# Drought Resistance
# in Spring Wheat Cultivars. III*
# Yield Associations with Morpho-physiological Traits

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*Abstract*

This paper describes associations between yield performance under drought and morpho-physio-logical traits, determined both under drought and non-drought conditions, for a large set of diverse cultivars of bread wheat (*Triticum aestivum* L.), durum wheat (*T. turgidum* L.), triticale (X *Tritosecale* Wittmack) and barley (*Hordeum vulgare* L). Performance under drought was considered in terms of grain yield and drought susceptibility, the latter being proportional to the decrease in yield relative to yield without drought.

Species effects are considered, but greatest attention is paid to associations amongst bread wheat cultivars ($n = 34$), based on phenotypic and genotypic correlations, multiple linear regression and principal components analysis. Under drought, which reduced yield on average 60%, greater yield was most closely associated with greater total dry weight at maturity. Variation in traits associated with plant water relations had only a minor influence. The best prediction of yield under drought, from traits measured in the absence of drought (non-drought traits), was given by a linear model containing total dry weight, kernel weight and leaf waxiness, all with positive coefficients.

Drought susceptibility, as defined, was unrelated to plant water relations under drought, but was related to various non-drought traits. It increased with increased non-drought yield, harvest index, kernels per sq metre, kernels per spike and leaf water potential, and with decreased plant height and waxiness. One part of these associations with drought susceptibility appeared to be related to variation in height, probably arising from the action of the Norin 10 dwarfing genes; part, however, was independent of height. The relationships suggested that direct selection for increased yield in the absence of drought, or selection via most of the non-drought traits, increased drought susceptibility and, depending on drought level, may increase or decrease yield under drought. No trait had clearly desirable effects on yield both in the absence of drought and drought susceptibility; total dry weight appeared to have the least undesirable effect on susceptibility.

## Introduction

Field experiments were conducted in north-western Mexico in which large and diverse sets of cultivars of wheat (*Triticum aestivum* L., *T. turgidum* L.), triticale (X *Tritosecale* Wittmack) and barley (*Hordeum vulgare* L.) were subjected to unrelieved drought in the latter half of the growing cycle. There were significant and consistent differences between cultivars in yield under drought ($Y_d$) and in an index ($S$) of drought susceptibility (Fischer and Maurer 1978). The latter was calculated after allowing for differences in yield potential ($Y_p$) as indicated by yield in the absence of drought. $S$, hereafter termed drought susceptibility, is proportional to $(1 - Y_d/Y_p)$ as seen in the following relationship:

$$Y_d = Y_p(1 - SD), \qquad (1)$$

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where $D$ is drought intensity, given by

$D = 1 - $(av. yield of all cultivars under drought)/(av. yield of all cultivars without drought).

Many studies have attempted to relate differences in the yield performance of temperate cereal cultivars under drought to numerical components of yields or to aspects of plant morphology such as awnedness or height (see reviews by Hurd 1974; Schmidt 1975). Because of the lack of rapid techniques until recently, only a few studies (Kaul 1969; Kaul and Crowle 1971, 1974; Shimshi and Ephrat 1972; Sojka 1974; Jones 1977) have included explicit consideration of differences in plant water relations. In our case, a special effort was made to measure morpho-physiological aspects of each cultivar in the largest of the drought experiments. Included were measurements of crop development, growth and morphology, components of yield, and, with the aid of rapid techniques, plant water relations. The preceding paper (Fischer and Sanchez 1979) examined drought and genotypic effects on plant water relations, including leaf water and osmotic potentials and leaf permeability, while the earlier paper (Fischer and Maurer 1978) covered drought effects on crop growth and yield components. Here we examine briefly genotypic variation in growth and yield components, and then in more detail, associations between yield performance under drought and all measured traits.

Since $S$ is an adjustment of $Y_d$ for differences in $Y_p$, it should be the best indicator of the presence of drought resistance mechanisms in cultivars and is therefore of greatest interest to physiologists. Wheat breeders may be more concerned with high $Y_d$, regardless of how it is achieved. For this reason trait associations with both $Y_d$ and $S$ are examined. Relationships with traits measured under non-drought as well as drought conditions are considered, because of interest in predicting performance under drought from information gathered in the absence of drought.

## Materials and Methods

The experiment, fully described by Fischer and Maurer (1978, experiment 3), was conducted during the 1974–75 season at CIANO (Centro de Investigaciones Agricolas del Noroeste) in Sonora, Mexico. There was an irrigated control treatment (non-drought or wet), and three unrelieved drought treatments of differing intensity resulting from irrigation termination at different dates before anthesis; results of drought treatments are averaged and known as drought or dry. A total of 53 cultivars (34 bread wheats, 6 durum wheats, 7 triticales and 6 barleys) were chosen to represent likely diversity in adaptation to drought, e.g. wheat *v.* barley; tall old dryland cultivars *v.* modern dwarf cultivars bred under irrigated conditions. There were three replications.

*Traits Associated with Crop Development, Growth and Morphology*

Traits relating to crop development, growth and morphology (see Table 1) included anthesis and maturity dates (AD and MD, respectively, as days from sowing) and total weight of above-ground material at maturity (TDW, g m$^{-2}$), as described in Fischer and Maurer (1978). Grain-filling days (GFD = MD − AD) was calculated. At 20 days after the mean date of anthesis, which was 13 March, all plots were scored for the degree of leaf waxiness (WAX, scale 0 to 3, 3 = most wax), and for spike tipping (STIP). Spike tipping often occurs in wheat with drought at around spike emergence; it was common on certain cultivars here and the percentage loss of spikelets (over all

spikes) was estimated. Plant height to the spike tip excluding awns (HT in centimetres), was measured on all plots just before maturity. The presence of awns was ignored as a variable in this study because all but five cultivars were awned. Finally, in order to examine the importance of differences in photosynthetic area between cultivars, the green ground cover (GC) of each plot was estimated visually on a 0–10 scale (10 = full cover) every week commencing on 6 March. Green cover at anthesis (GCA) was estimated by interpolation, and the duration of green cover from anthesis to maturity (GCD, days) was calculated by summation. The average persistence of green cover after anthesis (GCP, days) was calculated (GCP = GCD/GCA).

**Table 1.** Morpho-physiological traits considered in relationships to yield under drought and to drought susceptibility

| Trait | Units | Abbreviation |
|---|---|---|
| *Yield performance* | | |
| Grain yield or grain dry weight | $g\ m^{-2}$ | $Y$, GDW |
| Drought susceptibility | ratio | $S$ |
| *Development, growth and morphology* | | |
| Days from sowing to 50% anthesis | days | AD |
| Days from sowing to 50% maturity | days | MD |
| Duration of grain-filling | days | GFD |
| Mature plant height | cm | HT |
| Green ground cover on March 6 (0–10) | 0–10 scale | GC |
| Green ground cover at 50% anthesis | 0–10 scale | GCA |
| Mean persistence of green ground cover after anthesis | days | GCP |
| Duration of green ground cover, anthesis–maturity | days | GCD |
| Total dry weight at maturity | $g\ m^{-2}$ | TDW |
| Spike tipping | % | STIP |
| Waxiness | 0–3 scale | WAX |
| *Yield components* | | |
| Grain dry weight per unit of GCD | $g\ m^{-2}\ d^{-1}$ | $G$ |
| Harvest index | % | HI |
| Spike number per unit area | $m^{-2}$ | SNO |
| Kernels per spike | — | KPS |
| Kernel number per unit area | $m^{-2}$ | KNO |
| Kernel weight | mg | KW |
| *Plant water relations* | | |
| Leaf water potential | bars | $\psi$ |
| Leaf permeability | $\sqrt{(1000\ cm^2\ g^{-1}\ s)}$ | LP |
| Leaf osmotic potential | bars | $\pi$ |
| Leaf turgor pressure | bars | $P$ |

*Yield and Yield Components*

At maturity, $1\cdot8\ m^2$ was harvested from the centre of each plot for measurement of TDW and the dry weight of grain (GDW, $g\ m^{-2}$; also wet GDW $= Y_p$, dry GDW $= Y_d$). Two random samples of 100 kernels were weighed to give kernel weight (KW, mg); grain or kernel number (KNO, 100 $m^{-2}$) and harvest index (HI = GDW/TDW) were calculated. Spike number (SNO, $m^{-2}$) was counted on $0\cdot6\ m^2$ of plot several weeks

before harvest; kernels or grains per spike (KPS) were calculated. Finally, grain yield per unit green cover duration after anthesis ($G = \text{GDW} \times 10/\text{GCD}$, g m$^{-2}$ d$^{-1}$) was calculated.

