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PROJECT NO. US-335-80

Development and Physiological Evaluation of Barley (*Hordeum Vulgare*) Populations Divergently Selected for Drought Tolerance

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Development and physiological evaluation of barley (Hordeum vulgare)
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ABSTRACT

The relationships of 50 two-row and six-row barley cultivars to drought stress parameters were studied with field-grown plants at several environments in 1982, 1983, and 1984. Measured physiological parameters were osmotic (OP) and water (WP) potentials, percent dry matter, conductance (6l), resistance, dry-down rates, and membrane damage from PEG6000 simulated drought stress using leaves and IR thermometer temperatures of plant canopies. The regression parameters, slopes, and predicted varietal yields for mean site yields of 10 bu/acre (Y10) previously determined by Eslick (29) from linear yield stability analysis were related to physiological parameters and grain yield at dry field sites. All measured parameters were related to regression coefficients, other physiological parameters and to grain yield under some conditions. More correlations were obtained for 6-row varieties and for drought susceptible varieties. Physiological parameters of divergent barley populations with five generations of natural selection for drought stress were evaluated under irrigation and dryland in 1984. The two populations frequently differed under dryland conditions but seldom under irrigation, the dryland derived population often having more negative values for OP and WP, higher percent leaf dry weight, and 1°C warmer plant canopies near solar noon.

Blum, in 1982, showed large varietal differences in seedling growth from PEG6000 simulation of drought stress. These differences were not correlated with Eslick's regression parameters. Blum showed that varietal differences in awn and ear photosynthesis (CER) and transpiration were associated more with ear surface area than with rate differences. The ratio CER/transpiration for barley averaged 50% higher than for wheat and was 4 to 10 times higher for barley awns than for barley flag leaves, supporting the importance of awns to drought stress resistance in cereals.

LITERATURE REVIEW

Plant physiological attributes related to drought adaptation have been reviewed by 32, 37, 50. Drought resistance in relation to the genetic improvement of crop plants has been reviewed and discussed by 1, 53, 28, 39, 5, 6, 51, 62.

Several authors (53, 39, and 62) have concluded that at present, much of the knowledge on the physiology of plant water stress is apparently inapplicable to selection work, mainly because breeding involves testing en masse based on rapid methodology. They concluded that the major avenue by which drought resistance may be improved is by selection for yield under conditions of stress.

While yield performance under conditions of stress is the target, Blum (5, 6) presented some doubts whether selection for yield under stress should be employed as a major selection criterion. He proposed additional physiological criteria, to be employed in addition to yield, in a selection program. Such criteria, he points out, should be developed into rapid methodology amenable to selection in large populations. Thus, several physiological selection criteria were developed as screening techniques in the cereal crops.

O'Toole and Chang (51) record plant wilting on a visual scale, in water-stressed rice nurseries in addition to yield performance. Drought avoidance (maintenance of a relatively higher plant water potential under conditions of soil moisture stress) has been shown to vary genetically in various crop plants (61, 5, 51). Its estimation in the field with the pressure chamber method (59) is slow. An indirect rapid method for estimating drought avoidance in wheat was developed by Blum (14). By this method, leaf canopy temperatures are monitored remotely by the use of the

infrared thermometer (40). A correlation was established in wheat, whereby lower canopy temperatures under stress were indicative of drought avoidance reaction.

Whatever are the components of tolerance to water stress, their integrated effect should be revealed in plant growth under stress. Thus, Blum developed a seedling growth test under controlled stress for wheat (14). By this method, seedlings are grown in nutrient solution and in PEG-containing nutrient solution. The reduction in growth rate in PEG medium, as compared with the potential rate, in nutrient solution, is taken as an index of integrated plant tolerance, in terms of growth.

Ample proof is available that a major component of tolerance in growth is the photosynthetic performance of the leaf tissue, as controlled by stomatal and substomatal factors (14, 25, 37, 61).

Plant water stress affects photosynthesis directly and also indirectly by causing stomatal closure, controlled by turgor pressure of guard cells. Below a critical threshold level of ψ , ψ_p , or RWC, which varies drastically with crop species and growth conditions, stomata close rapidly (63). Barley has a very low threshold value of -30 bars (2). Blum (11) has shown a wide range of stomatal conductances among 14 different sorghum genotypes in the field. The range of critical threshold values of ψ_p appears to be small (0 to 3 bars) (63), but ψ_p is harder to determine than ψ because it is obtained as a difference. While the initial decline in photosynthetic rates is usually due to stomatal closure, work with isolated chloroplasts indicates severe stress also interferes with photosynthesis directly. Measurement of photosynthesis in stressed breeding populations requires rapid methodology. The common methods for measuring photosynthesis in

field grown plants are fairly slow (59). A comparatively rapid method was developed recently by Clegg et al. (19).

The above discussion demonstrates that in recent years, genetic variation was revealed in plant physiological responses to drought stress in several crop plants. It was further shown that for several plant physiological responses, fairly rapid methodology, amenable for selection, was developed. However, the most critical link, that between given physiological stress responses and yield performance under stress, is not well established. Doubts were increased by suggesting there could be negative associations between some drought adaptation reactions and yield (6).

It is therefore most critical, at this point in time, to use an integrated breeding and physiology research program for the evaluation of such associations.

The genetic resources for such an investigation must be available. Such genetic resources should clearly differentiate yield performance between stress and non-stress environments. In this research, divergent genetic materials, in terms of yield performance under conditions of drought stress, will be made available for physiological studies. These physiological studies attempted to establish the drought adaptation responses for which these genetic resources differ, and thus arrive at a conclusion on the most desirable drought resistance mechanism to be used in future selection programs.

Plant water potentials may be related by the equation:

$$\psi = \psi_p + \psi_s + \psi_m$$

Where: ψ = Water potential of plant tissue

ψ_p = Pressure potential (Hydrostatic or "turgor")

ψ_s = Solute or osmotic potential

ψ_m = Matric potential (adsorption by tissue matrix)

Plant tissue can respond to moisture stress by increasing the solute concentration and by decreasing cell wall elasticity; "osmotic adjustment" and increasing the modulus of elasticity, respectively.

One form of drought resistance is based on the ability of plant cells to adjust osmotically.

A comparatively simple method for measuring osmotic adjustment was utilized by Cutler et al. (22) for rice. The method is based on pressure-volume relationship when a leaf sample is subjected to testing in a pressure chamber. This method is appropriate for evaluation in barley.

Membrane Damage by Water Stress - Sullivan (61) developed in sorghum a rapid in vitro test of drought tolerance. The method evaluates injury to cell membranes by a given standard level of moisture stress. Stress is applied to leaf disks immersed in a solution of polyethylene glycol (PEG). Injury by stress is measured subsequently by ion efflux from pre-stressed disks, using the electroconductivity method. This method has been evaluated and adapted to wheat and barley by Blum (9).

Pressure/Volume Determinations of ψ , ψ_p , ψ_s , and RWC -- The pressure chamber can be used to measure ψ and to calculate RWC (64). In conjunction with a thermocouple psychrometer (65), ψ_s of sap from frozen tissue can be measured. Scholander et al. (55) obtain these values using only the pressure chamber with a "pressure/volume" technique in which reciprocal

internal chamber pressures are plotted against cumulative volume of sap evolved. The right-hand linear side of the curve corresponding to ψ_s at zero turgor, when extrapolated to the ordinate gives $1/\psi_s$ of the original tissue and to the abscissa gives volume of osmotically active water (excluding apoplastic water). Matric potential is determined with the pressure chamber (12) or the hydraulic press (56). ψ_p is obtained by subtraction, often ignoring e_m . Values of e_m may also be calculated by this procedure (22).

Dry Down Rate of Plant Tissue (Water Retention) -- Dedio (24) found dry down rates of young and of headed wheat plants were negatively associated with drought resistance. Fink (30), however, had only limited success using this technique with barley, possibly because his plants were only subjected to mild stresses at Bozeman, Montana.

A mild water stress, below -4 to -2 bars, reduced nitrate reductase activity in barley (38). Lower nitrate reductase activity resulted from lower protein synthesis rather than reduced nitrate uptake.

Severe water stress causes amino acids, especially proline, to accumulate. This has been extensively studied in barley, but its significance is still uncertain (34).

Hockett et al. (1968) discussed the 101 spring and 115 winter genetic male sterile barley stocks available at that time (36). Those male steriles arose from at least 19 different genetic mutations at at least 16 non-allelic loci. Eslick (1979) contrasts the effectiveness of a) male sterile facilitated recurrent selection (MSFRS) to b) the use of composite crosses (CC) obtained without male steriles, and to c) a pedigree breeding program (27). The first two methods both speed up the development of genetic "resource material" which is a prerequisite to "exploitation" (release of

genotypes for crop production). MSFRS is considered the best technique for giving maximum gene recombination, obtaining unusual genotypes, easily adding desirable genotypes, and the accumulation of minor genes.

Ceccarelli (69) evaluated the magnitude of response after six cycles of phenotypic natural selection for culm length in barley. They report that the exhaustion of genetic variability for this trait differs in the two directions of selection. Spike length was closely associated with culm length but heading date was independent.

RESEARCH CONDUCTED IN THE USA

Materials and Methods - General

'Yield stability analysis' has been done with the Reference Varieties used in this study which are two-row and six-row barley varieties tested in the Western USA and in southern Alberta and Saskatchewan. Drought often limits production in these areas. Extensive data from 1936 to 1976 have been analyzed by Eslick (30). Data from 49 widely-grown varieties were tested by, essentially, a linear regression of yields for each variety against calculated mean yields for individual nurseries (method E) (30, 31, 46). This is depicted in Figure 1. Since Eslick used linear regression (not logarithmic as in reference 31), his calculated slope for each variety gives the predicted yield increase per unit increase in mean nursery yield level. These regression equations help select "drought resistant varieties" that have slopes significantly less than one and predicted yields significantly higher than mean nursery yields at the 538 kg/ha (10 bu/A) yield level (Table 1 and Figure 1). Some varieties designated as "drought susceptible" were selected by the converse procedure, i.e., slopes greater than one and low predicted yields at the 538 kg/ha yield level. Varieties

were also classified by experienced barley breeders. Varieties selected (Reference Varieties) should represent extremes of drought resistance.

In March 1981, 28 diverse barley populations were intercrossed using male sterile plants in the field at Mesa, Arizona*. About 110,000 seeds resulting from these hand crosses were field planted in Montana in 1981. Divergent natural selection with optimum irrigation versus limited moisture (dryland) was imposed for two generations per year by alternating production between winters in Arizona and summers in Wyoming. In March, 1982, only heads from 2-row by 6-row crosses were saved to prevent loss of the less prevalent 2-row types from the populations.

Materials and Methods - 1982

Physiological parameters measured in 1982 include measurements of all 50 Reference Varieties including membrane damage, Pressure/Volume determination of $\psi\pi$, dry down rates, and percent dry matter, conventional dry down rates, transpiration rate measurements (Tables 2 & 3), and infrared canopy temperatures. Most of the work on the 50 Reference Varieties was done on several runs of a single replication of material grown in the field at Bozeman, Montana.

Pressure/volume measurements were taken on 50 barley varieties in the summer of 1982 from plots planted in Bozeman, MT. The youngest fully expanded leaves were excised at sunrise and placed in plastic bags on ice and transported to the lab. Each leaf was individually weighed and then placed into a rubber stopper and inserted into the pressure chamber of Soil

* Dr. Tom Ramage and Mr. Rex Thompson helped J. Brown make these crosses.

Moisture Equipment Corporation pressure bomb. The chamber was pressurized until an end point was obtained. The end point was determined as the first sign of sap exuded. The initial balance pressure after the end point was recorded and the leaf was removed and placed on the counter for 10 minutes. The leaf was weighed and pressurized for seven readings. The measurements were plotted with the reciprocal of the Y total ($1/Y$) versus the percent relative water content (RWC). The osmotic potential was determined by extrapolation (22,64). This work extended over a period of one month during the late vegetative stages.

Materials and Methods - 1983 and 1984

Techniques used to measure physiological parameters during the 1983 and 1984 growing season include infra-red canopy temperatures, thermocouple psychrometer determination of osmotic potential, pressure bomb determination of total leaf water potential, static, mass flow (57), determination of leaf conductance, and transient, moisture diffusion (Li-Cor-700) porometer determination of leaf resistance to water vapor. Canopy temperatures were measured from all 50 six- and two-row barley varieties previously reported. Osmotic potential, total potential, and leaf porosity were determined for only the 25 six-row varieties, because 1982 data showed more correlations among 6-row varieties.

The major U.S.A. effort of this project attempted to characterize the physiological behavior of reference barley varieties in the field. Plants were studied in both semiarid locations (Logan, MT, 1983; Three Forks, MT, 1984; and Powell, WY, dryland) and in more moist locations (Bozeman, MT and Powell, WY, irrigated).

During the final year of the project, massive amounts of data were collected from 25 reference varieties and 2 divergently selected populations grown under both dryland and irrigation at Powell, Wyoming. The results from the field-grown populations are given in Tables 5, 6, and 7 plus Figures 2 through 24. Studies of reference varieties in 1983 and 1984 are presented in Tables 8 through 14 and related to Table 1 and Figure 1 (from Eslick) and our earlier work reported in Tables 2, 3, and 4.

To circumvent the difficulties described above in 1983, in 1984 we used a partially balanced incomplete block (PBIB) design to better control local variation when studying varieties. We also monitored parameters, using only the 6-rowed varieties, more times from daylight to early afternoon to look for differences in rates of change. The PBIB design provides two measurements of time/location effects that are reported in all 1984 variety tables. The term "replication" refers to a subunit containing all varieties and is the same as block in the 1983 variety tables. The term "block" is applied to a strip of plots across one-fifth of replication. Since sampling was done one small block at a time, the PBIB design could better adjust for changes in measured parameters with time.

