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Drought Resistance in Spring Wheat Cultivars. I Grain Yield Responses

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Abstract

With a view to understanding the basis of cultivar differences in yield under drought, a wide range of cereal cultivars representing durum wheats (*Triticum turgidum* L.), triticales (X *Tritosecale* Wittmack), barleys (*Hordeum vulgare*), and especially tall and dwarf bread wheats (*T. aestivum* L.) were studied in field experiments in north-western Mexico over three seasons. Drought was created in this rain-free environment by permanently terminating irrigation at various stages before anthesis. Control treatments were well watered throughout the growing period. Detailed measurements of plant water status, leaf area and dry matter production, anthesis date, yield components and grain yield were made. This paper presents primarily the grain yield data.

Drought levels were such that the mean yield of all cultivars under drought ranged from 37 to 86% of control yield, corresponding to irrigation cut-offs varying from 69 days before mean anthesis date to only 10 days before. In each experiment the grain yield under drought showed highly significant cultivar differences, which appeared consistent between years. Yields were adjusted for drought escape by using a correction factor which ranged from 2·9 to 8·5 g/m^2 per day advance in flowering, being greater in experiments with less severe drought.

The demonstration of linear relationships between cultivar yield and drought intensity, as indicated by the mean yield of some or all cultivars, prompted the consideration of cultivar yield under drought as the function of yield potential (Y_p, yield without drought), drought susceptibility index (S), and intensity of drought. The cultivar groups showing lowest S values (most drought-resistant) were tall bread wheats and barleys; dwarf bread wheats were intermediate, and durum wheats and triticales were the most susceptible. However, because dwarf wheats have a higher yield potential (Y_p) than tall bread wheats, it is suggested that, as a group, tall bread wheats would outyield dwarf wheats only under very severe drought. Also there was considerable within-group variability of S and Y_p. Cultivar S values were consistent across experiments. Yield responses of tall and dwarf bread wheat groups obtained in these experiments agreed with those seen in extensive international trials under dryland conditions.

Introduction

The introduction of spring wheats with dwarfing genes derived from Norin 10 to irrigated regions throughout the world has led to striking increases in productivity (Borlaug 1968). Increases in yields in dryland situations, although evident (e.g. Laing and Fischer 1977), have not been as spectacular. The growing gap in yields between these two situations stimulated our interest in the yield of dwarf wheats under dry conditions.

Plant breeders and physiologists have been concerned with drought resistance for many years. Various mechanisms by which crops, including wheat, may resist drought have been summarized. May and Milthorpe (1962) classify these into (i) drought escape, (ii) drought endurance with high internal water content, and (iii) drought endurance with low internal water content. Levitt (1972) defines mechanism (ii) as drought avoidance and mechanism (iii) as drought tolerance, terms which along with drought escape ((i) above) will be used throughout these papers. Also we consider that drought resistance comprises avoidance and/or tolerance, but not escape.

Some workers have tried to devise simple tissue tests for drought resistance (e.g. Sullivan 1978). Owing to the likely multiplicity of factors and factor interactions contributing to drought resistance in crops in the field, these efforts have met with very little success. Other physiologists have proposed plant ideotypes for drought-prone situations, and the incorporation into existing cultivars of characters likely to increase their drought resistance (e.g. Passioura 1972). However, these proposals are largely based on theory and, as thorough assessment of the value of such characters is very time-consuming (Moss *et al.* 1974), it is not surprising that little such testing has been done.

In view of the lack of sound information on specific drought resistance mechanisms, plant breeders selecting for drought resistance are still largely guided by grain yield and its stability under dry conditions. This is necessarily a slow and difficult process. Also high yield could arise as a result of drought escape or high yield potential (yield in the absence of drought), rather than, or as well as, the possession of adaptations specifically favouring performance under drought, i.e. drought resistance mechanisms. Separation of these influences upon yield under drought could in itself facilitate breeding and selection, and the identification of drought resistance mechanisms. This approach, with yield performance used as the guide to drought resistance, ought to complement the contrasting approach which proceeds from understanding plant–water relationships at the physiological level to postulate drought-resistant ideotypes.

Our study aimed to compare the yield under drought of a large number of old and recent, tall and dwarf, cereal cultivars. A range of drought treatments as well as adequately watered control treatments were used to separate the effects due to the operation of resistance mechanisms from those of drought escape and differences in yield potential. As a further indication of the presence of such mechanisms and their nature, data were collected on important and readily measured aspects of cultivar traits such as anthesis date, yield components, harvest index, green area, plant morphology, leaf water potential and stomatal opening. This paper concentrates upon the grain yield results, their adjustment for drought escape, and the separation of effects due to differences in yield potential. A second paper will examine relationships between yield and the other features of the cultivars which were measured.

Material and Methods

The work was carried out at the Centro de Investigaciones Agricolas del Noroeste (CIANO), located near Ciudad Obregon, Sonora. The climate in this part of north-western Mexico (latitude 27° N.) is semiarid with an average of only 50 mm of rain falling during the winter cropping season. Wheat is normally irrigated; drought was created by withholding irrigations. Experiments were conducted during the December to April period in the years 1971–1975. Long-term weather averages for these months are shown in Table 1. The experiment of 1972–73 is not considered here because of interference from rainfall (104 mm December–April), but there was zero rainfall in the other three seasons and one major experiment was satisfactorily completed in

Table 1. Long-term monthly weather means for CIANO, Sonora, Mexico

Variable	Years	Month: Dec.	Jan.	Feb.	Mar.	Apr.
Rainfall (mm)	1960–1975	18	14	8	3	1
Temp. max. (°C)		24·1	23·2	24·7	27·1	31·2
Temp. min. (°C)		8·4	6·7	6·8	8·2	10·3
Sunshine (% max.)		81	78	79	84	84
Solar radn (MJ m^{-2} day^{-1})	1970–1975	12·2	13·1	16·7	21·5	24·9
Evaporation[A] (mm day^{-1})		3·4	3·1	3·7	5·2	7·5

[A] U.S. Weather Bureau Class A pan.

each (Table 2). Certain irrigation experiments at CIANO (Fischer *et al.* 1977) and other minor drought experiments also contributed to the relationships to be presented here.