### Plant Water Relations

When all cultivars or all bread wheat cultivars are being considered, we use several averages of leaf water potential ($\psi$, bars) and leaf permeability (LP, arbitrary units) as outlined in the preceding paper (Fischer and Sanchez 1979). Briefly they are as follows: wet $\psi$, wet LP (non-drought samplings); dry $\psi$, dry LP (drought samplings); early $\psi$, early LP (early samplings—mostly pre-anthesis); and mean $\psi$, mean LP (all samplings). The last three averages are considered dry traits since these averages are dominated by drought treatments.

Additional samplings of $\psi$ and LP, as well as measurements of leaf osmotic potential ($\pi$, bars) were made in the case of 17 cultivars, which were considered representative of the diversity of the whole cultivar set (Fischer and Sanchez 1979). Averages across samplings of $\psi$, LP, $\pi$, and turgor potential ($P = \psi - \pi$, bars), for each of these so-called representative cultivars were calculated in a similar manner to that listed above. Note that $\psi$ and $\pi$ are negative numbers, generally decreasing with increased water limitation.

### Genotypic Effects

We consider briefly species effects, passing then to within-species effects, where most attention is paid to relationships for bread wheat cultivars. These are grouped into height classes (tall, E1, E2 etc.) as described earlier (Fischer and Maurer 1978) to facilitate examination of the major variation in mature plant height, due largely to effects of Norin 10 dwarfing genes. Another key trait was anthesis date, since early anthesis favoured a degree of drought escape (Fischer and Maurer 1978). Before examination of genotypic associations, all dry traits, including $S$, were corrected by covariance analysis for differences in anthesis date as measured under the wet conditions. Generally this procedure weakened associations discernible in the data, but strong associations resulting from the familiar advantage of earliness would have obscured other possible traits influencing performance under drought.

### Associations of Traits with Yield and S

Associations with yield performance were examined with use of phenotypic and, where possible, genotypic correlations (Kempthorne 1969). The usefulness of wet and, separately, dry traits as predictors of dry GDW and $S$ was tested initially by multiple regression analysis. Traits calculated from dry GDW (dry HI, $G$ and KNO) or used to calculate $S$ (wet GDW, dry GDW) were excluded as independent variables. A forward selection procedure was used, and only independent variables for which $P < 0.05$ were included. Because of the obvious interrelation of many of the independent variables, the multiple regression procedure had limitations and principal components analysis was also used, being applied to the correlation matrices of untransformed wet and dry traits. Dry GDW and $S$ were then regressed against the derived principal components (wet PC's or dry PC's) as independent variables (see Dudzinski 1975), the multiple regression procedure outlined above being used. Trait loadings were assumed to be significant if equal to or greater than $0.29$ (Dudzinski 1975).

## Results

### Crop Development Growth and Morphology

Cultivar effects were significant for all the wet and dry traits listed under this heading in Table 1. Table 2 summarizes the more important results, the wet and dry means being uncorrected at this stage for AD differences. The following results are not shown in Table 2: for wet conditions, STIP (it was zero), WAX (low, averaging 0·8) and GC (average 9·5, range from lowest to highest cultivar, 7·5–10·0), and for dry conditions, AD (average 86·8 days) and HT (average 73 cm), cultivar effects for both being closely correlated with those under wet conditions. Also GCA, GCP and GFD are not shown for either condition. Wet GCA (average 8·6, range of cultivar means 7·5–10·0) was closely correlated with wet GC, and dry GCA (average 7·2, range of cultivar means 5·8–9·6) was closely correlated with dry GC. GCP varied little between cultivar groups: wet mean was 30·0 days (range 22–42), and dry mean was 19·8 days (range 16–25). Similarly GFD varied little: wet mean was 43·7 days (range 36–48), and dry mean was 35·0 days (range 29–40).

Since there was a major species effect on AD, barley being earlier than other species, and there was evidence that AD influenced some traits (Table 2), results were corrected for AD differences before examination of species effects. Following correction there were significant species effects for most traits (Table 3). These arose largely because barley relative to other species had a greater GC, especially under drought, and a greater dry GCD and dry TDW. On the other hand, barley showed a reduced GFD compared with other species. Triticale had greater WAX than other species, and dry GCD was greater than that of bread and durum wheat, but less than barley. The bread and durum species did not differ significantly for any growth or morphological traits. Within the bread wheat species, the short E3 and especially E4 groups showed low GC, GCD and TDW.

Phenotypic correlations with AD and HT not shown in Table 2 include significant correlations for wet GC (0·31* with AD, 0·47** with HT), wet GCA ($-0·63$** with AD) and dry GCA ($-0·39$** with AD, 0·30* with HT); GCP was unrelated to AD and HT. Wet GFD was negatively correlated with AD ($r = -0·64$**) but, curiously, dry GFD was unrelated to AD. The general picture was one of positive associations between growth, and lateness and height under wet conditions, and growth and only height under dry conditions. It is worth noting that variation in wet GCD across cultivars was related largely to variation in wet GCP ($r = 0·88$**), whereas variation in dry GCD was due equally to variation in dry GCP ($r = 0·70$**) and variation in dry GCA ($r = 0·63$**).

### Grain Yield Components

Cultivar effects, uncorrected for anthesis date differences, were highly significant for all the grain yield components shown in Table 4; GDW and $S$ are included for convenience, having been presented previously (Fischer and Maurer 1978). Wet $G$, HI, KPS and SNO (not shown) averaged respectively 20·4 g m$^{-2}$ d$^{-1}$, 42·5%, 40·0 and 307 m$^{-2}$, being closely correlated ($r = 0·7$ to 0·9) with group dry values in Table 4.

