



Growth and developmental responses of height and leaf color isogenic barley, *Hordeum vulgare* L., lines to cultural treatments
by Bharat Prasad Singh

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY in Crop and Soil Science
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Abstract:

In 1970, the responses of a two row commercial cultivar, Compana (C), and its medium height isogenic, Erectoides Compana (Ec), and a six row commercial cultivar, Titan (tall Titan, TT), and its height isogenics, Titan Belonee (medium Titan, MT), and Titan Beebee (short Titan, ST), to N fertilization, irrigation, and row spacing (population) treatments were compared. Vegetative plant characteristics studied included number of adventitious roots/plant, number of tillers/ unit land area, leaf number/plant, area/leaf, maximum leaf area/plant, leaf dry weight/plant, and plant dry weight/unit land area. Grain yields, grain yield components, and grain protein percentage were also obtained. N fertilization affected plant growth and grain yield much more than either irrigation or row spacing. For C, Ec, TT, MT, and ST with N fertilization maximum leaf areas/plant were 163, 154, 283 2.38, and 148 dm², plant dry weights were 71, 66, 71, 76, and 52 g/1.8 dm², and grain yields were 4257, 4283, 3910, 3695, and 2945 kg/ha, respectively. These values represent average increases in maximum leaf area/plant, plant dry weight/unit land area, and grain yield of 116, 105, and 50%, respectively. Vegetative, grain yield, and grain protein responses to N fertilization, irrigation, and row spacing of the short statured lines were similar to, or greater than, their normal isogenic lines except for area/leaf and leaf area/plant. The results indicate that the use of well adapted short statured barley lines will not reduce returns from investments in N fertilization and irrigation. In addition, the risk of loss from lodging would be reduced by changing from present tall commercial cultivars to the shorter lines.

In 1971, we studied the vegetative growth and water use of a normal green leaf color commercial cultivar, Liberty (L), and its two lighter leaf color isogenics, Pale Green Liberty, (PGL) and Golden Liberty (GL), grown at 8, 24, 49, 100% of full sunlight. Number of tillers/plant, number of leaves/plant, leaf area/plant, leaf dry weight/plant, dry weight/plant, specific leaf weight (SLW), and chlorophyll content were obtained. For 8, 24, 49, and 100% of full sunlight, mean values for maximum leaf areas were 270, 278, 328, and 310 cm²/ plant, and dry weights at harvest were 1.7, 2.9, 3.6, and 4.7 g/plant, respectively. Mean values for L, PGL, and GL were maximum leaf areas 217, 319, 353, cm²/plant, and dry weights at harvest 3.1, 2.9, 3.9 g/ plant, respectively. Leaf area development of GL was much slower than for L but dry matter yields were not reduced. Depletion of available soil water was delayed about 1 week by shading (24% of full sunlight) and about 2 weeks by the lighter leaf color of the GL line. Further research is needed to study the water use efficiency of light green barley lines.

GROWTH AND DEVELOPMENTAL RESPONSES OF HEIGHT AND LEAF COLOR ISOGENIC

BARLEY, HORDEUM VULGARE L., LINES TO CULTURAL TREATMENTS

by

BHARAT PRASAD SINGH

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ABSTRACT

In 1970, the responses of a two row commercial cultivar, Compana (C), and its medium height isogenic, Erectoides Compana (Ec), and a six row commercial cultivar, Titan (tall Titan, TT), and its height isogenics, Titan Belonee (medium Titan, MT), and Titan Beebee (short Titan, ST), to N fertilization, irrigation, and row spacing (population) treatments were compared. Vegetative plant characteristics studied included number of adventitious roots/plant, number of tillers/unit land area, leaf number/plant, area/leaf, maximum leaf area/plant, leaf dry weight/plant, and plant dry weight/unit land area. Grain yields, grain yield components, and grain protein percentage were also obtained. N fertilization affected plant growth and grain yield much more than either irrigation or row spacing. For C, Ec, TT, MT, and ST with N fertilization maximum leaf areas/plant were 163, 154, 283, 238, and 148 dm², plant dry weights were 71, 66, 71, 76, and 52 g/1.8 dm², and grain yields were 4257, 4283, 3910, 3695, and 2945 kg/ha, respectively. These values represent average increases in maximum leaf area/plant, plant dry weight/unit land area, and grain yield of 116, 105, and 50%, respectively. Vegetative, grain yield, and grain protein responses to N fertilization, irrigation, and row spacing of the short statured lines were similar to, or greater than, their normal isogenic lines except for area/leaf and leaf area/plant. The results indicate that the use of well adapted short statured barley lines will not reduce returns from investments in N fertilization and irrigation. In addition, the risk of loss from lodging would be reduced by changing from present tall commercial cultivars to the shorter lines.

In 1971, we studied the vegetative growth and water use of a normal green leaf color commercial cultivar, Liberty (L), and its two lighter leaf color isogenics, Pale Green Liberty, (PGL) and Golden Liberty (GL), grown at 8, 24, 49, 100% of full sunlight. Number of tillers/plant, number of leaves/plant, leaf area/plant, leaf dry weight/plant, dry weight/plant, specific leaf weight (SLW), and chlorophyll content were obtained. For 8, 24, 49, and 100% of full sunlight, mean values for maximum leaf areas were 270, 278, 328, and 310 cm²/plant, and dry weights at harvest were 1.7, 2.9, 3.6, and 4.7 g/plant, respectively. Mean values for L, PGL, and GL were maximum leaf areas 217, 319, 353, cm²/plant, and dry weights at harvest 3.1, 2.9, 3.9 g/plant, respectively. Leaf area development of GL was much slower than for L but dry matter yields were not reduced. Depletion of available soil water was delayed about 1 week by shading (24% of full sunlight) and about 2 weeks by the lighter leaf color of the GL line. Further research is needed to study the water use efficiency of light green barley lines.

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INTRODUCTION

Present day agriculture relies heavily on the use of commercial fertilizer and irrigation for higher yields. Most of the present commercial cultivars of barley, however, are susceptible to lodging when fertilized and irrigated. We probably have not been able to find the maximum yield potential of the available cultivars because when a certain high level of management for yield is reached, the crop lodges, grains fail to fill properly and harvest losses increase. In an effort to prevent damage from lodging, short and stiff strawed lines have been developed. Thorough knowledge of how semi-dwarfing genes influence various aspects of morphological plant development is needed to exploit the agronomic value and adaptation of this plant characteristic to the fullest extent. It is also essential to know the response of semi-dwarf plants to various cultural treatments in comparison to the present commercial cultivars of barley.

This investigation was designed to study the response to nitrogen fertilization, irrigation, and row-width of short statured two row and six row barley lines in comparison to the responses of their normal commercial isogenics.

LITERATURE REVIEW

Response of cereals to Nitrogen (N) fertilization and irrigation

N fertilization

The results of numerous fertilizer experiments up to 1942 have been reviewed by Olson and his associates. Most of the experiments have shown an appreciable yield response from nitrogen fertilizer alone or in combination with P and K. The magnitude of response and the significance of cultivar-fertilizer interactions, however, have varied considerably. Pendleton et al. (1953), in Illinois, found a significant difference in the yield response of barley cultivars to varying levels of nitrogen fertilization. Brown et al. (1961), in Georgia, studied the response of seven oat cultivars to different levels of fertilization and obtained significant cultivar x N fertilizer interactions for plant height, straw weight, grain yield, and grain protein content. In a four year experiment with barley, Frey et al. (1952) obtained a significant interaction between cultivars and fertilizer treatments only during those two years in which the Michigan weather was not favorable for barley production. During the other two years of this study when the weather was favorable for barley growth, no cultivar x fertilizer interaction for grain yield was obtained. Gregory and Crowther (1928), in England, reported no differential grain yield response for five cultivars of barley produced at different combination levels of N, P, and K. The cultivars, however, showed differential responses of yields of straw, roots and

and total top weight with different fertilizer treatments. Brown (1971)^{1/}, working on dryland in Montana's Gallatin Valley reported significant interactions between barley cultivars and N rates for plant height, straw yields, grain yield, test weight, grain protein, plumpness, and grain weights.

The grain yield is a function of (a) the number of spikes per unit area, (b) the number of grains per spike, and (c) the average weight per grain. Woodward (1966), in Utah, found that increase in yield of wheat by nitrogen fertilization was mostly due to increased culms per unit area. There was no increase in kernels per spike or in grain weight from N fertilization. Gasser and Iordanou (1967), in England, observed an increase in the number of spikes, total dry weight, and grain yield of barley with the application of N fertilizers. N application did not affect the weight per spike. Reisenauer and Dickson (1961), in Washington, found that yield increase from 80 to 120 lbs per acre of nitrogen resulted from the production of more but smaller kernels.

Hunter et al. (1958) found that protein content of Oregon grown pastry wheats was not increased appreciably by N fertilizer unless more was applied than necessary for maximum or near maximum yields. Martin and Mikkelsen (1960), working with barley in

^{1/} Brown, P. L. 1971. Annual Research Report. USDA, ARS-SWC, Northern Plains Branch, Bozeman, Montana.

California found that high rates of N fertilization were required to raise the percent grain protein appreciably on soils which were deficient in nitrogen. Even their lowest rates of N increased the protein level of the grain on soils which were not N deficient or in years when drought prevented yield responses on N deficient soils. McNeal and Davis (1954), in Montana, observed a decrease in percent grain protein of wheat from low N fertilization rates. Higher N fertilizer rates, however, significantly increased the protein content of the grain.

Irrigation

Bauer, Young and Ozbun (1965), in North Dakota, reported increased yields of wheat and barley with an increase in the available soil water, both with and without fertilizers. Bendelow (1958) and Sosulski and Bendelow (1964) also obtained significant increases in grain yield of barley grown under irrigation in Alberta, Canada. Irrigation increased the weight of the grain but invariably lowered the nitrogen content of the grain. Harris and Pittman (1922) reported an increase in plant height, tillering, grain weight, and head size of barley grown under irrigation in Utah. Widtsoe and Stewart (1912) found that there was an increase in the relative amount of ash and a decrease in per cent protein with irrigation of cereal grain grown in Utah.

Robins and Domingo (1962), in Washington, observed spring

wheat yield depressions of 10-35 per cent from severe moisture stress. Reductions were greatest when moisture stress was imposed during and following heading or during the maturing process. Moisture stress immediately preceding heading resulted in marked second growth which increased spike population but delayed the date of maturity. Moisture stress during and following heading generally resulted in fewer productive spikes, fewer spikelets per spike, and fewer grains per spikelet. Spike and grain productions were generally decreased by moisture stress late in the development of the plant. Grain weight was greatly reduced by moisture stress immediately preceding maturity. Plant height at harvest was depressed by moisture stress prior to or during heading.

Gaastra (1959) reported that moisture stress increased resistance to gas movement through the leaf mesophyll. Brouwer (1961) found that moisture stress tends to cause closure of stomata, thereby increasing resistance to diffusion of gases (water vapor and CO₂) through stomata. Moss et al. (1961) suggested that moisture stress reduces photosynthesis by limiting CO₂ supply to the chloroplast. Baker and Musgrave (1964) reported approximately 50 per cent reduction in photosynthesis in corn under moisture stresses where signs of wilt were barely visible.

N fertilization x irrigation

Luebs and Laag (1967) emphasized the importance of the ratio of

available water to available nitrogen for barley grain yield under non-irrigated conditions, particularly in winter rainfall areas where moisture is usually deficient from heading to crop maturity. Stanberry and Lowrey (1965), in Arizona, obtained much greater barley yield increases from application of N than from cultivar or irrigation treatments. N increased yields about 400%, whereas the "wet" moisture treatment exceeded the "dry" treatment by only 36%. When these two treatments were combined, however, the increase exceeded 570%, indicating that each treatment contributed its maximum effect only when the other was adequate. Barley without added N used about 80% as much moisture and produced less than 20% as much grain as barley receiving adequate N. Consequently, moisture utilization efficiency (M.U.E.) for grain production was about three times as high with abundant N as with no added N.

Ramig and Rhoades (1963), using different levels of preplant moisture with nitrogen application in Nebraska, found markedly greater straw-grain ratios in winter wheat when the moisture level was low. This indicated that with a low moisture level, nitrogen resulted in marked vegetative growth but moisture limited grain yield. Robins and Domingo (1962) in a study of the effect of moisture and nitrogen on spring wheat at Pullman, Washington found no significant interaction between the effects of nitrogen and moisture on yield.

Response of cereals to population density-Maize

Maize researchers have been advocating high plant populations to achieve high grain yield. Allison and Watson (1966) reported that when maize was grown at low populations in Rhodesia more leaves were produced than needed to fill the grain. When some leaves were removed, the grain received a larger fraction of the dry matter produced after flowering. High populations resulted in more ears per unit of land, thus creating a larger "sink" for the photosynthate. Denmead et al. (1962) reported a greater absorption of radiant energy with narrower row width and thus an increase in the energy available for photosynthesis. Colville and Burnside (1963) noted that inadequate plant populations caused inefficient light interception which in turn increased soil temperature and contributed to greater evaporative compared to transpirative water losses. Excessive light reaching the soil surface also increases weed growth. Yao and Shaw (1964) observed increased efficiency of water use and greater light interception with narrow rows. However, Timmons et al. (1966) and Olson (1971) observed that populations did not effect total water use in maize; the efficiency of water use was proportional to yield.

Response of cereals to population density-small grains and sorghum

Hansen et al. (1962) reported that narrower row spacing resulted in greater oat yields. Foth et al. (1964) in a three year study to evaluate the effect of row spacing on oats performance found that

oats grown in the narrow rows consistently had more panicles (or culms) per unit area and a higher yield of grain and straw than with the wider spaced rows. Of the yield components, seed weight was effected the least by row spacing and had the least effect on yield.

Working in Canada with wheat, oats, and barley, at three locations and over a three year period, Guitard et al. (1961) reported an increase in the number of plants per acre and a decrease in the number of fertile spikes per plant with successive increases in the seeding rate. There were reduction in the number of kernels per spike and in the 1,000-kernel weight. Demirlicakmak et al. (1963) observed that the heaviest rate of seeding produced the lightest weight kernels, and vice versa. Fewer tillers were produced under heavy competition.

Middleton et al. (1964), in North Carolina, grew three cultivars of winter barley at row widths of 8 and 16 inches and 3 rates of seeding in the row to study the effect of seeding rate and row width on yield and yield components. Decreasing the rate of seeding decreased the number of fertile spikes per unit area and increased the number of seeds per spike. The weight of 1,000 seeds and test weight per bushel were not affected significantly. Significant differences in yields were not found between 8 and 16 inch rows or at different seeding rates in the row.

Woodward (1956) observed that lower rates of seeding spring

barley, oats, and wheat, on irrigated soils in the Western United States, resulted in stiffer straw, larger spikes, and higher test weight. Day and Thompson (1970) noted that the conventional barley planting rates of 112 kg/ha in Arizona could be decreased by 50% without decreasing grain yields. They noted, however, that as the date of seeding was delayed beyond the optimum for grain production, the seeding rate should be increased. This is because later planted crops have a shorter vegetative period for tillering and root development.

It has been shown in many instances (Arnon and Blum, 1965, Grimes and Musick, 1960, Karchi and Rudich, 1966, Stickler, 1964, and Stickler and Younis, 1966) that grain yield of sorghum is not drastically affected by a wide range of plant densities. This is due to its ability to compensate by shifting grain yield components in response to available space. Under severe drought conditions at Hays, Kansas, Brown (1959) found that wider row spacing and low plant population increased grain sorghum yields significantly.

Siemans (1963) reported that grain protein content in spring wheat increased from 15.1 to 18.5% as distance between rows was increased from 15 to 76 cm. He found no cultivar x row spacing interaction in a test involving four wheat cultivars.

Interrelationship between different crop characteristics

Black (1970) observed that the number of spikes per ha in wheat

was linearly related to adventitious roots per plant at the end of tillering. The regression of grain yield on number of adventitious roots per plant accounted for 93% of the variation in grain yield.

Demirlicakmak et al. (1963) reported that tillering capacity, taken alone, was not a good indicator of yield in barley. In their experiment, the cultivar 'Gateway' produced the most tillers, but was lowest in yield.

Loomis and Williams (1963) have stated that the leaf area, manner of leaf display, and CO₂ supply are the major limiting factors to total seasonal yields in maize. The maximum possible production efficiency was calculated to be a conversion of 53 per cent of solar radiation to chemical energy, or 15 micrograms net dry matter per calory of solar radiation. It should be noted that these calculations are for maize plants which have a photosynthetic pathway that differs from that of wheat, oats, and barley. Allison (1969) pointed out that the leaf area of maize remains nearly constant for much of the time between flowering and maturity. So to maximize the supply of dry matter to the grain, plant density should be such that optimum leaf area index is reached at the time of flowering.

Watson et al. (1939) reported that there was very little carbohydrate translocation to the spike from below the flag leaf in barley. Thorne (1965) reported that CO₂ fixation by ear and flag leaf between ear emergence and maturity accounted for most of the final grain dry

weight. Photosynthesis in the flag leaf and the net CO₂ uptake by the spike each provided about half of the carbohydrate in the grain. Saghir, Khan, and Worzella (1968) shaded various parts of the culm from the lowest internode to the spike and found that the spike was the most critical plant part effecting grain development of wheat and barley. The removal of the top leaf had an effect on grain yield that was second to shading of the spike. Shading the stem or removal of the lower leaves caused an effect similar to but less marked than removal of the top leaf. Frey-Wyssling and Buttrose (1959) have cited the following evidences favoring the proposal that spike, rather than non-spike materials are preferentially used in grain filling (and floret respiration); (a) the proximity of awns and glumes to grains, as compared to stem and leaf sheath; (b) carbon fixed within a floret is not transported outside that floret; and (c) consideration of sugar and nitrogen transport in the plant suggests that the material elaborated in the spike is preferentially used by grains.

Neatby and McCalla (1938) observed that high yielding barley cultivars had a marked tendency to be low in protein. Correlation coefficients from a number of their experiments were all negative for the comparison of yield and protein content and ranged in magnitude from -0.21 to -0.88. Meredith et al. (1942) obtained a decrease in the nitrogen content of barley grain with an increase in 1,000 kernel weight. Middleton et al. (1961) determined protein percent-

age of 18 barley cultivars grown in a uniform nursery. The differences in protein content among cultivars were highly significant, but there was no significant correlation between grain yield and protein content of cultivars.

Genetics of plant height in barley

Plant height in barley is a very complex characteristic and is only partially determined by the H loci (Nilan, 1964). Shakudo and Kawase (1951) observed that the genes, LK, I, Uz, and rn inhibitors (factors for fertility of lateral florets) determines the height of culms through their pleiotropic influence on the length of awns and spikes. Leonard, Robertson, and Mann (1956) showed that the genes Uz and br acted in a complementary manner to determine plant height. Kump (1947) observed that long stem was dominant to short stem and it was controlled by a single gene.

EXPERIMENTAL PROCEDURES

Experimental site

This study was conducted in 1970 at the Field Research Laboratory, West of Bozeman, Montana. The soil at the Field Research Laboratory is Amsterdam silt loam. The nitrate nitrogen contents of the successive layers of the experimental plot were:

<u>Layer</u>	<u>Nitrate Nitrogen (ppm)</u>
0 - 15 cm	3.80
15 - 30 cm	1.75
30 - 61 cm	2.15
61 - 91 cm	1.25
91 - 122 cm	6.05
122 - 152 cm	4.05
152 - 183 cm	6.65

Climate and weather conditions

The Field Research Laboratory is situated at 45°41'N latitude and 111°09'E longitude. It has a semi-arid, temperate climate. A summary of the climatic data by months for the calendar year 1970, and average for the period 1958-1970 at the Field Research Laboratory, are given in Appendix Table 15^{1/}.

^{1/} Caprio, J. M. 1971. Weather data at Agricultural Experiment Stations in Montana. Mimeographed report.

Experimental Material

Three six row height isogenics and 2 two row height isogenics of barley were grown.

Two row lines

1. Compana - Compana is one of the many selections made at the Field Research Laboratory, Aberdeen, Idaho, from the tenth generation composite of 32 different crosses. The selection was tested by the Montana Agricultural Experiment Station and released in 1941. It is a white seeded, semi-smooth awned, drought resistant, early to mid-season maturing, high yielding barley cultivar. Seeds are large, plump, and thin hulled. Straw is weak and susceptible to lodging. It is classified as feed barley.^{1/}
2. Erectoides Compana - It is a spontaneous, medium statured, mutant derived from Compana.

Six row lines

1. Titan - Titan was obtained as a result of the cross Trebi x Gabron, made at the University of Alberta, Edmonton, Canada. It was released in 1943. It is a mid-season, stiff straw cultivar of barley with small to medium sized kernels. It is classified as a feed barley.^{1/}

^{1/} Barley Variety Dictionary, 1970. Malting Barley Improvement Association, Milwaukee, Wisconsin.

