Leaf Growth, Phenological Development and Yield of Wheat Grown Under Different Irrigation Treatments

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Abstract

An experiment with wheat grown in the field at Roodeplaat, near Pretoria, is described in which leaf growth, water use and yield were measured. Water use in three of the four water application treatments was monitored with weighing lysimeters.

Leaf growth, when not limited by a water deficit was highly responsive to diurnal temperature. Ambient temperatures at night were sufficiently low to inhibit leaf growth. Reduced leaf growth due to water deficits was reflected in the measured leaf area within several days.

Mild water stress after the time of floral differentiation caused anthesis to be earlier than in the well watered control plants. A more severe stress during this time delayed anthesis. There was also evidence that this severe stress caused some grains to abort following anthesis. The sensitivity of plants to water deficits at different development stages can be affected by the rate of increase and severity of the deficit. This was deduced from the yield component analysis of well adapted dryland plants and other treatments which had less time to adapt to an increasing water deficit.

Introduction

It has been established that the growth of plant leaves is highly sensitive to environmental variables such as water supply (Acevedo, Hsiao and Henderson, 1971), nutrient supply (Greenwood, 1976) and temperature (Johnson, 1969; Watts, 1974). Leaves are the intercepting surfaces for radiant energy and are the sites where the processes for photosynthesis and transpiration occur. The importance of leaf area in affecting the rate of soil water depletion and thus the onset of water stress has been demonstrated and used in the water balance model of Ritchie (1972). Thus a complete understanding of the main factors that affect leaf growth under field conditions must be gained before accurate simulations of yield and evapotranspiration (ET), utilizing the development of leaf area, can be made.

In order to improve grain yield predictions, an understanding of crop responses to various environmental conditions and especially to water stress must be gained. It has generally been found that any plant organ is most sensitive to stress during its period of most rapid development (Begg and Turner, 1976). Observations of phenological development made concurrently with observations of environmental variables can do much to improve the understanding of the time and manner in which the components of grain yield are affected.

This paper presents data on the growth of wheat *(Triticum aestivum)* leaves as affected by temperature and plant water status. It traces the development of a wheat crop under various water regimes and finally examines the effects of the treatments on yield and its components.

Materials and Methods

The study was carried out during 1978 at Roodeplaat, approximately 30 km north of Pretoria. Wheat (variety SST3) was sown on 4 ha of previously irrigated (100 mm on 15 May) and fertilized (20 kg ha^{-1} of P, 100 kg ha^{-1} of N) soil (Rhodic Paleustalf and Typic Ustropept according to the USDA system; Shorrocks and Glendale series according to the South African system) on 1 June. Rows were 200 mm apart and about 160 plants per m^2 were established. A general irrigation of 21 mm was applied to

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all treatments on 7 June.

Irrigation

Irrigation of plots (12 m x 12 m) was provided through a microjet system suspended 1 m above the ground surface. The system comprised nine PVC lines (1 m apart) connected to a common supply line. Microjets spraying downwards were positioned along these lines at a spacing of 1 m. Water application was monitored via a water meter and tests showed that spray distribution was very even over a 10 m x 10 m area within the experimental plot.

Treatments

Plots within the experimental area were assigned one of the following four treatments:

(1) Well watered (WW) where irrigation to replenish the water deficit was applied once 50% of the plant available water in the root zone had been extracted. This treatment was assigned to three plots, one of which included a lysimeter. The lysimeter was used to monitor ET. Previous experience suggested that the water available to full grown plants in the lysimeters was 136 mm. Thus irrigations were given when 68 mm had been depleted. More recently, plant available water has been found to be nearer 160 mm because the lysimeter profile held 23 mm more water at field capacity than was originally estimated.

(2) Well watered initially, thereafter allowing plants to dry the profile (WD); plants were irrigated in a manner similar to that for the WW treatment until 30 July (Julian day 211); thereafter no further irrigation water was applied. Only one lysimeter plot received this treatment.

(3) Drying of the soil profile allowed but water supplied to prevent the plants from dying (D). Irrigation to replenish the accumulated water deficit was given on 14 August (Julian Day 226). Two lysimeter plots received this treatment.

(4) Dryland (DL) where, apart from the initial irrigation given to aid germination no further irrigation water was supplied. This treatment was replicated on three plots.