After five generations of divergent selection, the "wet" and "dry" populations were each evaluated under dryland and irrigated conditions at Powell, Wyoming during the summer of 1984. The main objective of this study was to determine whether shifts in physiological parameters had occurred.

Three replications of each of the four treatments, dry population on dryland (dry on dry), dry population with irrigation (dry on wet), wet population on dryland (wet on dry), and wet population with irrigation (wet on wet) were sampled four times at two-week intervals during the growing

season. Sampling dates were June 14, June 28, July 12, and July 26, 1984. The irrigated portion of the plots had not received any additional water by June 14.

Because of the large plant to plant variation within populations, we sampled 10 leaves per plot to estimate osmotic potential, percent dry weight, water potential, air conductance through leaves (using the Shimshi mass-flow porometer), and water vapor diffusive resistance from leaves (using the Li-Cor model 700 autoporometer). Canopy temperatures, which average a number of plants, were taken at three locations within each plot using an Everest model 110 infrared thermometer. Plant samples were collected throughout the growing season at each of the locations. leaf sample was taken from 3 replications for each of 25 varieties, 3 to 4 times a day. Daily plant sampling began at sunrise (5:15 AM-5:30 AM) and continued at regular intervals ending by 3:30 PM.

Plant samples used to determine osmotic potentials with a thermocouple psychrometer consisted of the youngest fully expanded leaves (excluding the flag leaves). A leaf was excised from a plant and immediately placed into liquid nitrogen. Next the leaf was wrapped first in parafilm, then aluminum foil, and finally placed into a zip-loc plastic bag and placed on dry ice until returning to the lab. Samples were stored in a freezer until the osmotic potentials were measured.

The osmotic potentials were measured in 1983 with a Wescor HR-33 dewpoint microvolt meter and a Decagon SC-10 sample chamber; and in 1984 with a Decagon NT-3 nanovolt meter and a Decagon SC-10A sample changer. The microvolt meter and the nanovolt meter were both calibrated with NaCl solutions ranging from .05 to .90 molalities. Calibration curves were determined by plotting my readings vs. their known bar (MPa) potentials.

When the measurements were taken, each frozen leaf sample was removed individually from the freezer, unwrapped, and weighed with a digital Mettler scale to determine frozen weight. Four leaf disks were punched from each leaf and placed into a sample cup and then into the chamber. At times NaCl solutions were used to insure that accurate readings were being obtained. After 3 hours of equilibration (for temperature and vapor equilibration), measurements were taken. Three-minute equilibration intervals were allowed between each sample and measurements were taken when a constant reading was obtained. After taking readings, the samples were then dried in a dehydrating oven for 24 hours and dry weights taken. The percent dry weight was calculated from the frozen and dry weight measurements. (Note: In 1983, fresh sample weights were obtained in the field and then compared to their frozen weights. It was determined that water loss was insignificant and therefore field weighing was omitted in 1984. It was felt that speed was important to minimize water loss.)

The samples were kept frozen at all times until placed into the sample chamber to insure that metabolic processes are kept to a minimum. The leaves were handled with tweezers to prevent contamination.

Materials and Methods - Divergent Populations - 1984

Osmotic potential, water potential, percent dry weight, leaf conductance (Shimshi), leaf resistance (Li-Cor model 700), and infrared canopy temperatures were compared between the two divergent populations both on dryland and on irrigation in 1984. "Pressure potential" was calculated as the difference between water potential and osmotic potential. No statistical analysis is presented on this calculated parameter. Since most of the significant population treatment effects occurred on dryland, the

dryland results will be emphasized. In Figures 2 through 24 the symbol PD shows significant population treatment effects on the dryland half of the experiment, indicating measurable divergence after five generations of natural selection in populations containing a decreasing proportion of male sterile plants. PI indicates significant population by irrigation interaction. P, D-, and W- indicate population effect, dry population, and wet population, respectively, on June 14, 1984 immediately before the differential irrigation treatment was imposed.

All measurements except IR canopy temperatures are reported as average values for 30 leaves. It appears that this is a minimum number of observations to characterize the average osmotic potential of populations. OP values were obtained from all plots for the three sampling dates after the start of differential irrigation (June 28, July 12, and July 26).

Results - 1982 - Reference Varieties

The 1982 USA work is summarized in Tables 2 and 3. Table 2 compares 2-row versus 6-row barley varieties and "resistant" versus "susceptible" varieties. These comparisons are rather inconclusive.

All significant correlations between pairs of independent parameters are in Table 3. Significance is at $p = .05$ unless double asterisks appear to indicate $p = .01$. "Susceptible" varieties appear to have more significant correlations than do "resistant" varieties (numbers refer to parameters given in Table 2). Barleys with 6-row head types show more significant correlations than those with 2-row head types. This and the negative versus positive correlations of percent solute leakages versus $\psi\pi$ for 2-row versus 6-row barleys confirm our previous observation that barleys with these two head types behave divergently.

Results - 1983 - Reference Varieties

Significant differences were found among the barley varieties for each of the parameters measured in 1983 (Table 4). Correlation analyses indicate large variation among varieties in the parameters measured. Even when correlation was statistically significant, R^2 values were usually less than .20. The significant, negative relationship between Eslick's predicted yield at 10 bu/acre (Y_{10}) and measured yield at Powell raises an interesting point.

Eslick's series of regression lines of individual variety yields vs. mean yield of the nursery result in a fulcrum point at around 30 bushels per acre through which most of the lines intersect (Fig. 1). The mean yield at Powell, Wyoming was also approximately 30 bushels/acre. Correlations would change sign as the mean nursery yield passed through this fulcrum, unless the physiological response to environmental conditions also changed. At a yield environment of 30 bu/acre, no correlation with yield would be expected.

Another problem encountered during 1983 was in acquiring the necessary precision to determine varietal differences in physiological parameters. When measuring plant water potential, for instance, measurement of 25 varieties required about one hour, and therefore there was a significant correlation of potential with time of measurement. Obtaining a comparative set of data over a short time during a period of differential stress can be difficult. Differential stress may be a transient phenomenon whose time of occurrence may depend upon interaction among temperature, cloud cover, soil water status, and crop growth stage. Rate of recovery from stress may differ, resulting in residual effects on a physiological parameter long after a favorable change in the stress vector.

Leaf porosity data obtained in 1983 and its relationship with other parameters are most promising. Comparisons of drought resistant and susceptible varieties were significant in almost all cases (Table 1) and very consistent. The more drought resistant varieties had less porosity. Porosities were studied only in a relatively high moisture environment, however (Bozeman, Montana); in 1984 we will determine whether the relationship will change in a low moisture environment (Powell, Wyoming). Both methods of measuring leaf porosity yielded similar results. Leaf porosity was negatively correlated with drought resistance (Eslick's predicted yield at 10 bu/acre, Y10.)

Total leaf water potential and leaf osmotic potential were similarly related to drought resistance. Comparison of four resistant with four susceptible varieties indicated that the more resistant varieties had lower (absolute) potentials. This probably is not associated with osmotic adjustment, as water potential was significantly correlated with relative moisture content.

Comparisons of infra-red canopy temperatures between resistant and susceptible varieties were not significant. On several occasions, canopy temperatures were positively correlated with yield at the Powell site, both in A.M. and P.M. On one occasion, at the Logan, Montana dry site, a negative correlation of canopy temperature in the A.M. with yield was obtained.

In 1983, leaf blade areas and leaf dimensions of both flag and second leaves were determined at Bozeman, MT (Table 8). As would be expected, highly significant differences in leaf size were observed both within 2-row varieties and within 6-row varieties. Six-row varieties usually had larger leaf blades than did 2-row varieties (5.08 cm^2 vs. 2.80 cm^2 for flag leaves

and 12.20 cm² vs. 8.24 cm² for second leaves). The ranges in leaf area (Table 8), however, show that there was overlap in leaf size between 2-row and 6-row varieties.

Both leaf porosities (Shimshi) and leaf resistances (Li-Cor) differed among varieties at the relatively moist Bozeman site on August 16 and 17. These measurements were taken late in the growing season after almost all leaves at the two drier sites had lost their green color.

At Powell, WY in 1983, (Table 10) varieties differed in PM plant canopy temperatures on July 7 AM and PM, WP on July 12, PM W on July 27, and both AM and PM OP on July 27. Highly significant block effects on IR canopy temperatures with no block effects on osmotic potential appear to be related to the observed rapid changes in canopy temperatures with time.

Results - 1983 - Yield Stability Analysis

We have previously discussed yield stability analysis as worked out by Eslick (29). (See Tables 1, 2, & 3 and Figure 1). Eslick's slopes are meaningful yield ratios from linear-linear plots rather than the uninterpretable log-log" slopes of Finlay & Wilkinson (30). Does this form of regression analysis allow us to predict which varieties will yield best under drought stress and do Y10 and/or slope correlate with any measurable physiological parameters?

Table 14 presents correlation coefficients using physiological measurements that are averaged over all three 1983 field locations, actual grain yields at the two dry sites (Powell, WY and Logan, MT), and regression parameters for 22 six-row barleys. Slope E was derived by Eslick as the slope between predicted yields for individual varieties at mean site

(nursery) yields of 30 and 90 bu/acre (Figure 1) and was related to physiological parameters by Fink (29). Both slope B and Slope F are also derived from Eslick's data base. Slope F is calculated between predicted varietal yields of 30 and 70 bu/acre while slope B considers only mean site yields less than 40 bu/acre.

Grain yield at Powell in 1983 is significantly correlated with slope F and is correlated with slopes B and E and Y10 at $p=.10$ (Table 14). Powell grain yields of 1983 appeared to be positively associated with AM canopy temperatures ($p=.06$). Grain yield at Logan was associated only with grain yield at Powell, WY. This data provides very limited support for the use of regression parameters to select drought tolerant genotypes.

Each of the three physiological parameters, water potential, osmotic potential, and plant canopy temperature was correlated with one or more regression parameters at one sampling time, but not both. Of the correlated parameters, osmotic potential in the PM and water potential in the early morning are most closely associated with regression parameters. These data suggest that Y10 and regression slopes may be associated more closely with physiological data than with grain yields under drought conditions.

Results - 1984 - Reference Varieties

On July 7, 1984 in Bozeman, MT, plant leaves sampled at three successive times showed significant varietal effects for all measured parameters except leaf conductance (Shimshi) (Table 11). Osmotic potentials differed among varieties at all sampling times while water potential, percent leaf dry weight, and leaf transpiration resistance differed only for samples

taken early in the day. For all significant measurements on this day, earlier sampling resulted in closer association with varietal differences.

At the dryland Three Forks location on July 3, 1984, four successive samplings were taken rather than three (Table 12). Varieties differed significantly in osmotic potential at all four sampling times and in percent leaf dry weight for three of four sampling times. These two parameters (OP and %DW) are somewhat interdependent.

Physiological parameters were measured for reference varieties grown on adjacent dryland and irrigated land areas at Powell, WY, again in 1984 (Table 13). On June 27, early in the growing season, significant varietal effects were found with both dryland and irrigation. On dryland only leaf osmotic potential at sunrise and the associated percent dry weight differed among varieties. Under irrigation, percent leaf dry weight differed among varieties for the two earlier sampling times while osmotic potential differed only for the third sampling. Leaf water potential canopy temperatures showed varietal effects with early sampling under irrigation. It is not certain why varietal differences were more prevalent with irrigation, but several of the irrigated correlations were obtained at sample time one when the average calculated "pressure potential" (the difference between WP and OP) and therefore leaf turgidity was greater under irrigation (1.37 MPa) than under dryland (1.12 MPa). At the latest sampling time, calculated average leaf pressure potentials differed by only 0.12 MPa.

On July 11, 1984 at Powell, WY, the measurement at the third sampling time of both osmotic potential and water potential showed varietal differences. Under irrigation, the only varietal differentiation was from osmotic potentials of leaves sampled at time one.

By July 25, 1984, the dryland varieties were too mature for sampling and some upper leaves under irrigation had lost their green color. Therefore, only the irrigated plots could be sampled. Both water potential at the third sampling time and leaf conductance at sunrise showed varietal effects. Plant canopy temperatures differed among varieties, but this characteristic was probably influenced most by maturity since values are averages of a number of contiguous plants rather than individual selected leaf blades as for other measurements on this date. This is probably the most extreme example of possible bias of plant maturity on the interpretation of physiological parameters.

Results - Divergent Populations - 1984

Populations had very similar osmotic potentials at the earliest sampling time (Figures 2, 3, and 4). OP values differed at the second and third sampling times on June 28 and July 12, with the dryland population usually more negative. It is interesting that the temporal OP patterns are similar for the June 28 and July 26 dryland populations, even though the populations did not differ by July 26. At the later date, plants were senescing to the point that only select upper leaves on dryland remained green enough for evaluation. This may account for the paucity of significant differences on July 26, 1984.

As with most parameters, populations did not differ in water potential (WP) at the earliest sampling time (Figures 5, 6, 7, and 8). WP values differed at the second time three of four dates and at the third time on July 12. As with osmotic potentials, three of four times the dry population had the more negative value. While no significant population effects

were detected at the last sampling date, the population by irrigation interaction was significant at each sample time.

Leaf percent dry weight (%DW) values (Figures 9, 10, and 11) give some indication of the relative maturity of the uppermost expanded leaf blades which were sampled. Populations differed in %DW at times one and three on June 28 and at times two and three on July 12. Time course patterns on these two dates were similar to, and probably related to, those for osmotic potentials. As with OP and WP in three of four cases the dry population had readings of a greater magnitude, sign ignored.

