants. The changes in the CO₂ level were a reflection of the net CO₂ exchange by the plants. There were no calculations of respiration effects or of true photosynthesis.

Growing the Plants

Six barley seeds of a given variety were sown in a plastic container of dimensions app. 10 cm. x 10 cm. x 10 cm., equipped with a drainage hole. The rooting medium was vermiculite. This was irrigated at two day intervals with a normal Loaglands solution (Hoagland and Arnon, 1950). The plants were grown in a controlled environment growth cabinet (Ormrod, 1962), illuminated by cool white fluorescent tubes with an intensity of ca. 1200 ft. candles at the plant surface. There was no humidity control for these chambers. Photoperiod was 18 hours, the day temperature being maintained at approximately 25 degrees C and the night temperature at approximately 16 degrees C. At the end of one week the plants were thinned to four plants per pot.

A. Temperature Effects on CO₂ Exchange.

When the plants were 21 days old, the pot was removed from the growth chamber and the plants were irrigated with water.
The pot was then sealed within the chamber of the Vapor-Temp apparatus. The plants were allowed to photosynthesize with the lights on for 15 minutes at each of 16 temperatures ranging from 4 degrees C to 36 degrees C in 2 degrees C increments. The CO₂ uptake by the plants during this time was indicated indirectly by the CO₂ reading of the infra-red analyzer. After each 15 minute interval the CO₂ level in the system was restored to slightly above 300 p.p.m. CO₂, the approximate ambient level. This procedure was replicated four times with different pots of plants for each of the twelve varieties analyzed.

After the response of the plants had been measured the plants were cut off at soil level and dried in a forced-draft oven at ca. 60 degrees C for a minimum time of 40 hours. The dry weight of the plants was taken and with this figure the amount of CO₂ taken up per gram of dry weight of plant was calculated.

B. Light Intensity Effects on CO₂ Exchange.

For this experiment only four varieties were used: OAC-21, Olli, Stavropal, White Gatami. The plants were grown in a manner similar to those in the previous experiment.

Twenty-one day old plants were placed in the chamber of the Vapor-Temp as for the previous experiment. For this and succeeding experiments the volume of the system was increased from 55 liters to 65 liters and the Drierite absorber was dispensed with. Three light intensities were produced by using.
6 V.H.O. reflector fluorescent tubes, 2 tubes, and darkness. The light intensities thus produced were 2400 ft. candles, 800 ft. candles, and 0 ft. candles at soil level. All light was excluded from the 0 ft. candle trial by the use of an aluminum foil hood for the chamber. For each light intensity three temperatures were tested: 12 degrees C, 22 degrees C and 32 degrees C. The relative humidity was maintained at 60%.

The procedure for this experiment was the same as for the previous experiment, the plants being allowed to photosynthesize for 15 minutes at each combination of light intensity and temperature, with the CO₂ level being replenished when needed between each measurement. The number of additions of CO₂ can be minimized by alternating between light and dark conditions when possible. The experiment was replicated four times for each of the four varieties.

Following measurement the plants were cut off as before and the leaf area was measured by means of Ozalid paper. This was carried out by placing the leaves flat on this paper and illuminating it. Those places covered with leaf are protected from light and when fumed with NH₄OH turn deep blue. These areas were out and weighed and the weight compared to that of a sample of a known area. Following this
process, the plants were dried and weighed. The amount of
$\text{CO}_2$ taken up was then calculated per gram of dry weight and
dm.$^2$ of leaf area.

C. Effect of Relative Humidity on $\text{CO}_2$ Exchange.

For this experiment four varieties were used: OAC-21, Olli, Stavropal and White Gatami. The plants for this experi-
ment were grown in a manner similar to that in the previous
experiments. Twenty-one day old plants were placed in the
chamber of the Vapor-Temp as for the previous experiments.
Three relative humidities were created in the chamber by
making appropriate adjustments to wet and dry bulb temperatures.
The effects of relative humidities of 30%, 60% and 90% were
measured at 12 degrees C, 22 degrees C and 32 degrees C.
Light intensity was 2400 ft. candles at ground level. Four
separate replications were carried out with each variety.
After $\text{CO}_2$ uptake had been measured, the plants were cut off
at ground level, and leaf areas were taken as in the previous
experiment.