Measurement of water use

Four precision weighing lysimeters were utilized. The lysimeters (referred to as L1, L2, L3 and L4) had surface dimensions of 2 m x 2 m and a depth of 1 m. Further information about the design and construction of the lysimeters is given by Hutson, Green and Meyer (1980). The treatments were assigned such that L4 had the WW treatment, L2 had the WD and both L1 and L3 had the D treatment. Water use by plants in the dryland treatment was found by soil sampling for water content on a number of occasions during the growing season, and using these values in a simulation of the water balance (Ritchie, 1972, as modified by Meyer, Walker and Green, 1979).

Measurement of leaf growth and leaf area

A small steel peg was driven into the ground beside the plant whose leaves were to be measured. The top of the peg was used as a fixed reference point and the distance from it to the tip of the growing leaf was measured daily. Thus 'leaf' growth includes both the growth of the leaf lamina and the stem to which it is attached. Growth increments each day for each leaf on a plant were added together to give a total daily growth increment for the plant. Cumulative growth for each plant was obtained by accumulating these daily growth increments. Four plants each within L2, L3 and L4 were measured and the mean of these plants calculated. Leaf area was measured weekly by sampling five plants adjacent to the lysimeters and using a commercially available leaf area meter (Model: LI — 3000, Nebraska, USA).

Measurement of leaf water potential

Fully expanded, healthy leaves were cut one third of the distance along the lamina and the pressure potential was measured with a pressure chamber (Model: P.M.S., Oregon, USA).

Phenological observations and yield measurements

Throughout the growing season plants were sampled each week for determination of the growth stages according to the Feekes Scale (Large, 1954). Detailed observations, using microscopic examination of the developing apex were made at the time of spikelet differentiation. Spikelet differentiation was defined as the time of double ridge formation (Fisher, 1973).

For yield determination, an area of 1 m^2 was harvested, from each replicate of each treatment. Harvesting of all treatments other than the WW treatment was on Julian day 303. The WW treatment was harvested on day 306. Numbers of plants, tillers and heads were counted. Thirty heads were selected and numbers of total spikelets, fertile spikelets, and grains were counted. Individual grain mass was determined from the counted seeds. Finally the remaining heads from the 1 m^2 sample were thrashed and total grain mass determined.

Results and Discussion

Water Use

The lysimeter records of water use for treatments WW, WD and D are shown in Figs. 1a, 1b and 1c respectively. A discussion of the determination of the total amount of available water is given elsewhere (Meyer and Green, 1980). Figures 1b and 1c indicate that the total plant available water for the lysimeters with a soil depth of 0,9 m was about 160 mm. The lysimeters with the D and WW treatments were incompletely filled at the start of the experiment. Total available water in the field (dryland DL) was assessed at 230 mm. Dryland water use was simulated (Fig. 1d) using the Ritchie model (1972) as modified by Meyer, Walker and Green (1979). From observations of plant growth it is suspected that the rate of actual water use between days 200 and 230 was less than that simulated. This is supported by the difference in rate between this treatment and the D treatment during days 190 and 215 when growth of plants in the two treatments was similar. Thus it is suggested that there was more water available between days 230 and 240 than was simulated (Fig. 1d). It is further suggested that the amount of water available to plants in the DL treatment around the time of heading was about the same as that available in the WD treatment since,in both treatments the numbers of heads which emerged per tiller were less than in either of the D or WW treatments. It is apparent then that the model does not accurately describe the situa-