Values of OP and %DW considered together give additional indication of whether the two populations differ in maturity. It appears that at least the uppermost fully expanded leaves of the dry population are not consistently more mature based on two considerations. At each date the two populations had almost identical OP early in the morning at the time of minimum moisture stress. Secondly, %DW of the dryland population never exceeded that of the wet population at all three sampling times, was less for time one on June 28 and was numerically 2 to 3% less than the wet population on July 26, even though this difference was not significant.

OP and %DW can also be considered together to show appreciable osmotic adjustment beyond the concentrating effects of diurnal desiccation. The mean diurnal osmotic adjustment for individual treatment combinations ranged from -0.25 to -0.45 on July 12 and -0.4 to -0.65 on July 28 after adjusting for diurnal water loss.

Pressure potentials (PP) presented in Figures 12, 13, and 14 are calculated from the osmotic potentials and comparable water potentials. Errors are additive and no adjustment is made for matric potential. Therefore no statistical analyses were run on PP.

Pressure potentials change markedly during the day, but the response varies from day to day. On June 28 calculated PP dropped from values of 1.02 to 1.19 MPa at time one to 0.03 to 0.28 MPa time two with similar readings at time three. On July 12, PP values dropped from the 0.1 to 0.6 range to calculated values at or below zero followed by recovered turgidity during early afternoon cloud cover preceding rain at 2:50 PM local time. On July 26 PP declined from 1.2 to 1.9 MPa to 0.5 to 1.3 MPa at time two and then three of four treatments remained essentially constant to time three.

Leaf conductance (LC) (cm/s) data as measured by the Shimshi (1977) mass-flow porometer is presented in Figures 15-18. LC differed between the two populations at both the first and third sampling times on June 28, 1984, but in different directions. Differences in LC at the second time on July 12 and the first time on July 26 were also in the opposite direction. Population differences in LC of 8 to 10 cm/s at the high conductance values on June 14 suggest that LC measurements may differentiate better under moist environments. This is also supported by more correlations among drought stress parameters under irrigation than under dryland.

Leaf resistance (LR) (s/cm) data as measured by a water vapor diffusion porometer are shown in Figures 19 and 20. An annoying characteristic of this instrument is that even minute amounts of free water on leaf surfaces disabled the instrument for the duration of the field trip.

Limited LR data suggest that resistance is more likely to differ between cultivars at a later sampling date (28 June) than for LC. For both significant differences, the dry population had a higher LR than the wet population.

Figures 21 and 22 compare leaf conductance (LC) of air to leaf conductance (approx. $1/LR$) of water vapor on June 14 and Jun 28. Inverted LR values for the Li-Cor instrument have been scaled up by two and one orders of magnitude to allow comparison on the same graph. It appears that on June 28 both dryland populations had increased transpiration rates at T2 without increased porosity. This suggests a major role for cuticular transpiration of these relatively immature leaves. Transpiration is also more responsive to heat load than is air flow

Figures 23 and 24 show canopy temperatures for June 28 and July 26. Temperatures were higher for the dryland population at the third sampling time for both dates but this difference was only 1°C . Canopy temperatures were rather uniform within treatments, but the populations never differed by over 1°C on dryland, and irrigated differences were non-existent. Remote sensing of plant canopies has the advantages of being rapid and also of averaging readings from many different plants.

The effect of irrigation on drought stress parameters is indicated in Table 6. All significant population by irrigation interactions are also indicated in Figures 2 through 24. Since no differential irrigation treatment had been imposed before June 14, 1984, the effect of irrigation could not be tested on that date.

Irrigation did not effect OP, %DW, leaf conductance, or diffusive resistance at the earliest sampling time, or leaf conductance or %DW at the latest sampling time on June 28, 1984. The only other case where additional water had no measurable effect was for IR canopy temperatures at the earliest sampling time on July 26, 1984. Irrigation effected 85% of the measurements reported in this study. Population by irrigation interactions occurred 30% of the time.

With irrigation, populations differed only 11% of the time while on dryland, populations differed 38% of the time. This demonstrates that it is much easier to compare these divergent barley selections on dryland than under irrigation.

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Table 1. Six-row barley varieties classified as resistant or susceptible to drought.

Variety	Number	Drought Response	Regression Slope	
			(B) (Eslick)	$\hat{y}_{10}$
Larker	12	Resistant	0.86	12.7
Steptoe	32	Resistant	(1.27)	(3.3)
Beecher	34	Resistant	0.86	12.3
Nordic	46	Resistant	0.50	12.7
Harlan	16	Susceptible	1.15	6.9
Hiland	18	Susceptible	1.14	7.3
Bonneville	26	Susceptible	1.04	9.2
Steveland	38	Susceptible	1.09	8.0

Table 2. Barley Reference Varieties: Mean values for parameters.
U.S.A., 1982.

MEASUREMENT		DATA MEANS			
Number	Type	16 Varieties		50 Varieties	
		"Resistant" (8)	"Susceptible" (8)	2-Row (25)	6-Row (25)
<u>Ψπ (-bars)</u>					
1	I	13	14	(15)	11
2	II	11	11	11	11
3	III	14	12	13	15
<u>Dry Down Rate</u> mg H ₂ O (<u>gFW min</u>)					
4	I	3.1	2.6	3.2	2.3
5	II	2.0	2.0	2.2	1.7
6	III	2.2	1.6	1.8	1.9
<u>% Dry Matter</u>					
7	I	22	20	24	20
8	II	22	21	21	21
9	III	26	21	24	24
<u>% Solute Leakage</u>					
10	I	78	71	76	78
11	II	59	59	65	57
<u>Regression (Stability)</u> <u>Analysis (Eslick)</u>					
12	$\hat{y}_{10} (y_0)$	13.2	7.2	10.8	10.6
13	Slope (b)	0.87	1.14	0.96	0.87
<u>Leaf</u> <u>Resistance (sec/cm)</u>					
14	(22 July, WY, A.M.) I	5.0	6.4	6.1	6.4
15	(29 July, MT, P.M.) II	4.7	6.8	4.6	4.7
16	(8 Aug., MT, A.M.) III	6.6	8.9	7.8	6.9

a) I, II & III refer to three different runs.

b) WY = Wyoming, 14 & 15 are from Eslick, other values from Bozeman, MT.

c) "Resistant" & "Susceptible" cultivars as hypothesized in the research proposal.

Table 3. Barley Reference Varieties: Significant correlation coefficients (p = .05 and p = .01**) among independent parameters. U.S.A., 1982.

	16 Varieties		50 Varieties		
	"Resistant" (8)	"Susceptible" (8)	2-Row (25)	6-Row (25)	All (50)
Dry Down Rate vs _____		+4vs2		+4vs2** +5vs1**	+4vs2 +5vs1**
% Dry Matter vs _____	+8vs3**	+8vs4 +9vs1		+7vs5 +9vs4 +9vs5	+9vs5
% Solute Leakage vs _____			-10vs2	+10vs2** +10vs4 +10vs5 +10vs8 +10vs9 -11vs5	+10vs6 +10vs2 +11vs7**
		-11vs3**			
Regression Analysis vs _____		-12vs8 +12vs11 -13vs11	-12vs2 -13vs11		
Leaf Resistance vs _____				+14vs4 +14vs5 +14vs9** -14vs11 -15vs10** -16vs10**	+14vs2 +14vs9 -14vs11** -15vs10** -16vs10**
	-14vs11 -15vs10 -16vs10	-15vs4 +16vs2 +16vs4 +16vs5	-14vs11 -15vs10 -16vs6 -16vs10** -16vs11**		

a) Numbers in the body of this table refer to Table 2.

b) Numbers 12 (predicted yield at a 10 bu/A yield level) & 13 (slope) are from Eslick (see research proposal), 14 is from Powell, Wyoming, all other data are from Bozeman, Montana.

c) "Resistant" & "Susceptible" cultivars as hypothesized in the research proposal.

Table 4. Results of analysis of variance for varieties and orthogonal comparisons of resistant (R) versus susceptible (S) varieties for physiological variables throughout 1983 growing season.

Date	Variable	ANOV P-Value	ORTH Comp. (R vs S) P-Value
<u>Powell, Wyoming</u>			
July 12	Total potential	.10	N.S.
July 27	" "	.01	.05
July 12	Osmotic potential	N.S.	N.S.
July 27	" "	.01	N.S.
July 12	IR Canopy Temp.	N.S.	N.S.
July 27	" " "	.03	N.S.
<u>Logan, Montana</u>			
July 7	Total potential	N.S.	N.S.
July 18	" "	N.S.	N.S.
July 25	" "	.02	N.S.
July 7	Osmotic potential	N.S.	N.S.
July 18	" "	N.S.	N.S.
July 25	" "	.08	N.S.
July 7	IR Canopy Temp.	N.S.	N.S.
<u>Bozeman, Montana</u>			
August 5	Total potential	N.S.	.08
August 16	" "	N.S.	N.S.
August 9	Osmotic potential	.01	N.S.
August 5	IR Canopy Temp.	.01	N.S.
August 5 (A.M.)	Porosity (Shimshi)	.01	.09
August 5 (P.M.)	" "	.01	.05
August 16 (A.M.)	" "	N.S.	.01
August 16 (P.M.)	" "	.02	N.S.
August 17 (A.M.)	" "	.01	.01
August 17 (P.M.)	" "	.01	.01
August 16 (A.M.)	Porosity (Li-Cor)	.01	.01
August 16 (P.M.)	" "	.01	.01
August 17 (A.M.)	" "	.01	.01
August 17 (P.M.)	" "	.01	.01
August 6	Flag leaf area	.01	.01
August 6	2nd Leaf area	.01	.01

Table 5. Mean standard deviation of individual observations, significance level, and number of observations (n) for two divergent barley populations grown for five generations under dry or irrigated conditions, tested at Powell, Wyoming in 1984. NS indicates significance levels above $p = .05$. OP = Leaf Osmotic Potential (-MPa); WP = Water Potential (-MPa); %DW = Leaf Dry Weight; LC = Leaf Conductance (cm/s) (Shimshi); LR = Leaf Resistance (S/cm) (LI-Cor); °C = Plant Canopy Temperatures (°C).

Variable	Means						SDx	Significance Level			N=	
	Dry		Wet		Wet	Dry		Wet	PI	Blocks		
	Dry	Wet	Dry	Wet								
	June 14											
WP1							1.15	1.01	0.26	.04	.01	0
WP2							1.17	1.18	0.17	NS	.01	60
WP3							3.40	4.19	1.33	.02	.01	60
LC1							2.27	2.16	0.92	NS	.02	60
LC2							3.32	2.27	1.71	.02	.02	60
LC3							--	--	--	--	--	0
LR1							4.56	4.20	1.00	NS	.01	60
LR2							3.05	3.05	0.80	NS	NS	60
LR3							--	--	--	--	--	0
°C1							20.92	20.83	0.39	NS	.02	12
°C2							--	--	--	--	--	0
°C3												
	June 28											
OP1	1.65	1.70	1.69	1.73	1.68	1.71	0.21	NS	NS	NS	NS	120
OP2	1.94	1.75	2.20	1.83	1.84	2.01	0.24	.01	.01	.05	NS	120
OP3	2.15	1.92	2.01	1.87	2.03	1.94	0.20	.01	.01	NS	.02	120
WP1	0.64	0.61	0.71	0.54	0.63	0.63	0.16	NS	NS	.02	.01	120
WP2	1.66	1.54	1.79	1.54	1.60	1.66	0.21	NS	.01	NS	NS	120
WP3	1.73	1.55	1.76	1.51	1.64	1.64	0.19	NS	.01	NS	.05	120
%DW1	21.14	21.55	22.37	21.97	21.34	22.17	3.11	NS	NS	NS	NS	120
%DW2	23.24	22.46	23.70	22.05	22.85	22.88	3.42	NS	.05	NS	NS	120
%DW3	24.03	23.09	22.49	22.15	23.56	22.32	2.27	.01	NS	NS	NS	120

(Table continued)

(Table continued)

Table 5 (cont.)

Variable	Means						SDx	Significance Level				N=
	Dry		Wet		Wet			Pop	Irr.	PI	Blocks	
	Dry	Wet	Dry	Wet	Dry	Wet						
LC1	1.09	1.11	1.02	0.96	1.10	0.89	0.86	NS	NS	NS	.02	120
LC2	1.77	8.38	2.07	10.14	5.08	6.10	7.50	NS	.01	NS	.01	120
LC3	1.32	1.63	1.88	1.95	1.47	1.91	1.46	NS	NS	NS	NS	120
LR1	11.63	13.23	15.60	11.43	12.43	13.52	13.52	NS	NS	NS	.01	120
LR2	3.23	2.23	2.17	2.00	2.73	2.08	1.59	.03	.04	NS	.03	120
LR3	8.07	4.47	5.57	4.23	6.27	4.90	3.16	.02	.01	.05	NS	120
°C1	15.22	14.48	15.09	14.16	14.85	14.62	0.28	.02	.01	NS	.02	36
°C2	21.86	20.43	21.37	20.84	21.14	21.11	0.44	NS	.01	.01	.05	36
°C3	29.61	26.11	28.60	25.99	27.86	27.29	0.62	.01	.01	.04	NS	60
July 12												
OP1	2.12	1.72	2.10	1.56	1.92	1.83	0.35	NS	.01	NS	.01	120
OP2	2.76	1.83	2.44	1.91	2.30	2.18	0.44	NS	.01	.01	.04	120
OP3	2.62	1.93	2.45	1.96	2.28	2.20	0.29	NS	.01	.04	.01	120
WP1	1.48	0.86	1.26	0.77	1.17	1.01	0.44	.05	.01	NS	.01	120
WP2	3.07	1.99	2.44	1.93	2.53	2.19	0.49	.01	.01	.01	.02	120
WP3	2.77	1.74	2.14	1.68	2.26	2.04	0.47	.04	.01	NS	NS	100
%DW1	28.38	24.10	26.98	22.92	26.24	24.95	3.58	.05	.01	NS	NS	120
%DW2	32.02	24.75	28.86	26.37	28.38	27.61	4.15	NS	.01	.01	.02	120
%DW3	30.41	25.75	28.05	25.94	28.08	26.99	3.77	NS	.01	NS	.02	120
LC1	1.41	3.02	1.32	3.23	2.21	2.28	1.51	NS	.01	NS	NS	120
LC2	5.36	24.45	3.26	27.10	14.91	15.23	13.49	NS	.01	NS	NS	120
LC3	4.88	5.07	2.51	6.80	4.98	4.65	5.71	NS	.03	.05	NS	120

(Table continued)

(Table continued)

Table 5 (cont.)