2. Titan Belonee - It is a medium statured isogenic of Titan developed by back crossing at the Montana Field Research Laboratory.

3. Titan Beebee - It is a short statured isogenic of Titan developed at the Montana Field Research Laboratory.

Experimental Design

A split plot experimental design with 40 treatments replicated three times was used. The main plots were 48.8 m long and 6.1 m wide. The treatments within any split were allocated randomly. The allocation of treatments were made in the following manner:

Split	Treatments
First split	0 kg N per ha 72 kg N per ha
Second split	No irrigation irrigation
Third split	15 cm row-spacing 30 cm row-spacing
Fourth split	<u>Lines</u> Compana Erectoides Compana Titan Titan Belonee Titan Beebee

Field operations

Nitrogen as ammonium nitrate (33% N) was applied at the rate of 72 kg N per ha to the plots assigned the N fertilization treatment.

Phosphorus as triple superphosphate (45% P_2O_5), potassium as potassium chloride (60% K_2O) and sulfur as gypsum (18% S) were applied to all plots at the rate of 18 kg P and K and 9 kg S per ha. Fertilizers were broadcast before planting. A tractor mounted cone seeder was used for planting the entire field in 30 cm rows. A manually operated single row cone seeder was then used to obtain 15 cm row spacing.

A sprinkler irrigation system was used for irrigating plots assigned the irrigation treatment. Irrigation was applied three times during the growing season. Weeding operations were carried out manually.

Method of study

Vegetative growth

Sampling was done three times, first at the end of the tillering period on June 17, second at the end of the stem extension period on July 2, and last at the flowering period on July 20. Samples were collected from an area 60 cm long and 30 cm wide. The following observations were recorded:

- (i) Number of plants per sample
- (ii) Number of adventitious roots per plant - the estimate was based on the average of a random 10 plant subsample.
- (iii) Number of tillers per sample
- (iv) Number of leaves per plant - the estimate was based on the average of a random 10 plant subsample. Only the leaves

with open collar were included in the leaf count.

- (v) Area per leaf - area per leaf estimates were based on the average of the leaf area of 20 randomly selected leaves. An air-flow planimeter as described by Jenkins (1959) was used for measuring the leaf area. Leaf area measurements included only the area of the leaf blade.
- (vi) Leaf area of flag leaf - at the time of the third sampling, 20 randomly selected flag leaves were used to estimate the average flag leaf area.
- (vii) Leaf area per plant - leaf areas per plant were calculated only for the second sampling date. The second sampling was taken at the end of the vegetative phase, so it should give an estimate of the maximum leaf area per plant. Values for the leaf area per plant were arrived at by multiplying the number of leaves per plant by average area per leaf.
- (viii) Dry weight per plant leaf - dry weight per plant leaf was obtained at the second sampling date.
- (ix) Plant height - length of the main stem from the base to the topmost exposed collar was recorded as plant height at the first two sampling dates. Length of the plant from the base of the main stem to the end of spike, awn excluded, was recorded as plant height at the third sampling date.
- (x) Plant dry weight - the above ground plant parts of the sample were dried in the oven and recorded as plant dry

weight.

Components of grain yield, grain yield, and protein percentage

Just prior to harvesting all plants from samples 120 cm long and 30 cm wide area were collected for the yield component analysis. The number of spikes bearing mature grain and tillers without mature spikes were counted separately. One hundred randomly selected mature grain bearing spikes were used to determine the number of grains per spike. Weight per grain was estimated from weighing 1,000 grains.

The plants were trimmed immediately preceding harvesting from both ends so that only the central 2.4 meter remained in each row. The middle three rows in 30 cm row spacing and the middle six rows in 15 cm row spacing were harvested with a gasoline powered mower with a mounted catcher on the sickle bar. The sickle bar was at the ground level, resulting in recovery of essentially all spikes from harvested area. Threshing of the grain was done in the field with a Vogel plot thresher.

Lodging severity indexes were estimated for each plot at harvest. These values can be influenced greatly by adjacent plots and difference between replications. Lodging severity indexes were not indicative of the detrimental effect on grain yield, since most lodging occurred after grain maturation. Therefore these values are not reported.

Grain protein percentage was determined by the modified

Kjeldahl's method^{1/} (AOAC, 1965). Grain test weight was recorded by AACC method 84-10^{2/}

^{1/} Association of Official Agricultural Chemists. 1965. Official methods of analysis, (10th Ed.). The Association, Washington, D.C.

^{2/} American Association of Cereal Chemists. 1962. Cereal Laboratory methods, (7th Ed.). The Association. St. Paul, Minn.

RESULTS AND DISCUSSION

Plant life is associated with numerous physiological processes, from planting to the harvest of the crop. Both genetic and environmental considerations regulate the physiological processes of the plant. The interrelation of these processes dictate growth and development.

Murata (1970) has divided grain yield formation in grain crops into the following three phases: (i) the formation of organs for nutrient absorption and photosynthesis; (ii) formation of flower organs and the "yield container"; and (iii) production, accumulation translocation of grain yield contents.

The number of plants germinating per unit area under favorable germinating conditions is a function of the number of seeds planted. In this experiment, the number of seeds planted per row was kept constant. The plots with 15 cm row spacing were seeded with double the number of seeds per unit area as for the 30 cm spacing. Plant counts revealed no influence of nitrogen, irrigation or lines on the number of plants per unit area (Table 1, p 21). As expected, a highly significant increase in plants per unit area resulted from

Table 1. Analysis of variance for various barley plant characteristics: (Plants/1.8 dm²; Adventitious roots/plant, Tillers/1.8 dm²; Fully expanded leaves/per plant; Leaf area (cm²/20 leaves); Flag leaf area (cm²/20 leaves); Maximum leaf area/per plant (cm²/plant); Maximum leaf weight/per plant (g/plant); Plant height (cm); (Plant dry weight (g/1.8 cm²); Grain yield (g/2.3m²); No. of spikes/3.6 dm²; No. of grains/50 spikes; grain weight (g/1,000 grains); grain protein %; Test weight (lb/bu).

Source	DF	Plants/ 1.8 dm ²	MEAN SQUARES		
			No. of adventitious roots/plant		
			End of tillering	End of stem extension	Flowering
Rep (R)	2	46	1.1	13.	13
Nitrogen (N)	1	294	186.0*	294.	683*
Error a (Ea)	2	28	8.0	13.	17
Irrigation (I)	1	218	1.0	8	35
N x I	1	186	1.1	22	82
Error b (Eb)	4	204	1.4	7	9
Spacing (S)	1	21440**	1.0	302 *	1660**
N x S	1	94	1.4	42	32*
I x S	1	63	2.8	12.	4
N x I x S	1	104	14.0*	47	21
Error c (Ec)	8	42	1.9	43	6
Lines (L)	4	114	2.0	43 *	216**
N x L	4	106	1.9	3.3	16
I x L	4	120	1.2	4.5	38*
S x L	4	120	4.9**	7.2	37*
N x I x L	4	179	1.6	3.2	12
N x S x L	4	189	1.4	3.7	16
I x S x L	4	139	1.3	2.3	11
N x I x S x L	4	186	0.51	3.7	6
Error d (Ed)	64	100	0.98	3.6	12
Total	119				

* Significant at 0.05 level

** Significant at 0.01 level

Table 1. (continued)

Source	MEAN SQUARES					
	No. of tillers/1.8 dm ²			No. of fully expanded leaves/plant		
	End of tillering	End of stem extension	Flowering	End of tillering	End of stem extension	Flowering
R	2981	468	5057	1.2	8	51
N	37465**	63112**	78694*	99 **	469*	839 ***
Ea	342	559	1422	0.71	15	0.34
I	1002	464	11078*	1.1	3.3	93
N x I	529	472	5589*	4.2	5.6	134
Eb	654	675	341	2.0	9.0	23
S	47124**	25637**	16263**	1.2	149.**	909**
N x S	7520	2448	4118*	6.4*	1.4	57
I x S	853	74334	1549	1.0	2.5	20
N x I x S	832	661	2475*	1.5	7.2	52
Ec	375	838	440	0.7	2.4	21
L	3909**	4328**	3756**	3.7 **	9.0*	31**
N x L	691	449	1105	2.8 *	2.0	6
I x L	286	537	407	1.3	2.0	16*
S x L	233	894	1335	1.5	1.8	15*
N x I x L	406	532	2105*	1.5	1.2	10
N x S x L	554	1520*	619	0.5	5.1	6
I x S x L	760	471	434	1.2	1.7	9
N x I x S x L	803	379	845	1.1	1.5	14
Ed	368	557	728	1.0	2.6	5.4

Table 1. (continued)

Source	MEAN SQUARES					
	Leaf area (cm ² /20 leaves)			Flag leaf area (cm ² /20 leaves)	Max leaf area/plant (cm ² /plant)	Max leaf weight/plant (g/plant)
	End of tillering	End of stem extension	Flowering			
R	4969	3677	626	316	2606	0.06
N	23213*	479562**	486795**	123200**	108863*	6.2 **
Ea	785	3677	6524	250	5229	0.02
I	113	572	1286	1098	3321	0.006
N x I	130	1116	1752	2042	6554	0.013
Eb	125	641	1824	1054	4991	0.006
S	3532*	14083*	5507	1086	11995*	0.27
N x S	119	1825	15664	7285*	544	0.00
I x S	715	1790	1030	405	4496	0.00
N x I x S	298	3328	1801	686	1310	0.00
Ec	419	1974	1498	656	1187	0.04
L	1215*	31253**	21298**	18875**	25238**	0.20
N x L	375	6751**	11440**	4490**	9875**	0.02
I x L	409	1273	1123	661	2703	0.00
S x L	798	821	2509	990	2906	0.01
N x I x L	684	1261	6510**	1385	1796	0.04
N x S x L	375	1910	2425	1888**	1680	0.02
I x S x L	306	3084	2797	484	1470	0.03
N x I x S x L	370	782	2441	479	1894	0.01
Ed	453	1271	1319	419	2316	0.03

Table 1. (continued)

Source	MEAN SQUARES					
	Plant height (cm)			Plant dry weight (g/1.8 dm ²)		
	End of tillering	End of stem extension	Flowering	End of tillering	End of stem extension	Flowering
R	14	131	233	36	45	1630
N	236*	5177*	6912*	1877*	33852**	107700*
Ea	7.4	203	361	34	293	1896
I	3.5	56	788**	15	361	3549
N x I	8	323	620**	11	468	4605*
Eb	4	64	17	12	348	555
S	3	44	256**	640**	4314**	4467
N x S	9	199	14	182**	1998	1227
I x S	3	95	150**	16	121	1202
N x I x S	12	30	48	24	118	1120
Ec	1	47	12	6	209	852
L	134**	1184**	2009**	107**	1005**	5595**
N x L	5	80**	110**	25**	156	1090
I x L	1	17	29	13	123	1009
S x L	2	90**	48	4	395*	1885**
N x I x L	5	50	59*	15	177	1400*
N x S x L	3	41	23	6	261	442
I x S x L	1	20	16	13	93	337
N x I x S x L	1	24	30	14	128	875
Ed	2	20	20	6	129	491

Table 1. (continued)

Source	MEAN SQUARES					
	Grain yield (g/2.3 m ²)	No. spikes/ 3.6 dm ²	No. grains/ 50 spikes	Grain weight (g/1,000 grains)	Grain protein %	Test weight (lbs/bu)
R	92331	4077	13076	8	11	1.4
M	2024100**	78540**	84270*	20	187.*	1.2
Ea	100171	99	1613	9.6	2.7	9.2
I	331275*	29578**	33924	16.7	24**	1.2
N x I	242910	15732**	22908	16.4	1.1	5
Eb	34325	838	27393	12.4	0.75	1.7
S	7197	50020**	1689810**	3.2	0.74	1.3
N x S	4585	1442	4870	8.3	1.94	0.74
I x S	9346	1149	2822	23.8*	0.65	2.5
N x I x S	25433	2288	3876	4.5	0.60	0.82
Ec	7665	747	2419	4.0	0.87	0.92
L	315872**	15642**	2916950**	5071.***	8.9.**	27.9.**
N x L	6693	833	15082	4.7	4.7	0.67
I x L	24054	140	16437	4.1	1.2	0.63
S x L	13230	26	149545**	5.6	0.85	0.67
N x I x L	16819	395	8970	4.0	0.49	1.81
N x S x L	17223	592	13238	4.7	0.98	0.49
I x S x L	12800	451	15237	5.0	0.79	0.47
N x I x S x L	60524*	329	19142	3.2	0.72	0.78
Ed	17944	1005	13270	4.2	0.70	0.88

Table 2. Adventitious roots per plant as influenced by N, irrigation, and row spacing in five lines of barley (Flowering period).

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	10.5	13.9	13.8	13.2	17.4	13.8
72 kg N/ha	14.7	18.1	18.8	17.9	22.1	18.3
% increase	40	30	36	36	27	33 *
No irrigation	12.1	14.1	15.9	16.2	19.5	15.5
Irrigation	13.1	18.0	16.6	16.3	20.0	17.3
30 cm rows	15.8	20.0	19.7	17.7	24.3	19.5
15 cm rows	9.4	12.1	12.8	13.5	15.2	12.6
% increase	-40	-39	-35	-24	-37	-35 *

* The two means differ at the 0.05 level

decreasing the row spacing from 30 to 15 cm.

Adventitious root number responses of five barley lines to nitrogen, irrigation, and row spacing treatments are given in Table 2. Increase in the number of adventitious roots by the application of nitrogen fertilizer was significant and similar for all lines. Black (1970) has also obtained a significant increases in the number of adventitious roots from N application when adequate P was present in the soil.

No significant increase in the number of adventitious roots per plant from irrigation was observed. A significantly greater number of adventitious roots per plant were found in 30 cm row spacing than in 15 cm row spacing in two later samplings. An inter-row plant competition could account for the reduction in adventitious roots number at the later sampling dates. Significant inter-row competition probably was not present when the first sampling was taken at the late tillering period.

The maximum adventitious root number per plant in six row barley was greater (17.3 per plant) than in two row barley (14.2 per plant) (Table 2). Short statured Erectoides Compana attained 16.3 adventitious roots per plant in comparison to 12.2 for its normal isogenic line. Respective per plant adventitious root numbers for Titan, Titan Belonee, and Titan Beebee were 16.2, 15.1, and 20.5

This experiment failed to give any definite line by row spacing

interaction pattern for adventitious root development. A significant line x row spacing effect was found at the first sampling date when no significant effect of spacing on adventitious root number was observed. But at the second sampling, a significant row spacing effect was not accompanied by a significant line x row spacing effect. At the third sampling, both row spacing and line x row spacing effects were significant.

Tillers which ultimately form mature spikes are formed in the early stages of vegetative growth. Tiller proliferation requires a rapid formation of new cells which in turn increases the demand for structural protein. Seventy-two kg N/ha significantly increased the number of tillers per unit area. Nitrogen fertilization increased tiller production by 63% (Table 3). Short statured lines were similar to their normal isogenic lines in their response to N fertilization.

Irrigation did not influence tiller number per unit area of the first two samplings, but did at the third sampling date. A significant nitrogen x irrigation effect on tillering at the third sampling date indicated greater response to irrigation with added N. There was no irrigation by line interaction.

Decreasing the row spacing from 30 to 15 cm significantly increased the tiller number per unit area because of the greater number of plants in the 15 cm row spacing. The increase in the tiller number with narrower row was significantly greater in treatments receiving

Table 3. Tillers per 1.8 dm² as influenced by N, irrigation, and row spacing in five lines of barley (End of tillering period).

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	73	74	73	69	61	70
72 kg N/ha	131	129	109	112	91	114
% increase	79	74	49	62	49	63*
No irrigation	99	95	91	86	77	90
Irrigation	106	108	92	95	75	95
30 cm rows	84	86	75	73	75	79
15 cm rows	121	117	108	108	99	111
% increase	44	36	44	48	32	41*

* The two means differ at the 0.05 level

additional nitrogen fertilizer. No line by row spacing interaction for tillering was evident.

Lines differed significantly in the tiller number per unit area. Mean tiller numbers per 1.8 cm^2 for Compana, Erectoides, Compana, Titan, Titan Belonee, and Titan Beebee at the first sampling were 102, 101, 91, 90, and 76.

Dry matter production after the seedling stage is dependent on photosynthesis. Chlorophyll content and leaf area have been used to characterize the photosynthetic capacity of plants. However, most normal green plants contain at least the level of chlorophyll required for the saturation of their CO_2 assimilating capacity and the excess chlorophyll is not correlated with production (Loomis and Williams, 1970). They considered distribution of chlorophyll in plant leaves to be essentially in sheets whose surfaces are restrictive to CO_2 exchange, and whose lateral dimensions largely determine light interception. So leaf area gives a good estimation of photosynthetic capacity for the vegetative growth of a crop. Number of leaves per plant and leaf area per leaf determines the total leaf area of a plant. Calculations of leaf area index (LAI, defined as the ratio of leaf area on one side of leaf blades to the ground area) for a crop canopy would require the values for plant populations.

Table 4 shows the variation in the leaf number per plant caused by nitrogen, irrigation and row-spacing treatments. Nitrogen caused a

Table 4. Maximum number of leaves per plant as influenced by N, irrigation, and row spacing in five lines of barley.

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	10.1	10.3	9.6	9.1	9.7	9.8
72 kg N/ha	14.7	14.2	13.4	13.8	13.7	14.0
% increase	45	38	40	52	41	43 *
No irrigation	12.1	12.3	11.2	11.3	11.7	11.7
Irrigation	12.7	12.2	11.8	11.6	11.7	12.0
30 cm rows	13.2	13.7	12.9	12.5	12.6	13
15 cm rows	11.6	10.9	10.9	10.4	10.8	11
% increase	-12	-20	-15	-17	-14	-15*

* The two means differ at the 0.05 level.

significant increase in the number of leaves per plant. A differential response of leaf number to nitrogen application was observed among the five lines only for the first sampling. Irrigation had no significant effect on leaf number. Narrow rows had fewer leaves per plant. The maximum number of leaves per plant in two row lines was 12.3 in comparison to 11.5 in six row lines.

Nitrogen fertilization increased the maximum area per leaf (Table 5). Lines showed differential leaf expansion responses to nitrogen application when measured at the end of stem extension or at the flowering period. Increases in area per leaf from N for Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee at the end of the stem extension period were 46, 36, 94, 48, and 16%, respectively. This shows N fertilizer increased leaf area more in the normal lines. Irrigation did not influence area per barley leaf. A significant decrease in area per leaf with a decrease in row spacing from 30 to 15 cm was observed at the first two sampling dates. Maximum areas per leaf of Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 9.3, 9.4, 14.7, 13.0, and 9.8 cm², respectively.

The flag leaf in barley has been shown to play an important role in grain filling (Archbold, 1945, and Thorne, 1963, 1965). Table 1, p. 23 gives the variations in the flag leaf area caused by various cultural treatments. It is evident that flag leaf area responses to these treatments were similar to leaf area responses of other leaves.

Table 5. Maximum area per leaf as influenced by N, irrigation, and row spacing in five lines of barley (cm²/leaf).

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	7.6	8.0	10.0	10.5	9.1	9.0
72 kg N/ha	11.1	10.9	19.4	15.6	10.6	13.5
% increase	46	36	94	48	16	50 *
No irrigation	8.9	9.2	14.1	12.9	9.7	11.0
Irrigation	9.8	9.8	15.2	13.2	10.1	11.6
30 cm rows	9.7	9.9	16.5	14.5	10.3	12.2
15 cm rows	9.0	9.0	12.9	11.6	9.4	10.4
% increase	-7	-9	-22	-20	-9	-15 *

* The two means differ at the 0.05 level

Respective flag leaf areas of Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 3.6, 3.6, 5.8, 7.8, and 5.6 cm². The areas of barley flag leaves are always less than for the other leaves.

Table 6 gives the leaf area per plant at the end of the stem extension phase as influenced by the N, irrigation, and row-spacing. Addition of N increased the leaf area per plant of Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee by 112, 79, 186, 131, and 66%, respectively (Table 6). The leaf area increases by N in normal lines was significantly greater than for their shorter height isogenics. N increased leaf area per plant by producing more leaves and by increasing leaf size. Irrigation did not influence leaf area per plant significantly.

Decreasing the row spacing from 30 to 15 cm resulted in an average 20% decrease in leaf area per plant. The lower leaf area per plant with narrower row-spacing resulted from decrease in both the number of leaves per plant and area per leaf. Average leaf area per plant for Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 120, 120 191, 171, and 119 cm², respectively. While no differences existed in the average leaf area per plant between the 2 two row lines, normal Titan had significantly greater leaf area per plant than its height isogenics.

Table 7 gives the maximum leaf dry weight per plant of the five lines as influenced by the N, irrigation and row spacing (population)

Table 6. Maximum leaf area per plant as influenced by N, irrigation, and row spacing in five lines of barley (cm²/plant).