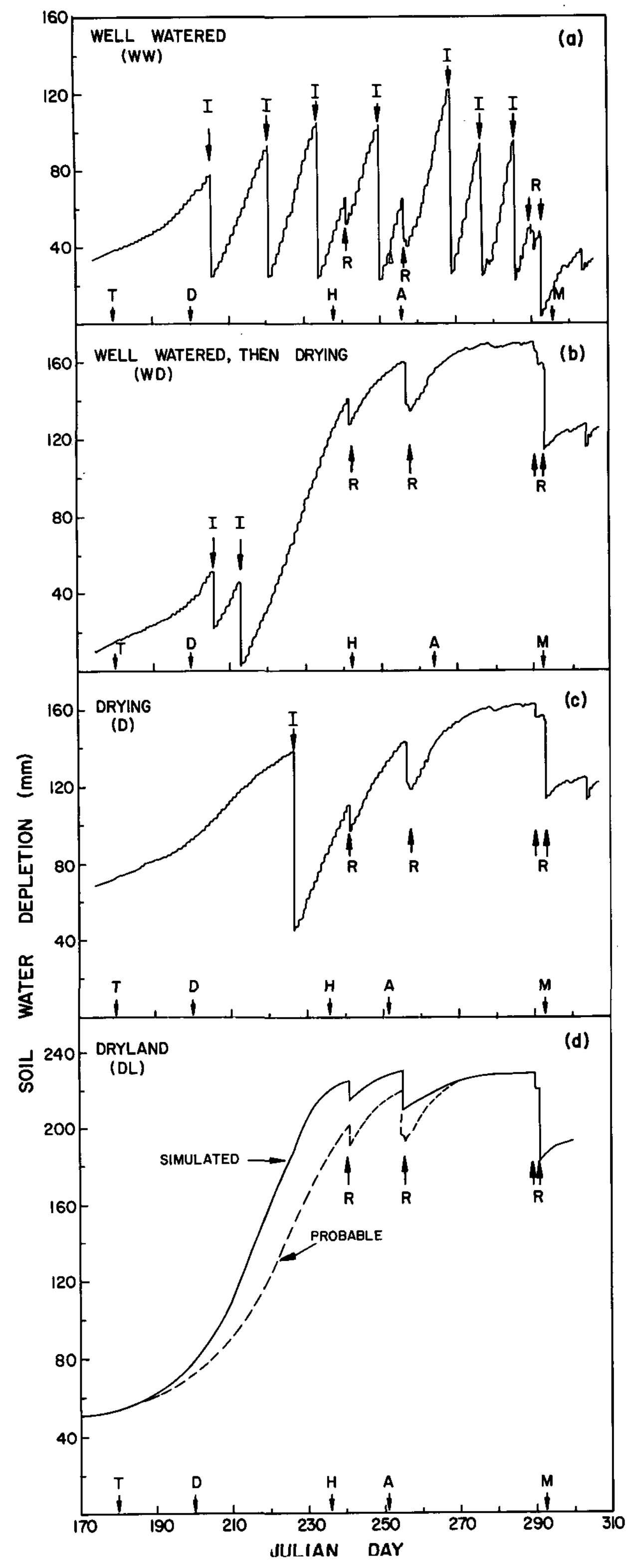

Figure 1
Water use and phenological development for the four treatments. Water use was determined from lysimeter records in a, b and c. In d, both the predicted (from the Ritchie Water balance model) and probable (a composite of water use similar to the D and WD treatments) are shown.
Treatments: WW = well watered, WD = initially well watered but then allowed to dry, D = drying and DL = dryland treatment.
Phenological development: T = tillering, D = differentiation of the floral apex, H = 50% heading, A = 50% anthesis, M = maturity (hard grain).
Water application: I = irrigation, R = rain.

tion where plants are subject to a slow increase in water deficit and are thus being conditioned. A curve of probable water use was composed of periods from both the D treatment (days 190–215) and WD treatment (days 235–290).

Diurnal leaf growth

Measurements of leaf growth were generally taken daily. During days 222 and 223 leaf lengths were measured every two hours. The rate of leaf growth during this time is shown in Fig. 2b. The highest growth rate of well watered plants occurred during the late afternoon. This is in agreement with the findings of Johnson (1969). It was expected that growth would be greatest during the night when leaf water potential (Fig. 2a) and thus turgor pressure were high (Boyer, 1968). The resemblance of the growth rate curve for the well watered plants to the diurnal temperature curve (Fig. 2c) indicates a dominating effect of temperature in this case. Johnson (1969) using wheat and Watts (1974) using maize (*Zea Mays*) grown in the field showed that leaf growth was highly sensitive to ambient temperature. However, Christ (1978) found little temperature effect on the growth of wheat leaves but he did not test temperatures less than 20°C. Christ (1978) attributed the reduction of leaf growth at night to the exhaustion of the previous day's accumulated starch. It is unlikely that this effect was important in the present situation because, in the first place, the level of accumulated starch in the field-grown plants would be expected to be higher since radiation levels were high and, secondly because there is no evidence of a lag between the observed leaf growth rate and temperature.

Cumulative leaf growth

As has been reported by others (Boyer, 1970; Acevedo *et al.*, 1971) there is a clear effect on the growth of leaves caused by decreasing soil water availability. The comparison between the growth of leaves of well watered plants and that of plants which were in a drying situation, showed that it is possible to accurately identify the time of initial decrease in leaf growth (Fig. 3b) caused by an increasing water deficit. In the present study this occurred when about 55% of the plant available water had been extracted from the soil profile (Meyer and Green, 1980). The decline in leaf growth of individual plants in the drying situation was very quickly reflected in the leaf area (Fig. 3a) and as pointed out by Begg and Turner (1976) this is a permanent effect and may subsequently affect potential crop yield.

