Irrig Sci (1985) 6: 131–140

Irrigation Science

Grain Yield, Yield Components, Drought Sensitivity and Water Use Efficiency of Spring Wheat Subjected to Water Stress at Various Growth Stages

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Received March 30, 1984

Summary. The influence of water stress at various growth stages on yield and yield structure of spring wheat (*Triticum aestivum,* L., cv. "Sappo") was investigated using lysimeters in the field, automatically protected from rain by a mobile glass roof. Each drought treatment consisted of a single period without irrigation. Irrigation was resumed when all available soil water (100 mm between field capacity and permanent wilting to a depth of 100 cm) had been used. The drought periods were defined as beginning when relative evapotranspiration decreased below one and ending at reirrigation. The first drought occurred during tillering and jointing and the final one during grain formation.

Drought which was terminated before heading caused the development of late tillers which appeared after heading had ceased. They contributed up to 50% of the final grain yield. When only normal tillers were considered, the grain yield was lowest – 42% of fully irrigated treatment, for drought occurring during tillering and jointing. For drought during grain formation the relative yield was 87%.

The drought sensitivity was estimated as relative yield decrease per stress day (*F/SD*) where *F* is relative yield decrease and *SD* is relative evapotranspiration deficit multiplied by time, and as yield response factor (*Ky*), i.e. ratio of relative yield decrease to relative evapotranspiration deficit. For drought during tillering-shooting, shooting-booting, booting-heading, flowering and grain formation *F/SD* was 0.113, 0.087, 0.049, 0.021 and 0.012, respectively, and the *Ky* values were 3.00, 1.50, 0.90, 0.57 and 0.32, respectively. Based on the relative evapotranspiration during the entire growing period the *Ky* values for the five stages were 2.85, 2.45, 3.36, 1.28 and 0.98, respectively.

Considering the yield of both normal and late tillers for drought occurring during tillering-shooting and shooting-booting, *F/SD* was 0.034 and 0.055, respectively and the *Ky*-values were 0.90 and 0.95, respectively, for the individual periods and 1.10 and 1.86, respectively, based on the evapotranspiration deficit in the entire growing period.

The late tillers ripened two weeks later than the normal tillers and delayed the harvest making it difficult to harvest the crop in a satisfactorily dry condition. For this reason the drought sensitivity was calculated with and without the grains from late tillers included in the final yield.

It is concluded from the above results that the drought sensitivity of the variety of wheat used in this investigation was greatest during tillering-shooting when the grain yield of only normal tillers was considered. Including the grain yield of both normal and late tillers, drought sensitivity appeared to be greatest during booting-heading stage.

In wheat production under limited water supply conditions it is essential to know the proper time for application of the water available for irrigation in order to obtain maximum grain yield and water use efficiency.

A number of growth stages has been identified as critical stages of water stress for scheduling irrigation. These include seeding to maximum tillering stages (Choudhury and Kumar 1980), crown rooting (Misra et al. 1969), tillering to heading (Dragland 1979), jointing (Day and Intalap 1970) and booting to early grain formation (Schneider et al. 1969).

These different results obtained may be due to variations in climatic conditions or to differences in experimental procedures. When crops are exposed to drought at different times, the climatically determined stress will vary. Drought or water stress can be defined in various ways. For a barley crop Mogensen (1980) found that relative evapotranspiration was the most sensitive expression of water stress. The stress day factor as defined by Hiler and Clark (1971) combines the effect of the severity of water stress during drought and of the duration of the drought period. The ratio of relative yield reduction to the number of stress days was used by Mogensen (1980) to compare drought sensitivity at various growth stages of barley.

Late tillers will develop when temporary water stress is imposed at early growth stages. Such late tillers, if allowed by climatic conditions to ripen and to be included in the final harvest, may contribute significantly to the final grain yield and consequently to the overall drought sensitivity.

The purpose of the present investigation was to determine drought sensitivity of spring wheat at various growth stages and to determine the significance of late tillers for the final grain yield, and for the overall drought sensitivity and water use efficiency.

Materials and Methods

This experiment was conducted in a lysimeter installation situated 20 km west of Copenhagen (55°40′N; 12°18′E; 28 m MSL).