D. Effect of Plant Age on $\text{CO}_2$ Exchange.

The plants for this experiment were prepared in a manner
similar to that in the previous experiments. The plant ages
at which $\text{CO}_2$ exchange was measured were 15 days, 30 days,
45 days and 60 days from seeding. During measurement of $\text{CO}_2$
uptake, humidity was maintained at 60% and illumination at
the soil level was 2400 ft. candles. The temperatures at
which $\text{CO}_2$ exchange was measured were 6 degrees C, 12 degrees C,
18 degrees C, 24 degrees C, 30 degrees C and 36 degrees C.
Following measurement of $\text{CO}_2$ exchange, the plants were cut off,
leaf area and dry weight taken and calculations made as in the previous experiment. Each of the four varieties tested were replicated independently four times at each of the four plant ages.

E. Photoperiod Effects on Development.

The experiments concerning the effects of photoperiod on the development of barley were conducted using small light-tight growth chambers with wheeled platforms (Ormrod, 1962). These were not fitted with any heating system but a baffled fan ensured uniform air circulation between the chamber and the atmosphere of the surrounding greenhouse. Minimum night temperatures were approximately 60 degrees F and day temperatures were approximately 75 degrees F. The wheeled platforms holding the pots of plants were wheeled out of the chambers at 8 a.m. and returned at 5 p.m. thus giving the plants 9 hours of daylight. In addition the chambers were provided with supplementary low intensity illumination provided by an equal wattage of incandescent and fluorescent lights yielding about 100 ft. candles at plant level. These lights were time switch controlled to provide equal additional periods of illumination before and after the day period. For the first photoperiod experiment, begun on August 16, 1965,
five such chambers were provided, giving photoperiods of 9 hours, 12 hours, 15 hours, 18 hours and 21 hours, while in the second experiment, begun on August 10, 1966, six chambers were used, the sixth having a 24 hour photoperiod or continuous light. Humidity was not controlled.

In both experiments, the twelve varieties of barley previously mentioned were sown in steamed greenhouse soil in one gallon plastic pots equipped with drainage holes. Eight seeds were sown in each pot, in the first experiment with a total of five pots of each of the twelve varieties being sown and in the second, six pots of each variety. In each experiment these varieties were placed in the same order on each of the wheeled platforms. The pots were watered approximately every three days. Periodic sulfur dusting and malathion spraying were necessary at the end of both experiments due to an infestation of aphids and mildew.

After emergence the plants were tested daily for evidence of the onset of internode elongation which started immediately after the completion of head differentiation. This was indicated by the appearance of a hard swelling in the plant stem above the soil level, easily detected by gentle tactile pressure. The date was recorded at which this stage was reached.
The plants were allowed to continue growth until evidence of heading was shown, that is until the head appeared through the collar of the leaf. This date was recorded and at this point the experiment was terminated.

Calculations

In the course of reducing the data of the CO₂ exchange experiments into a meaningful form some calculations were necessary:

1) P.P.M. CO₂/g. dry wt./15 min. = \( \frac{R}{M} \)

where \( R \) = reading in P.P.M. CO₂ per 15 min.

\( M \) = dry wt. in grams

2) P.P.M. CO₂/dm² leaf area/15 min. = \( \frac{100R}{A} \)

where \( R \) = reading in P.P.M. CO₂ per 15 min.

\( A \) = leaf area in cm.²

3) grams CO₂/dm²/hour = \( \frac{.786RV}{A} \)

where \( R \) = reading in P.P.M. CO₂ per 15 min.

\( V \) = volume of system in liters

\( A \) = leaf area in cm.²
RESULTS

A. Effect of Temperature on CO₂ Exchange.

There was a great difference in the amount of CO₂ taken up by the plants, both among varieties and also among temperature treatments within a single variety (Table 2). Furthermore there was among the varieties tested a great diversity of optimum temperature for CO₂ uptake (Figs. 1, 2, 3, 4). In general it was found that most varieties took up a maximum amount of CO₂ between 16 degrees C and 20 degrees C. Important exceptions to this were the varieties Vantage and Vantmore (Figs. 3, 4) which had a maximum uptake at 12 degrees C and 14 degrees C respectively and the variety White Gatami which had a maximum CO₂ uptake at 24 degrees C.