After correction for AD differences, species effects on all traits of Table 4 were statistically significant (see Table 3). Generally bread wheat, closely followed by durum wheat, had the highest $G$, HI, KNO and KPS, although triticale had the highest

Table 2. **Effect of drought, cultivar group and cultivar on crop growth and development traits[A]**

Data are uncorrected for differences in anthesis date

| Species group | Number of cultivars | AD Wet (days) | HT Wet (cm) | GC Dry (1–10) | GCD Wet (days) | GCD Dry (days) | TDW Wet (g m$^{-2}$) | TDW Dry (g m$^{-2}$) | STIP Dry (%) | WAX Dry (score) |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | *Bread wheats* | | | | | | |
| Tall | 8 | 93 | 120 | 7·5 | 252 | 134 | 1283 | 749 | 4 | 1·2 |
| E1 | 7 | 90 | 101 | 7·5 | 265 | 138 | 1326 | 720 | 4 | 1·6 |
| E2 | 13 | 91 | 96 | 7·4 | 262 | 136 | 1348 | 736 | 3 | 1·5 |
| E3 | 3 | 90 | 74 | 7·2 | 230 | 127 | 1206 | 687 | 1 | 1·9 |
| E4 | 3 | 88 | 53 | 6·3 | 253 | 119 | 1070 | 560 | 0 | 1·8 |
| | | | | *Durum wheats* | | | | | | |
| Tall | 3 | 97 | 117 | 7·7 | 226 | 111 | 1383 | 741 | 3 | 1·7 |
| E2 | 3 | 89 | 94 | 7·2 | 260 | 135 | 1365 | 726 | 0 | 1·9 |
| | | | | *Triticale* | | | | | | |
| Old | 1 | 93 | 132 | 7·8 | 280 | 154 | 1505 | 736 | 1 | 2·8 |
| Recent | 6 | 94 | 117 | 7·9 | 284 | 150 | 1450 | 728 | 6 | 2·4 |
| | | | | *Barley* | | | | | | |
| Recent | 6 | 82 | 101 | 9·2 | 276 | 196 | 1231 | 801 | 0 | 1·1 |
| | | | | *Overall* | | | | | | |
| Mean | 53 | 91 | 101 | 7·6 | 258 | 142 | 1315 | 729 | 3 | 1·6 |
| Highest cv. | — | 99 | 142 | 9·6 | 349 | 218 | 1617 | 905 | 19 | 3·0 |
| Lowest cv. | — | 79 | 46 | 5·8 | 204 | 103 | 948 | 531 | 0 | 0·6 |
| LSD (0·05) between cvv. | — | 3 | 11 | — | 47 | 20 | 166 | 95 | — | — |
| Correlation[B]: | | | | | | | | | | |
| With wet AD | — | 1·00 | 0·33* | 0·12 | −0·14 | −0·47** | 0·49** | −0·05 | 0·40** | 0·08 |
| With wet HT | — | 0·33* | 1·00 | 0·60** | −0·12 | 0·13 | 0·37** | 0·56** | 0·39** | −0·39** |

[A] See Table 1 for abbreviations.

[B] Phenotypic correlation within all species (*$P<0·05$; ** $P<0·01$).

wet KPS and a dry KPS equal to bread wheat; barley had the lowest values for these four traits. The dry SNO of triticale was significantly lower than the rest, with barley having highest SNO. Bread wheat, and to a lesser degree triticale, showed significantly lower KW than barley and durum wheat. Barley had a significantly lower wet GDW than other species. The dry GDW of titicale was significantly lower than bread wheat. *S* for triticale was significantly higher than barley.

**Table 3. Effect of species on morpho-physiological traits, grain yield and drought susceptibility**
All dry traits are corrected for differences in anthesis date

| Species | GC Wet | GC Dry | GCD Wet | GCD Dry (days) | GFD Wet | GFD Dry | TDW Wet | TDW Dry (g m$^{-2}$) | SNO Wet | SNO Dry (m$^{-2}$) | KPS Wet | KPS Dry |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bread wheat | 9·5 | 7·2 | 254 | 146 | 44 | 35 | 1290 | 724 | 319 | 287 | 40 | 29 |
| Durum wheat | 9·5 | 7·3 | 243 | 145 | 43 | 35 | 1374 | 745 | 263 | 245 | 42 | 26 |
| Triticale | 9·8 | 7·7 | 248 | 162 | 45 | 36 | 1458 | 723 | 249 | 221 | 49 | 29 |
| Barley | 10·0 | 9·2 | 270 | 196 | 43 | 32 | 1231 | 801 | 365 | 294 | 28 | 22 |
| Significance[A] | ** | ** | NS | ** | NS | ** | ** | * | ** | ** | ** | ** |

| Species | KNO Wet | KNO Dry (100 m$^{-2}$) | KW Wet | KW Dry (mg) | $\psi$ Wet | $\psi$ Dry (bars) | LP Wet | LP Dry | GDW Wet | GDW Dry (g m$^{-2}$) | S |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Bread wheat | 126 | 82 | 42 | 30 | −17·1 | −29·7 | 3·3 | 2·6 | 524 | 254 | 0·88 |
| Durum wheat | 107 | 66 | 49 | 35 | −16·5 | −30·0 | 3·2 | 2·9 | 532 | 227 | 0·98 |
| Triticale | 120 | 65 | 45 | 32 | −16·2 | −28·7 | 3·8 | 3·1 | 536 | 212 | 1·05 |
| Barley | 95 | 63 | 48 | 36 | −20·4 | −28·2 | 3·2 | 2·5 | 452 | 226 | 0·85 |
| Significance[A] | ** | ** | ** | * | ** | * | NS | * | * | * | * |

* $P < 0·05$.  ** $P < 0·01$.  NS, not significant.

[A] *F*-test for species differences: * $P < 0·05$. ** $P < 0·01$. NS, not significant.

Within the bread wheat species, the relative effect of drought on all traits in Table 4 was generally smaller for the tall cultivars (see also Table 7); in the case of KW, this was evident within durum wheats as well. Gabo (tall bread wheat), Yecora 70 (E3 bread wheat) and Cocorit 71 (E2 durum wheat) were highlighted by Fischer and Maurer (1978) as cultivars showing consistent differences in *S*. Their behaviour was similar to the average behaviour of their respective groups in Table 4.

Dry traits were usually negatively correlated with AD (Table 4), although dry KW had a weak positive association. Several traits were negatively associated with HT, but dry KW showed a weak positive association.

*Associations with Grain Yield and* S

Table 5 indicates the proportion of cultivar variation (sums of squares) in dry GDW and in *S* which remains to be explained after correction for effects of species and anthesis date differences. Data for wet GDW, for which variances are clearly greater than for dry GDW, are included for comparison. Table 5 also shows the portion of the remainder sum of squares which can be attributed to experimental error and, in the case of dry GDW and *S*, the portion which can be explained by regression models based on wet traits to be developed later.

**Table 4.** **Effect of drought, cultivar group and cultivar on components of grain yield, grain yield[A], and drought susceptibility (S)**

Data are uncorrected for differences in anthesis date

| Species group | Number of cultivars | G Dry (g m$^{-2}$ d$^{-1}$) | HI Dry (%) | SNO Dry (m$^{-2}$) | KPS Dry | KNO Wet (100 m$^{-2}$) | KNO Dry | KW Wet (mg) | KW Dry | GDW Wet (g m$^{-2}$) | GDW Dry | S |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | *Bread wheat* | | | | | | | |
| Tall | 8 | 16·9 | 32 | 275 | 24 | 106 | 66 | 42 | 34 | 447 | 225 | 0·86 |
| E1 | 7 | 16·4 | 34 | 250 | 29 | 130 | 71 | 43 | 32 | 554 | 225 | 1·02 |
| E2 | 13 | 17·1 | 34 | 263 | 29 | 136 | 75 | 41 | 32 | 553 | 234 | 0·99 |
| E3 | 3 | 19·1 | 38 | 266 | 29 | 124 | 78 | 45 | 32 | 555 | 240 | 0·98 |
| E4 | 3 | 16·2 | 37 | 222 | 29 | 126 | 66 | 40 | 30 | 498 | 195 | 1·04 |
| | | | | | *Durum wheat* | | | | | | | |
| Tall | 3 | 14·5 | 23 | 190 | 21 | 95 | 40 | 49 | 40 | 464 | 162 | 1·12 |
| E2 | 3 | 16·6 | 34 | 236 | 28 | 119 | 66 | 50 | 35 | 599 | 229 | 1·06 |
| | | | | | *Triticale* | | | | | | | |
| Old | 1 | 5·9 | 13 | 201 | 16 | 105 | 32 | 43 | 29 | 456 | 92 | 1·38 |
| Recent | 6 | 12·6 | 28 | 186 | 29 | 123 | 54 | 45 | 36 | 550 | 192 | 1·13 |
| | | | | | *Barley* | | | | | | | |
| Recent | 6 | 11·4 | 30 | 293 | 22 | 95 | 63 | 48 | 36 | 452 | 226 | 0·85 |
| | | | | | *Overall* | | | | | | | |
| Mean | 53 | 15·5 | 32 | 249 | 27 | 120 | 66 | 44 | 34 | 518 | 214 | 1·00 |
| Highest cv. | — | 20·6 | 41 | 426 | 37 | 162 | 87 | 56 | 44 | 696 | 313 | 1·38 |
| Lowest cv. | — | 5·9 | 13 | 134 | 16 | 85 | 32 | 33 | 23 | 352 | 92 | 0·55 |
| LSD (0·05) between cvv. | — | — | 3 | 33 | 4 | 22 | 11 | 3 | 2 | 78 | 39 | 0·16 |
| Correlation[B] | | | | | | | | | | | | |
| With wet AD | — | 0·13 | −0·45** | −0·31* | −0·19 | 0·17 | −0·52** | −0·24 | 0·28* | −0·01 | −0·39** | 0·35** |
| With wet HT | — | −0·33* | −0·47** | 0·00 | −0·30* | −0·38** | −0·30* | 0·09 | 0·32* | −0·34* | −0·06 | −0·21 |