The lysimeter facility (Kristensen and Aslyng 1971) consists of 36 tanks, each 2×2 m by 1 m in depth. In the field, the lysimeter tanks are positioned in two rows divided by a drainage tunnel. A mobile glass roof automatically protects the crop against rain and when rain ceases the roof is automatically removed. Each tank is supplied with an individually operated trickle irrigation system.

The present investigation was conducted in 18 tanks containing loamy sand. Soil water content in the tanks was 130 mm at field capacity ($pF = 2$) and 30 mm at permanent wilting ($pF = 4.2$), thus the amount of available water was 100 mm.

On April 14, 1980 the soil was prepared and fertilizer applied at a rate equivalent to 780 kg ha^{-1} (NPK: 16–5–12) viz. 125 kg N ha^{-1}, 38 kg P ha^{-1} and 93 kg K ha^{-1}. Spring wheat

Table 1. Dry matter yield (kg ha^{-1}), yield components and actual evapotranspiration (*Ea*, mm) in the different treatments. ASW is per cent of plant available soil water utilized before reirrigation after drought. LSD is least significant difference at the probability level of 0.05 for comparing the drought treatments to the reference treatment. *F* is the variance ratio for test of significance. $F.05 = 3.2$ and $F.01 = 5.2$ for 7/10 degrees of freedom

Treatment	Dry matter yield			Ears per m²	Grains per ear	Grains per m²	Grain weight	Ea	ASW
	Grain	Straw	Total						
Normal tillers									
1	4,420	6,170	10,590	504	25.8	12,970	34.1	360	45
2	1,860	2,890	4,750	282	22.1	6,220	29.9	272	81
3	2,200	2,980	5,180	334	21.5	7,150	30.8	286	89
4	2,240	3,460	5,700	324	20.8	6,730	33.3	287	89
5	2,770	4,450	7,220	375	21.1	7,880	35.2	319	94
6	3,560	5,120	8,680	444	24.0	10,560	33.7	304	96
7	3,890	5,720	9,610	467	27.5	12,620	30.9	290	97
8	3,770	6,050	9,820	467	24.9	11,630	32.5	330	91
LSD	611	1,622	2,176	108	5.6	1,425	4.5	75	20
F	44.4	12.3	19.9	10.3	3.2	68.2	2.7	3.2	18.2
Late tillers									
2	1,830	2,550	4,380	294	20.0	5,880	31.1	271	81
3	1,530	2,570	4,100	288	19.1	5,350	28.6	286	89
4	800	1,340	2,140	231	13.2	3,050	26.2	287	89
LSD	495	888	1,348	155	9.1	1,135	4.5	47	23
Normal plus late tillers									
1	4,420	6,170	10,590	504	25.8	12,970	34.1	360	45
2	3,690	5,440	9,130	575	21.1	12,100	30.5	272	81
3	3,730	5,550	9,280	622	20.3	12,500	29.9	286	89
4	3,040	4,800	7,840	554	17.7	9,780	31.1	287	89
5	2,770	5,030	7,800	375	21.1	7,880	35.2	319	94
6	3,560	5,120	8,680	444	24.0	10,560	33.7	304	96
7	3,890	5,720	9,610	467	27.5	12,620	30.9	290	97
8	3,770	6,050	9,820	467	24.9	11,630	32.5	330	91
LSD	668	1,701	2,286	132	5.9	1,568	4.5	75	20
F	11.5	1.5	3.5	5.5	5.1	20.7	3.1	3.2	18.2

(*Triticum aesticum,* L., cv. "Sappo") was sown on April 16, 1980 at a seed rate equivalent to 200 kg ha^{-1} and with a distance between rows of 11 cm.

Treatments 2 to 8 each included 2 tanks in which the crop was successively exposed to drought. Each drought treatment consisted of a single drought period which terminated when all available soil water had been used up (Table 1). Treatment 1 included 4 tanks in which field capacity was restored weekly. The mean results from this treatment were considered as reference. Analysis of variance and least significant differences for treatments of unequal sizes were calculated according to Snedecor and Cochran (1979).