Statistical analysis showed that there were significant differences among temperatures for all varieties except Stavropal (Table 3). At 12 degrees C there were significant differences among varieties (Table 4) but no significant differences at 22 degrees C or 32 degrees C. When optimum temperatures were directly compared highly significant differences among varieties were noted. The lowest average recorded was 4.67 mg. CO₂ taken up/g. dry wt./hour at 34 degrees C for the variety Husky. The highest average recorded was 15.29 mg. CO₂ taken up/g. dry wt./hour at 18 degrees C for the variety Parkland.
B. The Effect of Light Intensity on CO₂ Exchange.

In all varieties tested the maximum CO₂ uptake occurred at the highest light intensity but the magnitude of this maximum uptake and the temperature at which it occurred varied among varieties (Table 5, fig. 5). In the dark, all plants showed a net release of CO₂ from respiration. Under 800 ft. candles, the compensation point varied greatly among varieties.
Table 2. Effect of temperature on CO$_2$ Exchange by twelve varieties of barley mg. CO$_2$ taken up/gram dry wt./hour - average of four replicates.

<table>
<thead>
<tr>
<th>Degrees C</th>
<th>4</th>
<th>6</th>
<th>8</th>
<th>10</th>
<th>12</th>
<th>14</th>
<th>16</th>
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<td>10.76</td>
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<td>11.64</td>
<td>11.84</td>
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<td>6.79</td>
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<td>7.93</td>
<td>7.65</td>
<td>8.30</td>
<td>8.62</td>
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<td>8.19</td>
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<td>7.98</td>
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<td>7.62</td>
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<td>11.04</td>
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</tr>
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<td>6.67(2)*</td>
<td>9.06(2)*</td>
<td>9.42(3)*</td>
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<td>9.78</td>
<td>9.90</td>
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<td>9.75</td>
<td>9.29</td>
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<td>9.44</td>
<td>10.38</td>
<td>8.60</td>
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* Number in parentheses indicates number of replications averaged.
Table 2. Continued.

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<th>22</th>
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<td>7.53</td>
<td>7.24</td>
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<td>6.55</td>
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<td>5.63</td>
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</tr>
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<td>11.00</td>
<td>11.42</td>
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<td>7.69</td>
</tr>
<tr>
<td>Pirrka</td>
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<td>9.05</td>
<td>8.14</td>
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<td>7.42</td>
<td>6.96</td>
<td>6.62</td>
<td>5.84</td>
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<tr>
<td>Stavropal</td>
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<td>8.73</td>
<td>7.80</td>
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<td>5.87</td>
<td>6.83</td>
<td>5.83</td>
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</tr>
<tr>
<td>Trebi</td>
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<td>10.02</td>
<td>9.75</td>
<td>9.60</td>
<td>8.81</td>
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<td>Wolfe</td>
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<td>8.71</td>
<td>8.08</td>
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Fig. 1 Effect of temperature on carbon dioxide exchange for Asa, Husky, and OAC-21.
Fig. 2 Effect of temperature on carbon dioxide exchange for Olli, Parkland, and Pirrka.
Fig. 3 Effect of temperature on carbon dioxide exchange for Stavropal, Trebi, and Vantage.
Fig. 4 Effect of temperature on carbon dioxide exchange for Vantmore, White Gatami, and Wolfe.
Table 3. Results of analysis of variance for effect of temperature on CO₂ exchange.

* indicates significance at 5% level
** indicates significance at 1% level
n.s. indicates no significance at 5% level

<table>
<thead>
<tr>
<th>Variety</th>
<th>F Value</th>
<th>Variety</th>
<th>F Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asa</td>
<td>5.54**</td>
<td>Stavropal</td>
<td>1.45 n.s.</td>
</tr>
<tr>
<td>Husky</td>
<td>10.13**</td>
<td>Trebi</td>
<td>3.37*</td>
</tr>
<tr>
<td>OAC-21</td>
<td>4.83**</td>
<td>Vantage</td>
<td>7.78**</td>
</tr>
<tr>
<td>Olli</td>
<td>7.19**</td>
<td>Vantmore</td>
<td>4.34**</td>
</tr>
<tr>
<td>Parkland</td>
<td>5.04**</td>
<td>White Gatami</td>
<td>5.12**</td>
</tr>
<tr>
<td>Pirrka</td>
<td>7.86**</td>
<td>Wolfe</td>
<td>8.63**</td>
</tr>
</tbody>
</table>

Table 4. Results of analysis of variance for varieties at a given temperature and between optimum temperatures.