Phenological development

Sowing of the crop took place on Julian day 153. Development of the plants in all treatments was similar during the first third of the growing season. Tillering began around day 180 and differentiation of the reproductive apex occurred on day 200. On day 207 it was observed that apices had formed 18 to 21 spikelet primordia. Of these, 3 or 4 failed to develop further into spikelets containing entire florets. As can be seen from the development scale given with the water use figures (Figs. 1a, 1c and 1d), the D and DL treatments showed more rapid phasic development after differentiation than did the WW treatment plants. Heading and anthesis began two days before it did in the well watered plants. The time between anthesis and maturity (when the grain became hard) was similar for the D, DL and WW treatments but for the first two, grain filling occurred during a period of decreasing water availability.

For plants in the WD treatment, heading and anthesis

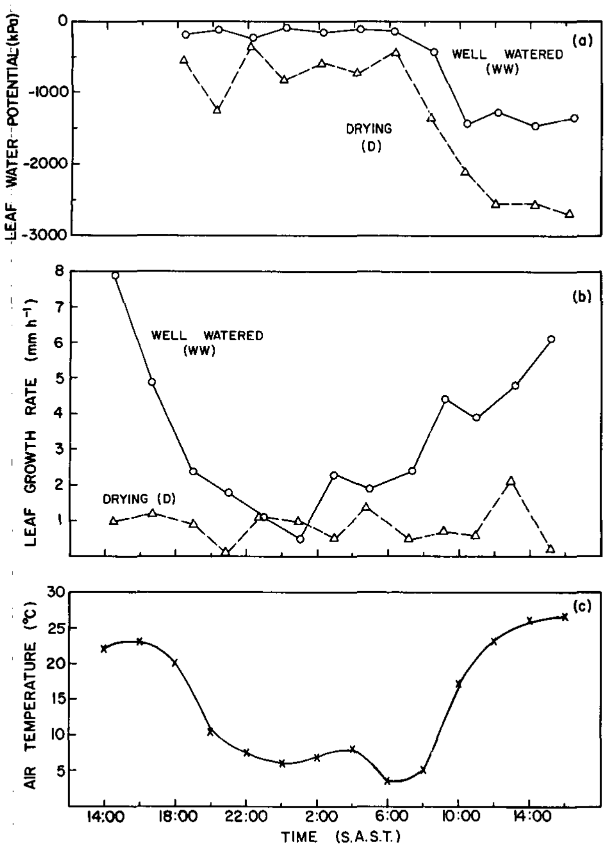

Figure 2
Measured values of (a) leaf water potential, (b) leaf growth rate and (c) air temperature during days 222 and 223

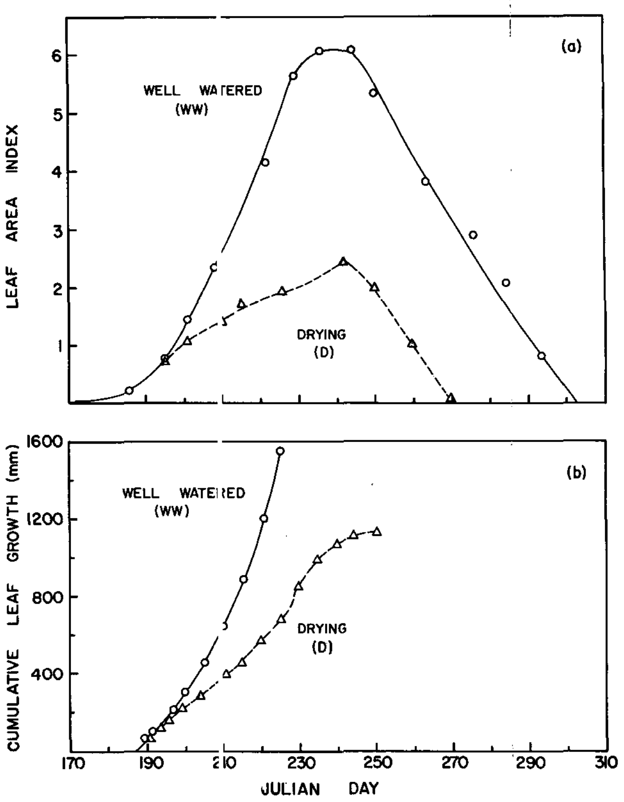

Figure 3
Cumulative leaf growth (l) and leaf area index (a) for the well watered and drying treatments

were delayed compared with the well watered plants. Thus the severity of stress influences the rate of phenological development. This finding agrees with that of Angus and Moncur (1977) who, in well controlled experiments with wheat showed that a mild stress between differentiation and anthesis caused anthesis to be earlier, but severe stress delayed anthesis when compared with well watered control plants.