Soil water content was measured three times a week by the neutron moderation method at 10, 20, 30, 40, 50, 70 and 90 cm depth. The calculated water deficit was restored at weekly intervals, except for the tanks which were in drought treatment. Actual evapotranspiration (*Ea*) was calculated from change in soil water content, supplied and percolated water.

The reference evapotranspiration (*Er*) was calculated as mean from treatment 1. To reduce random variations *Ea* and *Er* were calculated as moving average of three observations. The number of stress days was calculated from equation (1):

$$SD(j) = [1 - Ea(j)/Er(j)]\, N(j) \qquad (1)$$

where $Er(j)$ and $Ea(j)$ are evapotranspiration from fully irrigated treatment and drought treatment respectively, and $N(j)$ is the number of days in the period (j). The number of stress days ($SD(i)$) in the drought period corresponding to the development stage of i is:

$$SD(i) = \sum_{j=1}^{n(i)} SD(j) \tag{2}$$

where $n(i)$ is the number of periods in which $SD(j)$ is calculated. The crop was separated into grain and straw from normal and late tillers, respectively.

In tanks where late tillers developed, the ears of normal tillers were cut when they were ripe. Approximately 2 weeks later when the late tillers were ripe, the whole crop was harvested and the straws without ears (normal tillers) were sorted out. In the present study drought sensitivity (F) is defined according to Hiler and Clark (1971) as the relative yield reduction:

$$F(i) = 1 - Y(i)/Y(r) \tag{3}$$

where $Y(r)$ and $Y(i)$ are yield of the reference crop and the drought treatment, respectively $F(i)$ is the drought sensitivity during the growth stage (i). The yield response factor (Ky) is calculated from equation (4), in accordance with Doorenbos and Kassam (1979):

$$1 - Y(i)/Y(r) = Ky\,[1 - Ea(i)/Er(i)]. \tag{4}$$

The analysis included yield from normal and late tillers separately as well as the sum of yield of normal and late tillers.

Results and Discussion

The crop emerged on May 4, 1980 and the number of days of actual growth period was counted from that day. The climatic conditions during the growing season are given in Figure 1. From emergence (day 0) and until end of growth (day 106) the global radiation was 1,820 MJ m^{-2} and the evapotranspiration calculated after the Penman method was 325 mm. This was 7 and 11% less than long term average values for global radiation and evapotranspiration, respectively. As the solar radiation and the evaporative demand were relatively low during most of the growing season, the yield response to drought may be smaller than for a normal year.

In the present investigation the initiation of a drought period was defined as the time when relative evapotranspiration decreased below unity ($Ea/Er < 1$) and to terminate at the time of reirrigation. The number of stress days in each drought period was calculated from equation (1) and (2). As the drought periods in treatment 2 and 3 were terminated at a total green area index of approximately one and two, respectively, the evaporation from the wet soil surface in the reference treatment was not negligible compared with the transpiration, and greater than for the dry soil surface of the drought treatments. Therefore, the number of stress days in treatment 2 and 3 was calculated assuming that the reference transpiration was ½ and ¾ of the reference evapotranspiration for treatment 2 and 3, respectively. This simple correction is in reasonable agreement with the model of Kristensen and Jensen (1975).

The crop in treatments 2, 3 and 4 were exposed to water stress during each of the vegetative growth stage (tillering, jointing, shooting or booting), and for which the drought was terminated before heading, developed late tillers which appeared after heading of normal tillers had ceased (Table 1).

