EFFECTS OF DROUGHT IMPOSED DURING DIFFERENT DEVELOPMENTAL PHASES ON THE GROWTH AND YIELD OF SPRING WHEATS.

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ABSTRACT

A pot experiment was done in a glasshouse to investigate the sensitivity of different developmental phases to drought and to determine the relationship between plant growth rates and the number of ears per plant and grains per ear. A freely tillering and a sparsely tillering wheat (cvs. Oroua and Karamu) were subjected to drought from: emergence — six leaf stage (6L); 6L — flag leaf appearance (FL); FL — ear emergence (EE); EE to 10 days after anthesis. The number of stress days (SD) accumulated during each drought period was calculated.

Drought during any phase of development decreased grain yield to about 75% of the control although the early droughts, which accumulated slightly more SDs, depressed yield slightly more than the late droughts. The number of ears per plant formed by both cultivars was closely correlated with the growth rate per plant between the start of stem extension and ear emergence. The number of grains per ear was strongly correlated with the dry matter growth per culm during the period from 10 to 30 days before anthesis for both cultivars.

These data suggest that the response of wheat yield to a specific amount of drought is not influenced by the phase when the drought occurs. The effect of drought on ears per plant and grains per ear appears to be associated with slower growth rate per plant and per culm during the specific periods when these yield components are being determined.

Additional Key Words: Stress days, growth and development, sensitive periods.

INTRODUCTION

Drought is known to decrease the yield of wheat but the precise influence of the severity and timing of drought in decreasing yield is less clear. Some results apparently support the existence of moisture sensitive periods — phenological phases during which yield is particularly sensitive to drought (El Nadi, 1969; Fischer, 1973; Chowdhury and Kumar, 1980). But results from other experiments where attempts have been made to quantify the degree of drought experienced by small grains cereal crops show no such sensitive periods (Day *et al.*, 1978; French and Legg, 1979; Baird, 1985). There is evidently a need to determine generally applicable procedures for quantifying drought stress so that the existence of moisture sensitive periods can be rigorously tested for.

Hiler and Clark (1971) proposed a mean of quantifying both the degree and duration of drought based on measurements of evapotranspiration. They defined the number of stress days (SD) experienced by a treatment as

$$SD = \Sigma\,[(1 - E_d/E_w)N] \qquad (1)$$

where Σ signifies the sum of all the periods in the square bracket when drought was imposed, E_d is the evapotranspiration from a droughted treatment and E_w is the evapotranspiration from a well-watered treatment and N is the number of days over which E_d and E_w were measured. Mogensen (1980) used SDs to quantify the effect of drought on barley and found that yield decreased with every increase in SD with the stress imposed during jointing and booting stages decreasing yield slightly more than stress at other times. Sudar *et al.* (1981) found that maize yield decreased proportionately with the number of SDs accumulated. However, the concept has not been widely used.

The mechanisms underlying the response of various yield components to drought imposed during developmental phases are also obscure. There is a need to elucidate such mechanisms if the effects of drought on yield are to be understood and predicted. Monteith and Scott (1982) recently suggested that the formation of a large yield component is favoured by conditions which maximise the amount of available assimilate during a key developmental phase and per relevant organic unit i.e. per plant during the time stem number is being determined, and per ear when the number of grains per ear is being determined. Similar concepts have also been suggested by Charles-Edwards (1982) and van Keulen (1982). The possibility that drought may affect yield components by slowing growth during different developmental phases when particular components are being determined seems worth investigating, especially as the idea is already incorporated in a simulation model of wheat growth and yield (Penning de Vries and van Laar. 1982).

The main objectives of this experiment were to use the stress day concept to help determine whether yield is differentially sensitive to the stage at which drought occurs and to examine whether the influence of drought on the number of ears per plant and grains per ear is related to a measure of the assimilate supply to these structures during particular phases of development. In addition, two cultivars were used to test previously reported assertions

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that freely tillering cultivars are affected more by drought than sparsely tillering ones (Kirby and Jones, 1977; Fischer *et al.*, 1977).

MATERIALS AND METHODS

Site and plant establishment

The experiment was conducted in an unheated glasshouse between March and July 1982. Square pots (150 x 150 x 180 mm deep) filled with 4.5 kg air-dried soil (sand:soil:peat by volume) were used for the experiment. Six seedlings per pot were retained and the pots were arranged to give a plant population of about 200/m^2. Nitrogen (0.71 g ammonium sulphate) in 200 ml solution per pot was applied at emergence which was adequate for the rest of the growth period. A fourteen hour daylength was maintained throughout growth using mercury vapour lamps (Phillips HLRG 400) which provided a photosynthetic photon flux density (PPFD) of 32μmole/m^2/s measured 0.5 m above the pots. Daily maximum and minimum temperatures were recorded and the glasshouse was ventilated automatically when the temperature exceeded 25 ° C.