Variable	Means						SDx	Significance Level				N=
	Dry		Wet		Dry	Wet		Pop	Irr.	PI	Blocks	
	Dry	Wet	Dry	Wet								
				</								

Table 8. Mean, range, and standard deviation of individual observations, significance level, and number of observations (n) for 6-row barley reference varieties tested at Bozeman, MT in 1983 on dryland. NS indicates significance levels above $p = .05$. OP = Leaf Osmotic Potential (-MPa); WP = Water Potential (-MPa); %DW = Leaf Dry Weight; LC = Leaf Conductance (cm/s) (Shimshi); LR = Leaf Resistance (S/cm) (LI-Cor); °C = Plant Canopy Temperatures (°C).

Variable	Mean	Range	SDx	Significant Levels			
				Varieties	Block	R vs S	N=
<u>4 August 1983</u>							
Flag leaf area 2-row (cm ²)	2.80	1.75-4.32	1.17	**			
Flag leaf area 6-row (cm ²)	5.08	2.39-8.54	1.50	**			
2nd leaf area 2-row (cm ²)	8.24	5.60-11.74	2.11	**			
2nd leaf area 6-row (cm ²)	12.20	8.09-15.00	2.33	**			
2nd leaf length 2-row (cm ²)	94.69	78.00-114.6	18.44	**			
2nd leaf length 6-row (cm ²)	101.20	77.40-129.40	18.18	**			
Flag leaf width 2-row (cm ²)	7.40	5.85-9.20	1.35	**			
Flag leaf width 6-row (cm ²)	10.80	7.30-13.35	1.40	**			
2nd leaf width 2-row (cm ²)	10.28	8.05-13.00	1.14	**			
<u>5 August 1983</u>							
OP AM	1.64	1.29-2.02	0.17	**	--		75
OP PM	2.37	1.87-2.98	0.32	**	--		75
WP AM	14.14	1.23-1.64		**	--		50
WP PM	20.50	0.78-2.35	2.10	NS	--		50
LC AM	14.03	74-166		NS		*	90
LC PM	162.4	138.5-179.8	20.6	**		NS	90
°C AM	19.8	18.6-20.7		*	**	NS	120
°C PM	30.2	29.1-32.7	1.17	**	**	NS	120
Δ°C (PM-AM)	10.4	9.1-12.6		**	**	NS	

(Table continued)

Table 8 (cont.)

Variable	Mean	Range	SDx	Significant Levels			
				Varieties	Block	R vs S	N=
<u>16 August 1983</u>							
LC AM	3.99	3.11-4.79		**			100
LC PM	5.99	3.17-9.21	1.28	**			100
LR AM	.77	0.66-1.01		*			100
LR PM	1.50	0.98-2.13	0.11	**			100
°C AM	24.3	22.9-26.0		*			100
°C PM	30.0	29.5-30.5	1.24	NS			100
<u>17 August 1983</u>							
LC AM	6.62	5.49-7.83		**	--	**	100
LC PM	8.11	5.35-12.07	0.70	**	--	--	125
LR AM	1.15	0.86-1.31					
LR PM	1.74	1.30-2.40	0.11				
°C AM	23.4	22.0-24.2		NS	--		100
°C PM	28.9	28.4-29.4	0.43	NS	--		125

Table 9. Mean, range, and standard deviation of individual observations, significance level, and number of observations (n) for 6-row barley reference varieties grown at Logan, MT in 1983 on dryland. NS indicates significance levels above $p = .05$. OP = Leaf Osmotic Potential (-MPa); WP = Water Potential (-MPa); %DW = Leaf Dry Weight; LC = Leaf Conductance (cm/s) (Shimshi); LR = Leaf Resistance (S/cm) (LI-Cor); °C = Plant Canopy Temperatures (°C).

Variable	Mean	Range	SDx	Significant Levels			N=
				Varieties	Block	R vs S	
<u>7 July 1983</u>							
OP-AM	1.61	1.41-2.06	0.21	NS	--	50	
OP-PM	1.99	1.71-2.40		NS	NS	50	
WP-AM	1.30	1.05-1.50	0.21	NS	NS	100	
WP-PM	1.94	1.70-2.20		NS	NS	100	
IR-AM-2 row	15.3	15.0-15.9	0.54	NS	**	100	
IR-AM-6 row	15.2	14.8-15.8	0.41	NS	**	100	
IR-PM-2 row	34.5	32.9-36.5	1.14	.07	*	100	
IR-PM-6 row	34.5	33.0-35.6	1.01	NS	**	100	
<u>8 July 1983</u>							
WP-AM	1.69	1.43-2.41	0.35	NS	NS	50	
WP-PM	2.12	1.68-2.56		NS	NS	50	
<u>18 July, 1983</u>							
OP-AM	1.88	1.53-2.51	0.27	NS	NS	50	
OP-PM	2.15	1.77-2.71		NS	NS	50	
WP-PM	1.83	1.50-2.15		NS	NS	50	
IR-AM-2 row	29.7	27.7-30.8	1.41	NS	**	75	
IR-AM-6 row	29.8	29.0-30.7	1.10	NS	**	75	
<u>21 July 1983</u>							
OP-AM	1.94	1.74-2.38	0.27	NS	NS	75	
OP-PM	2.46	1.56-2.71	0.43	.09	NS	75	
WP-PM	1.94	1.52-2.36	0.25	.02	NS	75	
<u>Final Grain Yield (Kg/ha)</u>							
25 6-row	1,582	934-1,864	276	**	NS	100	
25 2-row	1,479	1,002-1,900	298	**	NS	100	

Table 10. Mean, range, and standard deviation of observations and significance levels for 6-row barley varieties at Powell, WY in 1983. NS indicates significance levels above $p = .05$. OP = Leaf Osmotic Potential (-MPa); WP = Water Potential (-MPa); %DW = Leaf Dry Weight; LC = Leaf Conductance (cm/s) (Shimshi); LR = Leaf Resistance (S/cm) (LI-Cor); °C = Plant Canopy Temperatures (°C).

Variable	Mean	Range	SDx	Significant Levels			
				Varieties	D vs W	Block	N=
<u>7 July 1983</u>							
WP-AM	0.98	0.52-1.44		NS			
WP-AP	2.25	1.01-2.75	0.22	NS			
°C-AM	22.8	21.3-23.9	0.2	NS			
°C-PM	34.3	32.7-36.3	0.6	*			
<u>12 July 1983</u>							
WP-AM	1.00	0.67-1.38	0.16	NS	*	--	100
WP-PM	2.13	1.85-2.40	0.10	NS	*	--	100
°C-AM	19.8	19.1-21.0	2.73	NS		**	75
°C-PM	30.6	29.3-32.6	3.58	NS		**	75
<u>27-29 July 1983</u>							
OP-AM Dry	3.30	2.59-4.39	0.89	**	--	NS	69
OP-PM Dry	3.10	2.38-3.89	0.71	**	--	NS	70
Dry WP PM	2.37	2.01-2.92	0.29	**	--	**	100
27 JL DP	29.85	28.3-33.7		NS		NS	75
°C WP	29.80	28.0-33.5	1.20	NS	NS	NS	50
28 JL DA	26.2	25.1-28.0		NS		**	50
°C DP						**	50
29 JL WA	26.2	24.7-27.3	2.37	NS	NS	**	50
°C WP							25
29 JL DA	21.49	20.0-23.0		NS	**	**	50
°C WA	23.57	22.0-22.5	2.51				50
<u>Mean Grain Yields</u>							
Dryland = 1,913 kg/ha							
Irrigated = 2,704 kg/ha							
<u>Maturity Ratings 27 July 85</u>							
1 = all green plants							
5 = most plant tissue non-green							
27 JL Maturity							
Rating Dryland	2.34	1.17-3.33	0.61	**		*	75

Table 11. Mean, range, and standard deviation of individual observations, significance level, and number of observations (n) for 6-row barley varieties at Bozeman, MT in 1984 on dryland. NS indicates significance levels above $p = .05$. OP = Leaf Osmotic Potential (-MPa); WP = Water Potential (-MPa); %DW = Leaf Dry Weight; LC = Leaf Conductance (cm/s) (Shimshi); LR = Leaf Resistance (S/cm) (LI-Cor); °C = Plant Canopy Temperatures (°C).

Variable	Mean	Range	Significance Levels			
			SDx	Varieties	Reps	Blocks
<u>July 7, 1983</u>						
OP1	1.85	1.56-2.26	.163	**	**	*
OP2	2.21	1.92-2.60	.202	*	NS	NS
OP3	2.33	1.88-2.72	.213	*	NS	NS
WP1	0.84	0.43-1.12	.169	*	**	**
WP2	1.67	0.38-1.88	.207	NS	NS	NS
WP3	1.78	0.97-3.62	.720	NS	NS	NS
%DW1	21.1	16.1-24.7	2.4	*	NS	**
%DW2	21.3	15.3-27.3	3.7	*	NS	NS
%DW3	22.5	17.8-27.9	3.0	NS	NS	NS
LC1	15.72	6.8-30.1	5.25	NS	NS	NS
LC2	18.13	5.0-121.3	14.81	NS	NS	*
LC3	11.46	1.7-31.0	5.61	NS	NS	NS
LR1	4.50	1.4-14.5	1.62	**	**	**
LR2	3.25	0.9-7.4	1.68	NS	NS	NS
LR3	4.13	0.9-24.3	3.02	NS	NS	NS
°C1	--	--	--	--	--	--
°C2	24.3	23.3-25.4	0.51	**	**	*
°C3	25.9	24.3-27.4	0.69	**	**	*

(Table continued)

Table 11. (cont.)

Variable	Mean	Range	Significance Levels			
			SDx	Varieties	Reps	Blocks
<u>July 19, 1984</u>						
OP1	1.805	1.540-2.00	0.14	NS	NS	NS
OP2	21.12	1.880-2.42	0.22	NS	NS	NS
OP3	23.64	2.120-2.67	0.18	NS	*	NS
OP4	22.64	1.970-2.61	0.20	NS	*	NS
WP1	.195	.03-.50	0.11	NS	*	NS
WP2	1.79	0.60-2.80	0.33	.07	**	**
WP3	2.05	1.42-2.82	0.25	NS	NS	NS
WP4	2.00	1.04-2.59	0.24	NS	NS	NS
%DW1	24.4	19.8-26.7	2.6	NS	NS	NS
%DW2	25.6	21.0-30.6	3.6	NS	*	NS
%DW3	27.3	23.3-30.5	3.0	NS	*	NS
%DW4	25.5	19.6-29.5	4.4	NS	NS	NS
LC1	2.76	0.3-13.3	1.95	NS	**	NS
LC2	2.42	0.9-6.0	1.24	NS	NS	NS
LC3	2.57	0.7-9.0	1.96	NS	NS	NS
LC4	0.91	0.3-2.6	0.41	NS	*	**
LR4	369	181-999	165	NS	*	NS
°C1	12.2	10.9-13.6	0.62	NS	NS	NS
°C2	22.8	21.0-24.3	0.72	NS	**	**
°C3	24.8	23.1-28.1	0.87	NS	NS	NS
°C4	27.3	26.3-31.3	0.71	NS	NS	NS

(Table continued)

Table 11. (cont.)

Variable	Mean	Range	Significance Levels			
			SDx	Varieties	Reps	Blocks
<u>August 2, 1984</u>						
WP-1	0.18	0.02-0.42	.09	NS	NS	
WP-2	1.84	0.98-2.70	.33	NS	**	
WP-3	2.42	1.90-3.50	.31	NS	**	
LC-1	111.8	0.3-195	81.8	NS	**	
LC-2	13.6	0.7-65	18.6	NS	*	
LC-3	1.22	0.3-6.7	0.9	NS	NS	
°C-1	10.6	10.0-11.3	0.3	.10	NS	
°C-2	22.9	20.6-25.5	1.0	.09	*	
°C-3	25.6	22.2-28.0	1.2	NS	NS	
<u>Grain Yields (Kg/ha)</u>						
6-row Varieties	2,930	1,474-4,159	504	**	NS	
2-row Varieties	2,557	1,106-4,834	446	**	*	

Table 12. Mean, range, and analysis of variance for 6-row barley varieties grown at Three Forks, MT on dryland in 1984. NS indicates significance levels above $p = .05$. OP = Leaf Osmotic Potential (-MPa); WP = Water Potential (-MPa); %DW = Leaf Dry Weight; LC = Leaf Conductance (cm/s) (Shimshi); LR = Leaf Resistance (S/cm) (LI-Cor); °C = Plant Canopy Temperatures (°C).