Table 2. Outline of major experiments at CIANO

Experiment (year)	Treatments[A]	Cultivars[B]
1 (1971–72)	1. Sown 9 Dec., well watered 2. Sown 22 Nov., last irrign 10 Feb. (10) 3. Sown 9 Dec., last irrign 10 Feb. (20) 4. Sown 21 Dec., last irrign 10 Feb. (29)	9 (6 BW, 1D, 1T, 1B)
2 (1973–74)	1. Sown 6 Dec., well watered 2. Sown 24 Nov., last irrign 4 Feb. (20) 3. Sown 6 Dec., last irrign 4 Feb. (29) 4. Sown 18 Dec., last irrign 4 Feb. (40)	10 (6 BW, 2D, 2T)
3 (1974–75)	1. Sown 14 Dec., well watered 2. Sown 14 Dec., last irrign 6 Feb. (36) 3. Sown 14 Dec., last irrign 16 Jan. (57) 4. Sown 14 Dec., last irrign 4 Jan. (69)	53 (34 BW, 6D, 7T, 6B)

[A] Last irrigation in days before mean anthesis date of the treatment, or of treatment 1 (experiment 3), given in parenthesis.
[B] BW, bread wheat; D, durum wheat; T, triticale; B, barley.

Cultivars

Cultivars representing several species (bread wheats, *Triticum aestivum* L.; durum wheats, *Triticum turgidum* L.; triticales, X *Triticosecale* Wittmack; and barley, *Hordeum vulgare* L.), were studied (Table 2), although the major emphasis was upon bread wheats, including both tall and dwarf cultivars. Wheat breeders at CIMMYT have developed a nominal grading system for degree of dwarfism in cultivars assumed to carry major dwarfing genes generally originating from Norin 10. This is used here to classify dwarf wheats into single (E1), double (E2), triple (E3) and extreme (E4) dwarfs, corresponding to the following approximate mature plant heights at CIANO under high fertility in the absence of drought: >105 cm, 90–105 cm, 70–90 cm and <70 cm respectively. Tall wheats usually exceeded 120 cm. Cultivars, unless bread wheats, are designated durum wheats, triticales and barleys by the postscripts (D), (T) and (B) respectively. Most dwarf cultivars, and all triticales, were derived from Mexican breeding programs and usually had a history of selection under irrigated conditions. Tall cultivars were older varieties from Australia, Mexico, North Africa and India. They have no Norin 10 dwarfing genes and had been selected under non-irrigated conditions. All barleys had performed well in recent non-irrigated trials in North Africa, the Middle East and Australia.

Irrigation

The soil at CIANO is a cracking clay with very slow water penetration after initial wetting. In a separate study, a 2 hr flooding gave about 110 mm of available water in the top 100 cm, while a further 22 hr flooding increased this by only 10 mm, and there was little available water below 100 cm (L. H. Stolzy and R. J. Laird, unpubl. data). To standardize the initial conditions of any drought cycle, the irrigation preceding drought always involved 3 hr of full submergence by flooding. The onset of stress was gradual: signs of wilting were not noticed until 20–35 days after such an irrigation (see also Fig. 1). This study concentrated upon drought arising in the latter half of the crop's life cycle, to attempt to simulate the type of drought commonly seen by wheat in regions with Mediterranean climates. Thus a drought treatment, once initiated, was not relieved. Different severities of drought were established by giving the final irrigation at different stages of crop development. In general experiment 1 involved mild droughts and experiment 3 severe ones, with experiment 2 intermediate (Table 2). Irrigations were sufficiently frequent to avoid stress until drought treatments were imposed.

The inclusion of many diverse cultivars inevitably led to differences between cultivars in stage of development when irrigation was terminated and therefore when water stress arose. In experiments 1 and 2, drought treatments comprised a range of seeding dates with a single date for the final irrigation for all drought treatments (Table 2). Experiment 3, however, adopted a single seeding date and a range of irrigation cut-off dates. Both experimental strategies were planned to permit correction of yield results for differences between cultivars in rate of development (drought escape).

Experimental Design

A split plot design was used with drought levels as the main treatments, cultivars as subtreatments, and four replications (three in 1974–75). The main plots occupied from one to three adjacent irrigation basins depending on the number of cultivars; each basin was *c.* 12 m by 12 m and was completely flooded during an irrigation. Special precautions were taken to prevent seepage into drought plots from nearby canals in the cracking soil. In experiments 1 and 2, the size of the cultivar subplot was 3 m by 3 m (width across rows × length), from the centre of which 2 m^2 was harvested. Plot size was reduced in experiment 3 to 1·5 m by 3·0 m, from which 0·9 m by 2·0 m was harvested.

Agronomic management varied little between experiments. Row spacing was 30 cm and seeding density ranged from 60 to 100 kg/ha, with 40 kg/ha for barley in experiment 3. Fertilizers applied per hectare were: 100 kg nitrogen and 36 kg phosphorus (experiment 1), 50 kg nitrogen and 27 kg phosphorus (experiment 2), and 75 kg nitrogen and 18 kg phosphorus (experiment 3), variation which is unlikely to have influenced comparisons between experiments. Weeds and diseases were controlled.