A 2 x 5 factorial randomized complete block design with four replicatins was used. Two cultivars (Oroua and Karamu) were exposed to five drought treatments.

Control = Well watered;
E – 6L = Drought from emergence (E) (Zadoks (Z) 12) to six leaf (6L) stage (Z30);
6L – FL = Drought from 6L to flag leaf (FL) stage (Z39);
FL – EE = Drought from FL to ear emergence (EE) (Z55);
EE – A + 10d = Drought from EE to 10 days after anthesis (Z72).

The freely tillering cultivar, Oroua was bred at Palmerston North, New Zealand and is a cross between the South African cultivar Skemmer and CIMMYT line 66RN395. The sparsely tillering cultivar Karamu originated from CIMMYT, was selected at Wagga Wagga, Australia as WW15 and introduced to New Zealand in 1972. Both cultivars are semi-dwarfs.

Water application

The weight of the pot with air dried soil was 4.5 kg and at field capacity was 5.7 kg. The unstressed plants were watered to field capacity once a week initially and twice a week after 6L stage and the amount of water applied was recorded at each time. No corrections were made for increased plant weight. Plants subjected to drought were not watered until the leaves curled inwards (wilting point). Plants were then watered to field capacity and the drought cycle restarted. However, plants reached wilting point only once in their life cycle. The pots were weighed at the start and at the end of each drought cycle. The water used by plants during each phase of development and the cumulative total water use were calculated. The intensity and duration of drought was expressed in terms of stress days (Equation 1).

Sampling and measurements

At the beginning and end of each drought period destructive harvests were made from all six plants in pots preselected at random. Mainstems (MS) and tillers were separated and counted, dried to a constant weight at 75 ° C and weighed. At maturity, individual yield components, as well as straw yields, were measured for all mainstems and tillers. When the weight of a plant or organ had to be estimated at a stage between two growth harvests, the value was read from a curve drawn by eye through the growth measurements made on each replicate. The statistical analyses were done using the Genstat and Minitab statistical packages. Tests of significance were made using the following single degree of freedom contrasts:

C1 = Control vs mean of all drought treatments;
C2 = E – 6L vs 6L – FL;
C3 = FL – EE vs EE – A + 10d;
C4 = Mean of (E – 6L) + (6L – FL) vs mean of (FL – EE) + (EE – A + 10d).

RESULTS

Water use and accumulation of stress days

Figure 1 shows the pattern of water use and soil moisture content. The soil water deficit at the onset of leaf curling was about 1050 ml except for the first drought period when it was slightly less. By chance, each drought period coincided with only one drying cycle. Karamu used significantly less water than Oroua (P< 0.001) (Table 1). Plants subjected to drought during any phase of development used significantly less water than the well-watered control (P< 0.001) but there was no significant difference in water use between the drought treatments. A similar number of stress days was accumulated by the two cultivars and by plants subjected to drought irrespective of developmental phase though stress was slightly greater when imposed early.

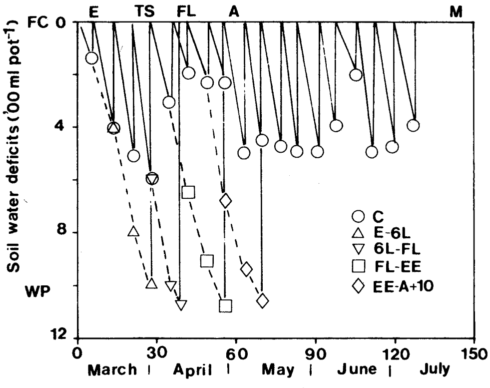

Figure 1: Development of water deficit in different drought treatments (E = emergence; TS = terminal spikelet; FL = Flag leaf ligule emergence; A = anthesis; M = maturity; FC = field capacity and WP = wilting point.).

TABLE 1: Effect of drought during different developmental phases on yield and yield components, water use and accumulation of stress days.

Treatments	Grain yield per plant (g)	Ears per plant	Grains per ear	Weight per grain (g)	Water use per pot (1)	Total stress days
Oroua	4.23 (81)a	5.24	25.6	32.7	11.80	16
Karamu	3.90 (75)	4.46	23.3	36.8	9.88	18
LSD (0.05)	0.135	0.150	0.68	0.99	0.529	2.9
Drought treatments						
Control	5.22(100)	5.67	26.3	38.8	12.96	0
E−6L	3.65 (70)	4.54	23.2	32.8	10.44	22
6L-FL	3.72 (71)	4.42	24.1	33.0	10.11	21
FL−EE	3.84 (74)	4.63	24.6	34.5	10.50	19
EE−A+10d	3.90 (75)	5.00	24.0	34.4	10.17	18
SEx	0.104	0.116	0.53	0.76	0.409	2.3
C.V.%	7.2	6.7	6.1	6.2	10.3	40
Contrasts:						
C1	***	***	***	***	***	**
C2	NS	NS	NS	NS	NS	NS
C3	NS	*	NS	NS	NS	NS
C4	NS	**	NS	*	NS	NS

*, **, *** are significant at $P<0.05, <0.01$ and <0.001, respectively.

a. Figures in the parentheses indicate yield as percent of control.