<table>
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<th>Temperature</th>
<th>F Value</th>
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</thead>
<tbody>
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</tr>
<tr>
<td>22 degrees C</td>
<td>4.17 n.s.</td>
</tr>
<tr>
<td>32 degrees C</td>
<td>1.39 n.s.</td>
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<tr>
<td>Optimum temperature</td>
<td>11.53**</td>
</tr>
</tbody>
</table>
The greatest rate of CO₂ uptake as well as the greatest rate of CO₂ evolution was shown by the variety Stavropal (fig. 5), which also showed the greatest increase in CO₂ uptake between 800 ft. candles and 2400 ft. candles. For three of the four varieties analyzed, the compensation point was reached between 22 degrees C and 32 degrees C at 800 ft. candles light intensity. For the variety Stavropal the compensation point was found by extrapolation to be 35 degrees C.

In the light intensity experiment the dark respiration figures were added to the 2400 ft. candle photosynthesis figures in an attempt to determine the variation of true photosynthesis with temperature increase. The resulting figures showed a slight increase in mg./CO₂/dm.²/hour at 22 degrees C over 12 degrees C and 32 degrees C. An example is the variety OAC-21 with 8.87 mg./dm.²/hour at 12 degrees C, 9.65 mg./dm.²/hour at 22 degrees C and 9.20 mg./dm.²/hour at 32 degrees C.

C. Effect of Humidity on CO₂ Exchange.

There was great variation in responses between varieties and among temperatures within varieties (Table 6, Figs. 6, 7, 8, 9). The results of this experiment which gave figures for 30% and 90% relative humidities were combined with the previous experiment which gave results for 60%.
In two varieties, Stavropal and White Gatami, the rates of CO₂ uptake were significantly higher at 60% relative humidity than at either 30% or 90% relative humidity and of the two remaining varieties, Olli had a significantly lower rate of CO₂ uptake at 60% than at either 30% or 90% while OAC-21 showed no significant difference among humidities. In all cases, the 30% relative humidity and 90% relative humidity figures showed relatively little difference.
Table 5. Effect of light intensity on CO₂ by four varieties of barley

CO₂ uptake in mg./dm.² leaf area/hour - average of four replicates.
- figures indicate CO₂ uptake
# figures indicate CO₂ output

<table>
<thead>
<tr>
<th>Variety</th>
<th>2400 ft. candles</th>
<th>800 ft. candles</th>
<th>0 ft. candles</th>
</tr>
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<td>22</td>
<td>32</td>
</tr>
<tr>
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</tr>
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<td></td>
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<td>-1.95</td>
<td>-1.27 #</td>
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<tr>
<td></td>
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<td>-9.64</td>
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<td></td>
<td>-1.72</td>
<td>-1.98 #</td>
</tr>
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</tr>
<tr>
<td></td>
<td></td>
<td>#6.23</td>
<td></td>
</tr>
<tr>
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<td>-8.07</td>
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</tr>
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<td>-3.07</td>
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</tr>
<tr>
<td></td>
<td></td>
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<td>#4.31</td>
</tr>
</tbody>
</table>
Fig. 5 Effect of light intensity on carbon dioxide exchange.
Table 6. Effect of humidity on CO₂ exchange by four varieties at three temperatures.

CO₂ uptake in mg./dm.² leaf area/hour - average of 4 replications

<table>
<thead>
<tr>
<th>Variety</th>
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<th>22</th>
<th>32</th>
<th>12</th>
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<th>32</th>
<th>12</th>
<th>22</th>
<th>32</th>
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</thead>
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<td>5.63</td>
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<td>7.08</td>
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<tr>
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<td>7.15</td>
<td>5.90</td>
<td>6.64</td>
<td>6.07</td>
<td>3.68</td>
<td>8.02</td>
<td>7.15</td>
<td>4.44</td>
</tr>
<tr>
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<td></td>
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<td>7.92</td>
<td>2.49</td>
<td>9.48</td>
<td>9.64</td>
<td>6.08</td>
<td>7.97</td>
<td>6.34</td>
<td>.86</td>
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<tr>
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<td>4.98</td>
<td>5.23</td>
<td>5.30</td>
<td>4.33</td>
</tr>
</tbody>
</table>
Fig. 6 Effect of humidity on carbon dioxide exchange for OAC-21.
Fig. 7 Effect of humidity on carbon dioxide exchange for Olli.
Fig. 8 Effect of humidity on carbon dioxide exchange for Stavropal.
Fig. 9 Effect of humidity on carbon dioxide exchange for White Gatami.
Table 7. Results of analysis of variance of effect of humidity on CO₂ exchange at particular temperatures.