Measurements

At the maturity harvest, total above-ground dry matter was determined by either oven-drying or field-drying the plant material for at least 1 week. All grain was oven-dried at 70°C and yields are presented on an oven-dry basis. Harvest index (%) was calculated as the ratio of grain weight to total dry matter. When total dry matter was obtained by field-drying, oven-dry grain wheat was increased by 8% moisture for the harvest index calculation. Kernel weight was determined from the weight of two samples of 100 grains. Grain number per m^2 was calculated. Observations were made on date of 50% anthesis (dehisced anthers) and 50% maturity (spikes without green colour), but anthesis was estimated from observations of 50% spike emergence (spike above flag ligule) in experiment 2. Because drought retards and even prevents the full emergence of spikes from the flag leaf sheath, spike emergence is not a satisfactory indicator of anthesis under severe drought for some cultivars. For example, with droughted barley in experiment 3, observation of anthesis involved dissection of the flag leaf sheath because anthesis occurred before any part of the spike had emerged. Leaf water potential was measured in experiment 3 with a pressure chamber (Fischer *et al.* 1977).

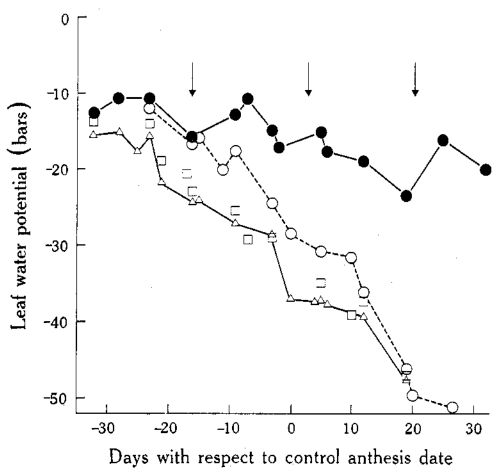

Fig. 1. Change in minimum daily leaf water potential (pressure chamber) with time for control (●——●) and drought treatments 2 (○----○), 3 (□), and 4 (△——△) in experiment 3. Mean of Yecora 70 (E3), Penjamo (E1) and T64-2-W (tall). Arrows indicate control irrigations.

Results

Main Effects on Plant Water Potential

Plant water potential averaged for three representative bread wheat cultivars for each main treatment in experiment 3 are shown in Fig. 1. Plant water potential fell steadily but slowly (about 0·7 bar/day) following the onset of drought; water potential was only slightly higher for treatment 3 than in treatment 4, but clearly higher for treatment 2 until maturity was approached. The rate of decline in plant water potential with drought in experiments 1 and 2 is likely to have been similar to that shown in Fig. 1. However, measurements in experiment 2 (R. E. Sojka, unpubl. data) did show that, despite the same irrigation cut-off date for all treatments, the water potential at any given date during drought was from 5 to 10 bars higher for treatment 4 than in treatment 2, with treatment 3 intermediate. This arose because plant water potential began to fall sooner for the earlier-sown crop.

Main Effects on Yield and Yield Components

All drought treatments reduced the grain yield significantly, although the range in yields between treatments experiencing drought in any experiment was not large (Table 3). Total dry matter production was reduced relatively less than grain yield,

Table 3. Effect of drought on grain yield and its components, experiments 1, 2 and 3
Values are means of all cultivars

Treatment	Grain yield (g/m²)	Grain yield (%)	Total dry[A] matter (g/m²)	Harvest index (%)	Grain number (100/m²)	Kernel weight (mg)
			Experiment 1			
1	472	100	1425	35·9	129	36·4
2	408	86	1317	33·7	123	33·3
3	324	69	1155	30·4	122	26·7
4	246	52	1015	26·0	99	25·2
LSD (5%)	26		85	0·8	8	1·4
			Experiment 2			
1	520	100	1363	38·4	132	39·7
2	328	63	1005	32·9	108	30·5
3	302	58	1026	29·5	104	29·5
4	214	41	740	28·6	72	29·7
LSD (5%)	45		115	2·4	15	1·3
			Experiment 3			
1	516	100	1315	42·5	119	44·0
2	253	49	870	31·3	78	33·1
3	192	37	664	31·0	58	33·6
4	197	38	648	32·4	58	34·5
LSD (5%)	75		163	3·5	20	1·6

[A] Field-dry weight in experiments 1 and 3, oven-dry weight in experiment 2.

so that the harvest index fell with drought, but once the drought was severe enough to reduce yield by 50%, greater levels of drought did not further reduce the harvest index (experiments 2 and 3). The milder drought treatments (less than 50% yield reduction) led to a greater relative reduction in kernel weight than in grain number. As drought severity increased, grain number was reduced relatively more.

Cultivar Effects and Cultivar × Drought Interactions

Cultivar and cultivar × treatment interactions were highly significant for yield, grains/m² and kernel weight in all experiments (Table 4). However, when the analysis was restricted to those treatments involving drought (i.e. excluding the adequately watered control) the interactions for grain yield were, with one exception, no longer significant, although the cultivar effects remained highly significant. This occurred presumably because drought treatments were not markedly different in each experiment, and it means that cultivar yield averaged across drought levels is an appropriate summary of the cultivar yield differences under drought in each particular experiment. Averaging across several treatments gives a gain in precision of cultivar comparisons, which is very desirable in view of the generally high coefficient of variability under drought. The exception referred to above was a significant interaction in experiment 1 when yield was analysed across treatments 2, 3 and 4; exclusion of one of the nine cultivars, Cocorit 71 (D), reduced the interaction to non-significance.