No significant interaction was noticed between the cultivars and the drought treatments either in water use or accumulation of stress days.

Yield and yield components

Karamu yielded 8% less grain than Oroua. Drought decreased grain yield by about 25% although the earlier droughts had a slightly more severe effect which was associated with a slightly greater accumulation of stress days (Table 1).

Karamu produced about one less ear per plant and 9% less grain per ear than Oroua but grains of Karamu were 12% heavier than Oroua. Drought decreased number of ears per plant, the effect being less marked the later the drought occurred. Drought during any phase of development also decreased the number of grains per ear by about 10% and weight per grain by about 13% (Table 1).

There was no significant interaction between the cultivars and the drought treatments either in yield or yield components.

Interrelationship between growth and yield components

Increase in plant dry matter were calculated between the periods 4L−6L, 6L−FL, FL−EE and EE−A+10d and correlated with the number of ears per plant although the number of days were not the same for the different periods. The correlation with dry matter growth between 6L−EE was the strongest (Figure 2).

Table 2 gives the correlations between the number of grains per ear and the dry matter growth per culm present at anthesis determined over a range of periods about the time of anthesis. The number of grains per ear was correlated most strongly with growth per culm during the periods from 10 to 20 days and 10 to 30 days before anthesis. Although grains per culm during 10 to 20 days before anthesis looks more consistent than 10 to 30 days, the former incurred greater intercepts implying significant number of grains per ear without any growth. This might be due to production of spikelets before the period in context was actually started. As the dry matter growth during 30 to 10 days before anthesis reduced the slopes considerably, this correlation was preferred. Figure 3 shows that the

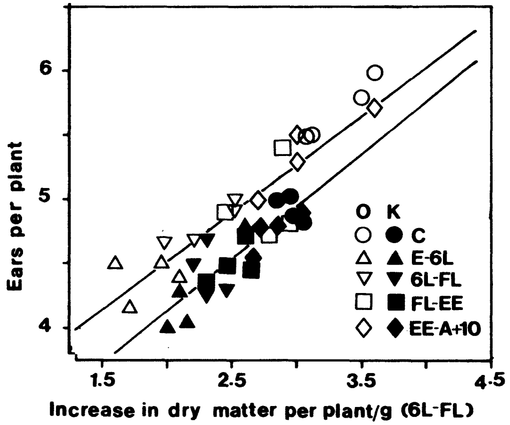

Figure 2: Relationship between ears per plant and increase in dry matter per plant of wheat grown under drought:

O = Oroua ($Y = 2.95\ (\pm0.205) + 0.781\ (\pm0.75)X$, $R^2 = 0.87$);

K = Karamu ($Y = 2.51\ (\pm0.282) + 0.81\ (\pm0.109)X$, $R^2 = 0.75$).

TABLE 2: Correlation coefficients of grains per ear of Oroua and Karamu wheat with increase in dry matter per culm during different developmental periods.

Developmental periods	Correlation coefficients Oroua	Karamu
A to A + 10d	0.326 NS	0.149 NS
A – 10d to A	0.605 **	0.307 NS
A – 10d to A – 20d	0.877 ***	0.804 ***
A – 20d to A – 30d	0.509 *	0.513 *
A to A – 20d	0.766 ***	0.513 *
A – 10d to A – 30d	0.886 ***	0.785 ***

A = Anthesis time of mainstems.

*, **, *** are significant at $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

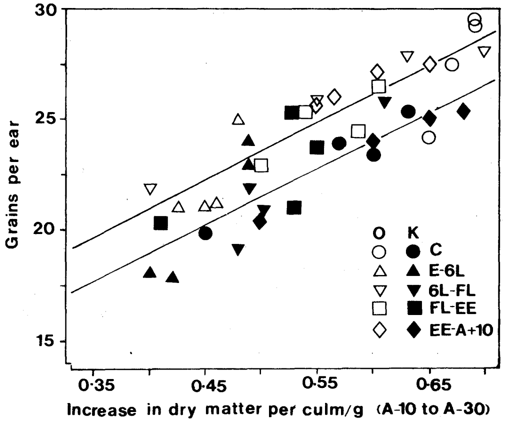

Figure 3: Relationship between grains per ear and increase in dry matter per culm of wheat grown under drought:
O = Oroua ($Y = 10.8\ (\pm 1.82) + 25.5\ (+3.15)X$, $R^2 = 0.78$);
K = Karamu ($Y = 9.3\ (\pm 2.46) + 24.5\ (\pm 4.57)X$, $R^2 = 0.63$).

intercepts were slightly different for the two cultivars with Oroua producing more grains per ear per unit of dry matter growth than Karamu. The relationship between weight per grain and post-anthesis dry matter growth per grain was highly anomalous and is not presented.