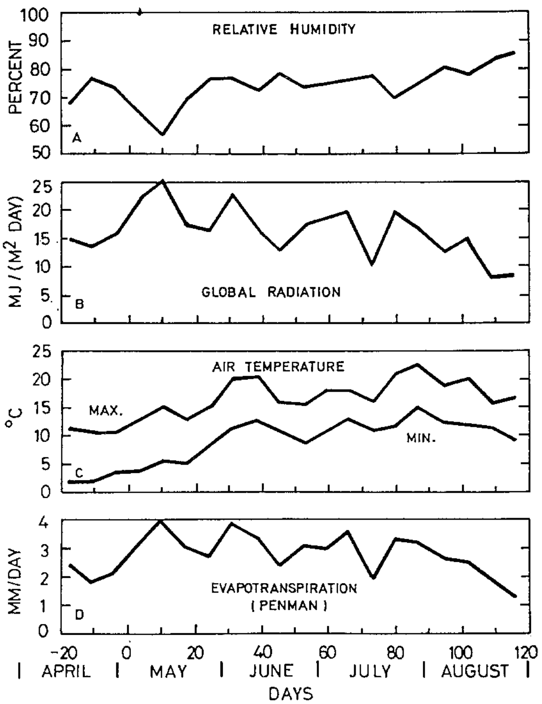

Fig. 1. Climatical conditions during the growth period

The later in the growth period the water stress occurred the greater the decrease in both straw and grain yield of late tillers (Table 1 and Fig. 2). For treatments 2, 3 and 4 the grain yield of late tillers amounted to 50, 41 and 26% of total grain yield. The late tillers, however, ripened two weeks later than the normal tillers. This delay in harvest date may be important because the days are getting shorter and the evaporative demand is decreasing. Thus, it becomes more and more difficult to harvest the crop at a satisfactorily low water content. If the grains have too high water content at harvest, artificial drying is necessary.

For a barley crop Mogensen (1980) reported that late tillers developed after drought during vegetative growth. The late tillers were not threshed but in some treatments they amounted to about one third of total yield. In Great Britain, Day et al. (1978) stated that late tillers induced by early drought contribute very little to final yield. In Finland late tillers often fail to ripen and thus do not significantly influence the final grain yield (Kivisaari and Elonen 1974). In Norway drought during tillering doubled the number of ears in barley and delayed the harvest by two weeks (Dragland 1979). For wheat the increase in number of ears was not significant. The late tillers delayed the harvest and some tillers failed to ripen.

Considering normal tillers the total yield of grain plus straw as well as grain yield increased the later in the growth period the drought occurred (Table 1 and Fig. 2) in spite of the greater number of stress days in the drought period. Analysis of variance applied to grain, straw and total yield showed significant differences among treatments at the 0.05 level of significance. For normal plus late tillers there

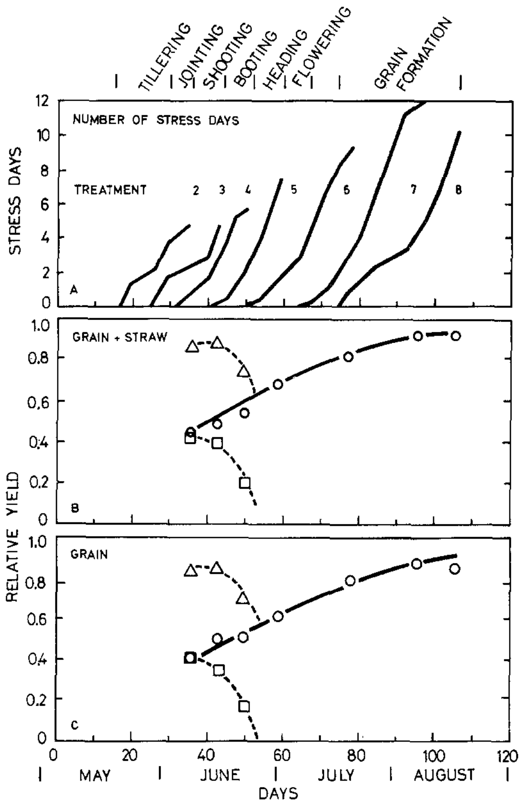

Fig. 2A – C. Number of stress days in the drought periods for the different treatments (**A**). Relative yields as a function of the time at the end of the drought periods. Total yield (**B**), grain yield (**C**). Normal tillers ○——○, late tillers □-----□, normal + late tillers △-----△

were significant differences among treatments for grain yield and for yield of grain plus straw.

To investigate the drought sensitivity (*F*) at the various growth stages the differences in water stress in the various drought treatments must be considered. For this purpose the ratio of drought sensitivity to the number of stress days (*F*/*SD*) was calculated. Equal drought sensitivity at all stages of development would give the same magnitude of *F*/*SD* and the curve in Fig. 3 C would be a horizontal line. In the present investigation the drought sensitivity of normal tillers decreased from treatment 2 to treatment 6.