Table 4. Summary of the statistical significance of cultivar (G) and cultivar × treatment (G × E) interaction for experiments 1, 2 and 3

Experiment	Treatments included	Variable	Significance G	Significance G × E	Coefficient of variability (%)
1	All	Grain yield	**	**	9·9
		Grain no./m²	**	**	10·3
		Kernel wt.	**	**	6·7
	Only 2, 3, 4	Grain yield	**	*	11·0
	Only 3, 4	Grain yield	**	NS	12·5
2	All	Grain yield	**	**	10·6
		Grain no./m²	**	**	10·7
		Kernel wt.	**	**	5·9
	Only 2, 3, 4	Grain yield	**	NS	12·8
3	All	Grain yield	**	**	14·7
		Grain no./m²	**	**	15·6
		Kernel wt.	**	**	6·3
	Only 2, 3, 4	Grain yield	**	NS	19·5
		Grain no./m²	**	NS	18·9
		Kernel wt.	**	**	7·1

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

Considering the minimal yearly variation in weather, the artificial control over drought, and the absence of soil differences, cultivar yield differences under drought in this study should have been consistent from year to year. Evidence of consistency of cultivar yield responses was sought by plotting the yields of individual cultivars in all treatments of all experiments against an environmental index representative of the degree of water stress (as in Eberhardt and Russell 1966). Ideally some physical quantity descriptive of environment should be used as the environmental index, but none of the measurements made here appeared to serve as an index of stress as well as cultivar yield itself. Normally the mean yield of several or many cultivars is used, but in Fig. 2 the environmental index was taken to be the yield of the E3 dwarf bread wheat cultivar Yecora 70, since this was the only cultivar common to all experiments. All experiments in which Gabo and Cocorit 71 (D) appear, and all treatments, are included in Fig. 2. Relationships were assumed to be linear, an assumption which obviously cannot be true as zero yield is approached, but which nevertheless fits the data well.

The approach of Fig. 2, with the mean of the yields of Yecora 70 and Cocorit 71 (D), varieties which appeared in most experiments, taken for greater precision as an environmental index, was used to calculate linear regressions for all the data available on each of a number of frequently tested representative cultivars (Table 5). The close

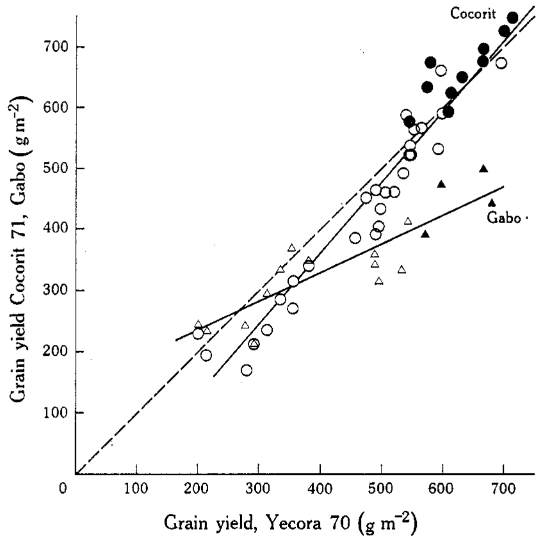

Fig. 2. Grain yield of cultivars Cocorit 71 (D) and Gabo as a function of the yield of Yecora 70; all treatments in all available experiments. The linear regressions were: Cocorit 71 (D): $Y = -102 + 1 \cdot 16X$ ($r = 0 \cdot 954^{**}$), and Gabo: $Y = 151 + 0 \cdot 44X$ ($r = 0 \cdot 883^{**}$). Closed symbols, well-watered control treatments. Dashed line, 1:1 relationship.

fits obtained for each cultivar in Fig. 2 and Table 5 are evidence of consistent responses to water stress. The very close relationships for Yecora 70 and for Cocorit 71 in Table 5 are obviously partly spurious, but the relationship of Cocorit 71 yield to Yecora 70 yield in Fig. 2 is not so, and is also close ($r = 0 \cdot 954$).

Table 5. Relationship of yield to environmental index (mean of Yecora 70 and Cocorit 71 (D) yields) and other variables for key cultivars: all experiments

Cultivar	Height class	Anthesis[A] (days)	n	Yield (g/m²) (X = env. index)	Standard error of b	Correlation coefficient	Predicted yield (g/m²) $X = 650$	Predicted yield (g/m²) $X = 230$	Drought yield[B] (g/m²)
Gabo	Tall	92	17	$160 + 0 \cdot 44X$	0·06	0·897	446	262	258
T64-2-W	Tall	94	13	$135 + 0 \cdot 47X$	0·06	0·923	441	244	248
Nainari 60	Tall	91	13	$101 + 0 \cdot 57X$	0·06	0·942	472	233	249
Pitic 62	E1	95	13	$18 + 0 \cdot 76X$	0·06	0·969	510	193	200
Siete Cerros 66	E2	97	13	$37 + 0 \cdot 87X$	0·07	0·966	602	237	232
Ciano 67	E2	85	17	$180 + 0 \cdot 50X$	0·07	0·870	505	295	252
Yecora 70	E3	90	38	$57 + 0 \cdot 91X$	0·02	0·988	642	267	241
Cocorit 71 (D)	E2	91	38	$-58 + 1 \cdot 10X$	0·02	0·992	657	196	221
Armadillo (T)	Tall	93	17	$-29 + 0 \cdot 70X$	0·07	0·935	426	133	92

[A] Days to anthesis in well-watered treatment, experiment 3.
[B] Mean of treatments 2, 3 and 4, experiment 3.