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	77	86	99	103	89	91
72 kg N/ha	163	154	283	238	148	197
% increase	112	79	186	131	66	116*
No irrigation	115	112	182	168	116	139
Irrigation	126	127	199	174	122	150
30 cm rows	135	129	222	183	129	160
15 cm rows	105	110	160	159	108	128
% increase	-22	-15	-28	-13	-16	-20*

* The two means differ at 0.05 level

Table 7. Maximum leaf dry weight per plant as influenced by N, irrigation, and row spacing in five lines of barley (mg/plant).

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	293	293	426	396	318	345
72 kg N/ha	583	545	788	788	589	658
% increase	99	86	85	99	85	91*
No irrigation	411	416	572	566	444	482
Irrigation	465	421	641	618	463	522
30 cm rows	451	470	680	648	509	551
15 cm rows	386	406	534	526	398	450
% increase	-14	-14	-21	-23	-22	-18*

* The two means differ at 0.05 level.

treatments. Addition of nitrogen increased the leaf dry weight per plant by an average of 91%. A major portion of leaf dry weight is composed of chloroplast and about 50% of this weight of the chloroplast is composed of various proteins (Bonner, 1952). This emphasizes the special role of N in determining the dry weight of the plant leaves. As reported earlier, addition of N increased plant leaf area. Increased leaf area would provide the plant greater efficiency to synthesize photosynthates, some of which can be stored in the leaf itself. It should be noted that while N application caused different plant leaf area responses of lines, all lines showed similar increases of leaf dry weight.

Irrigation did not cause significant increases in leaf dry weight per plant. Decreasing the row spacing from 30 to 15 cm (thereby doubling the plant population) decreased the leaf dry weight per plant by an average of 18%. Average leaf dry weights per plant of Compana, Erectoides Compana, Titan, Titan, Belonee, and Titan Beebee were 438, 418, 607, 592, and 453 mg, respectively.

A 105% increase in plant dry weight per unit area was obtained with the application N fertilizer (Table 8). Increased leaf area by N application would enable the plant to produce more dry matter. Fujiwara (1965) has reported a very close, positive correlation between the nitrogen content of the rice leaf and its photosynthetic activity. So, additional nitrogen could also have increased photosynthetic

Table 8. Plant dry weight per 1.8 cm² as influenced by N, irrigation, and row spacing in five lines of barley (End of stem extension period) (g/1.8 dm²).

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	34.4	34.1	33.9	37.3	23.3	32.8
72 kg N/ha	70.7	65.5	70.9	76.2	52.1	67.5
% increase	105	92	109	104	124	105 *
No irrigation	49.8	49.8	50.8	56.4	37.3	48.8
Irrigation	55.8	52.7	54.0	57.1	38.1	51.5
30 cm rows	44.4	43.1	51.0	47.2	26.4	42.4
15 cm rows	60.7	59.5	53.8	66.2	49.0	59.2
% increase	37	38	5	40	86	40 *

* The two means differ at the 0.05 level

efficiency of the plant. Responses of short statured lines to N for plant dry weights were similar to their normal isogenic lines.

No significant increase in dry matter production by the application of irrigation during the vegetative phase of plant growth was evident. Sampling at the flowering phase revealed that while practically no increase in dry weight occurred from irrigation without fertilizer, an increase in dry weight of approximately 111% was obtained from irrigating N added plots. As no significant increase in dry matter production was evident in the vegetative phase, this increase could be attributed to greater spike weight in N fertilized irrigated plots. Robins and Domingo (1962) have reported that favorable moisture conditions increase the number of spikes formed in cereals.

Dry matter production was increased approximately 40% by decreasing the row spacing from 30 to 15 cm. Lines varied in the effect of row spacing on dry matter production. Increase in dry matter production by reduction in row spacing was only 5% for the normal Titan, in comparison to 40% for the medium tall Titan, and 86% for the short statured Titan. The reason for a smaller dry matter increase in the normal Titan could be that an optimum vegetative growth was achieved at the 30 cm row spacing. Such a possibility could be envisioned considering that normal Titan had the greatest leaf area per plant. The barley seeding rate at the 30 cm row spacing used in this experiment was a common rate used by farmers in Montana. So, at the

15 cm row spacing, the number of plants would be about double the population usually planted. This could result in inter-rows competition for plant nutrients and moisture. Adverse effects of mutual shading on nitrogen and carbohydrate metabolism is also a possibility. Knipmeyer et al. (1962), studying three maize hybrids which were artificially shaded or placed under competitive plant shading, observed that shading did not change the per cent N but increased nitrate accumulation. They attributed it to the decreased nitrate reductase activity under shaded conditions. In terms of leaf area Titan Belonee is in the middle of the three six row lines. Its response to dry matter production (40% increase) under increased plant density was also in the middle of these three lines. For Titan Beebee, which had minimum leaf area, the increase in dry weight with increased plant density was maximum. The above results point out that in deciding the optimum seeding rate for dry matter yield, various plant morphological characteristics of a line have to be taken into consideration.

Plant dry weights per 1.8 dm^2 produced by Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee at the end of the vegetative phase were 53, 51, 52, 57, and 38 g, respectively. At this point, it should be noted that the leaf areas per plant of Compana and Erectoides Compana were comparable to Titan Beebee and less than Titan or Titan Belonee, but they equalled Titan, and Titan Belonee in dry matter production.

The three isogenics for shorter height used in this experiment can be separated into the following three categories based on their leaf area development and dry matter production abilities - (i) Erectoides Compana - reduction in plant height did not reduce plant leaf area or dry matter production (ii) Titan Belonee - reduction in height reduced the plant leaf area, but did not effect the dry matter production. The reduction in plant leaf area was caused by reduction in area per leaf (iii) Titan Beebee - reduction in height reduced both leaf area and dry matter production. So, different height genes seem to modify the vegetative structure of the plant to different limits.

Analysis of variance for plant height at the end of tillering, end of stem extension, and in the flowering period is given in Table 1, p. 24. The effect of nitrogen on plant height was significant at all three sampling dates. No response to irrigation and row spacing was noted at the first two sampling dates. Plant height at the flowering period, however, was significantly influenced by N, irrigation, and row spacing treatments. The plant height of the five lines at different cultural treatments are given in Table 9. Plant heights increased an average of 31% with the application of N, and 9% with irrigation. Decreasing the row spacing from 30 to 15 cm decreased the plant height by an average of 5%.

Average plant heights of Compana, Erectoides, Compana, Titan, Titan Belonee, and Titan Beebee at flowering were 62, 49, 69, 54, and 47 cm respectively.

Table 9. Plant height (cm) as influenced by N, irrigation, and row spacing in five lines of barley (Flowering period).

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	53.4	41.7	58.5	46.3	42.4	48.4
72 kg N/ha	70.2	55.9	78.8	62.3	51.1	63.6
% increase	31	34	35	34	20	31 *
No irrigation	59.3	47.6	65.0	50.7	44.9	53.5
Irrigation	64.3	50.0	72.4	57.9	48.5	58.6
% increase	8	5	11	14	8	9 *
30 cm rows	63.8	49.5	72.4	55.2	46.8	57.5
15 cm rows	59.8	48.1	65.0	53.4	46.7	54.6
% increase	-6	-3	-10	-3	0	-5 *

* The two means differ at the 0.05 level

A 50% increase in grain yield was obtained from N fertilization (Table 10). With low soil nitrate values an increased grain yield is expected with the application of nitrogen. Olson et al. (1942) have reviewed numerous papers to conclude that appreciable yield increases from nitrogen are obtained either alone or in combination with P and K. Nitrogen constitutes a significant portion of grain weight as a component of grain protein. Nitrogen also has a stimulatory effect on the rate of photosynthesis (Fujiwara, 1965). But it should be noted that the 50% increase in grain yield by N was far less than the 105% increase in total dry matter by N.

It was very encouraging to note that the height isogenics were similar to their respective normal lines in their responses to N fertilization. This would indicate that a farmer using N fertilizer may expect to obtain the same returns on his investment by growing a high yielding short statured line as from the present commercial lines, without running the risk of losses from lodging.

Grain yield of barley is a function of (i) the number of spikes per unit area, (ii) the number of grains per spikes, and (iii) the average grain weight. Addition of N caused an average 42% increase in the number of spikes per unit area (Table 11). Since application of N increased the tiller number, an increase in the spike number was expected. No differential N response among lines was observed for spike formation. N increased the number of grains per spike by an

Table 10. Grain yield as influenced by N, irrigation, and row spacing in five lines of barley (kg/ha).

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	2953	3034	2524	2331	1851	2538
72 kg N/ha	4257	4283	3910	3695	2945	3818
% increase	44	41	55	58	59	50*
No irrigation	3426	3394	3022	2619	2094	2911
Irrigation	3784	3923	3417	3403	2704	3446
% increase	10	16	13	30	29	18*
30 cm rows	3592	3740	3340	2981	2367	3204
15 cm rows	3619	3578	3098	3044	2430	3153

* The two means differ at the 0.05 level

Table 11. Number of spikes per 3.6 dm² as influenced by N, irrigation, and row spacing in five lines of barley.

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	152	138	110	99	104	121
72 kg N/ha	201	205	146	157	150	172
% increase	32	48	33	58	44	42*
No irrigation	162	155	116	110	109	130
Irrigation	191	188	140	145	145	162
% increase	18	21	21	32	33	25*
30 cm rows	156	152	108	106	107	126
15 cm rows	198	190	148	150	147	167
% increase	27	25	37	41	37	32*

* The two means differ at the 0.05 level

average of 6% (Table 12). Wada (1961) has established that in cereals the differentiation of spikelets is strongly promoted by nitrogen supply and the final number of spikelets is closely related to the nitrogen supply. Grain formation of short stature lines and their normal isogenics responded similarly to N. N did not effect 1,000 grain weight (Table 13).

Irrigation increased grain yields by an average of 18% (Table 10). The increase in grain yield from irrigation was caused by an increase in the spike number per unit ground area. Spike differentiation took place in June. June 1970 was a dry month. Irrigation resulted in a 25% increase in the number of tillers forming spikes. The increase in spike number with the application of irrigation was 74% in plots with added N, as compared to 8% in plots to which no N was added. Irrigation had no influence on number of grains per spike and 1,000 grain weight.

Reduction in row spacing from 30 to 15 cm did not cause any significant increase in grain yield (Table 10). Middleton et al. (1964) reported no difference in grain yields between 8 and 16 inch row spacings in winter barley. Grain yield components compensated for each other resultin in no increase in grain yield with 15 cm row spacing. The 15 cm row spacing produced approximately 32% more spikes per unit ground area than the 30 cm row spacing. But this increase was compensated for by a 20% decrease in grain number per spike.

More spikes per unit ground area can be envisioned to increase

Table 12. Grain number per spike as influenced by N, irrigation, and row spacing in five lines of barley.

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	12.8	13.6	26.2	23.9	25.9	20.5
72 kg N/ha	13.6	14.2	27.7	24.4	28.5	21.7
% increase	6	4	6	2	10	6 *
No irrigation	13.0	13.6	26.9	23.7	27.0	20.8
Irrigation	13.4	14.2	27.0	24.6	27.5	21.3
30 cm rows	14.1	14.4	30.8	27.1	30.8	23.4
15 cm rows	12.4	13.4	23.0	21.2	23.6	18.7
% increase	-12	-7	-25	-22	-23	-20 *

* The two means differ at 0.05 level

Table 13. 1,000 grain weight as influenced by N, irrigation, and row spacing in five lines of barley (g/1,000 grains).

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	57.2	57.5	35.4	35.0	26.4	42.3
72 kg N/ha	58.2	59.1	36.9	35.7	27.0	43.4
No irrigation	58.2	58.7	36.2	35.7	27.1	43.2
Irrigation	57.3	57.8	36.2	35.1	26.7	42.6
30 cm rows	58.1	58.5	35.8	35.4	26.2	42.8
15 cm rows	57.3	57.6	36.6	35.4	27.2	42.8

the competition for nutrients, water, and light. Table 1. p 25 does not show any nitrogen or irrigation by row spacing interaction for spike formation. Mutual shading at high tiller density, however, could limit the CO₂ assimilation by individual tillers resulting in fewer filled grains per spike. Row spacing did not effect 1,000 grain weight. No line by row spacing interaction for either spike number or grains per spike was observed.

Average grain yields for Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 3658, 3605, 3217, 3013, and 2398 kg per ha, respectively. The average grain yield of two row lines was 26% above that of six row lines. No significant difference existed between the grain yield of Compana and Erectoides Compana, or between Titan and Titan Belonee. Both Titan and Titan Belonee significantly out-yielded Titan Beebee.

The number of spikes per 3.6 dm² for Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 176, 171, 128, 127, and 127, respectively. So, spike number per unit area in two row barley was 36% over six row barley. This, at least in part, explains the yield superiority of two row lines over six row lines. The height isogenics within two or six row lines had almost identical spikes numbers per unit area.

The number of grains per spike for Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 13.2, 13.9, 26.9, 24.1, and 27.2, respectively. So, six row lines had 92% more grains per

spike than two row lines. This, of course, would be expected as there are three fertile spikelet at each rachis node of six row barley compared to only one fertile spikelet at each rachis node of two row barley. Differences in the grain number per spike between Compana and Erectoides Compana, and Titan and Titan Beebee were not significant. Both Titan and Titan Beebee had significantly more grains per spike than Titan Belonee.

The 1,000 grain weight of Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 59, 58, 36.1, 35.1 and 27 g, respectively. The 1,000 kernel weight of Titan Beebee was lower than for Titan and Titan Belonee. Two row barley had 77% heavier grains than six row barley. As already discussed, no difference in average grain weights of the lines used in this experiment were obtained from any of the cultural treatments. Yield differences from cultural treatments were caused by differences in the other two yield components. This would indicate strong genetic control of grain weight expression.

The three shorter height isogenics used in this experiment can be separated into the following three categories based on their grain yielding abilities - (i) Erectoides Compana - grain yield was similar to the normal line because no significant differences existed in the grain yield components.- (ii) Titan Belonee - grain yield was not significantly different from normal Titan even though a significant difference existed in one of the grain yield components (grain number per spike) and (iii) Titan Beebee - grain yield was significantly

reduced as compared to the normal line. A low 1,000 grain weight of Titan Beebee was responsible for this yield difference. So, like the vegetative characteristics of the plant, different height genes seem to have different effects on the grain yielding ability of the plant. It is very encouraging, however, to note that in every case the response of the shorter height isogenics to cultural treatments was similar to that of the normal lines.

Grain protein percentage was increased by 21% with the addition of nitrogen (Table 14). Martin and Mikkelsen (1960) also reported an appreciable increase in barley grain protein by high rates of N fertilization. Nitrogen is a major constituent of protein. Increase in the amount of available N may account for the increases in grain protein at high N rates. Lines differed in their per cent grain protein responses to N. The increases for Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 29, 27, 20, 23, and 8%, respectively.

Irrigation significantly decreased per cent grain protein. Bendelow (1958) and Sosulski et al. (1964) have reported that increases in grain yield of barley by irrigation are accompanied by decreases in the grain protein percentage. The decrease in the per cent grain protein is attributed to the dilution effect, because the total amount of grain protein per ha produced under irrigation was 441 kg compared to 398 kg in unirrigated plots. Because the increase in grain yield by

Table 14, Grain protein percentage as influenced by N, irrigation, and row spacing in five lines of barley.

Treatment	Lines					Mean
	Compana	Erectoides Compana	Titan	Titan Belonee	Titan Beebee	
0 kg N/ha	11.2	11.0	11.9	12.3	13.6	12.0
72 kg N/ha	14.4	14.0	14.4	15.0	14.6	14.5
% increase	28	27	21	22	7	21 *
No irrigation	13.3	12.7	13.6	14.1	14.8	13.7
Irrigation	12.4	12.3	12.7	13.2	13.4	12.8
% increase	-7	-3	-7	-6	-9	-7 *

* The two means differ at 0.05 level

irrigation (18%) was more than the increase in grain protein production (11%), the increase in grain protein was not sufficient to maintain the level of protein found in unirrigated grains. Row spacing treatments did not have any effect on per cent grain protein.

Grain protein percentages of Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 12.8, 12.5, 13.1, 13.6, and 14%, respectively. So, a given weight of grain of two row barley averaged 17% less protein than for six row lines. It is interesting to recall that two row barley yielded 26% more than six row barley. The total amounts of protein produced by two and six row barley were 459 kg and 392 Kg, respectively. So, two row barley produces 17% more grain protein per ha than six row barley. But since this protein had to be distributed over 26% more grain, the result was that the two row lines had a lower protein percentage than six row lines.

Grain test weights differed among lines but was not effected by cultural treatments (Table 1, p. 25). Test weights of Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 54.2, 52.4, 52.4, 51.2, and 5.2. pounds per bushel, respectively.

SUMMARY AND CONCLUSIONS

The objective of this investigation was to study the response of short-statured lines of barley and present commercial cultivars of barley under various cultural treatments. The responses of a two row commercial barley cultivar, Compana, and its height isogenic Erectoides Compana, and a six row commercial barley cultivar Titan, and its height isogenics Titan Belonee, and Titan Beebee to N fertilization, irrigation, and row spacing (population) treatments were compared.

The effects of cultural treatments on plant characteristics of barley lines differing in plant height:

1. N fertilization significantly increased the number of adventitious roots per plant. The narrower row spacing (resulting in higher plant populations) reduced the number of adventitious roots per plant. The maximum numbers of adventitious roots per plant in Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 12.2, 16.3, 16.2, 15.1, and 20.5.
2. N fertilization, irrigation, and narrow row spacing significantly increased the number of tillers per unit area at flowering. Average number of tillers per 1.8 dm² for Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 102, 101, 91, 90, and 76, respectively.
3. N fertilization significantly increased the leaf number per

plant. Narrower row spacing (and the resultant higher population) caused fewer leaves per plant. Maximum leaf number per plant in two row lines were 12.3 in comparison to 11.5 in six row lines.

4. N fertilization significantly increased the area per leaf. Increase in the area per leaf by N was more for the normal lines than for their height isogenics. Narrow row spacing significantly decreased the areas per leaf of the barley plant. Per leaf area of Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 9.3, 9.4, 14.7, 13.0, and 9.8 cm², respectively.
5. N fertilization significantly increased the maximum leaf area per plant. This increase in leaf area per plant was greater for the normal height lines. A significant decrease in leaf area per plant was observed with narrow row spacing. Average leaf area per plant for Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 120, 120, 191, 171, and 119 cm², respectively.
6. N fertilization significantly increased leaf dry weight per plant. Leaf dry weight per plant decreased with the narrow row spacing. Average leaf dry weights per plant of Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 438, 607, 592, and 453 mg, respectively.

7. N fertilization, irrigation, and narrow rows significantly increased plant dry weight per unit area at flowering. Plant dry weight per 1.8 dm^2 produced by Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee at the end of vegetative phase were 53, 51, 52, 57, and 38 g, respectively.
8. N fertilization and irrigation increased but narrow row spacing decreased maximum plant height. Average plant heights attained by Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 62, 49, 69, 54, and 47 cm, respectively.
9. N fertilization significantly increased the grain yield of barley by increasing the number of spikes per unit area and the number of grains per spike.
10. Irrigation significantly increased the grain yield of barley by increasing the number of spikes per unit area.
11. Row spacing (plant population) did not influence grain yield of barley. Yield components, however, were affected by row spacing. Narrower rows resulted in more spikes per unit area but fewer grains per spike.
12. Grain yields for Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee averaged over all treatments were 3658, 3605, 3217, 3013, and 2398 kg per ha, respectively. The number of spikes per 3.6 dm^2 for Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 176, 171, 128, 128,

and 127, respectively. The number of grains per spike for Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 13.2, 13.9, 26.9, 24.1, and 27.2, respectively. The 1,000 grain weight of Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 58, 58, 36, 35, and 27 g, respectively.

13. N fertilization increased and irrigation decreased per cent grain protein, but the total amount of protein produced per unit area was greater under irrigation. Per cent grain proteins of Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 12.8, 12.5, 13.1, 13.6, and 14%, respectively.
14. Cultural treatments did not effect grain test weight. Test weight of Compana, Erectoides Compana, Titan, Titan Belonee, and Titan Beebee were 54.2, 52.4, 52.4, 51.2, and 52.2 pounds per bushel, respectively.

From the above findings, it can be concluded that:

1. Reducing barley plant height changed other plant characteristics as well as height. The vegetative and yield characteristics that were affected differed among the three different short statured lines.
2. Vegetative responses to N fertilization, irrigation, and row spacing (different populations) of the short statured lines

were similar to, or greater than, their normal isogenic lines except for area per leaf and leaf area per plant.

3. Grain yield and grain quality of short statured lines were at least as responsive to N fertilization, irrigation, and row spacing (plant population) as the normal height lines.
4. Our results imply that a farmer should not expect the use of well adapted short statured barley lines to reduce his returns from his investment in N fertilization and irrigation.. In addition the risk of loss from lodging would be reduced by changing from the present tall commercial cultivars to the shorter lines.