[A] See Table 1 for abbreviations.

[B] Phenotypic correlation within all species (DF = 48, $r > 0.35$, $P < 0.01$; $r > 0.28$, $P < 0.05$).

*Bread Wheat Cultivars Only*

*Simple correlations.* After correction of all dry traits for anthesis date, phenotypic and genotypic correlations with GDW and S were calculated (Table 6). Some traits which showed non-significant effects have been excluded. Increased dry GDW was significantly associated with increased wet GDW, wet TDW, wet GC, wet GCA, wet KW and wet WAX (first column). S increased as wet GDW, wet HI, wet G, wet KNO and wet KPS increased and as wet HT decreased; S also increased as wet $\psi$ increased (second column). As an example of how correction of dry traits for anthesis date differences altered correlations, uncorrected dry GDW was most closely related to, amongst wet traits, wet GCA ($r = 0.62$**) and wet KW ($r = 0.55$**) rather than wet TDW ($r = 0.20$) (cf. Table 6, column 1).

Table 5.  **Sum of squares for cultivar means for dry GDW, S and wet GDW, and its partitioning amongst effects due to species, anthesis date, regression model and experimental error**

| Source of variation | DF | Dry GDW % (ss) | S % (ss) | Wet GDW % (ss) |
|---|---|---|---|---|
| | | *All species* | | |
| Cultivars | 52 | 100 | 100 | 100 |
| | | (78260) | (1·206) | (252980) |
| Less species | 3 | 22 | 33 | 12 |
| Less anthesis date | 1 | 12 | 8 | NS |
| Remainder | 48 | 66 | 59 | 88 |
| Less model[A] | 4, 2 | 23 | 16 | — |
| Residual | 44, 46 | 43 | 43 | — |
| Error[B] | — | 13 | 18 | 12 |
| | | *Bread wheats only* | | |
| Cultivars | 33 | 100 | 100 | 100 |
| | | (21549) | (0·361) | (134090) |
| Less anthesis date | 1 | 16 | 10 | NS |
| Remainder | 32 | 84 | 90 | 100 |
| Less model[A] | 3, 3 | 39 | 62 | — |
| Residual | 29 | 45 | 28 | — |
| Error[B] | — | 30 | 26 | 20 |

[A] Models developed by multiple regression of dry GDW and S on individual wet traits (see text).
[B] Error estimated via standard error of cultivar mean derived from analysis of variance by using drought treatments (dry GDW, S) error DF = 318, or wet treatment only (wet GDW) error DF = 107.

Table 6 also gives correlations within wet (column 3) and dry (column 4) situations. For both, GDW was closely and positively correlated with both TDW and HI, GCD and G, and with KNO and some of its components, but in neither situation was there a significant correlation with KW. The correlation of yield with TDW, GCA and SNO became stronger and that with KNO weaker under dry conditions; the HT correlation reverses, from being negative under wet to weakly positive under dry. Wet GDW showed a strong positive association with wet $\psi$, while dry GDW only showed weak, non-significant, positive associations with $\psi$. Under both wet and dry conditions,

yield was positively correlated with LP, although not always significantly. Genotypic correlations generally exceeded phenotypic ones under wet conditions, but the situation tended to be opposite under dry conditions; spurious influences on correlations involving traits calculated from yield were obviously minimal.

**Table 6. Phenotypic and genotypic (in parenthesis) correlations between dry GDW, $S$ and wet GDW, on the one hand, and wet and dry traits on the other**

Last column phenotypic correlations between wet and dry traits. For bread wheat cultivars only, all dry traits corrected for anthesis date (DF = 31)[A]

| Trait | Dry GDW v. wet traits | $S$ v. wet traits | Wet GDW v. wet traits | Dry GDW v. dry traits | $S$ v. trait response to drought[B] | Wet traits v. dry traits |
|---|---|---|---|---|---|---|
| GDW | 0·36 (0·51) | 0·67 (0·76) | 1·00 | 1·00 | 1·00 | 0·36 |
| TDW | 0·45 (0·70) | 0·17 (0·17) | 0·57 (0·63) | 0·74 (0·69) | 0·77 | 0·52 |
| HI | −0·06 (−0·08) | 0·59 (0·63) | 0·54 (0·63) | 0·46 (0·42) | 0·80 | 0·42 |
| GC | 0·44 | −0·13 | 0·23 | 0·44 | 0·23 | 0·73 |
| GCA | 0·38 | −0·15 | 0·15 | 0·47 | 0·02 | 0·47 |
| GCD | 0·29 (0·44) | 0·21 (0·30) | 0·47 (0·54) | 0·56 (0·50) | 0·46 | 0·41 |
| $G$ | 0·08 (0·12) | 0·50 (0·56) | 0·57 (0·61) | 0·62 (0·69) | 0·67 | 0·39 |
| KW | 0·40 (0·52) | −0·24 (−0·24) | 0·08 (0·10) | 0·32 (0·38) | 0·23 | 0·71 |
| KNO | −0·02 (0·03) | 0·70 (0·77) | 0·71 (0·67) | 0·53 (0·34) | 0·87 | 0·56 |
| SNO | 0·22 (0·33) | −0·02 (−0·13) | 0·19 (0·06) | 0·39 (0·36) | 0·01 | 0·75 |
| KPS | −0·16 (−0·22) | 0·70 (0·84) | 0·58 (0·65) | 0·11 (−0·01) | 0·51 | 0·62 |
| HT | 0·26 (0·33) | −0·60 (−0·65) | −0·39 (−0·47) | 0·27 (0·28) | 0·33 | 0·94 |
| WAX | 0·36 | −0·16 | 0·14 | 0·04 | 0·58[C] | 0·65 |
| STIP | — | — | — | −0·20 | 0·00 | — |
| Wet $\psi$ | −0·08 | 0·66 | 0·60 | — | — | — |
| Early $\psi$ | — | — | — | 0·25 | — | 0·80[D] |
| Dry $\psi$ | — | — | — | 0·28 | — | 0·26[D] |
| Mean $\psi$ | — | — | — | 0·24 | — | 0·48[D] |
| Wet LP | 0·21 | 0·15 | 0·35 | — | — | — |
| Early LP | — | — | — | 0·36 | — | 0·43[E] |
| Dry LP | — | — | — | 0·22 | — | 0·09[E] |
| Mean LP | — | — | — | 0·26 | — | 0·33[E] |

[A] For phenotypic correlations: $r > 0·45$, $P < 0·01$; $r > 0·35$, $P < 0·05$.
[B] Trait response to drought calculated for each trait and cultivar in a manner analogous to the calculation of $S$: Trait response $= (1 - $ dry trait/wet trait$)/K$, where $K$ is a constant for each trait across all cultivars analogous to $D$ of equation (1).
[C] Because of some zero values of this trait the response was calculated simply by dry WAX − wet WAX.
[D,E] Correlations with wet $\psi$ and wet LP respectively.