Significant differences in regression slopes between cultivars in Fig. 2 and Table 5 are indicative of cultivar × degree of water stress interactions. The differences are especially interesting in the case of Fig. 2 because the cultivars had similar anthesis dates. The interactions are appropriately summarized by the predicted yields at high (well-watered) and low (droughted) levels of the environmental index (Table 5). The low level of the environmental index ($X = 230$) adopted in Table 5 is equal to the mean index for treatments 2, 3 and 4 in experiment 3. Actual cultivar yields averaged over these treatments, shown in the next column, agree reasonably well with predicted yields, but the actual yields contributed three of the 13–38 points used to derive the prediction equations.

Given that the cultivar differences in yield responses to drought seemed consistent across experiments, most attention will now be paid to these differences in the largest of these experiments, experiment 3. Grain yield is summarized by species and cultivar group in the left of Table 6. E1 to E3 dwarf wheats, including durums, and recent triticales showed the highest yield potentials (control yields). E2 and E3 dwarf bread wheats gave the best yields under drought, but E1 dwarf and tall bread wheats, E2 dwarf durums and barleys were not far behind. Only E4 dwarf bread wheats, tall durums and triticales were clearly inferior. There was considerable variability within cultivar classes, the highest yield under drought being given by a two-row barley (WI2198, 313 g/m^2, 79 days to anthesis) and the second highest an E2 dwarf bread wheat (Cleopatra 74, 277 g/m^2, 82 days to anthesis).

Table 6. Mean grain yields, height and days to anthesis of cultivar groups in experiment 3

Species, group	*n*	Grain yield (g/m^2) Control mean	Drought[A] Mean	Drought[A] Lowest cv.	Drought[A] Highest cv.	Mean height[B] (cm)	Mean anthesis[B] (days)	Adjusted mean drought yield[C] (g/m^2)	Relative drought yield[D] (%)	Drought suscepti-bility index
Bread wheats										
Tall	8	447	225	153	258	120	93	231	51·7	0·83
E1	7	554	226	198	262	101	90	225	40·6	1·02
E2	13	553	234	193	277	96	91	237	42·9	0·98
E3	3	555	240	232	247	74	90	237	42·7	0·98
E4	3	498	195	171	227	53	88	187	37·6	1·07
Durum wheats										
Tall	3	464	162	121	197	117	97	180	38·8	1·05
E2	3	600	229	221	235	94	89	226	37·7	1·06
Triticales										
Old	1	456	92	—	—	132	93	98	21·5	1·34
Recent	6	550	192	144	221	117	94	201	36·6	1·08
Barleys										
Recent	6	452	225	162	313	101	82	201	44·5	0·95
All	53	516	217	92	313	101	91			

[A] Average of treatments 2, 3 and 4.
[B] Recorded on well-watered control, treatment 1.
[C] Adjusted to mean days to anthesis of experiment, 91 days, using 2·85 g/m^2 per day.
[D] Adjusted mean drought yield as percentage of control mean yield.

Drought Escape

Considering that drought in these experiments was unrelieved and in any treatment increased in severity with time, cultivars which flowered and matured earlier may have been favoured by partial escape from drought. For example, comparison of Ciano 67 with later-flowering Pitic 62 in Table 5 would suggest that Ciano 67 was favoured by escape: the predicted yields under well-watered conditions appeared similar, but the regression slope was lower with Ciano 67 and its yield under drought was superior.

The question of drought escape was approached in two ways. One approach was to plot the yield of each cultivar in each drought treatment against the time of last irrigation, expressed as the number of days before anthesis of the particular cultivar when this irrigation was given. Fig. 3 illustrates this approach for four contrasting cultivars from Table 5 and is based on data from all experiments. This figure permits cultivar comparisons which would be largely independent of differences in rates of development (days to anthesis) and hence effects of drought escape. For the Ciano 67 *v.* Pitic 62 comparison, allowing for drought escape in this manner does not completely eliminate the yield advantage of the earlier-flowering Ciano 67 evident in Table 5. Also it is important to note in Fig. 3 that the sensitivity of yield to irrigation cut-off time depends on the cut-off time itself as well as the cultivar. For an irrigation cut-off around 20 days before anthesis the sensitivity was as high as 6–8 g/m^2/day; at 60 days before anthesis it was only 1·5–2·5 g/m^2/day. Finally, it is obvious that the scatter of points under severe drought (cut-off before 40 days before anthesis) will make the identification of real cultivar differences difficult.

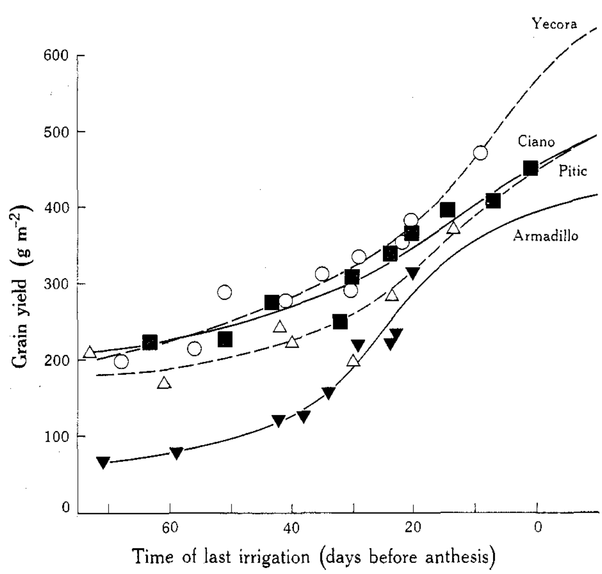

Fig. 3. The grain yield of Yecora 70 (○– – –○), Ciano 67 (■——■), Pitic 62 (△– – –△) and Armadillo (T) (▼——▼), as functions of the date with respect to anthesis when the last irrigation was given; all experiments. Curves hand-fitted to pass through mean control yield at 10 days after anthesis.