APPENDIX

Table 15. Summary of climatic data by months for the calendar year 1970 and averages for the period 1958-70 at the Field Research Laboratory, west of Bozeman, Montana.

	Month												
	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Total or Mean
Precipitation (inches)													
1970	0.24	0.31	1.57	1.43	3.62	1.57	3.38	0.49	2.21	1.92	1.26	0.50	18.50
1958-70	0.52	0.36	0.96	1.32	2.35	2.80	1.42	1.25	1.20	1.31	1.07	0.46	15.02
Maximum temperature (F°)													
1970	33.4	44.8	39.5	45.6	65.2	76.2	82.2	85.5	64.8	54.0	43.7	33.5	55.7
1958-70	32.5	37.7	41.8	53.0	65.4	72.1	82.2	80.8	69.0	59.3	43.9	34.7	56.0
Minimum temperature (F°)													
1970	14.1	24.7	18.1	25.9	39.1	46.7	50.1	49.4	36.9	28.1	22.4	12.0	30.6
1958-70	9.6	15.5	18.0	28.1	36.7	43.7	47.8	46.6	38.5	30.9	20.3	12.9	29.1
$\bar{X}$ temperature (F°)													
1970	23.8	34.8	28.8	35.8	52.2	61.5	66.2	67.5	50.9	41.1	33.1	22.8	43.2
1958-70	21.1	26.6	29.9	40.6	51.1	57.9	65.0	63.7	53.7	45.1	32.1	23.8	42.6

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INTRODUCTION

Light is often the limiting environmental factor in crop competition. The effects of light on the growth of small grains has been studied extensively in green houses and growth chambers, but not in the field.

In the dry land area of the Northern Great Plains, crop production is often limited by availability of water. This has necessitated research towards development of practices that will maximize water-use efficiency of crops grown in this area. Researchers at the Montana State University have developed a number of lines of barley which have lighter green leaves than the standard lines of barley. It is hoped that lighter color of the leaves will increase the albedo, thus reducing the evaporation from the crop surface.

This experiment was designed to study the effect of light intensity and leaf color on the vegetative growth and water use of barley.

LITERATURE REVIEW

Net photosynthesis and its relation to plant characteristics

Chlorophyll is essential for photosynthesis. But the amount of chlorophyll has not been found to be closely related to the photosynthetic (P) rate in the field (Leopold, 1964). Gabrielsen (1948) concluded that the P rate was proportional to chlorophyll content only at low light levels and that the chlorophyll factor reached its optimum at a concentration of 4 to 5 mg chlorophyll dm^{-2} . Any increase in chlorophyll content beyond this limit did not effect photosynthesis.

Burnside and Bohning (1957) tested the photosynthetic capacity of seven sun species (species whose natural environment is full sun) that had developed under low and high light. They found that the P rates of all but one species were reduced when plants were grown under low light intensity.

McClendon (1962) showed a close correlation between the net photosynthesis of deciduous plant leaves and their density-thickness ratios (the ratio of leaf fresh weight to leaf area). Heichel and Musgrave (1969) also observed a positive correlation between leaf fresh weight to area ratio and net photosynthesis in corn; but they failed to observe any correlation between leaf dry weight to area ratio (specific leaf weight, SLW) and net photosynthesis. Wolf and Blaser (1968), however, reported a significant correlation between net photosynthesis and SLW in alfalfa. Pearce et al. (1969) showed

a close association between the photosynthetic capability of the leaves of 13 alfalfa varieties grown in pots in a greenhouse and their SLW. Regression analysis revealed that 64% of the variation in net photosynthesis was due to variation in SLW. Dornhoff and Shibbles (1970) reported a similar relationship for 20 soybean varieties. Murata (1961) observed that low SLW was associated with low P rates and low productivity.

Effect of light intensity on plant characteristics

Light reduction has been shown to reduce photosynthetic activity with a consequent reduction in top and root growth (Gist and Mott, 1957; McKee, 1962; Pritchett and Nelson, 1951; Thomas, 1955; and Watkins, 1940). The response of plant growth to changes in light intensity may be linear or curvilinear depending upon light intensity and other factors (Bula et al. 1959; McKee, 1962; and Thomas, 1955).

In discussing plant growth under reduced light intensities, a distinction must be made between dry matter accumulation and elongation growth (cell enlargement). The former has been found to increase with an increase in light intensity, while the latter is suppressed by high light intensities (Stoughton, 1955).

Pendleton and Weibel (1965) reported that winter wheat grain yield was reduced 37, 70, and 99% and straw production was reduced 26, 52, and 88%, when light was reduced 30, 60, and 90%, respectively. Burton and Knox (1959) observed that the yields of coastal bermuda-

grass under 29% of full sunlight were 23 to 65% of yields under full sunlight.

Vegetative response of bromegrass to variations in light intensity was studied by Watkins (1940). He reduced light intensity to 300-800 footcandles (Ft c.) in field experiments resulting in a decrease in dry weight of all plants. The bromegrass growing under the lower light intensities also showed a decrease in the number of shoots, rhizomes, fertile shoots, and dry weight of all plant parts, but increase in the height of the plant. The shade grown plants were more succulent and had narrower, less vigorous and less deep-green leaves than plants grown in full sunlight. Mitchell (1953) reported fewer tillers per plant for shade grown ryegrass.

Klages (1942) concluded that plants grown under reduced light intensities develop structures common to shade plants. The leaves are modified, becoming larger and thinner in the shady habitat. Cooper and Qualls (1967) observed thinner leaves in alfalfa and birdsfoot trefoil under shade.

Rhykerd et al. (1950) reported low leaf weight to stem weight ratios in birdsfoot trefoil at low light intensities and a corresponding increase with increasing light intensities. But in alfalfa and red clover, this relationship was reversed, i.e. leaf weight to stem weight ratio was high at low light intensities and it decreased with an increase in light intensity. Cooper (1966) found

no change in leaf weight ratio for alfalfa or birdsfoot trefoil when light was reduced to 80% of full sunlight.

McKee (1962) observed that leaf area per plant increased for red clover under moderate shading, while leaf area per plant of alfalfa and birdsfoot trefoil decreased. Bjorkman and Holmgren (1963) observed a decrease in SLW with shading in Solidago vergaurea L.; but Penfound's (1931) finding revealed an opposite effect of shading in Helianthus leaves.

The rate of accumulation of chlorophyll in plant leaves is approximately autocatalytic after reaching a steady chlorophyll level in the mature leaf (Blaauw-Jansen et al. 1950). At this time the chlorophyll is in a state of turnover, as shown by radioactive tracers (Godnev and Shlik, 1955). The maximum chlorophyll content reached in the leaf thus represents a balance between the rate of formation and destruction.

The effects of different intensities of light, obtained by shading, on the chlorophyll content of a number of broad leaved plants have been studied by Shirley (1929). A reduction in the intensity down to about 1/5 that of daylight increased the chlorophyll content on a fresh weight basis, although the effect was not consistent when measured on leaf area basis. An increase in the chlorophyll content of alfalfa and birdsfoot trefoil leaves with reduced light has been reported by Cooper and Qualls (1967). Friend

(1960) found an increase in the chlorophyll concentration in Marquis wheat leaves from 200 to 1,000 ft c. at all temperatures between 10 and 30°C. Between 1,000 and 2,500 ft c. there was a marked interaction with temperature. At temperatures below 20°C the chlorophyll content decreased with increasing light intensity, whereas at higher temperatures chlorophyll content increased with increasing light intensities.

Maclachlan et al (1963) compared the response of normal and virescent barley mutants to high light intensity. They showed that the photoconversion of protochlorophyll to chlorophyll is rapid and complete in both lines, but the protochlorophyll formation is slower in mutant than in the normal. They did not observe a higher rate of photodestruction of chlorophyll in the mutant than in the normal line.

Land et al. (1971) studied the effect of light intensity and temperature on a yellow green mutant of Festuca pratensis. The high light intensities (72 and 157 Wm⁻²) in both high (minimum temperature of 15°C) and low temperatures regimes (15°C day and 10°C night) and low light intensities (4 and 33 Wm⁻²) at high temperature resulted in chlorosis of the mutant. The expression of chlorosis was greatest under high light high temperature conditions. With low light and low temperature the mutant appeared green. The ratio of chlorophyll a to b was increased in the chlorotic material relative to that in the normal tissue. As the expression of chlorosis decreased the

chloroplast number per cell increased. In low-light low-temperature grown material the chloroplast number per cell did not differ significantly from those found in normal plant.

Dean (1966) observed that leaves of virescent tobacco mutants turned greener as the season progressed, until they were almost the same shade as the normal green varieties. In Florida, this color change takes place in late June, when light intensity and day lengths are at a maximum. So this color change could not result from reduction of light intensity and day length, as suggested by Weybrew and Mann (1958). In Dean's opinion, change of color probably was the result of changes within the plant with the physiological maturity resulting in the development of green pigmentation. He noted that whenever one leaf of a virescent mutant partially shaded another, the shaded portion developed a darker green color. In his opinion, this could result from a detrimental effect of light on chlorophyll formation or from the photodestruction of the pigment after it is formed.

Ballantine and Forde (1970) observed striking contrasts in chloroplast ultrastructure between leaves of soybean plant grown under high and low light intensities. There was an abundance of grana in the leaves which developed under low light intensity, while the leaves from light intensities similar to sun-light showed fewer grana. High light intensity also resulted in an increase in starch

content accompanied by a decrease in general organization and in amount of chloroplast lipid and chlorophyll.

Land et al. (1971) found that the primary lamellae were aggregated in the center of the chloroplasts of the yellow green mutant of Festuca pratensis at high-temperature high-light conditions. The lamellae of the mutant had few invaginations and any paired regions occurred on the periphery of the aggregated lamellae. The abnormal structures became less apparent as the chlorosis was less pronounced under reduced light or reduced temperature conditions. Under low-temperature low-light, which produced the greenest tissue, the chloroplast structure closely resembled that of the normal tissue.

Chlorophyll deficient mutants

Mutations altering chlorophyll content are found in many algae and higher plants (Kirk et al., 1967). The majority of mutant plants which are very low in chlorophyll content die or grow very slowly. However, several mutants have been described which at high light intensities photosynthesize at rates comparable to the normal green plants (Goodenough et al., 1969; Schmid and Gaffron, 1967).

Boardman and Highkin (1966) described a barley mutant lacking chlorophyll b which appeared normal morphologically, and required a high light intensity for saturation. On a chlorophyll basis, the mutant photosynthetic rates were greater at light saturation than the normal plant. At low light intensities (less than 15000 lux),

however, the mutant had lower photosynthetic rates than the normal plant.

Highkin et al. (1969) reported a pea mutant which had about one-half the normal chlorophyll content per mg leaf dry weight. While normal pea plants reached light saturation at about 60,000 lux, P was still increasing at 113,000 lux in the mutant type. The normal pea plant gave a saturation rate of CO₂ fixation which was 46% of the rate obtained with the mutant barley plants. Hill reaction activity at saturating intensities on isolated chloroplasts with NADP as oxidant paralleled the CO₂ uptake rates of intact leaves.

A different type of light green (LG) mutant in soybean which has only 20% as much chlorophyll as the normal dark green (DG) type, but exhibits similar rates of CO₂ fixation at normal light intensities has been described Wolf (1963). Unlike the mutants mentioned earlier the LG mutant was light saturated at the same intensity as the normal.

Keck et al. (1970) isolated chloroplasts from these DG and LG soybean leaves and compared various biochemical functions. Photosynthetic reaction rates from isolated LG plastids were 3 to 5 times those of DG (on a chlorophyll basis). On a chloroplast lamellar protein basis, the mutant plastid rates were 1.5 to 2.5 times the normal type rates. Witt (1968) has suggested that the rate limiting step in photosynthesis is the oxidation of plastoquinones (PQ). Keck et al. (1970) found a range of three to five times more photo-

chemically active PQ/chlorophyll in the LG as compared to DG. So, the faster electron transport and phosphorylation rates in the LG compared to the DG chloroplasts could be related to the faster turnover of PQ in the LG. Kleinhofs et al. (1971) concluded that RuDP carboxylase activity of many chlorophyll deficient barley mutants was much less than normal green lines.

Ferguson et al. (1972) measured P, light saturation, and SLW of barley lines isogenic for leaf color. P and SLW of normal field grown isogenes were significantly higher than those of pale green or golden isogenes. Pale barley leaf blades had a higher light saturation point than normal green leaf blades grown in the green house.

Solar Radiation reflectance from leaves

The extensive literature on the radiation economy of leaves has been reviewed by Geiger (1965). He concluded that absorption accounts for about 90% of the incident radiation in the ultraviolet, that it diminishes with increasing wavelength, reached a minimum of about 25% in the yellow green, and after another slight rise, falls off to another minimum of between 5 and 10% in the near infra-red. Still further into infra-red a value of 10% is again reached at 1,000 nm, after which the absorption climbs to 65% at 2,400 nm.

Albedo of leaves in the ultraviolet region (below 360 nm) is small (below 10%). In the visible spectrum (360-760 nm), albedo

of leaves varies between 8 to 20% with a peak at 510 nm. In the infra-red region (over 760 nm), maximum albedo (about 45%) is obtained at 800 nm. Albedo decreases as we further go into the infra-red region. Average albedo values at 1,000, 2,400, and 10,000 nm, as reported by Geiger are 42, 9, and 5, respectively.

Transmissivity of leaves is less than 10% in ultraviolet, and between 5 and 20% in visible spectrum. In the infra-red region, maximum transmissivity (about 60%) is obtained at 800 nm. With further increase in wavelength transmissivity decreases, approximate transmissivity at 1,000 and 2,400 nm being 47 and 25%, respectively.

Several workers have recently studied the influence of leaf pigmentation on the optical properties of leaves (Gates et al., 1965; Pearman, 1966; Thomas et al. 1966). Gates and co-workers noted that reflection probably was the primary method used by desert plants to dispose of their heat load. They observed significant differences in reflectivity among mesophytic species. Leaf color markedly influenced the reflectance of light from the leaf surface. Aase (1971) found a 6% higher reflectance for a pale barley mutant than for its normal type. He had expected larger variations in the reflectivity based on the visual color differences.

Tanner and Lemon (1962) pointed out that plant color influenced transpiration by affecting albedo and therefore, temperature of crop surface. Seginer (1969) calculated that, on the average, an

increase in albedo from 0.25 to 0.40 reduced sensible heat flux by 25.6%; evaporation, 29.7%; maximum surface temperature 30°C; and net radiation, 30%. Fritschen (1967) suggested that increasing the albedo will result in water conservation. Aase (1971), in eastern Montana, observed similar total water use by both normal and pale isogenic lines of barley in an unusually humid year. Water use efficiency of the darker lines were higher than those of the pale isogenic lines.

EXPERIMENTAL PROCEDURES

This study was conducted in 1971 on an Amsterdam Silt loam soil at the Field Research Laboratory, west of Bozeman, Montana. This Field Research Laboratory is situated at 45°41'N latitude and 111°09'E longitude and has a semi-arid temperate climate. A summary of the climatic data by months for the calendar year 1971 and averages for the period 1958-1970 at this location^{1/} are given in Appendix Table 8.

Experimental Materials

Liberty, a commercial cultivar with a normal green leaf color, and its two isogenic lines having lighter leaf color were used in the study.

Liberty - Liberty^{2/} is a selection from the cross (Lion x Manchuria x Chevron) x Titan, made at the South Dakota State College in 1945. It was released in 1957. It is a midseason, stiff straw barley used mainly for feed purposes. The plant is modified Manchurian type, with spring growth habit. The head is six row, medium length with kernels overlapping slightly at tip of head. The hull is adhering and slightly wrinkled. The aleurone is colorless. The kernel is medium sized, smooth, tapering gradually to both ends.

^{1/} Caprio, J. M., 1972. Weather data at Agricultural Experiment Stations in Montana. Mimeographed report.

^{2/} Barley Variety Dictionary, 1970. Malting Barley Improvement Association, Milwaukee, Wisconsin.

Pale Green Liberty - Pale green Liberty differs from Liberty in two ways. It has a lighter leaf color that is linked with a pale lemma and awn. Pale leaf color is due to the light green (lg) gene which causes the leaves to be lighter in color throughout the season.

Golden Liberty - Golden Liberty has a very light green leaf color early in the season. Since this leaf color is controlled by a yellow virescent (yv) gene, these plants become darker green with maturity.

Plastic Saran shade cloth^{1/} was used for the purpose of reducing sunlight intensity to 40, 24, and 8% of full sunlight. Gaskin (1965) has reported that plastic Saran shade cloth produces light that is comparable in quality to that produced by the shading of trees when the cloths transmits more than 25% of the available light intensity. When the shade cloth transmits less than 25%, the light quality differs from comparable shading under trees. This is apparently due to increased absorption of blue light by tree leaves which does not occur with shade cloth. Pallas et al. (1971) also reported that Saran shade cloths may not have the same effect on the transmission of infra red radiation as tree canopies. Cooper and Qualls (1967), however, have found Saran shade cloths satisfactory for shading experiments intended to study plant growth and morphology.

^{1/} Lumite Saran Shade Cloth, Chicopee Manufacturing Company, Cornelia, Ga. 30531.

Experimental Methods - A randomized block design with a factorial arrangement of treatments was used. Three color lines, Liberty, Pale Green Liberty, and Golden Liberty were grown at full sunlight, and 49, 24, and 8% of full sunlight. Each treatment was replicated three times. Each of the 36 plots was 6 meter long and 1.8 meter wide.

Planting was done on May 7, 1971. Seeding rates were approximately 107×10^4 seeds per hectare with the seeding rates being corrected for viability. Planting was done with a tractor mounted cone seeder adjusted to a 30 cm row width. Weeding was done manually.

Saran shade cloths were placed above the plots designated for reduced light intensities on June 9, 1971 (middle of tillering period). They were placed 91 cm above ground level. They were kept at that height by wiring the four ends of the Saran shade cloths to fence posts and by running wires both ways across the plots at the edges and in the center of the plots and clipping the shade cloth to the wire. Shade cloths remained over the plots till August 16, 1971, when the plants were in the late ripening period.

A neutron moisture meter was used for measuring soil water content in all replications of the 24, and 100% sunlight Liberty and Golden Liberty plots. The principle of operation of the neutron moisture meter and its limitations have been described in detail by Holmes and Jenkinson, (1959), Pawliw and Spinks (1957), and Van Bavel

(1961). The first moisture readings were taken at the end of the flowering period and subsequent readings were taken at weekly intervals.

Chlorophyll estimations were made at the end of tillering and milky ripe stages. Chlorophyll concentration was expressed both on a leaf area (mg chlorophyll per dm^2) and on a leaf weight basis (mg chlorophyll per gm leaf blade dry weight). In the first chlorophyll concentration estimation, all the treatments were included. While in the second only Pale Green Liberty and Golden Liberty at 24, 49, and 100% light intensities were included. Top fully expanded leaves were used at the first estimation date and flag leaves were used at the second estimation date. Chlorophyll was determined with a Zeiss spectrophotometer following the method of Mackinney (1941) as modified by Arnon (1949).

Samples of 10 plants were used for growth studies. Number of tillers per plant, number of green leaves per plant, dry weight of leaf blades and total dry weight per plant were recorded. Leaf weight to plant weight ratios were calculated. From these samples, two plants were selected at random to measure the area per leaf and leaf area per plant. Area per leaf was obtained by the formula length x width x 0.60. Specific leaf weight (mg/cm^2) was also calculated. Four vegetative samples were taken, first at the end of tillering, second in the middle of the stem extension, third at the end of stem extension,

and last at the heading to early flowering stage.

Harvest was on August 30, 1971. 100 plants were uprooted from each plot. The roots were cut off and the plants were separated into spike and non-spike portions. Grains were not threshed, because the grains at the lower light intensities were severely shrivelled and thus difficult to thresh. Spike to straw ratios were calculated.

RESULTS AND DISCUSSION

Effect of leaf color and light intensity on plant growth and development.

The effects of light intensity and barley leaf color on plant characteristics will be shown primarily by figures in the text. Tables of numerical values will be given in the Appendix.

The number of tillers per plant for the three leaf color isogenic barley lines grown at different light intensities is plotted in Figure 1. Decreased light intensities reduced tiller numbers per plant. Plants growing at 100, 49, 24, and 8% sunlight had an average of 3.9, 3.3, 2.7, and 2.7 tillers per plant, respectively. Shading was provided when the plants were in the early tillering period. Reductions in light intensities have been shown to reduce the photosynthetic activity of the plant (Watkins, 1940; Gist and Mott, 1957). Reductions in the rate of photosynthesis may reduce carbohydrates in shaded plants. Hence, there may not be enough carbohydrate available for the tiller initials to develop. Mitchell (1953) has reported a decrease in the number of tillers in rye grass with a decrease in light intensity. No significant difference among lines in the tiller number per plant or in the response to different light intensities for tiller number was obtained in this study.