Variable	Mean	Range	Significance Levels			
			SDx	Varieties	Reps	Blocks
<u>June 22, 1984</u>						
OP1						
OP2	1.97	1.54-2.45	0.29	NS	**	NS
OP3	2.23	1.60-2.83	0.50	NS	NS	NS
WP1	1.00	.84-1.29	1.44	NS	NS	**
WP2	0.84	.69-0.98	1.03	NS	**	**
WP3	1.56	.96-2.05	3.51	NS	NS	*
%DW1						
%DW2	20.6	14.1-26.8	2.4	**	**	*
%DW#	23.1	15.0-29.2	4.4	NS	NS	NS
LC1	52.5	32.8-91.4	26.0	NS	NS	NS
LC2	49.6	28.5-108.1	19.5	NS	.06	NS
LC3	54.5	32.8-79.3	22.9	NS	**	NS
LC4	45.1	28.6-85.3	19.3	NS	**	NS
LR1						
LR2	4.3	2.7-5.9	1.7	NS	NS	NS
LR3	3.6	1.6-5.6	1.3	NS	NS	NS
LR4	4.4	1.6-7.1	1.6	NS	**	NS
°C1	9.1	8.3-9.1	0.3	NS	**	**
°C2	18.1	17.2-18.8	0.4	**	NS	NS
°C3	21.1	19.4-23.7	1.5	NS	NS	NS

(Table continued)

Table 12 (cont.)

Variable	Mean	Range	Significance Levels			
			SDx	Varieties	Reps	Blocks
July 3, 1984						
OP1	1.63	1.39-1.94	0.14	*	**	NS
OP2	1.78	1.51-21.2	0.13	**	NS	NS
OP3	1.88	1.69-2.47	0.17	**	NS	*
OP4	2.04	1.61-2.49	0.13	**	NS	*
WP1	0.38	0.18-0.56	0.11	*	**	*
WP2	1.38	1.11-1.63	0.15	NS	*	**
WP3	1.56	0.96-2.05	0.35	NS	NS	*
WP4	1.88	1.65-2.18	0.22	NS	**	**
%DW1	22.7	17.7-30.1	1.6	**	**	**
%DW2	23.3	17.7-29.2	4.2	NS	NS	NS
%DW3	24.5	19.9-29.7	2.3	**	NS	**
%DW4	25.1	19.8-30.40	2.5	**	*	*
LC1	1.51	0.30-3.90	1.26	NS	NS	NS
LC2	5.39	2.00-13.70	3.62	NS	**	NS
LC3	5.12	2.60-8.80	2.77	NS	**	NS
LC4	4.54	0.50-8.90	2.82	NS	**	NS
LR1	--	--	--	--	--	--
LR2	4.53	2.70-5.90	1.71	NS	NS	NS
LR3	3.48	1.60-5.60	1.32	NS	NS	NS
LR4	4.04	1.60-7.10	1.59	NS	**	NS
°C1	8.8	8.3-9.1	0.3	NS	**	**
°C2	18.2	17.2-18.8	0.4	**	*	NS
°C3	21.2	19.4-23.7	1.5	NS	NS	NS
°C4	22.2	20.9-24.2	0.7	*	**	NS

(Table continued)

Table 12 (cont.)

Variable	Mean	Range	Significance Levels			
			SDx	Varieties	Reps	Blocks
<u>July 17, 1984</u>						
WP1	0.62	0.16-0.89	0.18	*	**	
WP2	1.67	1.38-2.03	0.29	NS	NS	
WP3	1.94	1.50-2.38	0.29	NS	NS	
LC1	2.28	0.40-8.60	1.56	NS	NS	
LC2	3.56	0.70-12.4	2.63	NS	NS	
LC3	2.44	0.20-28.1	4.2	NS	**	
LR1						
LR2	16.30	6.20-46.2	8.07	NS	NS	
LR3						
°C1	11.1	7.7-11.9	0.15	NS	NS	
°C2	24.5	23.6-27.0	0.14	NS	**	
°C3						
<u>August 1, 1984</u>						
OP1	2.35	1.95-2.92	0.30	NS	**	NS
OP2	3.10	2.63-4.07	0.55	NS	NS	NS
OP3	3.15	2.60-4.12	0.55	NS	NS	NS
WP1	1.24	0.71-1.98	0.43	NS	NS	NS
WP2						
WP3						
%DW1	29.4	23.2-33.3	3.5	NS	NS	NS
%DW2	34.7	28.8-39.8	5.3	NS	NS	NS
%DW3	35.4	28.0-42.9	4.5	NS	NS	NS
LC1	.97	0.50-1.80	0.71	NS	*	NS
LC2	1.80	0.30-7.30	2.40	NS	NS	NS
LC3	.70	0.10-2.20	.83	NS	NS	NS
°C1						
°C2	28.3	26.8-30.2	1.3	NS	NS	*
°C3	30.9	28.9-32.7	1.2	NS	NS	NS
<u>Grain Yield (Kg/ha)</u>						
25 6-row	2,029	917-2,615	306	**	--	NS

Table 13. Means, ranges, and analysis of variance for 6-row barley varieties grown at Powell, WY on dryland and under irrigation in 1984. NS indicates significance levels above $p = .05$. OP = Leaf Osmotic Potential (-MPa); WP = Water Potential (-MPa); %DW = Leaf Dry Weight; LC = Leaf Conductance (cm/s) (Shimshi); LR = Leaf Resistance (S/cm) (Li-Cor); °C = Plant Canopy Temperatures (°C). N=75.

Variable	DRYLAND					IRRIGATED						
	Mean	Range	SDx	Significant Level			Mean	Range	SDx	Significant Level		
				Variety	Rep	Block				Variety	Rep	Block
June 27, 1984												
OP1	1.71	1.40-2.55	.37	*	*	NS	1.76	1.13-2.42	.33	NS	NS	NS
OP2	2.45	2.17-2.81	.33	NS	NS	NS	2.17	1.73-2.62	.26	NS	*	NS
OP3	2.55	2.07-2.94	.04	NS	**	NS	2.20	1.92-2.79	.17	**	NS	NS
WP1	.59	.19-.83	.25	NS	*	*	.39	.20-.67	.12	**	**	NS
WP2	1.71	1.42-2.16	.24	NS	NS	NS	1.61	1.34-1.94	.16	*	**	*
WP3	1.93	1.47-2.36	.30	NS	NS	NS	1.66	1.47-2.03	.16	NS	NS	*
%DW1	26.9	19.7-32.2	2.7	**	NS	NS	26.2	22.2-30.9	2.9	*	NS	*
%DW2	28.3	24.2-32.4	4.3	NS	NS	NS	28.2	23.7-32.1	2.6	*	*	NS
%DW3	27.9	21.3-32.4	3.0	NS	NS	NS	26.2	20.3-31.1	3.2	NS	*	NS
LC1	26.2	13.2-63.3	19.8	NS	**	NS	46.6	28.6-85.5	22.7	NS	**	NS
LC2	2.3	0.2-15.4	5.5	NS	NS	NS	20.2	3.6-44.1	15.0	NS	*	NS
LC3	1.7	0.1-52	2.1	NS	**	NS	4.0	0.1-15.1	5.3	NS	*	NS
LR1	6.0	2.3-18.0	7.4	NS	**	**	2.71	1.0-10.1	2.4	NS	**	*
LR2	4.9	1.2-8.6	2.8	NS	NS	NS	1.54	0.7-5.1	1.0	NS	NS	NS
LR3	9.4	1.1-41.6	10.0	*	NS	NS	2.88	1.0-7.7	1.6	NS	NS	NS
°C1							20.91	20.0-21.8	0.4	*	**	**
°C2	22.7	21.1-23.9	1.1	NS	**	NS	22.97	25.6-27.4	0.7	NS	NS	NS
°C3	30.8	28.2-32.8	1.7	NS	*	NS	26.51	25.7-27.6	0.7	NS	NS	NS

(Table continued)

Table 13. (cont.)

Variable	DRYLAND				IRRIGATED									
	Mean	Range	SDx	Significant Level			Block	Mean	Range	SDx	Significant Level			
				Variety	Rep	Block					Variety	Rep	Block	
July 11, 1984														
OP1	2.67	1.87-3.63	.75	NS	NS	NS	NS	1.17	1.57-2.37	.20	*	NS	NS	NS
OP2	3.61	2.69-4.90	.75	NS	NS	**	**	1.94	2.03-2.79	.31	NS	NS	NS	NS
OP3	3.99	2.43-5.42	.91	**	**	*	*	2.59	1.84-3.94	.66	NS	NS	NS	NS
WP1	1.71	1.05-2.82	.73	NS	NS	NS	NS	1.17	0.76-1.55	.28	NS	**	*	*
WP2	2.48	1.76-3.20	.52	NS	NS	NS	NS	1.94	1.59-2.31	.27	NS	*	*	NS
WP3	--	--	--	--	--	--	--	1.32	1.07-1.67	.26	NS	(**)	(**)	NS
%DW1	34.0	21.1-49.1	7.9	NS	**	**	**	28.2	22.2-39.5	5.2	NS	NS	NS	NS
%DW2	36.0	30.0-43.0	4.7	NS	**	**	**	28.6	23.3-31.2	3.6	NS	NS	NS	NS
%DW3	39.0	27.9-49.3	5.2	*	**	**	**	31.0	25.5-43.9	6.6	NS	NS	NS	NS
LC1	1.8	0.2-4.4	1.6	NS	*	NS	NS	3.6	1.1-6.7	2.5	NS	**	**	NS
LC2	1.5	0.2-3.7	1.7	NS	NS	NS	NS	2.1	0.3-4.6	1.8	NS	NS	NS	NS
LC3	1.7	0.3-3.5	1.3	NS	NS	NS	NS	1.6	0.6-3.4	0.8	NS	NS	NS	NS

(Table continued)

Table 13. (cont.)

DRYLAND				IRRIGATED									
Variable	Mean	Range	SDx	Significant Level			Variable	Mean	Range	SDx	Significant Level		
				Variety	Rep	Block					Variety	Rep	Block
July 25, 1984													
							OP1	1.52	1.33-1.75	.21	NS	NS	NS
							OP2	2.30	1.77-2.61	.43	NS	NS	NS
							OP3	2.48	1.44-3.55	.65	NS	NS	**
							WP1	3.1	0.7-7.60	.20	NS	NS	NS
							WP2	1.86	1.43-2.61	.37	NS	NS	*
							WP3	1.79	1.05-2.38	.20	**	NS	NS
							%DW1	27.3	22.9-31.6	4.2	NS	NS	NS
							%DW2	31.2	26.2-37.9	4.1	NS	NS	NS
							%DW3	42.6	32.4-56.4	9.3	NS	NS	NS
							LC1	5.1	0.5-13.90	3.6	**	NS	NS
							LC2	3.4	0.4-6.90	2.7	NS	NS	NS
							LC3	3.1	0.2-9.50	2.8	NS	*	NS
							°C1	19.65	18.8-20.0	0.26	*	**	**
							°C2	30.43	29.4-32.4	0.73	*	*	*
							°C3	29.10	27.6-30.5	0.69	NS	**	*
Grain Yield (Kg/ha)													
							6-row-Dry	1,052	419-1,587	406	NS		
							6-row-Irr	1,640	916-2,149	337	*		
							2-row-Dry	1,244	821-1,739	488	NS		
							2-row-Irr	1,774	1,243-2,266	363	*		

Table 14. Correlation coefficients for reference barley variety regression coefficients, grain yield at Powell, WY and Logan, MT and for leaf water potentials, leaf osmotic potentials, and plant canopy temperatures. WP, OP, and °C are averages for all days at all three locations, 1983. (1 and 20 degrees of freedom.)

	Yld-Pow	Yld-Log	Yld-E	Slope-E	Slope-B	Slope-F	WP-AM	WP-PM	OP-AM	OP-PM	°C-AM	°C-PM
Yld-Powell	1.000											
Yld-Logan	+.44/*	1.000										
Yld-E	-.38/.07	-.02/NS	1.000									
Slope-E	+.38/.07	-.02/NS	-.99/**	1.000								
Slope-B	+.32/NS	+.15/NS	-.11/NS	+.06/NS	1.000							
Slope-F	+.49/*	-.04/NS	-.88/**	.88/**	+.26/NS	1.000						
WP-AM	-.16/NS	-.02/NS	+.41/.06	-.48/*	+.02/NS	-.42/.06	1.000					
WP-PM	+.12/NS	-.12/NS	-.03/NS	+.04/NS	-.33/NS	+.02/NS	-.19/NS	1.000				
OP-AM	-.07/NS	-.02/NS	-.03/NS	+.03/NS	-.21/NS	+.06/NS	+.30/NS	+.33/NS	1.000			
OP-PM	-.24/NS	+.15/NS	+.45/*	-.46/*	+.01/NS	-.38/.07	+.38/07	+.01/NS	+.12/NS	1.000		
°C-AM	+.39/.06	+.29/NS	+.01/NS	-.05/NS	+.17/NS	+.08/NS	+.08/NS	+.21/NS	+.41/.06	-.08/NS	1.000	
°C-PM	+.12/NS	-.00/NS	+.04/NS	-.08/NS	+.12/NS	-.08/NS	+.08/NS	-.12/NS	-.05/NS	+.21/NS	+.26/NS	1.000
DRO #	-.11/NS	-.14/NS	-.02/NS	-.07/NS	-.08/NS	-.04/NS	+.48/*	-.34/NS	-.06/NS	-.12/NS	+.27/NS	+.34/NS

Fig. 1. Regression lines from Eslick's analysis for eight varieties. The lower left corner of the graph is enlarged showing the relative values of Y10.