The approach represented by Fig. 3 was used to adjust yields in experiments 1 and 2 for drought escape. The absence of significant cultivar × drought treatment interactions within each of these experiments (Table 4) meant that the level of drought (irrigation cut-off timing) to which yields were adjusted was not critical. The mean stages of development for irrigation cut-off (20 and 30 days before anthesis in experiment 1 and 2, respectively) were therefore chosen when adjusted drought yields were calculated later (see Table 7). For this purpose average slopes for all cultivars of 8·5 g/m^2 (experiment 1) and 5·5 g/m^2 (experiment 2) per day change in irrigation cut-off date were derived from plotting the data as in Fig. 3.

A second approach to drought escape was adopted in the case of experiment 3. Cultivar mean anthesis date for the control treatment, ranging from 79 to 99 days from sowing, was used as a covariable to adjust grain yield under drought (mean of treatments 2, 3 and 4) to a common anthesis date (91 days). The adjustment factor amounted to a $2 \cdot 85$ g/m^2 yield loss per day delay in anthesis ($r = 0 \cdot 40^{**}$). Adjusted mean yields for cultivar groups are shown in Table 6; they differed little from unadjusted yields, except in the case of barleys which averaged 9 days earlier than the experimental mean date of anthesis; their adjusted performance drops to that of triticales under drought.

Yield Potential and Drought Susceptibility

Fig. 2 and Table 5 show linear relationships between cultivar yield (Y) and water supply as reflected in the level of the environmental index (X). This suggests that yield under drought can be considered to depend on both yield potential (Y_p = yield without drought, when $X = X_p = c$. 700 g/m^2 in Fig. 2) and the slope ($\Delta Y/\Delta X$) of the yield *v*. environmental index relationship. However, Y_p and slope appear to be related: this is most obvious across the cultivars of Table 5 where the correlation between Y_p and slope was $0 \cdot 87^{**}$. Such associations are common. For example, Laing and Fischer (1977), in analysing the yield of 33 spring wheat cultivars over dryland sites, also found a strong positive correlation between regression slope and cultivar mean yield ($r = 0 \cdot 81^{**}$); their data imply an even stronger association between slope and cultivar yield potential.

From physiological considerations it is not surprising that the absolute reduction in yield for a given reduction in resource, i.e. water, is strongly influenced by the level of Y_p. High Y_p and low slope would seem biologically impossible although the opposite combination is possible (e.g. Armadillo (T) in Table 5). In order to remove the effect of variation in yield potential, relative yields (Y/Y_p) under drought were calculated. This approach has been used by many (e.g. Chinoy 1947; Blum 1973), and as an example was applied here to the yields of experiment 3 after adjustment of drought yields for drought escape (Table 6, second last column).

Relative yield (Y/Y_p) will depend on the level of the environmental index relative to its maximum value (X/X_p), but cultivar rankings for relative yield will remain unchanged with change in X/X_p provided Y *v*. X relationships are linear as in Fig. 2. The relative slope $[\Delta(Y/Y_p)/\Delta(X/X_p)]$ will, however, be independent of X, and should be more useful for comparisons between drought levels and experiments. This dimensionless slope is here termed the drought susceptibility index (S). Thus yield under drought (Y) is given by the following simple relationship:

$$Y = Y_p(1 - SD),$$

where D is defined as the drought intensity ($D = 1 - X/X_p$) and ranges from 0 to 1. This equation expresses the separate effects of yield potential and drought susceptibility on yields under drought, and in these terms lower drought susceptibility is considered synonymous with higher drought resistance, whether via greater drought tolerance or avoidance as defined in the Introduction.

Drought susceptibility indices were calculated for the cultivar groups of experiment 3 from the mean yields, and appear in Table 6 (last column). The rankings by definition are exactly the reverse of those derived from relative yield under drought. S values for some cultivars in various experiments appear in Table 7. Included are values calculated from the results of the 6th and 7th International Spring Wheat Yield Nurseries (ISWYN) by means of the regression of cultivar yield *v*. site mean yield (Table 7, last column). These trials involved 44 dryland sites throughout the world (Laing and Fischer 1977).

The first point to examine in Tables 6 and 7 is the consistency of S values for given cultivars. However, it should be remembered that, although S should be independent of drought intensity, its exact value will depend on the cultivars included in calculating the environmental index. For most cultivars there was reasonable agreement between S values calculated separately for experiments 1, 2 and 3; Armadillo (T) appears to be an exception. Values of S calculated from Table 5 probably represent the most precise comparison of drought susceptibilities. There were eight ISWYN cultivars from the study of Laing and Fischer (1977) common to experiment 3. In the case of 6, their S values (Table 7, last column) were closely

Table 7. Drought susceptibility indices for all cultivars appearing in at least two experiments plus some additional cultivars from experiment 3

Cultivar	Group	Drought susceptibility index[A] Expt. 1	Expt. 2	Expt. 3[B]	Table 5 data[C]	6–7th ISWYN
Gabo	Tall	0·52	0·73	0·78	0·64	—
Nainari 60		0·62	—	0·88	0·78	1·00
C306		—	—	0·90	—	1·08
T64-2-W		—	0·81	0·76	0·69	—
Pitic 62	E1	1·11	—	1·02	0·94	1·05
Sonalika		—	—	0·88	—	0·99
Siete Cerros 66	E2	—	1·00	0·98	0·94	1·04
Ciano 67		1·01	0·94	0·86	0·64	—
Penjamo 62		—	—	1·02	—	1·08
Tobari 66		—	—	0·95	—	0·90
WW15		—	—	1·02	—	1·08
Cleopatra 74		—	—	0·97	—	—
Yecora 70	E3	1·07	1·04	1·03	0·91	—
Cajeme 71		—	0·98	0·93	—	—
Cocorit 71 (D)	E2	1·36	1·33	1·09	1·09	—
D67-3 (D)		—	1·06	0·98	—	—
Armadillo (T)	Old	0·87	0·92	1·34	1·07	—
WI 2198 (B)	Recent	—	—	0·67	—	—