Numbers of green leaves during different growth stages in the three color lines and at different light intensities are plotted in Figure 2 and Figure 3. In the first sample taken at the end of tillering period, light intensity did not influence the number of

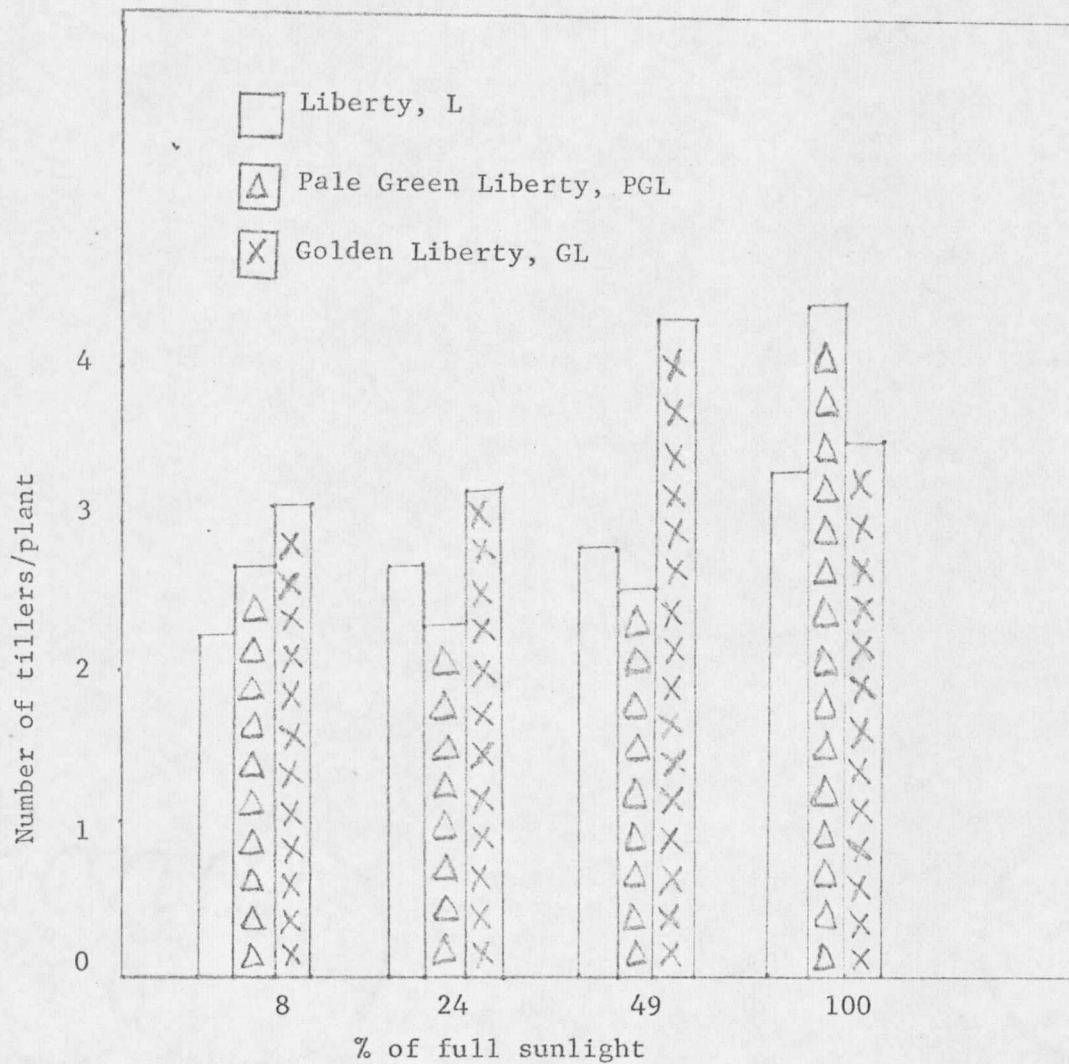


Fig 1. Number of tillers/plant for three leaf color isogenic barley lines grown at different light intensities.

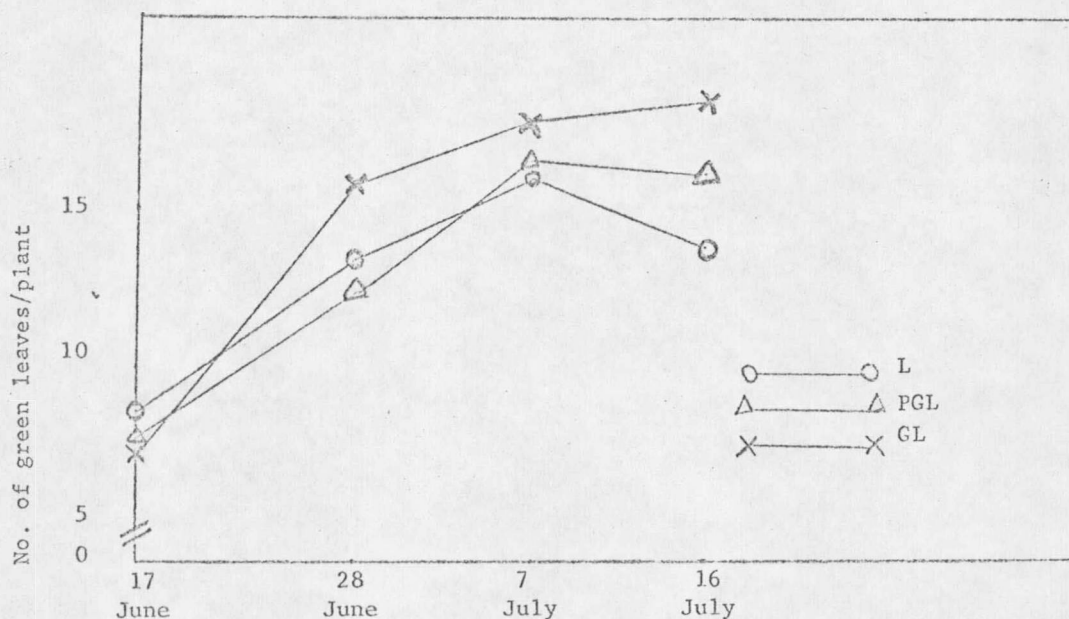


Fig 2. Number of green leaves/plant for three leaf color isogenic barley lines at different dates (Each value is the average of 4 light intensities).

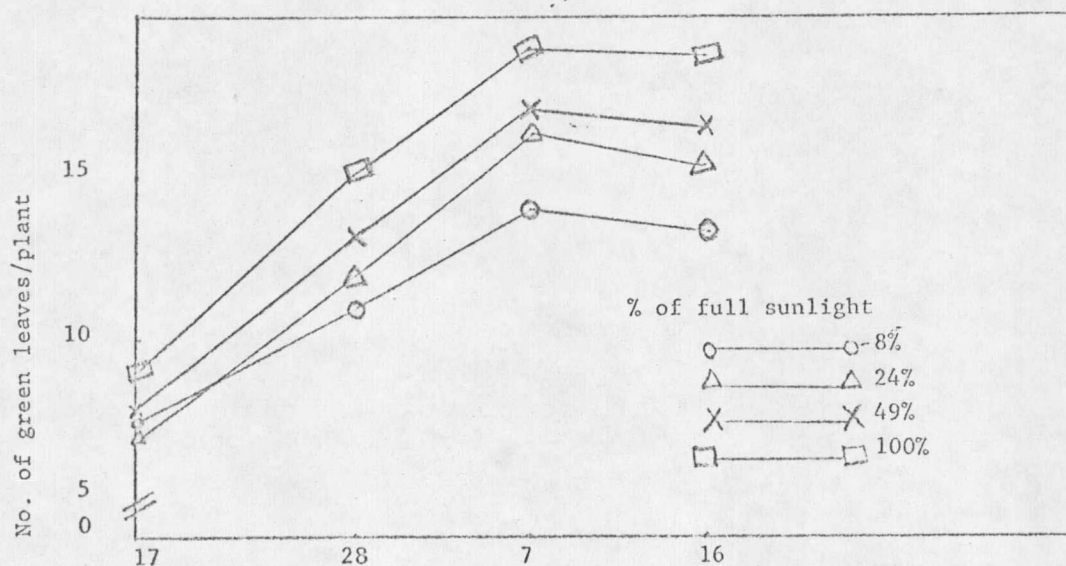


Fig 3. Number of green leaves/barley plant at different light intensities on different dates (Each value is the average of 3 lines).

leaves per plant. No significant difference existed among the three color lines for the number of leaves per plant. In the second sample, taken at approximately the middle of the stem extension period, a significant reduction in leaf numbers due to lower light intensity was observed. By this time Golden Liberty had developed significantly more leaves per plant (15.7) than Pale Green Liberty (12.4) and Liberty (13.4).

The third sample was taken at the end of the stem extension period. The effect of leaf color on number of leaves per plant was not significant. Leaf numbers per plant at 100, 49, 24, and 8% of sunlight were 19, 17, 3, 16.4, and 14.1, respectively (Figure 3). The last sample was taken at a date when the plants from different treatments varied from late heading to early flowering. Number of leaves for Golden Liberty, Pale Green, and Liberty were 18.3, 16.1, and 13.8, respectively. Number of leaves per plant at full sunlight averaged 18.8. At 49, 24, and 8% of full sunlight there were 16.6, 15.5, and 13.5 leaves per plant.

Maximum area per leaf (heading to early flowering) of the three color lines at the different light intensities are plotted in the Figure 4. Significant differences existed in the maximum area per leaf of the three color lines. Area per leaf of Pale Green Liberty was 19.4 cm^2 , followed by 17.3 and 15.3 cm^2 for Golden Liberty and Liberty, respectively. Reduction in light intensity generally

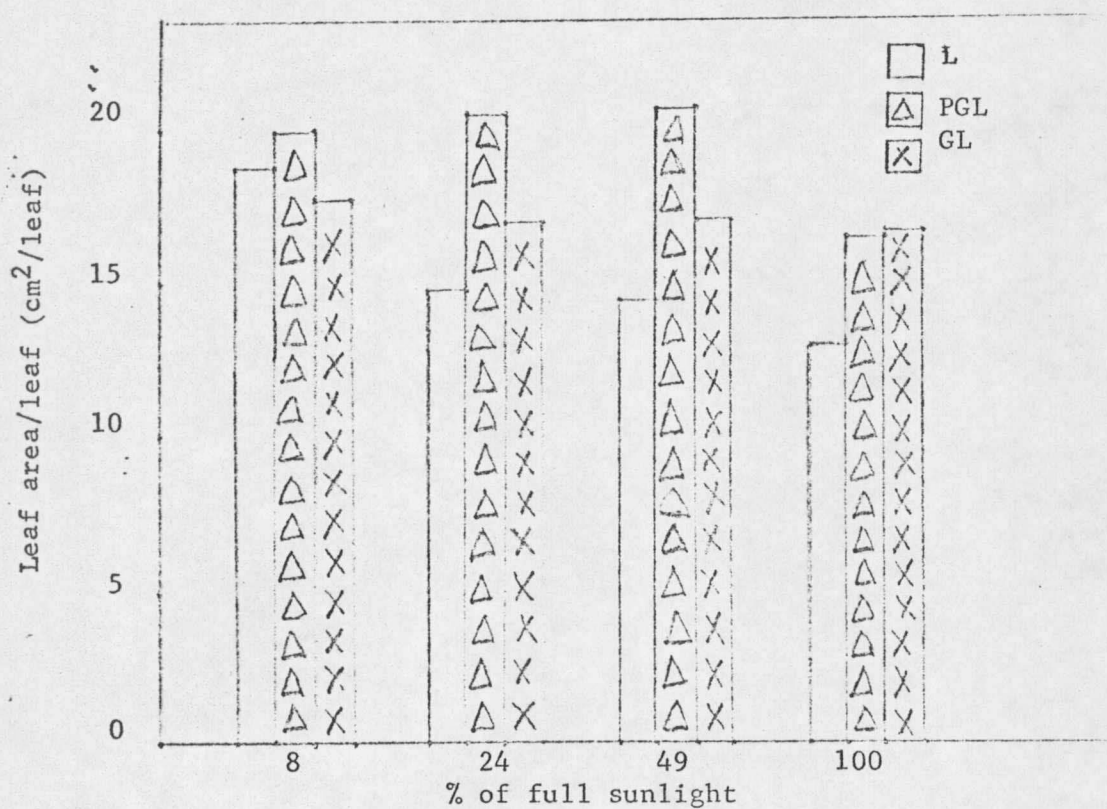


Fig 4. Maximum leaf area/leaf for three leaf color isogenic barley lines grown at different light intensities (cm²/leaf)

caused an increase in area per leaf. Area per leaf at 8, 24, 49, and 100% of sunlight averaged 18.8, 17.5, 17.6, and 15.4, respectively.

Patterns of leaf area development are shown a) in Figure 5 for each line grown in full sunlight, b) in Figure 6 for each line averaged across 4 light intensities, and c) in Figure 7 for each light intensity averaged across 3 lines. Light intensity had no statistically significant effect on leaf area per plant. This could be because the greater number of leaves at higher light intensities was compensated for by larger leaves at lower light intensities. In the first two samplings, Golden Liberty had significantly less leaf area than either Liberty or Pale Green Liberty. This could be because Golden Liberty is usually 4 to 7 days behind Pale Green Liberty and Liberty in maturity. In the third sampling (end of stem extension), leaf areas per plant of the three lines were not significantly different.

The maximum leaf areas per plant attained by Golden Liberty, Pale Green Liberty, and Liberty were 353, 319, and 217 cm²/plant (Figure 8). These greater leaf areas per plant for Golden Liberty and Pale Green Liberty than for Liberty were due to both more leaves per plant (Figure 2 and greater area per leaf (Figure 4).

Leaf dry weights per plant during different growth stages are plotted in Figure 9 for each color lines and in Figure 10 for each light intensity. From the second sampling on, a reduction in light intensity resulted in decreases in leaf dry weight (Figure 10). As has been

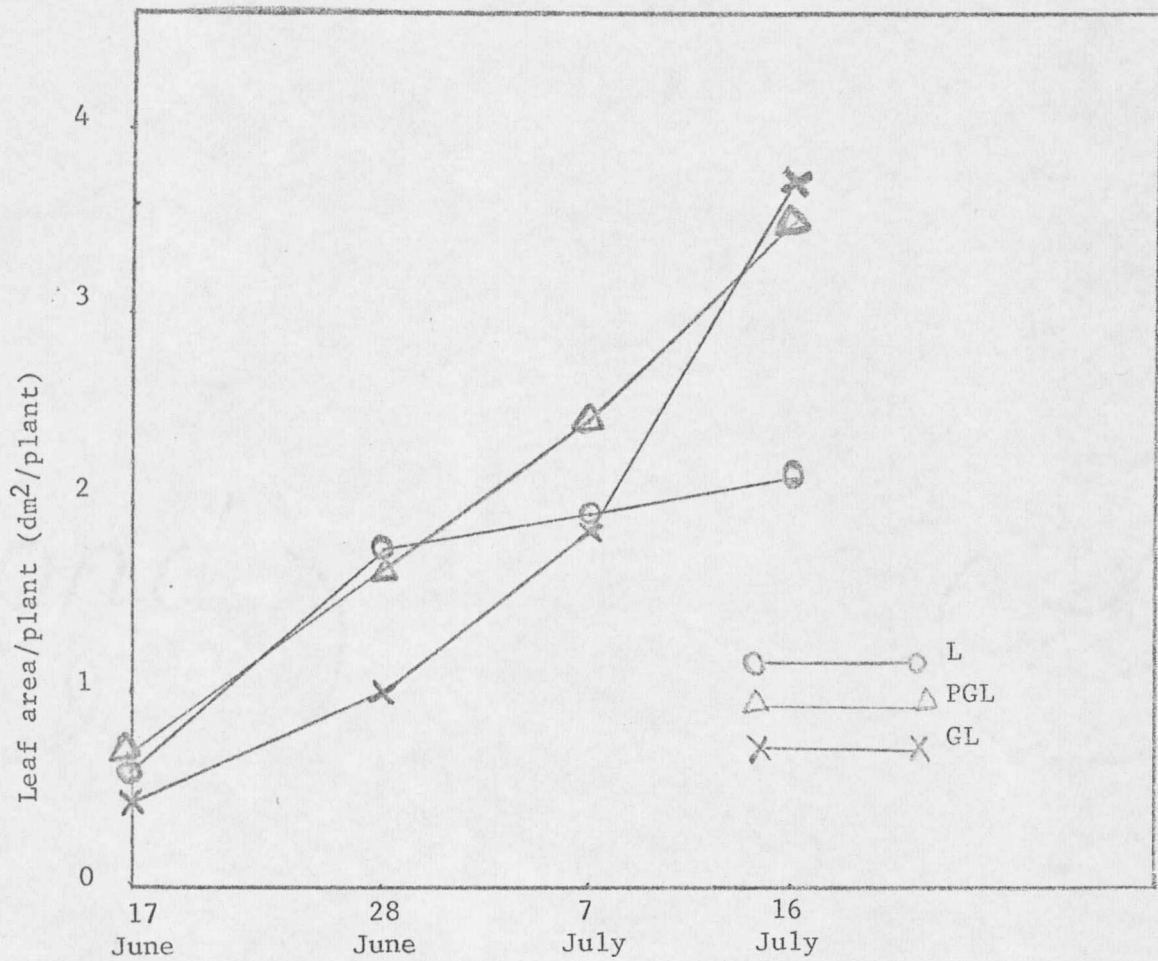


Fig 5. Patterns of leaf area development of three leaf color isogenic barley lines grown in full sunlight (dm^2/plant).

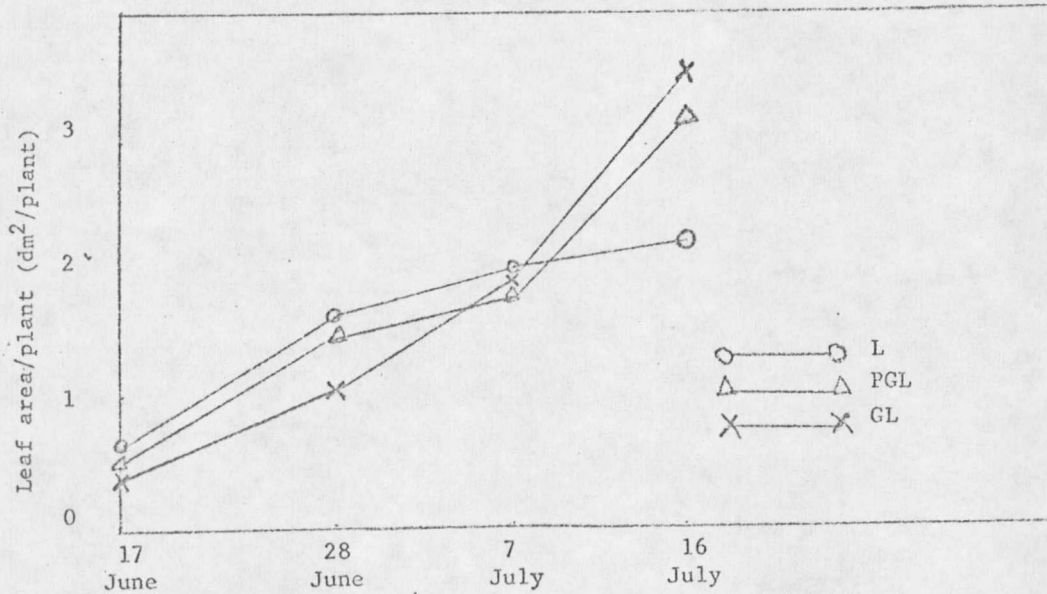


Fig 6. Patterns of leaf area development of three leaf color isogenic barley lines (dm²/plant) (Each value is average of 4 light intensities).

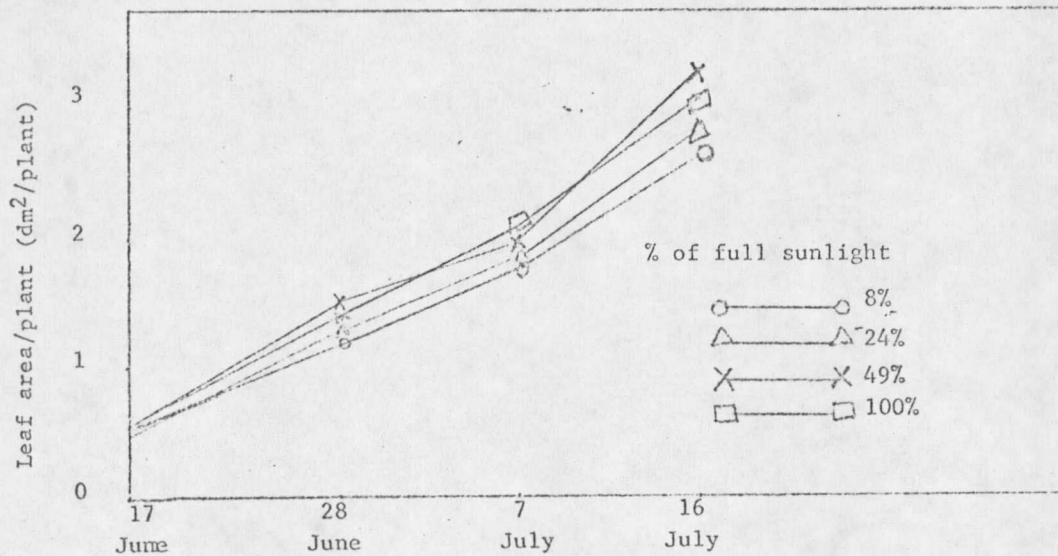


Fig 7. Patterns of leaf area development of barley plant at different light intensities (dm²/plant) (Each value is the average of 3 lines).