For a barley crop Mogensen (1980) found a curve similar to that reported here for a wheat crop. For the grain formation period a linear relationship was found between relative yield and *SD*. The drought sensitivity per stress day derived from the slope of the line corresponded to a grain yield reduction of 3.8% per stress day. It was concluded that a stress day could be interpreted as a day without grain production.

In the present investigation *F*/*SD* for the grain formation period was 0.012 corresponding to a grain yield loss of 1.2% per stress day. The grain formation period lasted for 35 days which means that the daily grain production was 2.9% per day of total grain yield. Thus, in the present investigation the grain yield depression per stress day was less than one half of that found for barley. This may be due partly to

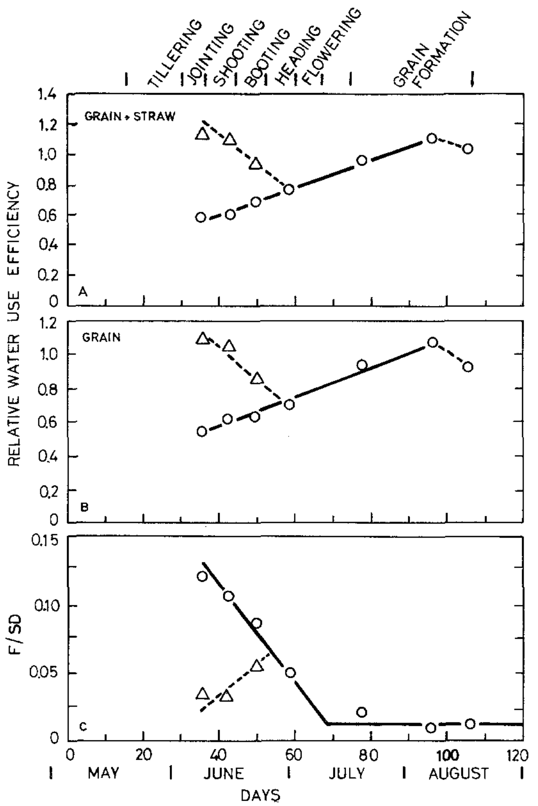

Fig. 3A–C. Relative water use efficiency of total yield (**A**) and grain yield (**B**). (**C**) is the ratio of drought sensitivity to the number of stress days (*F/SD*). All as a function of the time at the end of the drought periods. Normal tillers ○——○, normal + late tillers △-----△. Reference water use efficiency (treatment no. 1) is for grain + straw 29.5 and for grain yield 12.3 kg ha^{-1} mm^{-1}

low evaporative demand during the growing period and partly to a lesser drought sensitivity of wheat compared with barley.

Considering normal plus late tillers the drought sensitivity was greatest for drought occurring during booting and heading. Greater drought sensitivity was associated with a low water use efficiency (Fig. 3).

Values of the response factor (*Ky*) calculated by using *Ea* and *Er* values for the individual growth periods decreased from 3.00 for drought during tillering and jointing to 0.32 during grain formation (Table 2). When normal plus late tillers were considered the *Ky* values for the vegetative growth were 0.90–0.95 (Table 2). For spring wheat Doorenbos and Kassam (1979) found *Ky* values of 0.20, 0.63 and 0.55 for the vegetative growth, flowering and grain formation period, respectively. For a spring barley crop Mogensen (1980) found *Ky* values of 0.88 and 0.49 for the vegetative and grain formation period, respectively. This calculation was based on *Ea* and *Er* values for the individual growth periods and late tillers after drought during the vegetative growth were not included.

Values of the response factor calculated by using *Ea* and *Er* values for the entire growing period had the maximum value of 3.36 for drought during booting and heading when normal tillers were considered (Table 2). The minimum value (0.98) refers to drought during grain formation. For water deficit occurring equally over the entire growing period the *Ky* value was 1.15 (Doorenbos and Kassam 1979).