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<th>Variety</th>
<th>Temp. Deg. C</th>
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<td>Olli</td>
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<tr>
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<td>12</td>
<td>*</td>
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<tr>
<td>22</td>
<td>n.s.</td>
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<td>*</td>
</tr>
<tr>
<td>32</td>
<td>n.s.</td>
<td>32</td>
<td>*</td>
</tr>
<tr>
<td>Stavropal</td>
<td></td>
<td>White Gatami</td>
<td></td>
</tr>
<tr>
<td>12</td>
<td>*</td>
<td>12</td>
<td>*</td>
</tr>
<tr>
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<td>22</td>
<td>*</td>
</tr>
<tr>
<td>32</td>
<td></td>
<td>32</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

* indicates significance at 5% level  
** indicates significance at 1% level  
n.s. indicates no significance at 5% level
D. Effect of Age on CO₂ Exchange.

There was great difference in the response of the youngest plants (15 days) from that of the older plants (Table 8, Figs. 10, 11, 12, 13) in terms of rate of CO₂ exchange. In addition there was great variation in the response of different varieties and between temperatures in a given variety, as in previous experiments.

All varieties tested showed a decrease in the rate of CO₂ uptake expressed on a unit leaf area basis from the 15 day old plants to the 30 day old plants. However there was little or no difference among the 30, 45 and 60 day old plants tested with respect to the rate of CO₂ uptake.

E. Effect of Photoperiod on Development of Barley.

1) Days to Head Differentiation

There was considerable difference in the magnitude of the effect of photoperiod on head differentiation between varieties (Table 5). The variety Asa (Fig.14) had a time of 21 days to head differentiation at 9 hours decreasing to 18.5 days at 18 hours and increasing again to 20 days at 24 hours. The variety Husky took an average of 34.5 days at 9 hours decreasing to 21 days at 24 hours. The variety OAC-21 had a maximum time to head differentiation of 30.5 days at 9 hours and a minimum time of 21 days at 24 hours.
The variety Olli had a time of 18.5 days to head differentiation at 9 hour photoperiod, decreasing to 16 days at 18 hours and increasing to 21 days at 24 hours (Fig. 15). The variety Parkland took 26 days to head differentiation at photoperiods of 9 and 12 hours and a time of 19 days at 21 and 24 hours. The variety Pirrka had a maximum time of 28 days at 15 hours and a minimum of 16 days at 24 hours.

The variety Stavropal had a maximum time to head differentiation of 29 days at 24 hours and a minimum time of 19 days under continuous light (Fig. 16). The variety Trebi took 31 days at 9 hours and 19 days under 24 hour photoperiod. The variety Vantage took 33 days at 9 hours and 23 days at 24 hours.

The variety Vantmore (Fig. 17) had a maximum time to head differentiation of 34 days at 9 hours and a minimum of 23.5 days at 21 hours increasing to 24 days at 24 hours. The variety White Gatami took 33.5 days to differentiation at 9 hours, 22 days at 21 hours photoperiod and 23 days at 24 hours. The variety Wolfe had a maximum time of 36 days at 9 hours dropping to a minimum of 18 days at 21 hours.

2) Days to Head Appearance

Photoperiod affected the number of days to heading and some plants did not head at all under short day conditions (Table 10). In addition, as the age of these plants increased they were infected by mildew and infested by aphids.
Table 8. Effect of plant age on CO₂ exchange by four varieties at six temperatures.

mg. CO₂ taken up/dm.² leaf area/hour - average of 4 replicates.