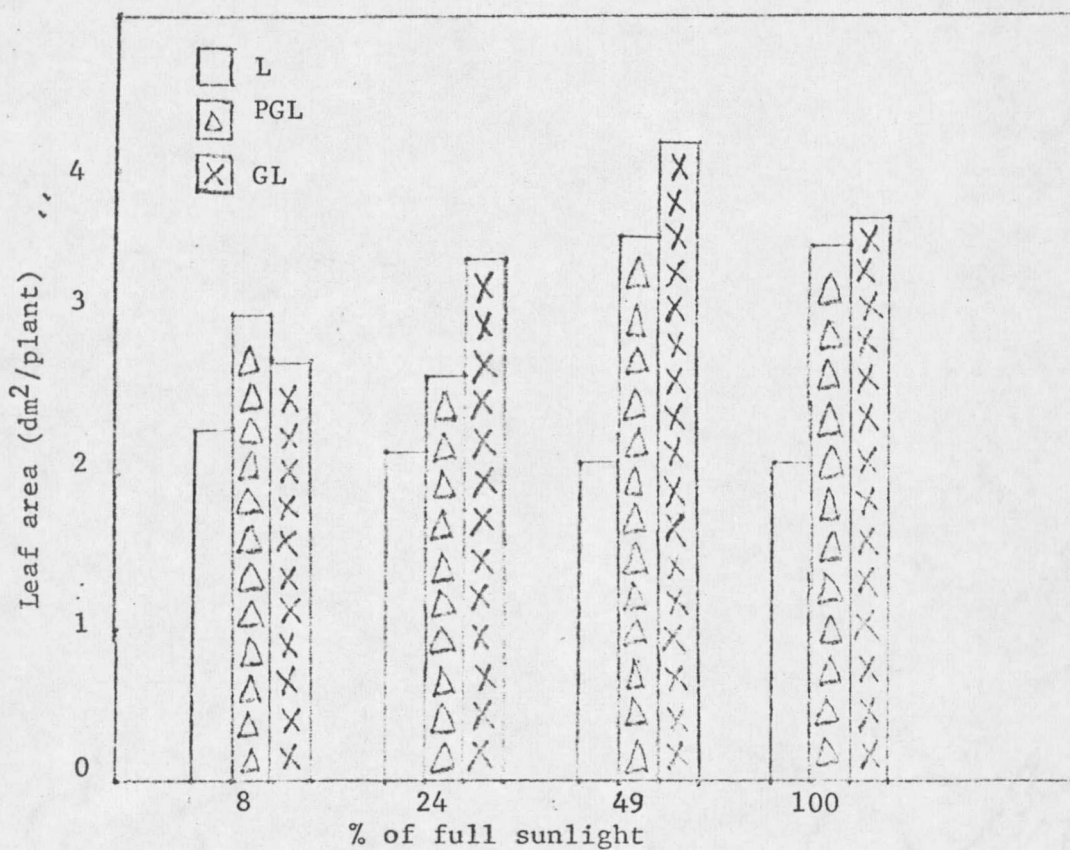


Fig 8. Maximum leaf area/plant for three leaf color isogenic barley lines grown at different light intensities (dm²/plant).

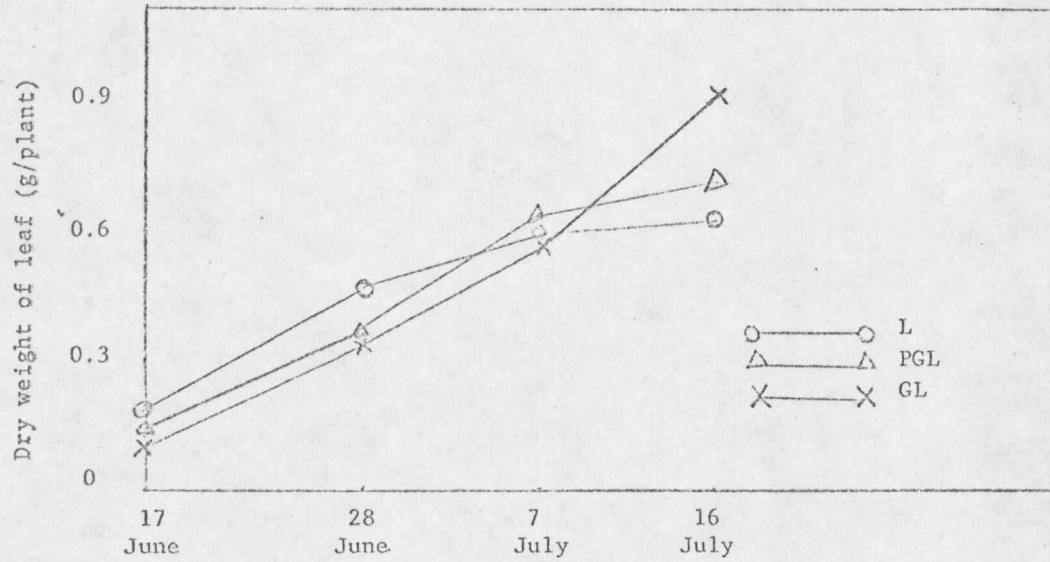


Fig 9. Leaf dry weight/plant for three leaf color isogenic barley lines at different dates (g/plant) (Each value is the average of 4 light intensities).

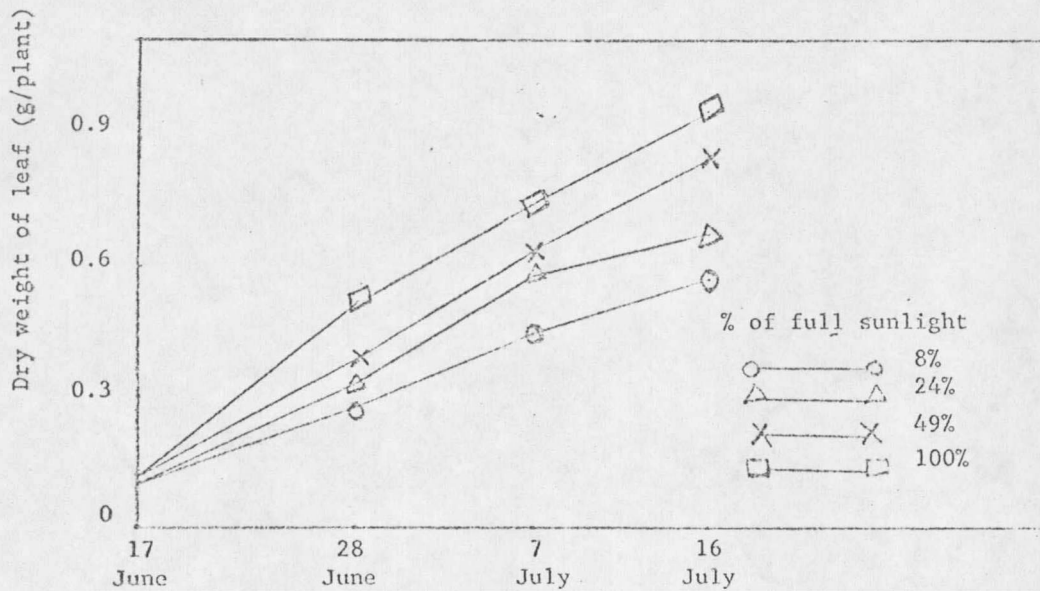


Fig 10. Leaf dry weight/plant at different light intensities on different dates (g/plant) (Each value is the average of 3 lines).

noted previously (Figure 7), light intensity had little effect on leaf area per plant. So, reduction in the weight of leaves of similar leaf area would result in thinner leaves in shade (lower specific leaf weights, SLW). Significant variation existed in leaf dry weight per plant among the three color lines at all except the third sampling date. At the first two sampling dates, Liberty had greater leaf weight per plant than that of its isogenic lines. By the third sampling, date Pale Green Liberty and Golden Liberty had caught up with Liberty, and no significant difference in leaf weight per plant among lines was evident. Leaf dry weight per plant in Liberty had reached a plateau by the third sampling date, while Pale Green Liberty and Golden Liberty were still increasing in leaf weight. Maximum leaf dry weight per plant for Golden Liberty, Pale Green Liberty and Liberty were 913, 744, and 637 mg, respectively (Figure 11). A comparison with Figure 9 shows that development of leaf area and leaf dry weight are nearly parallel.

In view of the numerous reports in the literature (Dornhoff and Shibles, 1970; Murata, 1961; Pearce et al. 1969; and Wolf and Blaser, 1968) of the close association between SLW and net photosynthesis, SLW at different light intensities for the color lines were calculated. Results are plotted in Figures 12 and 13. There was a gradual

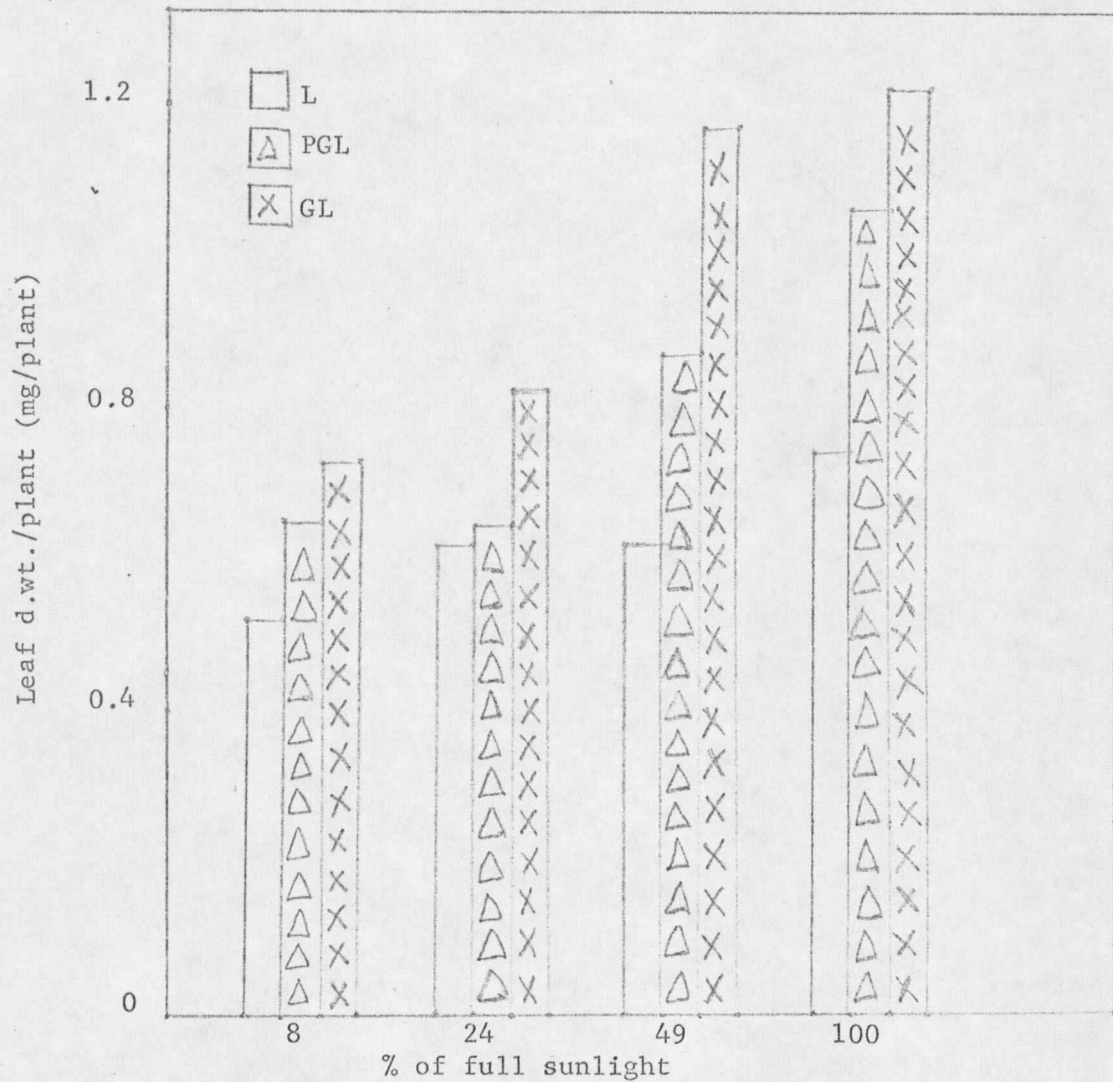


Fig 11. Maximum leaf dry weight/plant for three leaf color isogenic barley lines grown at different light intensities (g/plant).

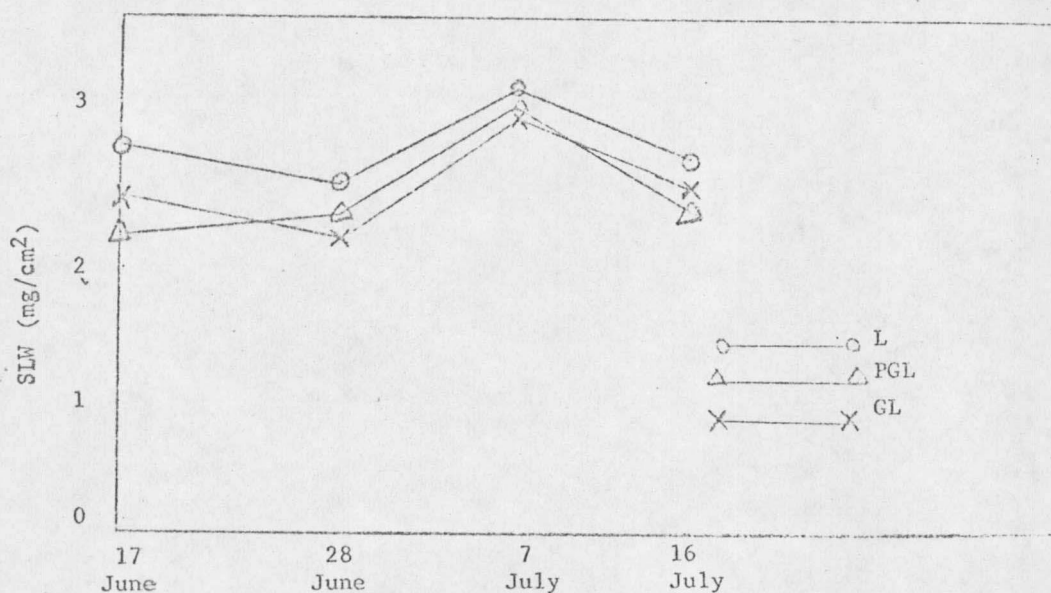


Fig 12. Specific leaf weight, SLW, for three leaf color isogenic barley lines at different dates (mg/cm²) (Each value is the average 4 light intensities).

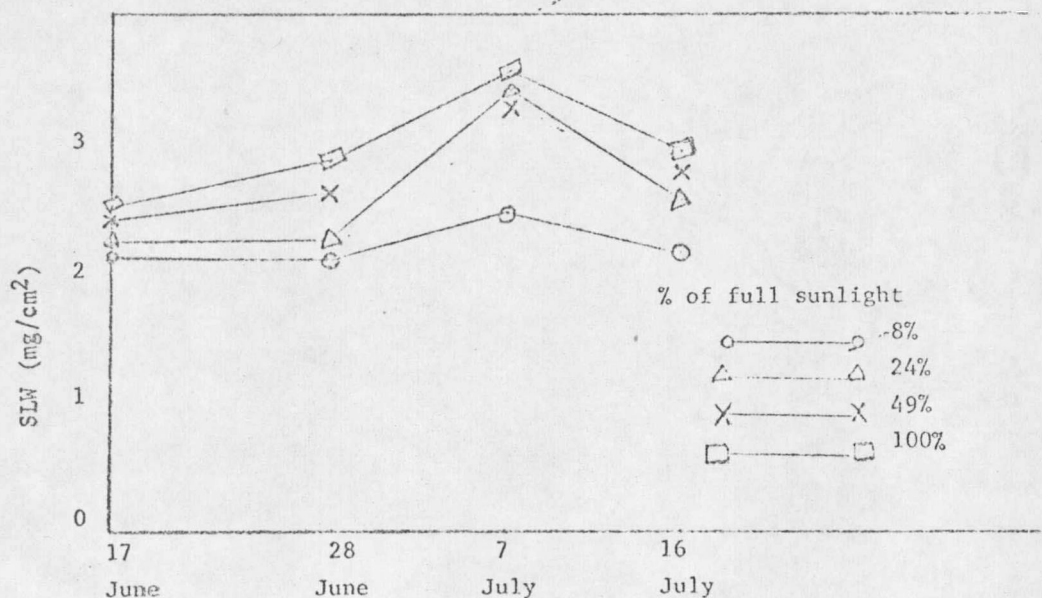


Fig 13. Specific leaf weight, SLW, of barley lines at different light intensities on different dates (Each value is the average of 3 lines).

increase in SLW with time for all three color lines at all light intensities up to the stem extension period after which specific leaf weights declined for all treatments Figure 12 and 13. Reduced light intensities resulted in significant reductions in SLW's. In legumes, Cooper and Qualls (1967) observed decreased SLW with reduction in light intensity. Maximum SLW attained by Liberty, Pale Green Liberty, and Golden Liberty averaged 3.26, 3.15, 3.15 mg/cm², respectively (Figure 12).

Plant dry weights per plant during different growth stages are plotted in Figure 14 for three color lines and in Figure 15 for different light intensities. Liberty had significantly greater plant dry weight at the first three sampling dates than Pale Green Liberty and Golden Liberty. Greater dry weight of Liberty than Golden Liberty at the first two sampling may be due to the fact that Liberty had greater leaf area than Golden Liberty during early growth periods which enabled it to assimilate more carbon dioxide. Liberty also had significantly greater SLW than Golden Liberty at the first two sampling dates indicating that Liberty had greater photosynthetic efficiency than Golden Liberty. No significant differences existed between Liberty and Pale Green Liberty in their leaf area per plant during the first two sampling dates. But Liberty had significantly greater SLW than Pale Green Liberty at the first two sampling dates. This indicates that Liberty was photo-

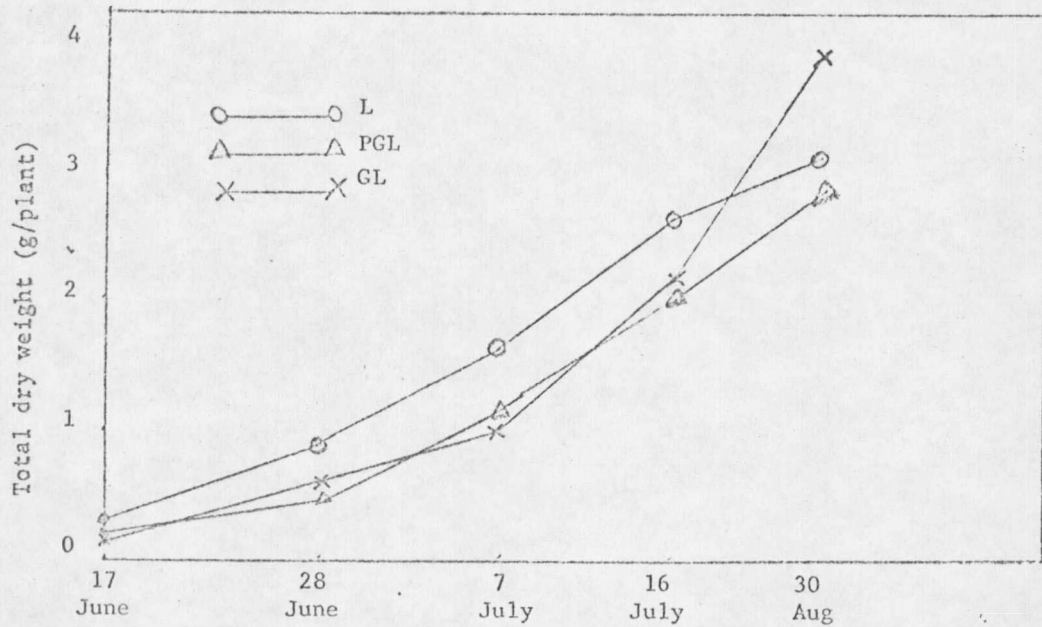


Fig 14. Plant dry weight for three leaf color isogenic barley lines at different dates (g/plant) (Each value is the average of 4 light intensities).