Table 2. The yield response factors (Ky) at various growth stages. Calculated for water deficits during the individual growth periods and for the total growth period

Treatment	Growth stages	Individual growth period		Total growth period	
		Normal tillers	Normal + late tillers	Normal tillers	Normal + late tillers
2 – 3	Tillering – shooting	3.00	0.90	2.85	1.10
4	Shooting – booting	1.50	0.95	2.45	1.86
5	Booting – heading	0.90		3.36	
6	Flowering	0.57		1.28	
7 – 8	Grain formation	0.32		0.98	

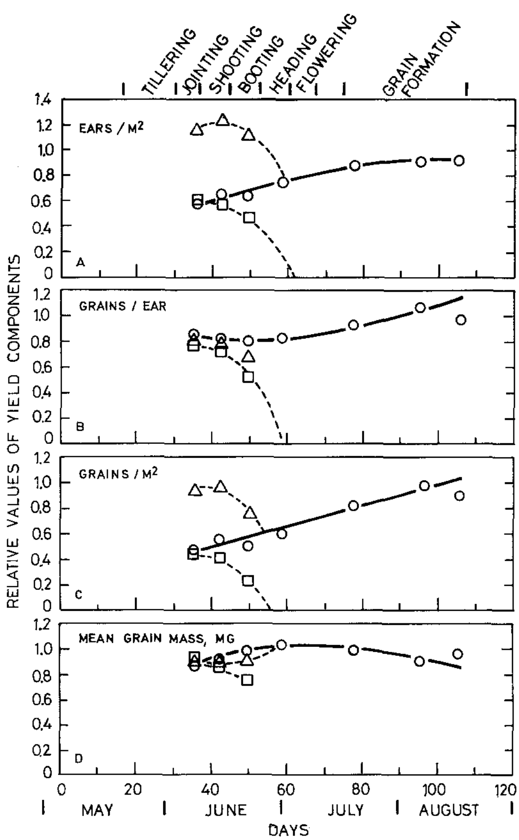

Fig. 4A – D. Relative yield components as a function of the time at the end of the drought period. Ears/m² (**A**), grains/ear (**B**), grains/m² (**C**) and mean grain mass (**D**). Normal tillers ○—○, late tillers □-----□ and normal + late tillers △-----△

In spite of the fact that the *Ea* and *Er* values for the total growing period are used for the calculations the *Ky* values are strongly related to the growth stages where the drought occurred. *Ky* values calculated for an individual growing period or for the entire growing period give different *Ky* values, however, which cannot be compared.

Compared to the yield response factors reported by Doorenbos and Kassam (1979) the yield response factors found for the vegetative growth stage in the present investigation are quite high. This may be attributed to the short growing period (106 days from emergence to end of growth). The late tillers which contributed significantly to the grain yield had a very short growing period (about 60 days) which may have affected the grain yield. The low yield response factor for drought during grain filling may be caused by a high relative humidity of the air (75%) during the grain filling stage.

Considering normal tillers the number of ears per unit area increased the later in the growing period the drought occurred (Fig. 4 A). The number of grains per ear was lowest for drought during shooting and booting (Fig. 4 B). Mean grain weight had maximum for drought during booting and heading (Fig. 4 D) but the effect was not significant (Table 1). These results are in reasonable agreement with those of Innes and Blackwell (1981).

For late tillers the number of ears per unit area, the number of grains per ear and the mean grain weight decrease the later in the growing period the drought occurred (Fig. 4). In treatment 2, 3 and 4 the yield components of late tillers differed significantly from the reference treatment (Table 1).

Considering normal plus late tillers the lowest number of ears and grains per unit area and the largest mean grain mass were found for drought during booting and heading stage (Fig. 4) where the lowest yield was obtained (Fig. 2). These results agree with those of Dragland (1979).

Conclusion

Drought during vegetative growth caused development of late tillers which appeared after heading had ceased. The grain yield of the late tillers contributed significantly to the total grain yield.

The late tillers ripened two weeks later than the normal tillers and delayed the harvest which made it difficult to harvest the crop in a satisfactorily dry condition. For that reason the drought sensitivity was calculated with and without the grains from late tillers included in the final yield.

When only grain yield of normal tillers was considered, drought sensitivity appeared to be greatest during the tillering-jointing stage. When grain yield of normal plus late tillers was considered drought sensitivity appeared to be greatest during heading stage.

These conclusions are valid for this one year and variety of spring wheat whether relative grain yield, ratio of relative yield reduction to the number of stress days, water use efficiency or ratio of relative yield reduction to relative water deficit were considered as the index of drought sensitivity.

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