<table>
<thead>
<tr>
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<th>12 D.C.</th>
<th>18 D.C.</th>
<th>24 D.C.</th>
<th>30 D.C.</th>
<th>36 D.C.</th>
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</thead>
<tbody>
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</tr>
<tr>
<td></td>
<td>30 days</td>
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<td>6.72</td>
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<td>2.84</td>
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</tr>
<tr>
<td>0111</td>
<td>15 days</td>
<td>9.56</td>
<td>12.43</td>
<td>12.13</td>
<td>12.16</td>
<td>11.93</td>
<td>9.13</td>
</tr>
<tr>
<td></td>
<td>30 days</td>
<td>5.28</td>
<td>6.34</td>
<td>5.99</td>
<td>4.89</td>
<td>3.81</td>
<td>2.47</td>
</tr>
<tr>
<td></td>
<td>45 days</td>
<td>6.59</td>
<td>7.04</td>
<td>7.76</td>
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<td>3.65</td>
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</tr>
<tr>
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<td>60 days</td>
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<td>7.76</td>
<td>7.51</td>
<td>6.34</td>
<td>3.45</td>
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<td>11.90</td>
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<td>10.37</td>
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<td>4.95</td>
<td>4.77</td>
<td>2.56</td>
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</table>

Figures in parentheses indicate number of replicates averaged.
Fig. 10 Effect of age on carbon dioxide exchange for OAC-21.
Fig. 11: Effect of age on carbon dioxide exchange for Olli.
Fig. 12 Effect of age on carbon dioxide exchange for Stavropol.
Fig. 13 Effect of age on carbon dioxide exchange for White Gatami.
There was a difference in response among varieties. The variety Asa (Fig. 14) had a maximum time to heading of 96 days with diseased plants at 12 hours photoperiod, while healthy plants at 9 hours took 69 days to head. The minimum time to head was 46 days at 24 hours. The variety Husky took a maximum of 103 days to head at 9 hours and a minimum of 43.5 days at 21 hours. The variety 0AC-21 had a maximum time to head of 82 days at 9 hours with a minimum of 45 days at 18 and 21 hour photoperiods.

The variety Olli took a maximum of 102 days to head at 9 hours, dropping to a minimum of 42 days at 24 hours (Fig. 15). The variety Parkland took 96 days to head at 9 hours with a minimum of 41.5 days at 21 hours. The variety Pirrka had a maximum time to head of 80 days at 9 hour photoperiod with a minimum of 38 days at 18, 21 and 24 hour photoperiods.

The variety Stavropal was not allowed to head at 9 hours because of physical damage. The longest time to heading observed was 101 days at 12 hours with plants also in a damaged state (Fig.16). The minimum time recorded was 42 days at 24 hours. The variety Trebi had a maximum time of 78 days at 12 hours while the minimum time was 41 days at 24 hours. The variety Vantage headed in 59 days at 12 hours and in 43 days at 21 hour photoperiods.
Table 9. Photoperiod effects on barley development.

a) Days to head differentiation

- First figure indicates 1965 results
- Second figure indicates 1966 results
- Dash indicates date not obtained

<table>
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<td>24</td>
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<td>19</td>
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<td>Trebi</td>
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<td>Avg.</td>
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Fig. 14 Photoperiod effect on development of barley for Asa, Husky, and OAC-21.
Fig. 15 Photoperiod effect on development of barley for Olli, Parkland, and Pirrka.
Fig. 16 Photoperiod effect on development of barley for Stavropal, and Trebi, and Vantage.
Fig. 17 Photoperiod effect on development of barley for Vantmore, White Gatami, and Wolfe.
The variety Vantmore (Fig. 17) had a maximum time to head of 61 days at 15 hours and a minimum time of 45 days at 21 hour and 24 hour photoperiods. The variety White Gatami at a 9 hour photoperiod headed in 77 days while it took 34.5 days at 21 hours. The variety Wolfe had a maximum time of 73 days at 9 hours and a minimum of 35 days at 24 hours.

In all varieties it was observed that vegetative growth increased as the daylength was shorter. The plants were lower in stature at short photoperiods than at long ones.

The greatest time to head differentiation was 36 days at 9 hours for the variety Wolfe and the minimum time 16 days at 24 hours photoperiod for variety Pirrka. Greatest variation from short to long photoperiod in its effect on differentiation was in Wolfe with 12 days between 24 hours and 9 hours. Asa and Olli were least sensitive with 2.5 days.

Maximum time to heading for a healthy plant was shown by OAC-21 with 82 days at 9 hours and minimum time was shown by White Gatami with a time of 34.5 days at 21 hours. It was difficult to determine sensitivity due to the number of diseased and damaged plants.
Table 10. Photoperiod effect of barley development.
   b) Days to head appearance.