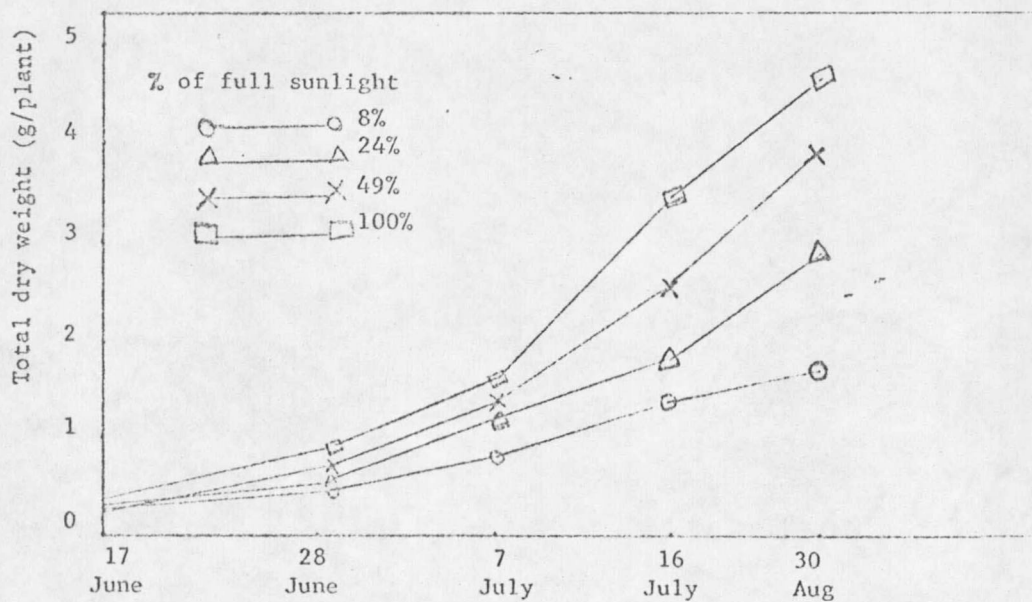


Fig 15. Plant dry weight at different light intensities on different dates (Each value is the average of 3 barley lines).

synthesizing more efficiently than Pale Green Liberty during the first two sampling periods resulting in greater plant dry weight for Liberty than Pale Green Liberty.

At the third sampling date, no significant difference existed among the color lines in leaf area per plant. There were significant differences in the SLW among the three color lines at the 10% level. A possibility exists that, due to relatively greater experimental error in SLW determination on this date, a significant difference in SLW was not obtained at 5% level. So, greater plant dry weight of Liberty than Pale Green Liberty and Golden Liberty might have been due to its greater photosynthetic efficiency per unit leaf area.

At the fourth sampling, no significant difference in the plant dry weight existed among the three color lines (Figure 14). At this time both Pale Green Liberty and Golden Liberty had significantly greater leaf area per plant than Liberty. But Liberty still had greater SLW than the other two lines. Probably greater photosynthetic efficiency of Liberty compensated for the greater leaf area of Pale Green Liberty and Golden Liberty, resulting in similar plant dry weight at the fourth sampling date for all three lines.

At harvest, dry weight per plant of Golden Liberty (3.9 g/plant) exceeded those of Liberty, and Pale Green Liberty (3.1 and

2.9 g/plant) (Figure 14). Average dry weight per plant at 100, 49, 24, and 8% of full sunlight were 4.7, 3.8, 2.9, and 1.7 g, respectively (Figure 15).

Table 1 gives the ratio of leaf dry weight per plant to plant dry weight (leaf weight ratio, LWR) at different times during the growth of the plant. No recognizable pattern of changes in LWR in response to different light intensities was obtained for the first two sampling dates. At the third sampling, reduced light intensity increased LWR. Reduced light intensity also increased LWR at the fourth sampling, taken at the heading to early flowering period. LWR values for 100, 49, 24, and 8% of full sunlight at the fourth sampling date were 0.28, 0.33, 0.38, and 0.43, respectively. At higher light intensities more photosynthate is produced and a greater proportion of it is translocated out of the leaf. At lower light intensities, less photosynthate is produced and a greater proportion of it is retained in the leaf. Our results in barley do not agree with the results of Blackman (1956), and Cooper (1966) for grasses. They observed no appreciable changes in LWR as a result of shading.

Cooper et al. (1967) noted that since the LWR of a legume is rather constant at different light intensities, reduction in the amount of dry matter available to the leaves is in proportion to the reduction in the dry matter productions at lower light inten-

Table 1. Leaf weight ratio (LWR) of three barley leaf color isogenic lines at different light intensities on different sampling dates (g leaf weight/g plant weight).

% of full sunlight						% of full sunlight					
	8	24	49	100	$\bar{X}$		8	24	49	100	$\bar{X}$
June 17, 1971 (End of tillering)						June 28, 1971 (Middle of stem extension)					
L	0.69	0.75	0.65	0.60	0.67	L	0.57	0.55	0.50	0.53	0.54
PGL	0.71	0.71	0.70	0.62	0.68	PGL	0.67	0.67	0.67	0.70	0.68
GL	0.71	0.72	0.71	0.72	0.70	GL	0.70	0.67	0.62	0.67	0.66
$\bar{X}$	0.70	0.73	0.69	0.65	0.69	$\bar{X}$	0.65	0.63	0.60	0.63	0.63
July 7, 1971 (End of stem extension)						July 16, 1971 (Heading to early flowering)					
L	0.47	0.40	0.36	0.33	0.39	L	0.30	0.28	0.23	0.20	0.25
PGL	0.65	0.60	0.57	0.54	0.59	PGL	0.46	0.41	0.36	0.27	0.37
GL	0.61	0.55	0.56	0.68	0.60	GL	0.54	0.46	0.40	0.38	0.44
$\bar{X}$	0.58	0.52	0.50	0.52	0.52	$\bar{X}$	0.43	0.38	0.33	0.28	0.35
L Liberty PGL Pale Green Liberty GL Golden Liberty											

sities. They suggested that reduction in SLW with reduced light intensity is an adaptive mechanism, whereby for each unit of dry matter partitioned into leaf, a greater amount of leaf area is exposed to available light. We find that reduction in light intensity also reduced specific leaf weights of barley. We also observed that reduced light intensity reduced the amount of dry matter produced, but a greater proportion of the dry matter is retained in the leaves of barley. Reduction in SLW in barley with reduced light intensities shows not only the reduction of photosynthates in the plant, but also a shift in partitioning of this photosynthate.

It is rather interesting to note that Liberty had a smaller LWR than the other two lines. We also know that Liberty had a significantly greater SLW than Pale Green Liberty and Golden Liberty. Thus, increase in SLW is accompanied by an increase in plant weight.

LWR decreased as the growing season of barley progressed. LWR at the end of tillering averaged 0.69. It decreased to 0.63 at the middle of stem extension and 0.53 at the end of stem extension. It further decreased to 0.35 at the end of heading to early flowering period.

Spike weights per plant at 100, 49, 24, and 8% of full sunlight averaged 2.2, 1.9, 1.2, and 0.6 g, respectively (Figure 16). This amounted to a decrease of 16, 83, and 267% with each successive decrease in light intensity. Straw weight in this experiment includes

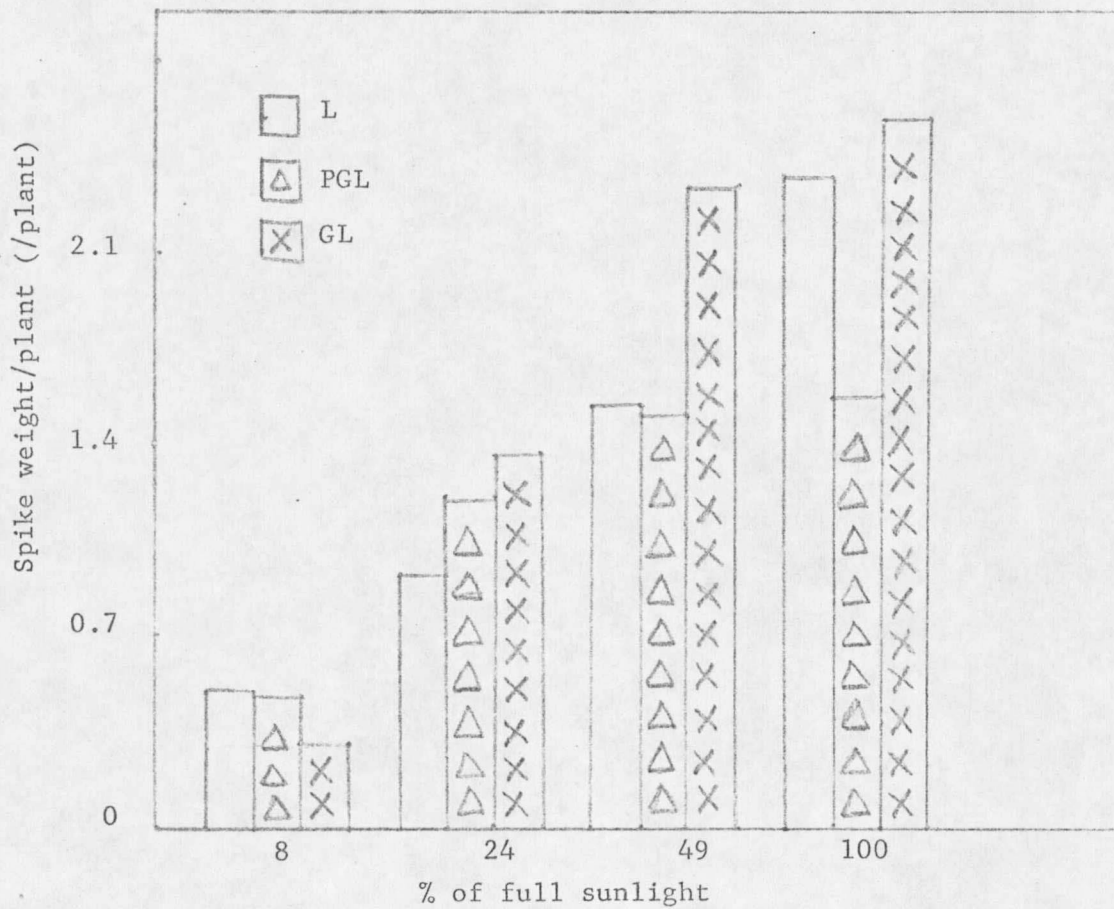


Fig 16. Spike weight/plant for three leaf color isogenic barley lines grown at different light intensities (g/plant at harvest).

only the above ground non-spike portions of the plant. Straw weights per plant at 100, 49, 24, and 8% of full sunlight were 2.6, 2.2, 1.7, and 1.3 g, respectively. This amounted to a decrease of 18, 53, and 100% with each successive decrease in light intensity. No marked difference in the spike to straw ration was observed between the two higher-light levels. But in plants grown at 8 or 24% of sunlight intensity, a considerable decrease in the spike-straw ratio was noted indicating a decrease in the spike weight in relation to the weight of the straw. This would imply that decreased light intensities, although decreasing both straw and spike weights, affect spike weight more than straw weight.

The grain filling stage in barley is of short duration. It has been established by several workers (Archbold, 1942, 1945; Asana and Mani, 1949; Buttrose and May, 1959; and Thorne, 1963, 1965) that the photosynthate used in grain filling in barley is mostly synthesized by the flag leaf and the spike. So, in the short time which the flag leaf and spike have to synthesize photosynthate for grain filling any limitation on the availability of light would be expected to be reflected in reduced spike weight. Pendleton and Weibel (1965) have reported a reduction in wheat grain yield of 37, 70, and 99% and straw production of 26, 52, and 88%, respectively, when light was reduced 30, 60, and 90%.

No significant difference existed in the spike yields among

the three lines but a significant line by light intensity interaction for spike weight was noted. Increase in spike weight from increased light intensity in Pale Green Liberty was less than in other color lines. Pale Green Liberty has white colored lemma indicating chlorophyll deficiency in the lemma of Pale Green Liberty. Insufficient chlorophyll in the spike prevents Pale Green Liberty from utilizing the increased light energy for grain production as well as the other two lines. Thorne (1965) has reported that half of the photosynthate for the grain is contributed from the spike in barley. The impact of chlorophyll deficiency in the spike on spike weight is important even though leaves can partially compensate for lack of chlorophyll.

Effect of leaf color and light intensity on the chlorophyll content of the leaf

Chlorophyll estimations made at the tillering period showed a higher concentration of chlorophyll in the leaves of plants grown at 24% sunlight intensity than for plants grown under other light intensities on both a leaf area, and a leaf weight basis (Figure 17 and Figure 18). Shirley (1929) has reported increase in chlorophyll content on a fresh weight basis of a number of broad leaf plants with reduction in light intensity down to about one-fifth of full sunlight. Cooper and Qualls (1967) have also reported an increase in the chlorophyll content of alfalfa and birdsfoot trefoil under partial shade conditions.

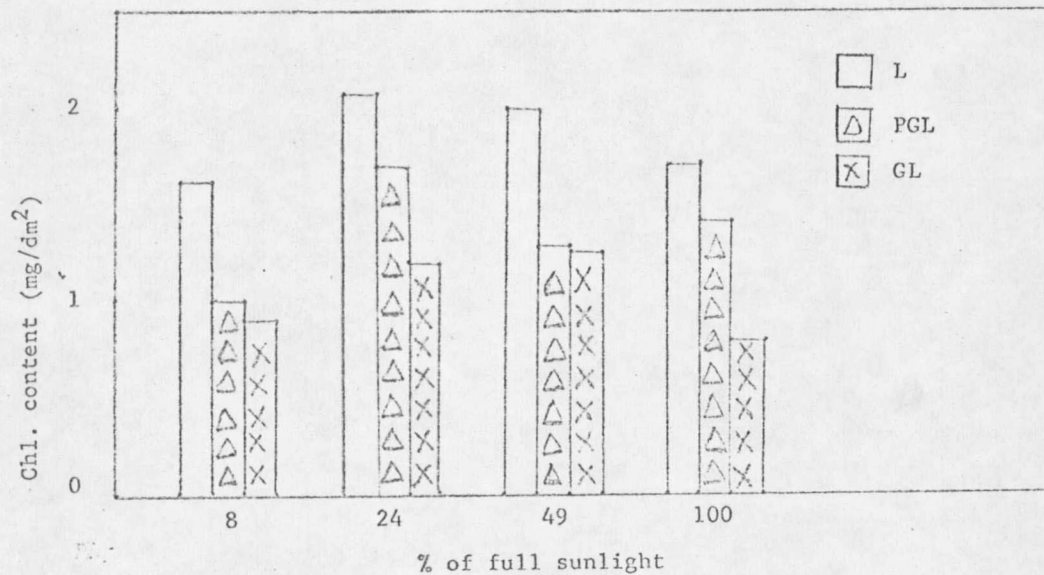


Fig 17. Chlorophyll content in the top leaf of three leaf color isogenic barley lines at different light intensities (mg/dm²) (End of tillering).

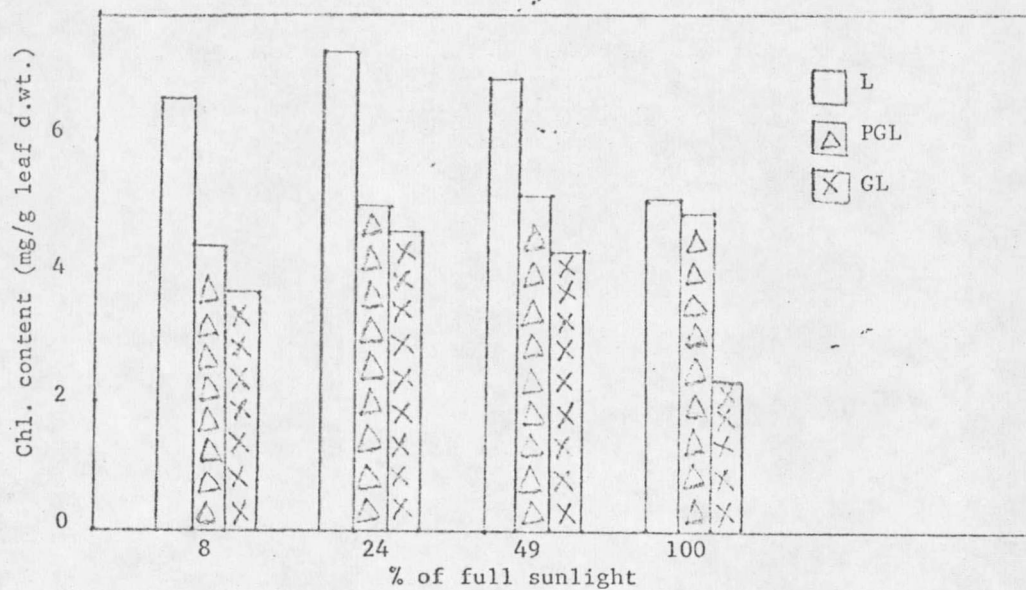


Fig 18 Chlorophyll content in the top leaf of three leaf color isogenic barley lines at different light intensities (mg/g leaf dry weight) (End of tillering).

The normal green color line, Liberty, had more chlorophyll at all levels of light intensity than Pale Green Liberty or Golden Liberty. The chlorophyll content of Pale Green Liberty exceeded that of Golden Liberty at all light levels. All three color isogenics, however, had maximum chlorophyll content at 24% light intensity and showed a decline in chlorophyll content with either an increase or a decrease in light intensity from this level.

Chlorophyll contents of the flag leaves of Pale Green Liberty and Golden Liberty at 24, 49, and 100% sunlight intensities was also estimated during the milk ripe stage (Figure 19 and Figure 20). The flag leaves of Golden Liberty had less chlorophyll (both on a leaf area and a leaf weight basis) than the Pale Green Liberty. At the early growing periods, the yellowish color of the Golden Liberty leaves makes it easily distinguishable from its isogenics. But, as the growing season progresses, Golden Liberty leaves start looking less and less yellowish. At the milk ripe stage, by visual observations, it is difficult to note any difference in leaf color between the upper leaves of Golden Liberty and Pale Green Liberty. But chlorophyll estimations revealed the continued difference in the chlorophyll content between Pale Green Liberty and Golden Liberty. A more frequent leaf pigment estimation (both chlorophyll and carotenoid) during the growing period will probably be required to understand the physiology of pigment formation in pale color lines in relation to greener color lines.

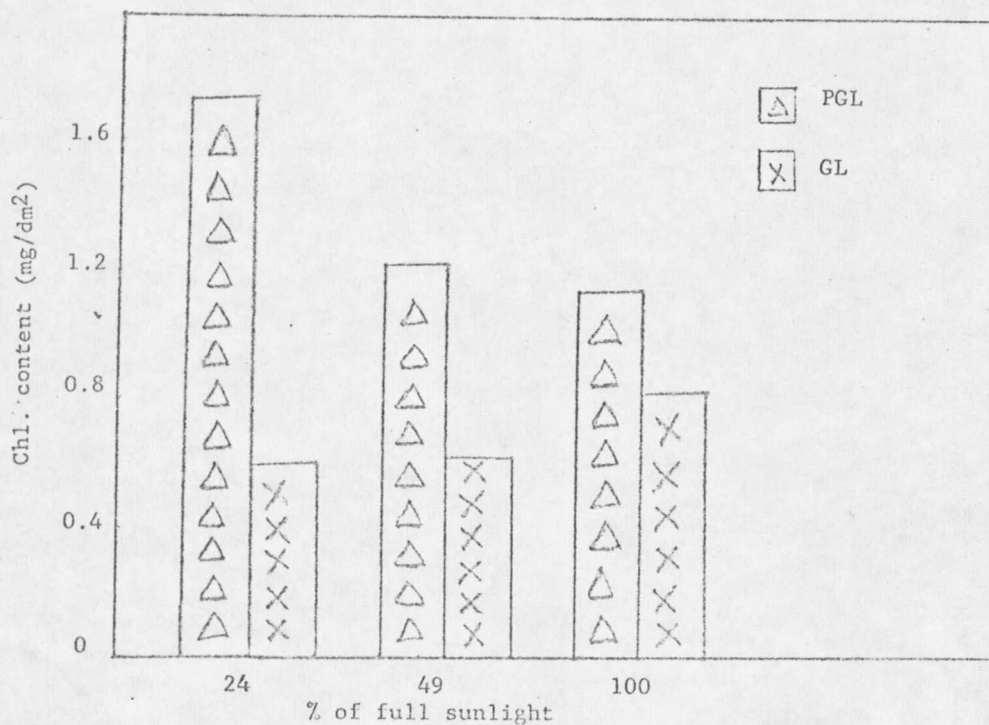


Fig 19. Chlorophyll content in the flag leaf of PGL and GL at 24, 49, and 100% of full sunlight (mg/dm²) (Milky ripe period).