$S$ is proportional to $1 - ($ dry GDW/wet GDW$)$, and it is not surprising that $S$ correlations with dry traits (not shown in Table 6) were similar but opposite in sign

to those for dry GDW (column 4). The correlation with HT was stronger in the case of $S$ (genotypic $r = -0.66$). $S$ was not significantly correlated with plant water relations under drought. The fifth column in Table 6 refers to correlations between $S$ and the response of each trait to drought, this response being calculated for each cultivar in the same manner as the response of yield ($S$) is calculated. Positive correlations with $S$ are to be expected, and these were strong for the responses of TDW, HI, $G$ and KNO. On the other hand, there was no relationship with the responses of GC, GCA, KW, SNO, and STIP to drought. Finally the sixth column shows the extent to which cultivar effects on each trait were correlated under wet and dry conditions. For example, wet and dry HT were closely correlated, in contrast to GDW, GCD, $G$ and some plant water traits.

Table 7. Effect of Norin 10 dwarfing genes *Rht 1* and *Rht 2*[A] on drought susceptibility ($S$) and yield (dry GDW) and associated wet traits in bread wheats ($\pm$standard error of mean): $S$ and dry GDW corrected to mean wet AD of experiment

| Genes present[A] | Cultivars | Wet HT (cm) | $S$ | Wet HI (%) | Wet KNO ($\times 100$ m$^{-1}$) | Wet KPS | Wet GDW (g m$^{-2}$) | Dry GDW (g m$^{-2}$) |
|---|---|---|---|---|---|---|---|---|
| None | Robin, Nainari 60, Gabo, C306, T64-2-W, Yaqui 50, Triple Dirk, Pusa 4 | 120 $\pm 4$ | 0·85 $\pm 0·033$ | 37·8 $\pm 1·2$ | 106 $\pm 4$ | 32·0 $\pm 1·1$ | 447 $\pm 17$ | 230 $\pm 10$ |
| *Rht 1* | Penjamo 62, Zaragoza 75, Siete Cerros 66, Jupateco 73, Tanori 71, Anza, UQ105 | 95 $\pm 3$ | 1·01 $\pm 0·020$ | 44·9 $\pm 0·6$ | 151 $\pm 4$ | 44·0 $\pm 2·7$ | 585 $\pm 8$ | 237 $\pm 4$ |
| *Rht 2* | Pitic 62, Tobari 66[B], Ciano, Sonalika[B], SXW771[B], SWX772[B], Nuri 70, Cleopatra 74 | 100 $\pm 1$ | 0·96 $\pm 0·023$ | 44·6 $\pm 1·1$ | 122 $\pm 5$ | 40·6 $\pm 1·6$ | 524 $\pm 13$ | 234 $\pm 5$ |
| *Rht 1* + *Rht 2* | Yecora 70, Cajeme 71, Hira[B], Fiserect 4A[B], Olesen | 64 $\pm 6$ | 1·03 $\pm 0·052$ | 50·4 $\pm 0·5$ | 126 $\pm 6$ | 41·5 $\pm 2·1$ | 523 $\pm 27$ | 215 $\pm 18$ |
| *Rht 3* | Tordo[B] | 56 | 1·09 | 48·5 | 125 | 44·5 | 542 | 196 |

[A] Notation as in Gale and Marshall (1978), *Rht 3* referring to the Tom Thumb dwarfing gene.
[B] Dwarfing genes deduced from pedigree; otherwise determined by test crossing (Gale and Marshall 1978).

To explain the few significant correlations between yield and plant water relations traits in Table 6, correlations between the plant water traits and yield components were examined. Under dry conditions only two correlations were significant, those between dry KPS and early $\psi$ ($r = 0.40^*$), and between dry KW and dry $\psi$ ($r = 0.41^*$). Under wet conditions wet $\psi$ was significantly correlated with wet HI ($r = 0.57^{**}$), wet KNO ($r = 0.59^{**}$), wet KPS ($r = 0.48^{**}$) and wet $G$ ($r = 0.42^*$). No yield components were correlated with LP. Also TDW was not correlated with either $\psi$ or LP. Finally dry plant water traits showed no significant correlations with yield component responses to drought, calculated as described for column 5 in Table 6.

Norin 10 dwarfing genes were a major cause of variation in height, yield potential and related traits in the bread wheat cultivars studied. Cultivars for which the specific dwarfing genes involved (*Rht 1*, *Rht 2*) have been determined (Gale and Marshall 1978) or can be deduced, are considered in Table 7. The results suggest that the Norin 10 genes increased $S$, as well as wet HI, wet KNO, wet KPS and wet GDW; the increase in $S$ may have been greater with *Rht 1* than with *Rht 2*. The variation in $S$ between groups in Table 7 was closely correlated with wet HI ($r = 0.94^*$) and wet HT ($r = -0.93^*$).

*Multiple regression with wet traits.* The multiple regression of dry GDW, and $S$, on wet traits led to the following models:

$$(\text{dry GDW}) = \text{constant} + 0 \cdot 07(\text{wet TDW}) + 2 \cdot 4(\text{wet KW}) + 16(\text{wet WAX}) \qquad (2)$$

$$S \times 10^2 = \text{constant} + 0 \cdot 91(\text{wet KPS}) + 2 \cdot 3(\text{wet } \psi) - 5 \cdot 7(\text{wet WAX}) . \qquad (3)$$

In the case of dry GDW, equation (2) explained 39% of the total sum of squares (Table 5), leaving, after allowance for error, 15% unexplained. This appears to be associated with five deviant cultivars, namely Olesen and We-GtoxKal-Bb with lower yields than expected from equation (2), and Tobari 66, Cajeme 71 and Gabo with higher yields. The regression model in the case of $S$ (equation 3) was more successful, explaining 62% of the total sum of squares (Table 5). Considering the estimated experimental error, there was no unexplained variation.

The regression of dry GDW and $S$ on wet PC's derived from principal components analysis produced models with three significant components each (Table 8). In order of importance, the fourth, third and 13th components entered in the case of dry GDW, explaining 43% of the total sum of squares (cf. 39% with equation 2). The sign of the latent vectors or loadings for these wet PC's in Table 8 is such that increases in the cultivar score are associated with increases in dry GDW. The top cultivar had the highest score for the particular PC concerned. In the case of $S$, wet PC 1, 2 and 7 entered the regression model (Table 8), which explained 66% of the total sum of squares for $S$ (cf. 62% for equation 2). The loading signs shown are such that increased cultivar score indicates increased drought susceptibility ($S$).

*Multiple regression with dry traits.* The analysis of dry GDW and $S$ as a function of dry traits (excluding yield-derived variables HI, $G$ and KNO) gave the following models:

$$(\text{dry GDW}) = \text{constant} + 0 \cdot 36(\text{dry TDW}) - 2 \cdot 5(\text{dry STIP}) - 0 \cdot 6(\text{dry HT}) + 1 \cdot 3(\text{dry KW}) \qquad (4)$$

$$S \times 10^2 = \text{constant} - 0 \cdot 50(\text{dry HT}) + 1 \cdot 1(\text{dry STIP}) - 2 \cdot 4(\text{dry GCP}). \qquad (5)$$

Equation (4) explained 66% of the total sum of squares for dry GDW, which is as much as could be expected from consideration of error. Because the model selected dry TDW first (see also Table 6, fourth column), it follows that the other three dry traits form a surrogate for dry HI. Equation (5) explains 52% of the total sum of squares for $S$, almost as much as could be expected from experimental error. It is notable that plant water traits did not enter equations (4) or (5).