[A] Drought yields adjusted for drought escape by estimating yields at irrigation cut-offs of 20 days before anthesis (experiment 1) and 30 days before anthesis (experiment 2) or by using anthesis date as a covariable (experiment 3); no adjustment was made for the Table 5 and ISWYN data.
[B] Standard error of cultivar mean was 0·065.
[C] Environmental index was the mean yield of Yecora 70 and Cocorit 71; for other columns the mean yield of all cultivars in the particular experiment constituted this index.

associated with those determined in experiment 3; the two exceptions were C306 and Tobari 66. Since the ISWYN contained 10 tall wheats and 18 dwarf ones (E2 and E1 dwarfs) of similar maturity, it is useful to compare the respective group mean Y_p and S values with the group means in experiment 3 (Table 6, last column). The ISWYN data gave mean Y_p values of $4 \cdot 11 \pm 0 \cdot 10$ t/ha ($\pm$standard error of the mean) for the tall wheats and $4 \cdot 95 \pm 0 \cdot 05$ t/ha for the dwarf wheats. These values were the mean predicted yields at a high site mean yield level (4·5 t/ha). S averaged $0 \cdot 96 \pm 0 \cdot 025$ and $1 \cdot 05 \pm 0 \cdot 04$ for the two groups respectively. These differences between tall and dwarf wheats agreed with those of experiment 3. Finally, an experiment similar to experiment 3 was conducted at CIANO in the 1975–76 season (P. C. Wall, unpubl. data); there were 23 cultivars common to experiment 3 and the correlation between their S values, corrected for drought escape, in the two experiments was highly significant (0·66**).

Discussion

Drought Levels

The drought which was simulated in this study was that commonly encountered by rain-fed autumn–winter-sown cereals in Mediterranean regions, and may not be representative of droughts seen by dryland wheat elsewhere. That yields under the most severe drought (around 2 t/ha) were still relatively high probably reflects good agronomic management, combined with a soil water storage capacity and texture conducive to gradual drying (Fig. 1), giving ample opportunity for physiological adaptation (Begg and Turner 1976). The responses to drought of yield and yield components (Table 3) were according to expectation. The sensitivity of grain number to drought at or just preceding anthesis (Fischer 1973; Fischer *et al.* 1977) is such that grain numbers are so reduced as to permit reasonable grain-filling, despite the fact that the intensity of the drought continues to increase and is greater during grain-filling than around anthesis (Fig. 1). This may contrast with the spring drought condition termed 'haying off' in southern Australia, which is characterized by a sudden increase in plant water stress during grain-filling, leading to a very reduced kernel weight (Fischer and Kohn 1966*b*). However, much of the data of these authors (Fischer and Kohn 1966*a*) shows that soil and plant water stress was often considerable at anthesis, and that relative differences in grains per sq. metre were as great as or greater than those in kernel weight (Fischer and Kohn 1966*b*). Thus effects on yield seen here, and probably often in Mediterranean environments, will depend as much, if not more, on the reaction of cultivars to mild drought before grain-filling as on their more obvious reactions to the same drought as it intensifies during grain-filling.

One interesting feature seen here is the apparent reduction in yield sensitivity to drought as the drought became more severe (Fig. 3). As a result there was no difference in yield between treatments 3 and 4 in experiment 3 (Table 3), although the latter received its last irrigation 12 days before the former. Plant water potential differences between these treatments, although usually in the expected direction, were never great (Fig. 1). This could have arisen because (i) evapotranspiration over these 12 days in January amounted to only a small loss of water (from pan evaporation multiplied by an appropriate crop constant it is estimated to have been $48 \times 0 \cdot 5 =$ 24 mm), and (ii) treatment 4, subject to the longer drought, adjusted by reducing crop water use and/or increasing root exploration, the trade-off in lost yield potential for this presumed adjustment being small. In contrast to all other drought treatments, neither treatments 3 or 4 in experiment 3 would have reached full (>90%) light interception.

Drought Escape

The importance of drought escape was seen in Fig. 3; it varied inversely with intensity of drought, being greater for experiment 1 (mild droughts) than for experiment 3 (severe droughts) and intermediate for experiment 2. In adjusting yields for drought escape, as implied in Fig. 3, either differences in sowing date (experiment 1, experiment 2) or in drying cycle weather (experiment 3) are confounded with developmental differences between cultivars. However, the effect of sowing date on yield under adequately watered conditions was small over the period of *c*. 30 days involved (R. A. Fischer, unpubl. data). The 20 day range in anthesis dates between cultivars in experiment 3 implies a maximum variation of *c*. 30% in pan evaporation rate for equivalent stages of development at that time of the year (March, Table 1). On the other hand, daily solar radiation would have increased by *c*. 20% as pan evaporation increased 30%, and the net confounding effect of weather differences may not be large.

The approach to drought escape represented by Fig. 3 is quite different from the general relationship between cultivar mean yield under drought and anthesis date which was used to adjust yields in experiment 3. The use of anthesis date as a covariable includes other factors, as well as the ontogenetic timing of the onset of drought, which across cultivars may be associated with anthesis date and yield; fortunately yield potential was not one of those factors in experiment 3, being unrelated to anthesis date ($r = 0 \cdot 19$). Also the approach is based on a linear response averaged over all cultivars, whereas Fig. 3 permits each cultivar's yield to be adjusted independently of other cultivars if necessary. On the other hand, since droughts were severe in experiment 3 (the mildest drought involving irrigation cut-off at 24 days before anthesis of the earliest cultivar), use of a linear response would, from Fig. 3, appear reasonable.