Fig. 2. Leaf osmotic potential of divergent barley populations evaluated at Powell, WY on June 28, 1984. The first letter refers to population (Dry or Wet) while the second refers to irrigation treatment in 1984 (Dryland or Wet). PD indicates that populations differed on dryland while PI indicates a population-irrigation interaction.

Figs. 3 & 4. Leaf osmotic potential of divergent barley populations evaluated at Powell, WY on July 12 and 26, 1984.

Figs. 5 & 6. Leaf water potential of divergent barley populations evaluated at Powell, WY on June 14 and 28, 1984.

Figs. 7 & 8. Leaf water potential of divergent barley populations evaluated at Powell, WY on July 12 and July 26, 1984.

Fig. 9. Percent leaf dry weight of divergent barley populations evaluated at Powell, WY on June 28, 1984.

Figs. 10 & 11. Percent leaf dry weight of divergent barley populations evaluated at Powell, WY on July 12 and 26, 1984.

Fig. 12. Calculated leaf pressure potential for divergent barley populations evaluated at Powell, WY on June 28, 1984.

Figs. 13 & 14. Calculated pressure potential for divergent barley populations evaluated at Powell, WY on July 12 and 26, 1984.

Figs. 15 & 16. Shimshi leaf conductance for divergent barley populations evaluated at Powell, WY on June 14 and 28, 1984.

Figs. 17 & 18. Shimshi leaf conductance for divergent barley populations evaluated at Powell, WY on July 12, and 26, 1984.

Figs. 19 & 20. Li-Cor leaf resistance for divergent barley populations evaluated at Powell, WY on June 14 and 28, 1984.

LEAF CONDUCTANCE: SHIMSHI VS LI-COR

LEAF CONDUCTANCE: SHIMSHI VS LI-COR

Figs. 21 & 22. Comparison of Shimshi and Li-Cor leaf conductances for divergent barley populations evaluated at Powell, WY on June 14 and 28, 1984.

Figs. 23 & 24. Infrared plant canopy temperatures of divergent barley populations evaluated at Powell, WY on June 28 and July 26, 1984.

RESEARCH CONDUCTED IN ISRAEL

Seedling Tolerance to Drought Stress

Sixteen barley varieties were chosen for this study. These varieties were among the ones classified by Eslick for their relative drought resistance in terms of productivity - using the standard Finley and Wilkinson "stability analysis". Three local Israeli wheat varieties and one local barley variety were included in the test.

Seedlings of each entry were grown in hydroponics in the growth chamber. Two treatments were applied: (1) growth in a nutrient solution with a water potential of 7 bars of PEG 6000 (stress) and (2) growth in pure nutrient solution (control, non-stress). The relative growth rates (RGR) of seedlings grown in the two media were determined. The extent of injury to seedling growth rate by stress was calculated as:

$$\text{Injury (\%)} = [(N-S)/N] \times 100,$$

where N and S were the relative growth rates in control and stress media, respectively.

The results obtained as well as the essential parameters of the stability analysis according to Eslick, are presented in Table 1.

The various entries differed significantly in the extent of injury to seedling growth by drought stress. No correlation was revealed across varieties between the extent of injury to seedling growth by stress and the potential (non-stress) seedling growth rate. Thus, seedling vigor under non-stress conditions was not predictive of varietal response to seedling stress.

No consistent relationship was revealed between drought resistance in terms of productivity (Eslick's analysis) and seedling drought tolerance in terms of growth rate.

The wheat cultivars tested were relatively medium or high in their susceptibility to seedling drought stress. Several of the barley cultivars such as 'Beecher', 'Hector', 'Compana', and 'Vireo', were relatively tolerant to seedling drought stress as well as relatively drought resistant in terms of plant production.

Table 15.

Variety	Injury by stress (%)	Non-stress growth rate (mg/plant/day)	Stability analysis	
			Regression slope (b)	YD ⁺
H-895 (wheat)	48.8	29.7	----	----
Ingrid	41.5	37.3	1.05	9.1
Maris Mink	35.2	45.1	1.50	-0.5
Hiland	34.5	37.6	1.14	7.3
Steptoe	29.1	30.0	1.27	3.3
Dekap	25.2	46.0	0.86	13.2
Bonneville	23.3	45.4	1.04	9.2
676 (Wheat)	22.8	28.6	----	----
Nordic	18.4	30.8	0.50	22.3
Barkace (Wheat)	17.9	25.7	----	----
Larker	17.0	33.9	0.86	12.7
Steveland	16.3	37.3	1.09	8.0
Vireo	15.5	28.8	0.72	20.5
Klages	14.3	32.5	1.04	9.3
Campana	14.1	34.3	0.84	12.5
Ruth (local)	9.9	38.9	----	----
Zephyr	7.9	30.2	1.12	7.2
Harlan	5.6	29.6	1.15	6.9
Hector	0.3	31.0	1.04	9.1
Beecher	0	30.8	0.86	12.3
LSD (P=0.05)	19.7			

⁺YD - predicted yield (bu/A) at a mean site yield level of 10 bu/A.

PHOTOSYNTHESIS AND TRANSPIRATION IN LEAVES, SPIKES, AND SPIKE COMPONENTS
OF UNIQUE GROUPS OF WHEAT AND BARLEY VARIETIES

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ABSTRACT

Carbon exchange rate (CER) and transpiration were measured in flag leaves, spikes, glumes (referring to the total area of glumes and lemmas) and awns, in 6 hexaploid spring wheats (Triticum aestivum L.), 7 tetraploid spring wheats (T. turgidum L.), 8 six-rowed barleys (Hordeum vulgare L.), and 5 two-rowed barleys (H. vulgare L.).

Differences among varieties and groups in total spike CER and transpiration were associated largely with differences in spike surface area rather than with rates per unit area. Spikes were less efficient than flag leaves in CER per unit area, by about 40 to 80%, depending on the group. Transpiration per unit area was less in spikes than in flag leaves by about the same proportion. However, since spike surface area was greater than flag leaf area by a factor of 1.1, 3.9, 5.5, and 4.4, in hexaploid wheat, tetraploid wheat, six-rowed barley, and two-rowed barley, respectively, total spike CER reached up to 90% of that of the flag leaf.

The contribution of awns to total spike CER depended largely on total awn surface area per spike, rather than on CER per unit awn area. Awn contribution to total spike CER was about 40 to 80%, depending on the group, while its contribution to total spike transpiration was only 10 to 20%. Thus, while transpiration ratio (CER/transpiration) was about the same in flag leaves and glumes, it was higher than both, by several orders of magnitude, in the awns.

A large amount of awns in the spike was therefore taken as a drought adaptive attribute in these cereals, where tetraploid wheat exceeded hexaploid wheat and six-rowed barley exceeded two-rowed barley, in this respect.

INTRODUCTION

Both the flag leaf and the inflorescence have a major role in affecting cereal grain yields. This has been shown, for example, by Simpson (1968), where the area above the flag leaf node was positively and highly correlated with grain yield across 120 wheat (Triticum aestivum L.) strains. While the area of the flag leaf is indeed important in this respect (Monyo and Whittington, 1973), the rate of carbon exchange per unit flag leaf area may also affect the yield variations among varieties of cereals (Shimshi and Ephrat, 1975; Brinkman and Frey, 1978).

The relative contribution of the spike to cereal grain yield has been dealt with and reviewed quite extensively (Evans, Wardlaw and Fischer, 1975). Estimates range anywhere from 13% (Biscoe et al., 1975) to 76% (Evans and Rawson, 1970), depending on the plant, the environment, and the experimental procedures. Undoubtedly, the spike assumes a greater role than flag leaves in supplying assimilate to the grain when water stress

develops (Evans et al., 1972; Johnson and Moss, 1976). The better ability of spikes than of leaves to supply assimilate to the grain under conditions of water stress depends partly on the greater availability to the grain of spike assimilate than of flag leaf assimilate (Carr and Wardlaw, 1965) and largely on the water relations of the spike. Spikelets maintain a higher water potential than leaves under conditions of water stress (Morgan, 1977) and they are more consistent than leaves in osmotic adjustment (Morgan, 1980). This has also been demonstrated by the fact that the spike becomes the major site for transpiration in severely water stressed wheat (Blum, Mayer and Gozlan, 1983).

The photosynthetic capacity of the spike is a function of its total green surface area, including the awns (Thorne, 1965; Derera and Stoy, 1973; Teare et al., 1972). The difference in spike surface area, as a function of the amount of awns, accounted for the greater spike photosynthesis in a barley variety (Hordeum vulgare L.) than in a wheat variety, at various levels of plant water potential (Johnson, Frey and Moss, 1974). In compiling the available data at the time, Grunbacher (1957) already concluded that the importance of awns in supplying carbohydrates to the grain increases as water stress develops. He cited results by Grantham (1919) from 26 tests of 1986 wheat strains, where awned strains yielded more than awnless strains, mainly because the former had less shrivelled grain. While most of the later work served to establish the same fact by using physiological parameters, the physiological advantage of the awns under conditions of water stress remains unclear. Based on limited anatomical observations, Grunbacher (1975) concluded that the awn has distinct xeromorphic features, such as a thick epidermis and cuticle and the predominance of sclerophyllous and conductive tissues. It is therefore unclear

why Teare et al. (1972) found that transpiration ratio (photosynthesis/transpiration) was greater in awnless than in awned isogenic lines of wheat.

This study was carried out in order to collect comparative data on photosynthesis and transpiration in flag leaves, spikes, and spike components of several distinct groups of cereals. In view of the reported differences in flag leaf photosynthesis among wheats of different ploidy levels and different evolutionary stages (Evans and Dunstone, 1970; Dunstone, Gifford and Evans, 1973; Austin, Mortan and Ford, 1982), tetraploid and hexaploid wheats were compared, among others, in this study.

MATERIALS AND METHODS

Plants used in this study were grown in a normal, non-stressed, disease-free field environment at Bet Dagan, during December-May 1983/84. Each variety was grown in one plot, 8 m long and 2 m wide.

A total of 6 hexaploid spring wheats (T. aestivum L.), 7 tetraploid spring wheats (T. turgidum L.), 8 six-rowed spring barleys (H. vulgare L.), and 5 two-rowed spring barleys (H. vulgare) were tested (Table 1). Four Triticum dicoccoides accessions, collected in the wild in various parts of Israel, were included among the tetraploid wheats.

Ten spike-bearing main stems were sampled from each variety, upon the onset of anthesis. Whole stems were placed with their cut end in water and brought to an air-conditioned laboratory, where temperature was 19 to 22 C and irradiance was 55 Watt.m^{-2} . The time elapsed between sampling and gas exchange measurement was 2 to 4 hrs, with replications distributed along time.

A closed system was used for carbon exchange and transpiration measurements, as described previously (Sullivan and Blum, 1985). Detached spikes were placed upright (in pairs) inside a 4.5 liter air-tight perspex chamber, with the peduncle passing through an air-tight silicon-rubber stopper into a beaker of water. The detached flag leaf lamina, connected to a section of its sheath with the enclosed stem section was placed in a perspex frame, so as to keep it flat. It was then placed horizontally, about 5 cm above the bottom of the chamber, with the leaf sheath section passing through an air-tight silicon-rubber stopper into water. The chamber contained a "Cole-Parmer" temperature-hygrometer probe. A heating element was connected to one of the walls inside the chamber. A small DC-operated fan vigorously mixed the air inside the chamber. The chamber was placed under a 750 Watt "Philips" mercury vapor lamp, giving $480 \text{ Watt} \cdot \text{m}^{-2}$ at 5 cm above the bottom of the chamber.

A leaf or a spike (pair) sample (five replications per variety) was placed in the chamber and the light was turned on. External air was pumped through a CO_2 and humidity trap (KOH pellets) into the chamber, in order to reduce initial CO_2 concentration to 310 ± 10 ppm and relative humidity to $35 \pm 5\%$. The desirable chamber temperature was attained by applying current to the heating element until a temperature of 24°C was reached. During the measurement period temperature was raised by the radiant energy to a maximum of 25.5°C . An equilibration period of 5 min was then initiated. Previous tests have shown that this time interval was sufficient for achieving a steady state of carbon exchange and transpiration. An air sample of 6 cc was then drawn from the chamber with a syringe through a minute hole, and 5 cc was injected into a "Beckman" infrared gas analyzer, for the measurement of CO_2 concentration, according to Clegg, Sullivan, and

Eastin (1978). The procedure was repeated after 10 min. Each time an air sample was drawn, chamber temperature and relative humidity were recorded and used for calculating transpiration rate.

After gas exchange measurement, organ area was measured. Flag leaf area was calculated from linear measurements of length and width. Spike surface area was measured and calculated after Teare and Petersen (1971), with respect to glumes, lemmas and awns. Since the green area of the palea is difficult to measure and since it is relatively insignificant in terms of total area per spike (Teare and Petersen, 1971), and net contribution to gas exchange (Evans and Rawson, 1970), it was accounted for by adding 2% to the total area of glumes and lemmas, which is hereon referred to as "glumes". Measurements were performed in each spike in four spikelets, two at the basal quarter and two at the apical quarter of the spike, and the average values were multiplied by the number of spikelets per spike. After surface area measurements the awns were clipped off and the spikes were returned to the chamber for gas exchange measurements. The difference in gas exchange between the same awned and de-awned spikes allowed the partitioning of gas exchange between awns and "glumes". The possible effect of awn clipping per se on gas exchange was evaluated in one wheat variety ('Bethlehem') and one barley variety ('Ruth'). Gas exchange was measured in de-awned spikes and in spikes where all the awns were carefully coated with a layer of silicon-grease. The results for both carbon exchange rate and transpiration in the two treatments were statistically (5 replications) the same.