- First figure indicates 1965 results.
- Second figure indicates 1966 results.
- Dash indicates data not collected.

<table>
<thead>
<tr>
<th>Variety</th>
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<td>-</td>
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<td>-</td>
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<td>41</td>
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<td>Pirrka</td>
<td>73</td>
<td>53</td>
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<td>36</td>
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<td>54</td>
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<tr>
<td>Avg.</td>
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<td>50.5</td>
<td>38.5</td>
<td>38</td>
<td>38</td>
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<tr>
<td>Vantage</td>
<td>-</td>
<td>59</td>
<td>57</td>
<td>57</td>
<td>42</td>
<td>-</td>
<td></td>
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<tr>
<td></td>
<td>-</td>
<td>76</td>
<td>48</td>
<td>44</td>
<td>46</td>
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<tr>
<td>Avg.</td>
<td>-</td>
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<td>61.5</td>
<td>52.5</td>
<td>43</td>
<td>46</td>
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<tr>
<td>Vantmore</td>
<td>-</td>
<td>-</td>
<td>54</td>
<td>-</td>
<td>47</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>-</td>
<td>-</td>
<td>68</td>
<td>54</td>
<td>43</td>
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<tr>
<td>Avg.</td>
<td>-</td>
<td>-</td>
<td>61</td>
<td>54</td>
<td>43</td>
<td>45</td>
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Table 10. Continued.

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<th>Variety</th>
<th>Photoperiod</th>
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<td></td>
<td>9 hrs.</td>
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<td>White Gatami</td>
<td>77</td>
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<td>Avg.</td>
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<tr>
<td>Wolfe</td>
<td>73</td>
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<td>Avg.</td>
<td>73</td>
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</table>
DISCUSSION

In all the barley varieties tested, the rate of net CO₂ uptake was found to increase with temperature increase to a certain optimum temperature, beyond which the rate decreased. This is in complete agreement with the results of other workers (Decker, 1944; Leopold, 1964; Whiteman and Koller, 1964). It has been stated that as the temperature is increased, progressively shorter periods of exposure of the plant result in a lowered rate of net CO₂ uptake, possibly due to enzyme inactivation (Meyer et al., 1960). However the rates of net CO₂ uptake by barley plants even at temperatures of 36 degrees C were constant over a period of time of 15 minutes, even though these rates were much lower than at the optimum temperature for that variety. It would seem that inactivation of the enzyme system is not primarily responsible for the lowered rate of net CO₂ uptake shown at high temperatures. It seems more likely that other factors such as a thermal increase in respiration (Thomas and Hill, 1949; Whiteman and Koller, 1964) and an increased stomatal resistance to CO₂ uptake are responsible for this lowering of the rate of CO₂ uptake at high temperatures (Leopold, 1964; Whiteman and Koller, 1964).

Many workers have found different varieties, races or species to have maximum photosynthesis rates at different temperatures and have in almost all cases attempted to correlate these differences with climatic differences in
habitat (Bjorkman et al., 1960; Miller, 1960; Mooney and Billings, 1960). The twelve varieties of barley examined were found to have optimum temperatures varying from 12 degrees C to 24 degrees C with nine of the twelve varieties being from 16 degrees to 20 degrees. This would tend to confirm the already well known fact that barley thrive in a relatively cool climate (Leonard and Martin, 1963). Unfortunately not enough data is readily available concerning climatic regions of growth of the exceptional varieties used in this study, there being no information readily available concerning the variety White Gatami for example which has its optimum at 24 degrees C. Vantage and Vantmore with optima of 12 degrees C and 14 degrees C respectively are genetically related (Weibe and Reid, 1961). They are both midseason varieties in the cool parts of the Canadian prairies and thus may be considered to perform more efficiently at cooler temperatures than other varieties of different provenance.