DISCUSSION

Stress days and yield

In this experiment the early stress treatments lasted longer than the later treatments but stress was less severe and stress days did not accumulate so quickly. The SD factor in this experiment provided a useful means of quantifying drought considering both intensity and duration of water stress. The fact that a similar number of stress days accumulated during each stress period and yield was decreased by a similar amount suggested that the periods were equally sensitive to drought. This contrasts with the results of El Nadi (1969) and Fischer *et al.* (1977) who reported a moisture sensitive period around the time of anthesis. However, intensity of drought was not measured in those experiments and drought imposed during an early stage might not be severe enough in the deep soil where they were working.

If a linear response of yield to stress days is assumed in the present experiment each stress day decreased yield about 1.4% below that of the control. This agrees well with 1.7% for barley (Day *et al.*, 1978) and 1.1% for wheat (Innis and Blackwell, 1981) whose data set were subject to similar analysis. However, Mogensen (1980) reported that yield was decreased by about 4% below that in a well-watered plot in his experiment but he calculated stress days only during the period when stress was imposed. A wider range of stress treatments is needed to establish whether decline in yield with stress days is really linear.

Drought decreased grain yield mainly through decreasing individual yield components. Heavier grains of Karamu failed to compensate for a smaller number of grains per plant arising from fewer ears per plant and fewer grains per ear. The grain yield reduction in droughted plants was a result of 12-20% decrease in ears per plant and 7-12% decrease in grains per ear. Innis and Blackwell (1981) and Rab *et al.* (1984) also reported 15-30% decrease in grains per ear due to drought during 20-25 days before anthesis. In this experiment weight per grain was decreased by 12-15% due to drought but Gales and Wilson (1981) and Parameswaran *et al.* (1984) found that when drought decreased the number of grains per ear there was a slight increase in weight per grain. However, Gales and Wilson (1981) reported that drought was not severe in a deep soil where they were working.

Interrelationship between growth and yield components

The strong correlation between ears per plant and dry matter growth during stem extension presented in Figure 2 supports the claim of Monteith and Scott (1982) that the number of ears formed by a plant is dependent on assimilate available during the time when stem number is being determined. Charles Edwards (1982), van Keulen (1982) and Gandar *et al.* (1984) suggested that to ensure the retention of each branch (tiller) on a plant or grain in a pod (or ear) there is a need for a minimum amount of dry matter to be produced for that organ during a particular developmental phase. The slope of the lines in Figure 2 suggest a requirement for about 1.25 g of dry matter to be produced between 6L – EE phase to ensure the survival of the tiller. However, the intercepts are larger than unity implying tiller survival without growth. This might be due to the presence of some late tillers which had the opportunity to mature in the E – 6L and 6L – FL treatments but the growth of those tillers was slow during 6L – EE period of the mainstems.

The strong correlation between grains per ear and growth per culm from 10 to 30 days before anthesis agrees with the results of Evans (1978) and Fischer and Stockman (1980) who both emphasized the importance of growth rate during the period 7-25 days before anthesis in determining grains per ear. Hawkins and Cooper (1981) also reported that the grains per plant of maize is dependent on plant growth rate during cob development before silking. The presence of positive and significant intercepts for both cultivars in Figure 3 indicates that dry matter production during other periods is also important to determine the number of grains per ear (cf. Table 2). Relationships such as those shown in Figures 2 and 3 may provide a useful approach to predicting the likely size of these yield components and one which Penning de Vries and van Laar (1982) adopted in a simulation model of wheat. However, there is a paucity of experimental results either supporting or refuting this approach. So care is needed when generalising.

CONCLUSIONS

The concept of stress days was useful in quantifying the degree and duration of drought in this experiment. Grain yield was reduced with every increase in stress days irrespective of developmental phases leaving little room for the existence of 'moisture sensitive periods'. Drought decreased grain yield by decreasing ears per plant, grains per ear and weight per grain. The decrease in ears per plant was associated with slower growth per plant during stem extension and that in grains per ear with slower growth per culm during the period between 10 and 30 days before anthesis. Drought and cultivar interactions were not significant.

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