In adjusting yields for drought escape or earliness of anthesis, no allowance was made for the acceleration of anthesis caused by drought itself. This is commonly observed with drought (e.g. Angus and Moncur 1977). Here the greatest acceleration was seen with the most severe drought (treatment 4, experiment 3), when it averaged 4 days across all cultivars. The presence of a highly significant cultivar × treatment interaction for days to anthesis in experiment 3 suggests that this acceleration varied between cultivars. The acceleration, averaged across all three drought treatments, was 3·6 days for all cultivar groups of Table 6, with the exception of recent triticales (2·2 days) and barleys (0·5 day), while the greatest acceleration in any given cultivar was 8 days. Whilst these cultivar differences are highly significant, it is not felt that they are large enough to constitute a separate drought resistance mechanism in itself.

It is concluded that either of the two approaches outlined for adjusting for drought escape is satisfactory under the conditions prevailing in these experiments, and provided the range in anthesis dates between cultivars is small (20 days or less) and the limitations of each approach are kept in mind. In other situations, for example where the drought is relieved, escape will depend on the drought missing the most sensitive ontogenetic period (anthesis) of the particular cultivar. For example, when drought began soon after sowing and was relieved before anthesis, early cultivars suffered relatively more than later ones (Fischer *et al.* 1977; R. A. Fischer, unpubl. data). Yield adjustment for such situations will be more cumbersome, but the approaches outlined should still apply.

Yield Potential and Drought Susceptibility

Before discussing cultivar effects on Y_p and S, it should be pointed out that, despite the use of relative slope (S), there still appears to be a positive association between Y_p and slope. For example, in experiment 3, Y_p was positively correlated with S across all cultivars ($r = 0 \cdot 41^{**}$, $n = 53$), and across bread wheats only ($r = 0 \cdot 68^{**}$, $n = 33$). The approach assumes that Y_p influences yield under drought because there are traits which favour yield in all situations. On the other hand, the existence of traits which are desirable under drought and undesirable under adequate watering, or vice versa, would lead to positive associations between Y_p and S. Notwithstanding the fact that error in estimating Y_p would add a spurious component to such positive associations, it appears that there were such traits in the cultivar set of experiment 3. This complex question of traits will be dealt with in a following paper. It suffices here to mention that a positive Y_p *v.* S association implies an optimum level of Y_p for maximum yield at any given expected intensity of drought, this value of Y_p being lower the more intense the drought. It should be added that environmental differences between experiments other than differences in water supply (e.g. nutrition, radiation, year etc.) may affect the expression of Y_p but should not alter S values.

The results of the tall *v.* dwarf bread wheat comparison appear to confirm some comment concerning the inferiority of the latter group under drought. In experiment 3 the tall group had a 19% lower Y_p than the E2 dwarf one and a 15% lower S; as a result the mean yield of former becomes superior at drought intensities (D) greater than 0·6. The corresponding ISWYN data indicates a crossover at $D = 0 \cdot 7$. However, these are quite severe drought intensities and may be approaching the lower limit of the linear relationship between yield and drought intensity (see Fig. 2). With less severe drought ($D < 0 \cdot 5$), the higher Y_p of dwarf wheats gives them a clear yield advantage over tall wheats. Also there was considerable variation within cultivar groups, and the most interesting question which arises is whether selection amongst progeny of crosses between tall and dwarf wheats can permit improvement of S without sacrifice of Y_p. This will also be discussed in the second paper.

In contrast to the tall *v.* dwarf bread wheat comparison, the performance of barley in experiment 3 (Table 6) appears to contradict the commonly stated belief that barley is more 'drought-resistant' than wheat. After adjustment of yields for drought escape, barley yields under drought were surpassed by all bread wheat groups except the extreme dwarf one. If allowance were made for the fact that the barley yield includes about 8% husk its performance is even poorer. The lower yield of barley was due to a lower Y_p, since the S value was better than other cultivar groups, with the exception of tall bread wheats. However, the major unique feature of barley in this context appears to be earliness, permitting drought escape. The yield advantage from drought escape may often be greater than that seen in experiment 3; for example, in experiment 1 it was three times as great.

Other cultivar groups in experiment 3 deserve brief comment. Amongst durums the difference between tall and dwarf cultivars seen with bread wheats was not found. However, the number of cultivars tested was small. The contrast in drought susceptibility between dwarf durums and dwarf bread wheats is well typified by the consistent responses of Cocorit 71 (D) and Yecora 70, seen for example in Fig. 2. Triticales in experiment 3 showed the highest drought susceptibility indices. This may be related to effects of the rye genome, or to lack of a selection history including exposure to drought, or to water stress interactions with floret fertility and grain-filling. Both these last two points appear to be relatively weak links in yield formation in triticales. Nevertheless, considerable progress has been made since the isolation of the Armadillo strain in 1968 (Zillinsky 1974), the one old triticale in experiment 3.

S values for individual cultivars (Tables 6 and 7) suggest that variation within cultivar groups is almost as great as that between groups, so that associations with height and species are not strong. Some dwarf bread wheats (e.g. Sonalika, Ciano 67) have relatively low S values, while two tall wheats (Gabo and T64-2-W) and one barley (WI 2198) appear to be the most drought-resistant (lowest *S*). The occurrence of large cultivar differences in *S* in experiment 3 (range 0·67–1·34 across all cultivars, 0·76–1·10 across bread wheats), and the consistency of yield responses when compared with other experiments suggest that the data on other plant traits collected in experiment 3 are appropriate for more detailed analysis. Thus a following paper will examine the relationship of various cultivar traits to adjusted yield under drought, and to the drought susceptibility index.

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