B. Effect of Light Intensity on CO₂ Exchange.

In all cases examined the net CO₂ uptake increased directly with light intensity. This has been also reported in clover (Beinhart, 1962), tomatoes (Porter, 1939) and barley variety Montcalm (Gfeller and Goulden, 1954). It has also been reported that at some light intensity varying with the plant and variety, a point is reached at which further increase
in light no longer brings about an increase in net CO$_2$ uptake (Bohning and Burnside, 1956). Perhaps this is due to a saturation of active chlorophyll molecules, which constitute a small fraction of the total present. In the present experiment, all varieties of barley showed an increase in net CO$_2$ uptake with increasing light intensity to 2400 ft. candles. Because barley is a field-crop its saturation intensity might be expected to substantially exceed 2400 ft. candles (Bohning and Burnside, 1956). In every respect the plants in this experiment behaved as expected. In the dark the CO$_2$ output increased with temperature giving an indication that increased respiration rates were the reason for a decreased net CO$_2$ uptake in the light at high temperature. The relationship of light respiration to dark respiration was not studied in the present work.

C. Effect of Humidity on CO$_2$ Exchange.

In the present experiments, three of the four varieties tested showed significant differences in net CO$_2$ exchange between humidities. The results of the present experiments would be difficult to explain on a physiological basis, especially since in all cases, the 60% relative humidity level rate was different from the 30% and 90% values which were relatively close. Furthermore, the 60% value in two cases
was higher and in two cases lower than the 30% - 90% group. The photosynthetic rate of Primula was found to be unaffected by relative humidity (Mitchell, 1936).

D. Effect of Plant Age on CO₂ Exchange.

Other workers have found plants decline in photosynthetic rate as they age (Singh and Lal, 1935). However, barley was found to decline in rate per unit leaf area only after the first four weeks (Thorne, 1960). In the present experiments, analyses of net CO₂ exchange rates on a unit leaf area basis at ages of 15 days, 30 days, 45 days and 60 days indicated a drop in the rate of CO₂ uptake between 15 and 30 days and apparently no difference between the rates at 30 days, 45 days and 60 days. Since at 60 days, the barley plants were not mature, it seems that the 30, 45 and 60 day rates indicate the standard rate for normally growing plants. The 15 day old plants however were definitely juvenile, before the end of head differentiation in all varieties as determined by photoperiod studies. At this stage, it might be expected that all metabolic rates including that of photosynthesis are higher than in later stages.

E. Effect of Photoperiod on Barley Development.

Barley has been considered a long day plant in all respects (Garner and Allard, 1923; Downs et al., 1959) and this has been confirmed again in the present experiments,
the optimum daylength for head differentiation in all
varieties being between 18 and 24 hours with the majority
being 24 hours. The optimum daylength for heading was in
all varieties either 21 or 24 hours which indicates perhaps
a slightly longer photoperiod requirement for heading than
for head differentiation. This however may be due to the
fact that the time to head differentiation may be in part
determined by the amount of nutrient in the seed itself while
the time to heading is almost completely independent of this
influence.

It had been found by many workers that long day
plants in short photoperiod, in addition to failing to flower
or flowering more slowly, are more vegetative with a tendency
to be sessile (Tincker, 1929; Allard and Evans, 1941;
Stuckey, 1942). This phenomenon was noted in the present
experiments.

Analysis of the Vapor-Temp Apparatus
The results obtained with the apparatus were well within
the order of magnitude expected for CO₂ exchange rates. However,
although the apparatus appeared to control temperatures
accurately, there was little or no corresponding data available
for the varieties under similar field conditions, therefore no
valid evaluation can be made, except that the machine is a good
tool for theoretical work.
Experiments were conducted with a Blue M "Vapor-Temp" controlled environment apparatus to show the effects of temperature, light intensity, relative humidity and plant age upon the rate of CO₂ exchange for twelve barley varieties. All varieties tested reacted in a similar manner to a gradual increase in temperature, that is, CO₂ uptake increased with an increase in temperature to a certain optimum point. So the temperature was increased beyond this point the rate of CO₂ uptake declined. This decrease does not seem to have been solely associated with enzymatic degradation. An increase in light intensity up to 2400 foot candles produced no light saturation in any variety. Three of the four varieties tested showed a significant change in rate of CO₂ uptake with a change in relative humidity. All varieties tested showed an initial decrease in rate of CO₂ uptake as the plants aged from 15 to 30 days. Above this age there was little change in rate of CO₂ exchange.

Experiments were also conducted in photoperiod chambers to determine the responses of twelve barley varieties to different photoperiods. The optimal photoperiod for head differentiation and for head appearance was 21 or 24 hours for all varieties.
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