Principal components analysis of the dry traits (excluding dry GDW and $S$) gave up to eight dry PC's which correlated sufficiently either with dry GDW or with $S$ to enter the multiple regression models. For simplicity only four components were allowed to enter each model, which explained 65% and 63% of the total sum of squares for dry GDW and $S$ respectively, results similar to those obtained with equations (4) and (5). For brevity, only the dry PC's of the dry GDW model are shown (Table 9). The sign of the loadings in Table 9 is such that the scores for each component are positively associated with dry GDW. It is interesting that one component (dry PC1) showing a correlation with dry GDW contained plant water traits (cf. correlations in Table 6, and equation (4)).

*Cultivars within All Species*

Associations were examined after all traits were corrected for species effects and all dry traits, including *S*, corrected for anthesis date. Simple phenotypic correlations are not presented because the correlations, including those with plant water traits, were generally similar to those shown for bread wheats in Table 6.

**Table 8. Principal components (PC's) derived from all wet traits, and their latent vectors**

Only components entering the models explaining variation in dry GDW and in *S* (corrected for anthesis date) are shown. Bread wheat cultivars only, the four cultivars having the most extreme scores being listed for each component

| Wet trait | Latent vector (loadings)[A] for principal components | | | | | |
|---|---|---|---|---|---|---|
| | PC's most important for GDW | | | PC's most important for *S* | | |
| | PC4 | PC3 | PC13 | PC1 | PC2 | PC7 |
| GDW | 0·24 | 0·22 | 0·11 | *0·33* | 0·19 | 0·10 |
| TDW | 0·28 | 0·20 | −0·33 | *0·29* | −0·23 | 0·02 |
| HI | −0·04 | 0·04 | *0·41* | 0·09 | *0·45* | 0·05 |
| GC | *0·42* | *0·29* | −0·36 | 0·03 | −0·21 | 0·19 |
| GCA | *0·33* | *0·33* | *0·30* | −0·20 | 0·16 | 0·06 |
| GCP | −0·35 | *0·33* | 0·01 | 0·25 | −0·11 | 0·01 |
| GCD | −0·17 | *0·50* | 0·21 | 0·14 | −0·03 | 0·05 |
| *G* | *0·39* | −0·25 | −0·10 | 0·21 | 0·23 | 0·03 |
| KW | 0·21 | *0·35* | 0·13 | −0·22 | 0·09 | −0·20 |
| KNO | 0·02 | −0·08 | 0·04 | *0·41* | 0·10 | 0·21 |
| SNO | −0·08 | 0·05 | 0·06 | 0·19 | −0·17 | 0·16 |
| KPS | 0·08 | −0·11 | 0·08 | 0·26 | 0·24 | 0·09 |
| HT | 0·21 | 0·05 | *0·45* | −0·15 | −0·37 | 0·17 |
| WAX | 0·16 | −0·02 | 0·07 | 0·11 | −0·04 | −0·79 |
| AD | 0·02 | −0·16 | *0·29* | 0·27 | −0·34 | −0·06 |
| MD | −0·22 | 0·05 | 0·13 | 0·27 | −0·30 | −0·12 |
| GFD | −0·30 | *0·34* | −0·33 | −0·13 | 0·24 | −0·04 |
| Wet $\psi$ | −0·08 | 0·05 | −0·06 | *0·29* | 0·24 | −0·06 |
| Wet LP | 0·10 | 0·12 | −0·02 | 0·17 | 0·02 | −0·39 |

*Cultivar score rankings*

| | | | | | | |
|---|---|---|---|---|---|---|
| Top cv. | Zacatecas 74 | Narro 74 | Sonalika | Zaragoza 75 | Fis4A | Tobari 66 |
| 2nd cv. | S. Cerros | Zaragoza 75 | Cajeme | Anza | Olesen | Yaqui 50 |
| 33rd cv. | Tordo | Yaqui 50 | Hira | C306 | T. Dirk | T64-2-W |
| 34th cv. | Olesen | ERAF | Tordo | Pusa 4 | Yaqui 50 | Fis4A |

*Correlation coefficients*

| | | | | | | |
|---|---|---|---|---|---|---|
| Dry GDW | 0·50 | 0·42 | 0·30 | 0·08 | −0·13 | −0·22 |
| *S* | 0·06 | 0·03 | −0·20 | 0·64 | 0·51 | 0·28 |

[A] Loadings > 0·29 italicized.

For dry GDW versus wet traits and *S* versus wet traits, multiple regression analysis explained only 23% and 16% respectively of the total sum of squares (Table 5). The largest unexplained residuals in each case were associated with several barley, triticale and durum wheat cultivars. Principal component analysis applied to wet traits, followed by multiple regression, did not produce better or more easily understood models of dry GDW and *S* than multiple regression alone. This is not surprising in view of the deviant cultivars encountered in the latter exercise.

*Representative Cultivars*

The only reason for consideration of this reduced set of 17 cultivars is that their water status was measured on more occasions and hence determined with greater precision. All traits, including plant water traits, were corrected for species effects, and all dry traits were corrected for anthesis date differences before correlations

**Table 9. Principal components (PC's) and latent vectors derived from all dry traits (excluding dry GDW and $S$)**

Only the first four components entering the multiple regression model for dry GDW are shown. All traits corrected for anthesis date before analysis. Bread wheat cultivars only, the four cultivars having the most extreme scores being listed for each component

| Dry trait | Latent vector (loadings)[A] for principal components | | | |
| --- | --- | --- | --- | --- |
| | PC3 | PC2 | PC4 | PC1 |
| TDW | *0·30* | *0·34* | 0·17 | −0·05 |
| HI | 0·06 | −0·17 | 0·14 | 0·26 |
| GC | *0·30* | *0·31* | −0·07 | −0·11 |
| GCA | *0·38* | 0·27 | −0·19 | −0·10 |
| GCP | −0·26 | 0·20 | 0·07 | 0·11 |
| GCD | 0·14 | *0·38* | −0·12 | −0·01 |
| G | 0·26 | −0·14 | *0·41* | 0·15 |
| KW | −0·14 | 0·28 | 0·09 | 0·10 |
| KNO | *0·41* | −0·09 | 0·10 | 0·04 |
| SNO | 0·19 | 0·00 | *0·47* | −0·08 |
| HT | 0·07 | *0·31* | 0·18 | −0·24 |
| WAX | 0·05 | −0·14 | −0·09 | 0·24 |
| STIP | −0·11 | 0·22 | −0·04 | −0·18 |
| AD | 0·00 | 0·14 | 0·13 | 0·26 |
| MD | −0·25 | 0·26 | 0·05 | 0·09 |
| GFD | *−0·32* | 0·23 | −0·04 | −0·09 |
| Early $\psi$ | 0·26 | 0·00 | −0·27 | 0·26 |
| Dry $\psi$ | 0·00 | 0·17 | −0·16 | *0·30* |
| Mean $\psi$ | 0·03 | 0·12 | −0·24 | *0·32* |
| Early LP | 0·03 | 0·12 | 0·11 | *0·37* |
| Dry LP | 0·10 | 0·14 | 0·20 | *0·31* |
| Mean LP | 0·07 | 0·13 | 0·19 | *0·34* |

*Cultivar score rankings*

| | | | | |
| --- | --- | --- | --- | --- |
| Top cv. | Cajeme | C306 | Gabo | Meng-8156 |
| 2nd cv. | S. Cerros | T64-2-W | T. Dirk | Yecora |
| 33rd cv. | Fis4A | Olesen | SXW772 | Pitic |
| 34th cv. | C306 | Pitic | Olesen | Yaqui 50 |

*Correlation coefficients*

| | | | | |
| --- | --- | --- | --- | --- |
| Dry CDW | 0·61 | 0·40 | 0·37 | 0·32 |
| $S$ | −0·02 | −0·41 | −0·51 | 0·15 |

[A] Loadings $> 0·29$ italicized.

with yield and its components were calculated. Leaf osmotic potential ($\pi$) and turgor potential ($P$) measurements were included, but there were no significant associations with $P$.