Statistical analysis of the data was performed through SAS program (Cary, North Carolina).

RESULTS

Means and ranges for the various variables are presented in Table 2 and the summary of the analysis of variance in Table 3.

Flag Leaf

Carbon exchange rate (CER) per unit leaf area ranged across all varieties from 6.8 to 32.1 mg dm⁻² with significant differences within each group. Crops and groups within a crop did not differ significantly in this respect. Total flag leaf CER was higher in wheat than in barley and higher in hexaploid than in tetraploid wheat. The differences between wheat and barley, in this respect, could be related to the smaller flag leaf area in barley, rather than to a difference in CER or unit area. The correlation coefficient (across all varieties) between total flag leaf CER and leaf area was 0.812 (p=0.0001), while the correlation between total flag leaf CER and CER per unit leaf area was only 0.423 (p=0.035). CER per unit leaf area was not correlated with flag leaf area (r=-0.099).

The four T. dicoccoides accessions differed significantly in CER per unit leaf area, within a range of 6.8 to 17.4 mg dm⁻²h⁻¹. CER per unit leaf area ranged from 8.1 to 11.1 mg dm⁻²h⁻¹ in the cultivated tetraploid wheats and from 8.5 to 21.8 mg dm⁻²h⁻¹ in the cultivated tetraploid wheats.

T. dicoccoides, as represented by the mean over the four accessions, did not differ in CER per unit leaf area from either the cultivated tetraploid or the hexaploid wheat.

Transpiration per unit flag leaf area differed significantly among all varieties, within a range of 226 to 1076 mg dm⁻²h⁻¹. Crops and groups within a crop did not differ significantly in this respect. T. dicoccoides was not different in this respect from either the cultivated tetraploid and the hexaploid wheat, with a range of 447 to 1076 mg dm⁻²h⁻¹, across the

four accessions. Mean total flag leaf transpiration was significantly higher in wheat than in barley, due mainly to a larger flag leaf area in wheat. Flag leaf transpiration ratio (CER/Transpiration) ranged across all varieties from 0.0108 to 0.1445, with significant differences among varieties within each group. No significant differences were revealed in transpiration ratio between crops and between groups within a crop. The highest transpiration ratio was observed among the wheats in cv. 'Bethlehem' (0.0544) and among the barleys in cv. 'Ruth' (0.1445). Flag leaf transpiration ratio was better correlated (across all varieties) with total flag leaf CER ($r=0.807$, $p=0.001$) than with total flag leaf transpiration ($r=-0.645$, $p=0.005$).

Spike

Mean total spike CER was 2.4, 3.8, 2.6, and 1.8 mg h^{-1} , in hexaploid wheat, tetraploid wheat, six-rowed barley, and two-rowed barley, respectively. The awnless hexaploid wheat ('Florence/Aurore') had a value of 1.6 mg h^{-1} . Total spike CER amounted to 31.6, 90.6, 86.7, and 78.3% of the total flag leaf CER, in hexaploid wheat, tetraploid wheat, six-rowed barley, and two-rowed barley, respectively. The low value in hexaploid wheat could be accounted for by the relatively high total flag leaf CER. Crops and groups within a crop differed significantly in total spike CER. Wheat was higher than barley; tetraploid was higher than hexaploid wheat; and six-rowed was higher than two-rowed barley, in this respect. These differences were not associated with respective differences in CER per unit glume area or CER per unit awn area (Table 3), although varieties differed significantly for each of these two variables, within each group. An examination of Tables 2 and 3 shows that differences between crops and between groups within a crop in total spike CER were largely associated

with respective differences in organ area. The differences in total spike CER between hexaploid and tetraploid wheat was associated with a respective significant difference in total glume and total awn area per spike. The difference in total spike CER between six-rowed and two-rowed barley was associated with a respective significant difference in total awn area per spike. The correlations presented in Table 4 support the conclusion that the variations among varieties in total spike CER were largely affected by variations in the area of spike organs, rather than by variations in CER per unit organ area. Glumes were more important in wheat and awns more important in barley, in this respect.

The contribution of awns to total spike CER was 48.7, 44.5, 78.7, and 48.3% in hexaploid wheat, tetraploid wheat, six-rowed barley, and two-rowed barley, respectively. This value was significantly higher in six-rowed barley mainly because it had the highest proportion of awns in total spike area (67.4%), as compared with the other three groups (49.6 to 58.4%).

CER per unit spike area was appreciably lower than CER per unit flag leaf area, amounting to 27.2, 23.1, and 19.3% in hexaploid, tetraploid, six-rowed barley, and two-rowed barley, respectively. These ratios were the same statistically and surprisingly consistent, when the large and significant variations among varieties in each of the two variables are considered. Some insight into the nature of this consistency in ratios may be gained by the observation that a positive and a significant correlation was found across all varieties between CER per unit leaf area and CER per unit glume area ($r=0.759$, $p=0.0001$). When genetic variation is considered, the glumes apparently behave in a correlative manner as the flag leaf, with respect to carbon exchange.

Mean total spike transpiration was 87, 160, 89, and 73 mg h⁻¹, in hexaploid wheat, tetraploid, wheat, six-rowed barley, and two-rowed barley, respectively. The awnless hexaploid varieties ('Florence/Aurore') had a rate of 117 mg h⁻¹. Mean total spike transpiration as percent of mean total flag leaf transpiration in the four groups was 29.4, 63.4, 62.6, and 76.8%, respectively. The ratio was significantly lower in hexaploid wheat as it had a relatively larger flag leaf area. The spike transpiration was higher in wheat than in barley and higher in tetraploid than in hexaploid wheat. The six-rowed and two-rowed barley were not different in this respect.

The greater total spike transpiration in wheat than in barley (Table 3) could be ascribed mainly to a higher total glume transpiration per spike, as affected by a larger glume area per spike, in wheat. The greater total spike transpiration in tetraploid than in hexaploid wheat could be ascribed mainly to a larger glume and awn area per spike in the tetraploid wheat, even though it was relatively inferior in transpiration rate per unit spike area. The correlations between total spike transpiration and its components (Table 5) support the conclusion that organ area rather than rates per unit area control genotypic differences in total spike transpiration.

The variations among varieties in transpiration per unit spike area were not large, but were significant among the tetraploid wheats and among the two-rowed barleys.

Transpiration rate per unit spike area was appreciably smaller than transpiration rate per unit flag leaf area, amounting to 26.5, 16.0, 11.0, and 18.3%, in hexaploid wheat, tetraploid wheat, six-rowed barley, and two-rowed barley, respectively.

The contribution of awns to total spike transpiration was appreciably smaller than that for CER, reaching only 11.4, 12.9, 21.4, and 23.5% in hexaploid wheat, tetraploid wheat, six-rowed barley, and two-rowed barley, respectively.

Transpiration ratio was higher in awns than in either glumes or flag leaves, by several orders of magnitude (Table 2). It was similar for the spike and the flag leaf, except for two-rowed barley, where the ratio was significantly higher in the flag leaf than in the spike. Crops and groups within a crop did not differ significantly in transpiration ratio of spike, glumes, or awns. Across all varieties, spike transpiration ratio was better correlated with total spike CER ($r=0.574$, $p=0.008$) than with total spike transpiration ($r=0.234$). Flag leaf transpiration ratio was better correlated with glume transpiration ratio ($r=0.930$, $p=0.0001$) than with awn transpiration ratio ($r=-0.306$).

DISCUSSION

The large and significant variations among varieties in most of the variables studied in this work underline the importance of sampling as many varieties as possible when seeking conclusions on a crop species or a group within a crop.

Total spike CER, as measured in this experiment, ranged in the various varieties from 0.9 to 6.4 mg h^{-1} , and it corresponded very well with values reported by others (Thorne, 1963; Teare et al. 1972; Johnson and Moss, 1974). Although varieties differed in CER per unit spike area, the difference among varieties, among groups within a crop, and among crops in total spike CER were largely affected by corresponding differences in spike area. The relative importance of glumes or awns, in this respect, was determined

by their relative proportions to the spike. Thus, for example, glumes were relatively more important in wheat than in six-rowed barley. The same conclusions are true also for spike transpiration.

Spikes were less efficient than flag leaves in CER per unit area, by about 80%. Transpiration rate was also less in spikes than in flag leaves, by about the same proportion. Teare, Law, and Simmons (1972) found that the total number of stomata in the wheat spike was only about 3 to 16% of the number in the flag leaf. Regretfully, they did not present values on stomata number per unit area. However, since spike area was at least as high as flag leaf area in this experiment, it can be concluded that stomatal density is far lower in the spike than in the flag leaf. This would account, at least partly, for the reduced rates of gas exchange in the spike, relative to the flag leaf.

In spite of the spike's low efficiency in CER per unit area it is an important source of carbon to the grain, mainly because of its relatively large area. Spike area was greater than flag leaf area by a factor of 1.1, 3.9, 5.5, and 4.4, in hexaploid wheat, tetraploid wheat, six-rowed barley, and two-rowed barley, respectively. The ratio of 1.1 in hexaploid wheat corresponds very well with data of Teare and Peterson (1971), for what they defined as "long awned" (hexaploid) wheats. McDonough and Gauch (1959) reported that the surface area of awns was equal to that of the ground surface. Data of this experiment, calculated for a reasonable spike density of 300 per m^2 , show that the area of spikes per unit ground area was 1.64, 4.41, 3.16, and $1.84 m^2 m^{-2}$ and the area of awns was 0.81, 2.57, 2.12, and $1.02 m^2 m^{-2}$, in hexaploid wheat, tetraploid wheat, six-rowed barley, and two-rowed barley, respectively. While these values may be slightly biased upwards due to measurements being limited to main spikes

and not including tiller spikes, they are still impressively high, especially for the tetraploid wheat and the six-rowed barley. Flag leaf area per unit of ground area ranged only within 0.42 to 1.45 m²m⁻², in the four groups.

Awn contribution to the total spike CER was around 40 to 80%, in the various groups, and it was proportional to the amount of awns in the spike, rather than to CER per unit awn area. In contrast, awn contribution to total spike transpiration was only around 10 to 20%. Hence, while transpiration ratio was about the same in glumes and in flag leaves, it was exceedingly higher than in both the awns. The importance of awns is therefore two-fold. They contribute largely to the photosynthetic area of the spike and they are highly efficient in water use.

The physiological uniqueness of the awn is exemplified also by the fact that variations across varieties in CER per unit area were correlated between the glumes and the flag leaf, but not correlated between the awns and either the glumes or the flag leaf. While the awn appears to show xeromorphic features (Grundbacher, 1957), the physiological basis for its high water-use efficiency remains to be explored.

A large amount of awns in the spike may be considered as a drought adaptive attribute in these cereals. By this criterion, tetraploid wheat is better adapted than hexaploid wheat, while six-rowed barley is better adapted than two-rowed barley. Still, the large variations in this respect among varieties within a group should be noted. Some of these variations were quite striking. For example, all of the hexaploid wheats, cv. 'Bethlehem' (previously reported also as selection '676') had the highest percent awns in total spike area and the highest transpiration ratio in both the spike and the flag leaf. This variety was specifically selected

for dryland conditions and its drought resistance has been established in both agronomical (Blum, 1983) and physiological (Blum, Mayer and Gozlan, 1983) terms.

This study did not show an influence of ploidity level or evolution on CER per unit flag leaf area at anthesis (Evans and Durnstone, 1970; Austin, Morgan and Ford, 1982) or on CER per unit spike area. The primitive T. dicoccoides did not differ in this respect from either the tetraploid or the hexaploid cultivated wheats. It was rather characterized by the large variations in CER per unit flag leaf area among the four accessions tested, which is typical of the large genetic diversity in this species (Nevo, Golenberg and Beiles, 1982). The results obtained here lend support to those of Holbrook, Keys and Leech (1984) who did not find a difference in the biochemistry of photosynthesis among tetraploid and hexaploid wheats. The reason for the disagreement among studies at this point may lie in the fact that while others measured intact leaves (Evans and Dunstone, 1970; Morgan and Ford, 1982), detached leaves were measured in this study. Dunstone, Gifford and Evans (1973) proposed that CER per unit flag leaf area can be different in wheats of different ploidity levels due to the existence of active sinks at the time of measurement in some wheats (such as growing tillers in diploid wheats). Work with detached leaves would therefore disassociate CER measurements from such interactions. This may be supported by the fact that while negative correlations were found between CER per unit leaf area and leaf area in intact leaves (Planchon, 1979; Austin, Morgan and Ford, 1982; Blum and Sullivan, 1985) no such correlation was found for detached leaves in this study.

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Table 1. Varieties of wheat and barley used in the experiment, all of which, except one, are awned.

Variety	Origin	Notes
<u>Hexaploid wheat (T. aestivum L.)</u>		
Barkaee	Israel	Dwarf
Miriam	"	Semi-dwarf
Bethlehem	"	"
H-895	"	"
Lachish	"	"
Florence/Aurore	North-Africa	Tall, awnless
<u>Tetraploid wheat (T. turgidum)</u>		
Inbar	Israel	Semi-dwarf
Nursi	"	Tall
Zenati/Bouteille	North-Africa	Tall
G-595	"	"
G-425	"	"
G-467	"	"
G-494	"	"
<u>Six-rowed barley (H. vulgare L.)</u>		
Larker	USA	Tall
Beecher	"	Tall
Steptoe	"	Tall
Nordic	"	Tall
Harlan	"	Tall
Steveland	"	Tall
CB 572	Mexico/Israel	Tall
CB 42	"	Tall
<u>Two-rowed barley (H. vulgare L.)</u>		
Ruth	Israel	Tall
Dekap	USA	Tall
Hector	"	Tall
Klages	"	Tall
CB 886	Mexico/Israel	Tall

Table 2. Means and ranges for 27 flag leaf and spike variables in hexaploid wheat, tetraploid wheat, six-rowed barley, and two-rowed barley. Data for the awnless wheat not included.