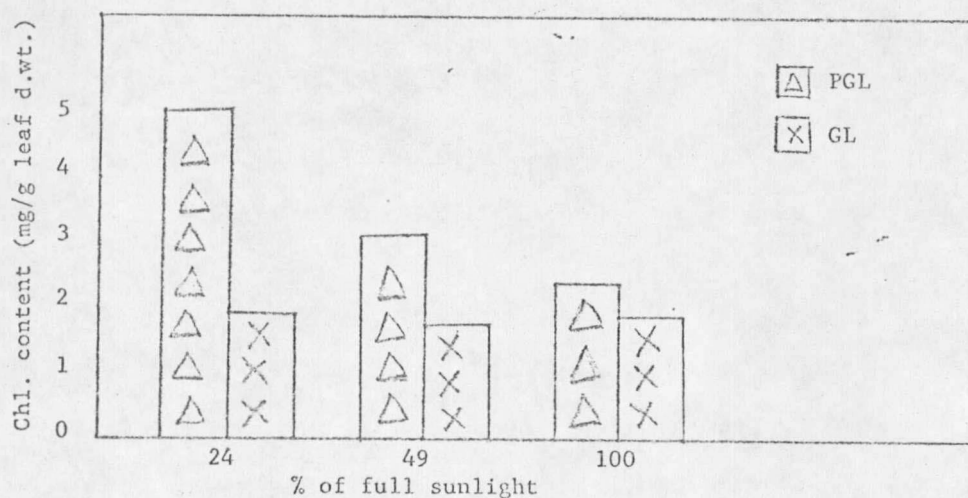


Fig 20. Chlorophyll content in the flag leaf of PGL and GL at 24, 49, 100% of full sunlight (mg/g leaf dry weight) (Milky ripe period).

Soil water utilization

Average annual precipitation at the Field Research Laboratory is about 38 cm. The rainfall for the year 1971 was 36 cm. Of this amount, 13 cm was received between May 10 and August 28 (barley growing period). On May 10, 1971 the average available water (0-15 cm) at the Field Research Laboratory was 12 cm. So, the total amount of water available for use during the barley growing season was 25 cm. We measured depletion of soil water by depths for Liberty and Golden Liberty at 24 and 100% of full sunlight. Soil water measurements were started in the early ripening period of the crop (Table 2). First readings were taken on July 25, 1971.

Assuming similar water loss from the ground surface any difference in the available soil water could be attributed to the difference in the water use by the plants. In estimating available water at different depths, the conventionally used 15 bar soil water tension was taken as the permanent wilting point.

Practically all the available water to a depth of 152 cm was used by July 23 in plots where Liberty was grown in full sunlight. There was considerable available water below the 152 cm soil depth. For those plots in which Liberty was grown at 24% of full sunlight, 1.6 cm water was still available to the 152 cm depth. Available water present to the 152 cm depth was 1.79 cm and 2.18 cm for Golden Liberty plots grown with 100 and 24% of sunlight.

By July 30, Liberty grown in full sunlight had used all

Table 2. Available soil water (cm) to a depth of 183 cm in plots with Liberty or Golden Liberty at 24 or 100% of full sunlight.

	Available soil water at different depths (cm)						
	0-30	30-61	61-91	91-122	122-152	0-152	152-183
<u>July 23, 1971</u>							
100% of full sunlight							
Liberty	0	0	0	0	0.10	0.10	1.70
24 % of full sunlight							
Liberty	0.03	0.37	0.83	0.07	0.30	1.60	1.45
100% of full sunlight,							
Golden Liberty	0	0	0	0	0.64	1.79	1.65
24% of full sunlight,							
Golden Liberty	0	0.43	1.00	0.30	0.45	2.18	2.00
<u>July 30, 1971</u>							
100% of full sunlight,							
Liberty	0	0	0	0	0	0	1.51
24% of full sunlight,							
Liberty	0	0.17	0.23	0	0.16	0.56	1.33
100% of full sunlight,							
Golden Liberty	0	0	0.19	0.11	0.62	0.92	1.87
24% of full sunlight,							
Golden Liberty	0	0.12	0.44	0.03	0.51	1.10	1.74

Table 2. (continued)

	Available soil water at different depths (cm)						
	0-30	30-61	61-91	91-122	122-152	0-152	152-183
<u>August 6, 1971</u>							
100% of full sunlight, Liberty	0	0	0	0	0	0	1.41
24% of full sunlight, Liberty	0	0	0.05	0.05	0.19	0.29	1.40
100% of full sunlight, Golden Liberty	0	0	0	0	0.40	0.40	2.10
24% of full sunlight, Golden Liberty	0.10	0.07	0.13	0.13	0.47	0.90	1.74
<u>August 13, 1971</u>							
100% of full sunlight, Liberty	0	0	0	0	0.06	0.06	1.60
24% of full sunlight, Liberty	0	0	0.06	0.06	0.18	0.30	1.54
100% of full sunlight, Golden Liberty	0	0	0	0.02	0.36	0.38	2.16
24% of full sunlight, Golden Liberty	0	0	0	0	0.18	0.18	2.0

available water to 152 cm. By August 13, both Liberty and Golden Liberty had used essentially all available water to 152 cm. By August 13, both Liberty and Golden Liberty had used essentially all available soil water at both light intensities.

It appears from Table 2 that depletion of available soil water was delayed about 1 week by shading (24% of sunlight) and about 2 weeks by the lighter leaf color of the Golden Liberty line (which matured 1 week later than Liberty).

No soil water below the 152 cm depth was extracted by plants. In spite of this, plants continued to develop after all soil water to 152 cm was held more tightly than 15 bars. This indicates that barley is able to extract soil water beyond the 15 bar tension. This is not unusual for dryland crops.

SUMMARY AND CONCLUSIONS

Barley breeders at Montana State University are involved in several phases of plant design which could increase water use efficiency. One of the efforts in this direction has been to develop barley lines with lighter green leaf color. It is hoped that lighter leaf color will increase the albedo, thus reducing the evaporation from the crop surface. Extensive efforts are now being made to gather information regarding the growth and developmental behavior of the light green color lines and the effects of climatic factors like light and temperature on them. Water use efficiency with these lines is also being investigated.

In this investigation we studied the vegetative growth and water use of a normal green leaf color commercial cultivar, Liberty, and its two lighter leaf color isogenics at different light intensities. The results obtained can be summarized as follows:

1. Decreased light intensities reduced tiller number per plant.

No significant differences in the tiller number per plant were observed among color lines or in the response of color lines to different light intensities.

2. The maximum number of leaves per plant attained by Liberty, Pale Green Liberty, and Golden Liberty were 16, 16, and 18, respectively. Fewer leaves were produced with reduced light intensities.

3. A significant difference existed among the color lines in maximum leaf area per leaf. Area per leaf of Pale Green Liberty was highest, followed in order by Golden Liberty, and Liberty. Area per leaf increased with reduced light intensities.
4. Maximum leaf area per plant of Golden Liberty, and Pale Green Liberty was significantly greater than Liberty. Light intensity did not have a significant effect on leaf area per plant. This was because the greater number of leaves at higher light intensities, was compensated for by larger leaves at lower light intensities.
5. A significant difference existed among the color lines in their maximum leaf dry weight. Maximum leaf dry weight obtained by Golden Liberty was 913 mg per plant, followed by Pale Green Liberty, and Liberty with 744 and 637 mg per plant, respectively. Reduction in light intensity resulted in significant decreases in leaf dry weight.
6. Liberty had significantly greater specific leaf weight than Pale Green Liberty or Golden Liberty. Reduced light intensities resulted in significant reductions in specific leaf weights.
7. At heading time, LWR of Liberty, Pale Green Liberty, and Golden Liberty were 0.25, 0.37, and 0.44, respectively.

Reduced light intensities resulted in reduced LWR.

8. At harvest, plant dry weight of Golden Liberty (3.9 g/plant,) exceeded those of Liberty and Pale Green Liberty (3.1 and 2.9 g/plant). Reduced light intensities resulted in significant reductions in plant dry weight.
9. Reduction in light intensity resulted in significant reduction in spike weight. Increase in spike weight with increase in light intensity was less in Pale Green Liberty than in the other two lines.
10. Liberty had the highest concentration of chlorophyll on both leaf area and leaf dry weight bases, followed by Pale Green Liberty and Golden Liberty, respectively. The highest concentration of chlorophyll was present in the leaves of the plants grown at 24% sunlight.
11. Depletion of available soil water was delayed about 1 week by shading and about 2 weeks by the lighter leaf color of the Golden Liberty line.

The above findings indicate that:

- (i) The reduced chlorophyll concentration of light green color lines may not adversely affect their vegetative growth.
- (ii) The absence of a line by light intensity interaction for any of the vegetative characteristics suggests

that the response of the light green color lines to different light intensities will be similar to that of the normal green color lines.

- (iii) Golden Liberty used water at a slower rate than Liberty. This might be advantageous for certain dry-land conditions, but much further research is needed to determine the comparative water use patterns and yielding ability.

APPENDIX

Table 3. Summary of climatic data by months for the calendar year 1971, and averages for the period 1958-70 at the Field Research Laboratory, west of Bozeman, Montana.

	Month.												
	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Total or Mean
Precipitation (inches)													
1971	0.40	0.51	0.41	3.09	2.07	2.85	0.25	0.97	2.10	0.71	0.67	0.21	14.24
1958-70	0.52	0.36	- .96	1.32	2.35	2.80	1.42	1.25	1.20	1.31	1.07	0.46	15.02
Maximum temperature (F°)													
1971	32.0	38.2	43.3	52.3	64.2	72.1	79.6	86.2	66.3	55.0	43.0	30.5	55.2
1958-70	32.5	37.3	41.8	53.0	65.4	72.1	82.2	80.8	69.0	59.3	43.9	34.7	56.0
Minimum temperature (F°)													
1971	14.9	19.8	21.6	27.8	37.7	43.1	46.4	50.4	36.9	29.6	23.6	8.8	30.05
1958-70	9.6	15.5	18.0	28.1	36.7	43.7	47.8	46.4	38.5	30.9	20.3	12.9	29.1
X temperature (F°)													
1971	23.5	29.0	32.5	40.1	51.0	57.6	63.0	68.3	51.6	42.3	33.3	19.7	42.6
1958-70	21.1	26.6	29.9	40.6	51.1	57.9	65.0	63.7	53.7	45.1	32.1	23.8	42.6

Table 4. Analysis of variance for various barley plant characteristics: Tillers/plant; Green leaves/plant; Leaf area/plant; Leaf dry weight/plant; Specific leaf weight; Dry weight/plant; and Spike weight/plant.

DF	SOURCE OF VARIATION				
	R	CL	LI	Cl x LI	E
Plant characteristics	2	2	3	6	22
Tillers/plant	0.45	2.34	4.28**	1.57	0.84
<u>Green Leaves/plant</u>					
End of tillering	2.35	5.71	6.65*	1.95	2.18
Middle of stem extension	27	35 **	30 **	4.8	4.9
End of stem extension	1.8	18	36 *	11	13
Heading to early flowering	26	92 *	53 +	32	22
Maximum leaf area/leaf (cm ² /leaf)	15	52**	18 **	6	3
<u>Leaf Area/plant (cm²/plant)</u>					
End of tillering	294	1267**	214	160	170
Middle of stem extension	4593	11131**	1652	1085	1323
End of stem extension	10413	1522	2716	3654	3137
Heading to early flowering	11340	58730**	7022	4868	7075
<u>Leaf Dry wt/plant (mg/plant)</u>					
End of tillering	3753	13418**	877	701	994
Middle of stem extension	25115	53056**	99104**	7046	6525
End of stem extension	26951	37488	109411	22585	34361
Heading to early flowering	29978	234781*	407671**	70728	61207

R = replication
CL = color lines

LI = light intensities
E = error

Table 4. (continued)

Plant characteristics	SOURCE OF VARIATION				
	R	CL	LI	CL x LI	E
Specific Leaf Weight (mg/cm ²)					
End of tillering	9	136**	19+	20*	6.4
Middle of stem extension	19	67**	121**	6	5
End of stem extension	67	23	34+	11	12.4
Heading to early flowering	4	40**	20**	2.5	2.5
Dry weight/plant (mg/plant)					
End of tillering	11733	36297**	10014**	2210	2076
Middle of stem extension	51952	517720**	517720**	37155	20324
End of stem extension	92150	1238189**	922138**	79458	125825
Heading to early flowering	389377	1592428+	22268576**	2492951**	494908
Harvest	453918	2280431*	14053712**	1273898*	401351
Spike weight/plant (mg/plant)	249342	337906	4635125	709310**	160843

+ Significant at 0.10 level

* Significant at 0.05 level

** Significant at 0.01 level

Table 5. Number of green leaves per barley plant for three leaf color isogenic lines at 8, 24, 49, and 100% of full sunlight.

% of full sunlight						% of full sunlight					
	8	24	49	100	$\bar{X}$		8	24	49	100	$\bar{X}$
June 17, 1971 (End of tillering)						June 28, 1971 (Middle of stem extension)					
L	8.7	8.3	8.3	9.2	8.6a	L	10.6	13.3	13.4	16.5	13.4a
PGL	7.7	6.2	7.5	8.5	7.5a	PGL	11.0	10.9	12.6	15.2	12.4a
GL	6.0	6.7	7.4	9.4	7.4a	GL	14.3	14.9	17.0	16.8	15.7b
$\bar{X}$	7.5a	7.1a	7.7a	9.0b	7.8	$\bar{X}$	12.0a	13.0ab	14.3bc	16.2c	13.8
July 7, 1971 (End of stem extension)						July 16, 1971 (Heading to early flowering)					
L	15.4	16.6	16.1	16.8	16.2a	L	10.9	15.8	13.4	15.3	13.8a
PGL	11.5	17.0	16.1	20.5	16.3a	PGL	13.7	14.3	14.9	21.6	16.1a
GL	15.5	15.7	19.7	19.7	17.6a	L	15.8	16.4	21.7	19.6	18.3b
$\bar{X}$	14.1a	16.4ab	17.3ab	19.0b	16.7	$\bar{X}$	13.5a	15.5ab	16.6ab	18.8b	16.0

L Liberty
PGL Pale Green Liberty
GL Golden Liberty

Means in the same column or row followed by the same letter are not significantly different at the 0.05 level according to Duncan's Multiple Range Test.

Table 6. Leaf area per barley plant (cm²/plant) of three leaf color isogenic lines at 8, 24, 49, and 100% of full sunlight.

% of full sunlight						% of full sunlight					
8	24	49	100	$\bar{X}$		8	24	49	100	$\bar{X}$	
June 17, 1971 (End of tillering)						June 28, 1971 (Middle of stem extension)					
L	56	60	54	59	57a	L	162	147	171	166	161a
PGL	55	42	50	69	54a	PGL	141	137	184	174	159a
GL	30	40	40	42	39b	GL	96	132	102	100	107b
$\bar{X}$	47a	47a	48a	57a	50	$\bar{X}$	133a	139a	152a	147a	142
July 7, 1971 (End of stem extension)						July 16, 1971 (Heading to early flowering)					
L	181	200	168	194	186a	L	230	219	208	211	217a
PGL	154	179	218	244	199a	PGL	305	265	357	350	319b
GL	214	178	186	187	191a	GL	274	350	420	368	353b
$\bar{X}$	183a	186a	191ab	208b	192	$\bar{X}$	270a	278a	328a	310a	296

L Liberty
PGL Pale Green Liberty
GL Golden Liberty

Means in the same column or row followed by the same letter are not significantly different at the 0.05 level according to Duncan's Multiple Range Test.

Table 7. Dry weight of leaf per barley plant (mg/plant) of three leaf color isogenic lines at 8, 24, 49, and 100% of full sunlight.

% of full sunlight						% of full sunlight					
	8	24	49	100	$\bar{X}$		8	24	49	100	$\bar{X}$
June 17, 1971 (End of tillering)						June 28, 1971 (Middle of stem extension)					
L	172	167	185	163	172a	L	315	423	449	657	461a
PGL	101	106	111	145	116a	PGL	253	267	358	495	343b
GL	79	84	128	113	101b	GL	279	296	387	418	345b
$\bar{X}$	117a	119a	141b	140b	130	$\bar{X}$	282a	329a	398b	523c	383
July 7, 1971 (End of stem extension)						July 16, 1971 (Heading to early flowering)					
L	501	660	599	663	606a	L	495	665	570	819	637a
PGL	437	660	585	832	628a	PGL	572	652	794	959	744ab
GL	397	487	701	800	596a	GL	646	702	1185	1118	913b
$\bar{X}$	445a	602b	628b	765c	610	$\bar{X}$	571a	673ab	850bc	956c	765

L Liberty
PGL Pale Green Liberty
GL Golden Liberty

Means in the same column or row followed by the same letter are not significantly different at the 0.05 level according to Duncan's Multiple Range Test.

Table 8. Specific leaf weight (mg/cm²) of three leaf color isogenic barley lines at 8, 24, 49, and 100% of full sunlight.

% of full sunlight						% of full sunlight					
8	24	49	100	$\bar{X}$		8	24	49	100	$\bar{X}$	
June 17, 1971 (End of tillering)						June 28, 1971 (Middle of stem extension)					
L	2.33	2.40	2.82	2.91	2.61a	L	2.20	2.63	2.78	3.28	2.72a
PGL	1.93	2.21	2.02	2.01	2.04b	PGL	1.95	2.06	2.38	2.60	2.24b
GL	2.19	2.06	2.44	2.58	2.31c	GL	2.11	2.06	2.66	2.70	2.38
$\bar{X}$	2.15a	2.22a	2.42ab	2.50b	2.32	$\bar{X}$	2.08a	2.25a	2.60b	2.86c	2.44a
July 7, 1971 (End of stem extension)						July 16, 1971 (Heading to early flowering)					
L	2.76	3.30	3.57	3.41	3.26a	L	2.27	2.76	2.94	3.51	2.87a
PGL	2.93	3.68	2.68	3.41	3.15a	PGL	2.12	2.39	2.44	3.06	2.50b
GL	1.85	3.22	3.76	3.78	3.15a	GL	2.07	2.43	2.79	3.29	2.64b
$\bar{X}$	2.48a	3.40b	3.33b	3.53c	3.18	$\bar{X}$	2.15a	2.52b	2.72c	3.28d	2.67

L Liberty
PGL Pale Green Liberty
GL Golden Liberty

Means in the same column or row followed by the same letter are not significantly different at the 0.05 level according to Duncan's Multiple Range Test.

Table 9. Dry weight per barley plant (g/plant) of three leaf color isogenic lines at 8, 24, 49, and 100% of full sunlight.

% of full sunlight						% of full sunlight					
	8	24	49	100	$\bar{X}$		8	24	49	100	$\bar{X}$
June 17, 1971 (End of tillering)						June 28, 1971 (Middle of stem extension)					
L	0.25	0.22	0.29	0.27	0.25a	L	0.55	0.76	0.90	1.2	0.85a
PGL	0.14	0.15	0.16	0.23	0.17b	PGL	0.37	0.40	0.53	0.70	0.50b
GL	0.11	0.12	0.18	0.16	0.14b	GL	0.40	0.40	0.62	0.60	0.50b
$\bar{X}$	0.16a	0.16a	0.21ab	0.22b	0.18	$\bar{X}$	0.44a	0.52a	0.68b	0.83c	0.61
July 7, 1971 (End of stem extension)						July 16, 1971 (Heading to early flowering)					
L	1.07	1.63	1.67	1.98	1.58a	L	1.65	2.38	2.44	3.83	2.57a
PGL	0.67	1.11	1.03	1.54	1.08b	PGL	1.25	1.57	2.19	3.51	2.13a
GL	0.65	0.88	1.26	1.18	0.99b	GL	1.20	1.51	2.97	2.94	2.15a
$\bar{X}$	0.79a	1.20b	1.32bc	1.56c	1.21	$\bar{X}$	1.36a	1.82ab	2.53b	3.42c	2.28

L Liberty
PGL Pale Green Liberty
GL Golden Liberty

Means in the same column or row followed by the same letter are not significantly different at the 0.05 level according to Duncan's Multiple Range Test.

Table 9. (continued)

August 30, 1971
(Harvest)

L	1.62	2.48	3.47	4.78	3.08a
PGL	1.88	2.67	3.19	3.75	2.87a
GL	1.64	3.48	4.91	5.60	3.90b
$\bar{X}$	1.71a	2.87b	3.85c	4.71d	3.28

L Liberty

PGL Pale Green Liberty

GL Golden Liberty

Means in the same column or row followed by the same letter are not significantly different at the 0.05 level according to Duncan's Multiple Range Test.

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