None of the wet plant water traits ($\psi$, $\pi$ and LP) showed significant correlations with dry GDW or $S$, but correlations with wet GDW, wet HI, wet KNO and wet KPS

were positive, being significant in six out of 12 cases. The highest coefficients were between wet KPS and wet $\psi$ (0·73**) and between wet KPS and wet LP (0·67*).

Considering dry plant water traits, and dry GDW, $S$ and dry yield components, there were noteworthy correlations between dry GDW and mean LP ($r = 0·58$*), dry KNO and early $\pi$ ($r = 0·59$*), dry KPS and mean $\psi$ ($r = 0·58$*), and dry STIP and early $\pi$ ($r = -0·62$*). Early $\psi$, the measure expected to have the greatest influence on spike fertility, just failed to show significant correlations with dry KPS ($r = 0·48$ NS) and dry STIP ($r = -0·50$ NS). Leaf permeability showed moderate positive correlations ($r = 0·3$ to $0·7$) with dry TDW, dry GCA and dry GCD.

## Discussion

### Species Effects

The most striking species effect was the superior green ground cover (GC) and growth (TDW) of barley under drought. Barley also had lowest leaf permeabilities (LP) under all conditions and lower leaf water potentials ($\psi$) under drought (see also Fischer and Sanchez 1979). These effects seemed to balance out, since barley was not superior in dry GDW. However, barley was the most drought-resistant (lowest $S$, although not much lower than bread wheat). This may be due to its greater early growth (GC in Table 3; Bidinger *et al.* 1977), so that drought stress later in the life cycle affects total growth and yield relatively less. The lower susceptibility of barley was reflected largely in smaller reductions in kernel number under drought (Table 3).

Triticale had the lowest dry yield and was most drought-susceptible (highest $S$). This was again related to kernel number, i.e. reductions in kernel number with drought. Growth or ground cover were not inferior (Table 3). Kernels per spike (KPS) seemed to be sensitive to drought in triticale, but leaf water potentials ($\psi$) under drought were not lower in triticales than in other species. This suggestion of greater sensitivity of spike fertility to water stress is not surprising for an interspecific hybrid like triticale.

### Between Bread Wheat Cultivars

In an attempt to encompass the greatest diversity of germplasm and derive relationships of more general relevance, associations within species across all cultivars were examined. However, with the exception of associations with plant water traits, results suggested that relationships within barley and triticale, in particular, were not the same as those within the more numerous bread wheat group. The remainder of the discussion will deal almost exclusively with the bread wheat results.

*Breeding for yield under drought.* Our results support the view that selection for dry GDW, at least in homozygous lines, can be made under non-drought conditions or by using certain dry traits other than dry GDW. Equations (2) and (4) suggest that selection indices may be useful for this purpose. For example, equation (2) explained much more of the variation in dry GDW after correction for anthesis (39/84 = 46% of sum of squares) than did wet GDW alone ($0·36^2 = 13\%$). Further examination of selection indices is beyond the scope of this paper. It is possible, however, to consider briefly single traits, either wet or dry ones, which may serve in the indirect selection for dry GDW. Those of greatest interest in Table 6, in terms of efficiency, are those which might be assessed rapidly, even perhaps on spaced plants, traits such as kernel weight (KW), waxiness (WAX), harvest index (HI) and height (HT).

The efficiency of indirect selection is given by Searle (1965). The calculation requires heritabilities, which we obtained by the variance-component method (i.e. heritability equals cultivar genotypic variance divided by cultivar phenotypic variance) and the genotypic correlations of Table 6. The relative efficiency of indirect selection for dry GDW through selection for wet GDW, wet TDW (total dry weight), wet KW, and dry HI was respectively 57, 72, 63 and 47%. Other wet traits showed low efficiencies, while other dry traits, which often had high correlations with dry GDW, were not tested, since their measurement is clearly more laborious than the determination of dry GDW itself. The results indicate significant but slower progress with indirect single-trait selection for dry GDW, slower progress perhaps partly because the heritability for dry GDW was quite high (63%), dry GDW being determined over effectively nine replicates (3 replicates × 3 drought levels).

For selection in common plant-breeding situations, obviously additional problems arise, including interactions with drought intensity, since dry GDW here refers to yield under drought of a given intensity ($D = 0 \cdot 6$). The approach to yield represented by equation (1) attempts to estimate yield for any known intensity of drought ($D$), given knowledge of $S$ and wet GDW ($= Y_p$). It is obvious from equation (1) and from the positive correlation between wet GDW and $S$ (Table 6) that cultivar rankings change with change in $D$. As $D$ approaches zero, rankings approach those for wet GDW, while as $D$ increases, the opposing influence of $S$ on rankings becomes increasingly important.

A positive correlation between wet GDW and $S$ can also be derived from the data of Laing and Fischer (1976), who examined a similar set of spring bread wheat cultivars at international sites, but there was no correlation in the results of Johnson et al. (1978) with a limited set of winter wheats. A positive correlation implies, as already pointed out by Fischer and Maurer (1978), that there is an optimal level of wet GDW for maximum $Y_d$ at any given level of $D$. However, because wet GDW and dry GDW were positively correlated in our experiment (Table 6), the general level of wet GDW was not excessive or superoptimal for maximum yield at $D$ as high as $0 \cdot 6$. The correlations of $S$ and wet GDW to wet traits (columns 2 and 3, Table 6) can be similarly examined. For traits where both correlations are strong and of similar sign, there arises the possibility of an optimal level of the given trait for maximum yield at a given $D$, since selection for the trait increases both wet GDW and $S$. Wet HT is a good example, for the general height of the cultivars tested was superoptimal for wet GDW (negative correlation) and suboptimal for dry GDW (positive correlation). Similar considerations suggest that wet KPS is tending to behave as does wet HT, while relationships for wet HI, wet $G$, wet KNO and wet $\psi$ suggest that their general levels were about optimal for maximum yield at $D = 0 \cdot 6$ (correlations with dry GDW close to zero), but clearly suboptimal at $D = 0$ (correlations with wet GDW positive). Curvilinear regressions of dry GDW against single wet traits would seem appropriate but were not attempted.

These results pointing to optimal levels of traits for maximum $Y_d$ agree with those of Finlay (1968) who observed that genotypes widely adapted for dryland cropping in South Australia tended to be intermediate in their characteristics. There were in fact no wet traits having a significant and desirable association with both $S$ and wet GDW, such that selection for the trait would increase yield at all levels of $D$ from zero to $1 \cdot 0$. The closest approach to the universally desirable trait is probably

wet TDW for which correlations (strong with wet GDW, almost zero with $S$) indicate positive and significant associations with yield at all levels of $D$ between 0 and 0·6 and probably higher. The trait wet GCD (duration of green ground cover) tended to behave like wet TDW. Within the limitations of this study (given type of drought, limited set of genotypes, etc.), these associations suggest general selection indices for yield under drought via selection under well-watered conditions, indices in which expected drought intensity $(D)$ is a variable. In other words the optimum phenotype will depend on $D$ in the target environment, and selection would be for specific adaptation to droughty environments. However, it should be pointed out that many recent cultivars, containing Norin 10 dwarfing genes and selected for general adaptation or even irrigated culture alone, have superior yields at all but severe levels of drought (Syme 1970; Shimshi and Ephrat 1972; Laing and Fischer 1976), because the adverse effects of dwarfing genes on $S$ are outweighed by the desirable effects on yield potential at least for the range $0 < D < 0·7$. The only exception to this in our present study appears to be very short cultivars, which tended to have inferior growth and yields at $D = 0·6$ (E4 group in Table 4; *Rht 1+Rht 2* and perhaps *Rht 3* in Table 7). However, general confirmation of the value of seeking specific adaptation to drought requires more examples of significant and consistent yield reversals as $D$ increases to high levels, levels at which experimental precision is inevitably poor.