Variable	Unit	Hexaploid wheat			Tetraploid wheat			Six-row barley			Two-row barley		
		Mean±SD	Range		Mean±SD	Range		Mean±SD	Range		Mean±SD	Range	
Flag leaf area	cm ²	48.1±9.8	32.0-55.1*		38.1±9.4	21.4-69.2**		19.0±7.5	11.6 - 30.4		13.9±7.1	5.8 - 25.0**	
CER per unit leaf area	mg dm ⁻² h ⁻¹	16.6±5.4	8.5-21.8*		11.7±4.0	6.8-17.4**		14.7±5.6	8.3-26.4*		17.6±9.8	8.3-32.1**	
Total CER per flag	mg h ⁻¹	7.6±2.2	4.3-9.9*		4.2±2.0	2.0-7.1**		3.0±2.2	1.2-7.6**		2.3±1.6	0.8-4.9**	
Transpiration per unit leaf area	mg dm ⁻² h ⁻¹	60.4±17.8	38.9-81.3*		630 ± 208	47-1076**		778±203	54.6-1076**		694±303	226-1000**	
Total transpiration per flag leaf	mg h ⁻¹	295±137	146-441**		252±152	97-465**		142±43	81-209**		95±78	34-231**	
Transpiration ratio, flag leaf	--	0.0306±0.0178	0.0125-0.0544**		0.0202±0.0100	0.0108-0.0360**		0.0207±0.0100	0.0112-0.0371*		0.0422±0.0573	0.0115-0.1445**	
Total glumes area per spike	cm ²	27.8±5.9	23.7-38.1		61.1±11.7	4.4-81.7*		34.2±11.0	20.4-56.1*		27.3±14.6	14.2-48.4**	
Total awns area per spike	cm ²	27.0±3.1	23.5-30.3		85.8±15.7	3.3-115.0*		70.7±15.8	39.0-89.0*		33.9±11.3	17.0-43.1*	
Total spike area	cm ²	54.9±8.1	47.2-68.4		146.9±21.0	22.5-173.5		105±23.5	63.0-145.5*		61.2±24.4	31.2-91.6*	
Awns in total spike area	%	49.6±3.7	44.4-54.1		58.4±5.8	51.9-66.6		67.4±6.1	61.6-80.0		56.6±7.8	47.0-68.0	
CER per unit glume area	mg dm ⁻² h ⁻¹	4.7±3.2	1.6-9.0**		3.2±1.7	1.1-5.4**		2.1±3.3	0.1-10.2**		4.2±4.6	1.3-12.3**	
CER per unit awn area	mg dm ⁻² h ⁻¹	3.8±2.0	1.4-7.0**		2.1±2.0	0.3-5.9**		3.0±1.1	0.6-4.4*		2.3±1.4	1.0-4.3**	
CER per unit spike area	mg dm ⁻² h ⁻¹	4.5±1.6	2.7-6.1		2.7±0.9	2.0-4.6*		3.4±1.1	2.5-5.9*		3.4±1.5	1.9-5.0**	
Total CER in glumes per spike	mg h ⁻¹	1.4±1.1	0.4-3.0**		1.9±0.9	0.5-3.2**		0.5±0.6	0.08-2.1**		1.0±0.9	0.3-2.4**	
Total CER in awns per spike	mg h ⁻¹	1.0±0.6	0.4-2.0**		1.8±1.7	0.2-5.1**		2.1±0.8	0.5-3.1**		0.8±0.5	0.3-1.6**	
Total CER per spike	mg h ⁻¹	2.4±0.8	1.4-3.4**		3.8±1.2	3.1-6.4**		2.6±0.6	1.8-3.5*		1.8±0.6	0.9-2.7*	
Awns CER/total spike CER	%	48.7±27.7	12.3-71.3**		44.5±30.6	6.5-84.0**		78.7±24.8	18.7-97.9**		48.3±31.2	10.3-85.3**	
Transpiration per unit glume area	mg dm ⁻² h ⁻¹	2.78±4.9	2.36-3.61		2.28±5.0	3.1-2.85*		2.06±2.7	1.72-2.45		2.36±1.70	3.2-4.67**	
Transpiration per unit awn area	mg dm ⁻² h ⁻¹	3.4±2.1	1.3-6.9*		2.6±1.7	5.4-9**		2.9±2.7	6-91**		5.4±8.7	7-209**	
Transpiration per unit spike area	mg dm ⁻² h ⁻¹	1.60±1.7	1.40-1.74		1.01±3.1	88-128**		8.7±3.3	60-156*		1.27±3.7	66-162*	
Total transpiration in glumes per spike	mg h ⁻¹	77±20	56-99		138±31	77-201**		69±15	49-96*		56±34	6-95**	
Total transpiration in awns per spike	mg h ⁻¹	9±6	4-20		22±14	6-41**		20±20	3-66*		16±24	1-59**	
Total spike transpiration	mg h ⁻¹	87±17	67-107		160±45	83-231**		89±18	73-23**		73±23*	49-100*	
Awns transpiration/total spike transpiration	%	11.4±8.6	3.8-25.8**		12.9±7.0	4.4-23.6**		21.4±16.9	4.4-53.9**		23.5±37.6	2.3-90.6**	
Transpiration ratio, glumes	--	0.0186±0.0139	0.0044-0.0361**		0.0153±0.0095	0.0039-0.0310**		0.0093±0.0139	0.0012-0.0424**		0.0853±0.1704	0.0033-0.3901**	
Transpiration ratio, awns	--	0.1316±0.0896	0.0532-0.2842**		0.1086±0.0958	.0101-0.2514**		0.2144±0.1929	0.0188-0.5342**		0.1843±0.1756	0.0048-0.4545**	
Transpiration ratio, spike	--	0.0289±0.0123	0.0150-0.0427*		0.0252±0.0101	.0154-0.0431**		0.0293±0.0032	0.0242-0.0337		0.0249±0.0096	0.0174-0.0410*	

*,** Differences among varieties within a group are significant at p>0.05 and p>0.01, respectively.

Table 3. Summary of the analysis of variance for 27 flag leaf and spike variables, comparing crops and groups within a crop. Data for the awnless wheat variety not included.

Variable	Unit	Differences between wheat and barley	Differences among groups with a crop	
			Hexaploid vs. tetraploid	Six-row vs. two-row
Flag leaf area	cm ²	** (W) ^a	NS	NS
CER per unit leaf area	mg dm ⁻² h ⁻¹	NS	NS	NS
Total CER per flag	mg h ⁻¹	** (W)	** (H)	NS
Transpiration per unit leaf area	mg dm ⁻² h ⁻¹	NS	NS	NS
Total transpiration per flag leaf	mg h ⁻¹	** (W)	NS	NS
Transpiration ratio, flag leaf	--	NS	NS	NS
Total glumes area per spike	cm ²	* (W) ^a	** (T)	NS
Total awns area per spike	cm ²	NS	** (T)	** (S)
Total spike area	cm ²	NS	** (T)	** (S)
Awns in total spike area	%	* (B)	** (T)	** (S)
CER per unit glume area	mg dm ⁻² h ⁻¹	NS	NS	NS
CER per unit awn area	mg dm ⁻² h ⁻¹	NS	NS	NS
CER per unit spike area	mg dm ⁻² h ⁻¹	NS	NS	NS
Total CER in glumes per spike	mg h ⁻¹	* (W)	NS	NS
Total CER in awns per spike	mg h ⁻¹	NS	NS	NS
Total CER per spike	mg h ⁻¹	* (W)	** (T)	* (S)
Awns CER/total spike CER	%	NS	NS	* (S)
Transpiration per unit glume area	mg dm ⁻² h ⁻¹	NS	NS	NS
Transpiration per unit awn area	mg dm ⁻² h ⁻¹	NS	NS	NS
Transpiration per unit spike area	mg dm ⁻² h ⁻¹	NS	* (H)	NS
Total transpiration in glumes per spike	mg h ⁻¹	** (W)	** (T)	NS
Total transpiration in awns per spike	mg h ⁻¹	NS	NS	NS
Total spike transpiration	mg h ⁻¹	** (W)	** (T)	NS
Awns transpiration/total spike transpiration	%	NS	NS	NS
Transpiration ratio, glumes	--	NS	NS	NS
Transpiration ratio, awns	--	NS	NS	NS
Transpiration ratio, spike	--	NS	NS	NS

*,** Significant mean squares at p>0.05 and p>0.01, respectively.

^a Letters in parentheses designate the superiority of one group over the other, where W-wheat, H-hexaploid, T-tetraploid, and S-six-rowed.

Table 4. Correlations (r), across varieties, between total spike CER and four components of total spike CER, in wheat and barley.

Crop	CER per unit area		Total area per spike	
	Glumes	Awns	Glumes	Awns
Wheat	-0.001	0.121	0.611*	0.456
Barley	-0.019	0.187	0.374	0.721*

* Coefficient of correlation significant at $p > 0.05$.

Table 5. Correlations (r), across varieties, between total spike transpiration and four components of total spike transpiration, in wheat and barley.

Crop	Transpiration per unit area		Total area per spike	
	Glumes	Awns	Glumes	Awns
Wheat	-0.054	0.049	0.876**	0.502
Barley	0.049	0.004	0.485	0.586*

*, ** Coefficient of correlation significant at $p > 0.05$ and $p > 0.01$, respectively.

EVALUATION OF THE RESEARCH ACHIEVEMENT

The objectives proposed for this project were:

1. To develop genetically broad-based, drought-resistant barley germplasm for use by plant breeders.
2. To evaluate population breeding in barley, under controlled drought resistance in barley.
3. To evaluate possible barley drought resistance mechanisms.

(Relate these to barley yield performance under stress.)

Blum, in 1982 (Table 15) measured barley seedling growth reduction from drought stress imposed by -0.7 MPa PEG6000 solution. Growth reduction ranged from 0 to 42%. The barley cultivars Beecher, Hector, Compana, and Vireo were tolerant to drought stress as predicted. There was no consistent relationship, however, between Eslick's regression analysis ratings and seedling stress tolerance.

Blum (report & 1985 reprint) reported that differences in awn and total ear photosynthesis and transpiration were associated more with surface area than with differences in rates. For photosynthetic rate (CER) the ratio of awn/total ear averaged 79% for 6-row barley versus 48% for 2-row barley which was more comparable to wheat. The ratio CER/-transpiration for barley averaged 50% higher than for wheat and was 4 to 10 times higher for barley awns (2-row and 6-row, respectively) than for barley flag leaves. His work supports the importance of awns to drought resistance in both barley and wheat. Blum's work supports objective 3 above.

Also in support of objective 3, reference varieties were evaluated in the USA for several physiological parameters. Measurements included membrane damage from an osmoticum, water potentials from pressure-volume work,

plant dry-down rates, osmotic potentials from a thermocouple psychrometer, water potential from a pressure bomb, leaf moisture content, Shimshi leaf conductance to air flow, Li-Cor leaf resistance, and IR plant canopy temperatures. The work was done all 3 years rather than the first 2 as proposed. The first year of the project we studied all 50 reference varieties rather than just the 16 proposed. The second and third years of the project we evaluated all 25 of the 6-row lines in the field after 1982 results suggested that physiological parameters gave more correlations with 6-row barleys.

Correlation coefficients among average values for all measured physiological parameters, regression coefficients, and grain yields at the two dryland sites were presented for 22 reference varieties (Table 14). All four regression parameters, Y10, slope E, slope B, and slope F were related to grain yield at Powell, WY ($p=0.10$), but not to grain yield at Logan, MT. Using the same average values, three of four regression coefficients were related to water potential in the morning ($p=.06$), while three of four coefficients are related to osmotic potential in the afternoon ($p=.07$) and slope B is correlated with PM canopy temperatures. These results suggest guarded optimism for the use of regression analysis to predict relative grain yields under stress. Regression coefficients are also related to physiological measurements in a number of instances (Table 14).

Differences were obtained between the dryland and irrigated populations after five selection cycles. These differences, which were exhibited more often on dryland than under irrigation, are best explained by Figures 2 through 24. Considering only the dryland (rainfed) comparisons, for osmotic potential, water potential, and percent leaf dry weight, the magnitude of measured values (sign ignored) for the dryland population

exceeded values for the irrigated population three of four times. These results and the significant population by irrigation interactions suggest complex interactions among drought stress parameters. Leaf canopy temperatures differed significantly by the last sample time both dates but this difference was only about 1°C.

We are very encouraged by these results and plan to release these two divergent selections to scientists after one or two more selection cycles. These populations should be useful to both plant breeders and physiologists.

DESCRIPTION AND RESULTS OF COOPERATION

A. Blum contributed greatly to the development of the research planning both before and during the project. He taught J. Brown his exosmosis technique and also demonstrated the use of a remote infrared thermometer to measure plant canopy temperature.

J. Brown was able to visit Israel where he observed, photographed, and learned to use the Shimshi leaf porometer as well as specially designed leaf punches. He also visited the major cereal production areas. Brown supplied Blum with seed of 16 reference varieties which he used in his studies. Using some of the same barley cultivars makes work done in the two countries more comparable.