*Physiology of yield under drought.* Physiological explanations of the genotypic variation in dry GDW can be sought in its associations, or lack thereof, with dry traits and dry principal components, but this is not easy. Thus Table 6 shows that dry GDW was not significantly correlated with dry KW, dry STIP and dry HT, yet the multiple regression model (equation 4) derives significant coefficients for all these traits because they become important predictors of HI once variation due to changes in dry TDW is accounted for. Nevertheless, one can state clearly that variation in TDW (assimilate production) between cultivars under drought is more important in explaining dry GDW variation than is variation in HI (assimilate distribution). Growth variation is partly associated with variation in ground cover (GC, GCA) and kernel number (KNO) in dry PC3 (Table 9), the most important dry PC for explaining variation in dry GDW. It could be called an early growth component. Hurd (1974) also refers to the importance of early growth to drought resistance. Growth variation is also found in dry PC2, the second most important component, this time associated with ground cover again (GC) and also with ground cover duration after anthesis (GCD), height (HT), and perhaps kernel weight (KW): PC2 can therefore be termed a late growth component. The third and fourth most important components, namely, PC4, a spike number or tillering component, and PC1, a plant water status component, reveal associations with dry GDW not so clearly evident from the correlations of Table 6. The presence of one cultivar (C306) at the top of dry PC2 and bottom of dry PC3 exemplifies the small chance of finding strong phenotypic correlations between dry GDW and any single trait. Nevertheless, a reasonable conclusion from these analyses is that greater dry GDW is favoured by greater ground cover and growth. The cause may lie in greater early growth before the onset of stress, as in the case of barley as a species, and explaining why wet TDW was a good indicator of dry GDW. The cause may also be due to greater total transpiration after the termination of watering, since growth is likely to be proportional to transpiration under water-limiting conditions (Fischer and Turner 1978). Greater transpiration could arise

through greater ground cover, thereby reducing soil evaporation, or through a more extensive rooting system. The latter could have led to changes in $\psi$, and dry PC1 may reflect such effects, but these suggestions regarding rooting systems must be regarded as very tentative. It should be remembered that all the plant water variation contained in this principal component explained only 10% of the variation in dry GDW. Other studies have also found disappointingly poor associations between plant water status and yield under drought (Kaul 1969; Kaul and Crowle 1971, 1974; Shimshi and Ephrat 1972; Sojka 1974; Jones 1977).

A more general and useful appreciation of the physiology of yield under drought may be obtained through consideration of wet GDW and $S$, rather than dry GDW. In the case of wet GDW, the phenotypic correlations with wet traits (Table 6) agree with other published results (e.g. Thorne *et al.* 1969; Syme 1970; Aguilar and Fischer 1975), especially when allowance is made for our study having lower fertilization than that necessary for maximum yield. This low level was chosen to better simulate dryland situations, and probably explains the somewhat inferior wet GDW of two-gene dwarf wheats (Table 7), cultivars which under high fertility and irrigation appear to have the highest yield potential of all (R. A. Fischer, unpubl. data). The positive correlation of wet GDW with LP has been confirmed in other studies at CIANO (R. A. Fischer, unpubl. data) and elsewhere (Shimshi and Ephrat 1972). The correlation of wet GDW with wet $\psi$, confirmed with the 17 representative cultivars, has not been reported before. Since wet $\psi$ was closely correlated with wet HT ($r = -0 \cdot 63**$), partial correlation coefficients (HT constant) with wet $\psi$ may be more illuminating. These remained significant for wet GDW ($r = 0 \cdot 50**$) and wet KNO ($r = 0 \cdot 48**$), but were non-significant for wet HI, wet KPS and wet $G$. Wet PC1 (Table 8) also seems to contain an element of these associations. It seems surprising that small genetic differences in $\psi$ under generally wet conditions (Fischer and Sanchez 1979) could influence wet KNO and hence wet GDW, although a number of studies with cereals do point to the great sensitivity of KNO to environmentally determined changes in $\psi$ (e.g. Fischer *et al.* 1977). Jones (1977) reported weak positive rank correlations between grain yield and $\psi$ under conditions of mild drought in the United Kingdom.

The causes of variation in $S$ are of major interest because it has been suggested that they may indicate drought resistance mechanisms. The three wet PC's which were positively correlated with $S$ (Table 8) are described as: a high kernel number–wet $\psi$ component (wet PC1), a high harvest index–short stature component (wet PC2), and finally showing the weakest correlation, a low waxiness component (wet PC7). This agrees with the multiple regression model for $S$ (equation 3) and with the simple correlations of Table 6. Equation (5) indicates that susceptibility to spike tipping, a trait which is only evident under drought, may also influence $S$. On the other hand, there was no correlation between $S$ and plant water status under drought (see Table 6 and dry PC1, Table 9), which rules out any major role for rooting differences in our drought situation.

The decrease in drought resistance (increased $S$) with lower leaf waxiness might be expected from physiological considerations, although waxiness increased markedly with drought but dry WAX was not associated with $S$. Regarding the two major associations with $S$ (wet PC1, PC2), it is interesting that height variation, and hence action of the major dwarfing genes, was implicated (wet PC2, see also Table 7), but that independently of height variation, $S$ was still related to yield components (i.e.

PC1, also partial correlation coefficients, height constant, of $S$ with wet KNO ($0 \cdot 64$**), wet KPS ($0 \cdot 60$**), wet $G$ ($0 \cdot 36$*), and wet $\psi$ ($0 \cdot 46$**)). Laing and Fischer (1976) have argued that traits making for high yield potential, such as high wet KNO and in particular high wet HI, ought to be advantageous even under stress conditions because they would lead to more efficient distribution of assimilate, assimilation being limited under stress. The associations with $S$ reported here clearly contradict these earlier suggestions. The breakdown in the argument seems to arise because, while high dry KNO and dry HI may be positively associated with yield under stress (as in Table 6), these traits are not so strongly correlated with the same traits under wet conditions (last column, Table 6).

What are the underlying physiological causes of these associations with $S$? Nothing can be clearly specified, but perhaps high yield potential, high wet KNO, high wet HI, low HT, etc., represent a strategy of allocation of resources by the plant that minimizes investment in organs, tissues, or tissue reserves of any kind, which would buffer yield and yield components against the effects of water stress. Reduced investment in roots or in stem reserves of assimilate would be simple examples. Clearly such plants would show higher values of $S$ in the face of drought. The fact that kernel weight in tall wheats of lower yield potential was less sensitive to artificial manipulation of post-anthesis assimilate level (Fischer and HilleRisLambers 1978), and to drought in this study, supports this hypothesis. Evans and Wardlaw (1976) also suggest a trade-off between yield potential and yield resistance to stress in recent cereal improvement. The suggested combination through breeding of the drought resistance of old tall dryland cultivars with the yield potential of modern short wheats (Laing and Fischer 1976) begins to look difficult from a physiological point of view.

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