Yield and its components

Table 1 presents data on the yield components which were used to calculate an expected yield and also gives the measured yield based on a sample area of 1 m^2. The discrepancy between the calculated and measured yield ranges from 16% for the WW treatment to 44% for the D treatment. The reasons for this discrepancy include the unintentional selection of better heads from the harvested sample, the multiplication of positive sampling errors of each component to obtain the calculated yield and the loss of small grains during the thrashing of the main sample. The thrashing loss was estimated to be about 10% but would have been greater in samples containing small grains. Despite the discrepancy the yield component analysis is extremely valuable for comparing the response of plants in the different treatments to water deficits at different times of development.

There was an expected compensation between plant number and tiller number. In the WW treatment where more plants grew to maturity, fewer tillers per plant resulted. Of the tillers which grew in the WW treatment 67% produced heads. This contrasts with 35% for the dryland plants and indicates that initial growth of these plants was fairly good but that stress began before heading. The WD treatment plants were affected in a similar manner. As discussed earlier, this probably indicates that the amount of available water left in the WD and DL treatments was similar at about this time. The similarity of the number of spikelets for the various treatments indicates that there was little difference in stress at the time of differentiation. However, it appears that at the time of anthesis and fertilization, differential stress occurred since there were differences in the number of florets which produced grain. It is, however, not possible to conclude that the fewer grains per spikelet of treatments D and WD were the result of poorer fertilization. Twenty days after anthesis there were 2,1 and 2,3 grains per spikelet for the D and WD treatments respectively. After a further eight days the counts were 1,4 and 1,7 and at harvest 1,7 and 1,9 respectively. Although sampling errors are apparent, only these two treatments showed a significant decrease in the number of grains per spikelet after anthesis. It is, therefore, suggested that there was little difference between treatments in the number of ovules fertilized at anthesis but that stress after anthesis was severe enough in the case of the D and WD treatments to cause ovule abortion.

There is now an apparent anomaly. The dryland plants produced very few heads per tiller, but at anthesis when available soil water was less than at the time of heading, fertilization

TABLE 1
COMPONENTS OF GRAIN YIELD, CALCULATED YIELD FROM A SUBSAMPLE OF 30 HEADS AND MEASURED YIELD FROM 1 m^2 OF EACH OF THE FOUR TREATMENTS

Treatment	Plants per m^2	Tillers per plant	Heads per tiller	Fertile spikelets per head	Grains per spikelet	Grain mass (mg)	Calculated yield* (kg ha^{-1})	Measured yield (kg ha^{-1})
Well watered (WW)	184	4,2	0,67	15,6	2,4	43,4	8413	7068
Dryland (DL)	159	5,1	0,35	14,8	2,2	33,7	3114	2129
Drying (D)	144	5,0	0,64	15,0	1,7	23,5	2761	1829
Well watered and then drying (WD)	142	6,2	0,43	16,8	1,9	20,6	2489	1931

*Calculated Yield (kg ha^{-1}) = Plants per m^2 x tillers per plant x heads per tiller x fertile spikelets per head x grains per spikelet x grain mass x 10^{-2}

was not severely affected. Observations suggest that the reason for this was the adaptation or conditioning of the dryland plants as opposed to those of the D and WD treatments. For the dryland plants the early restriction of water supply caused reduced leaf growth and fewer heads to emerge. Dryland plants had less than two heads on average but these heads were able to develop reasonably well, whereas plants in the WD treatment, although initially well developed, were subjected to a rapidly developed stress about the time of heading. The large leaf area present when irrigation ceased, caused stress to develop very rapidly, thus giving the plants little chance to adapt. It is clear that the rate of development of stress can cause large differences in plant response. This is particularly true when comparisons are made between water deficit treatments applied to container-grown and field-grown plants (Ritchie, 1973). The review by Turner and Begg (1976) points out that many of the experiments which have been done to determine the sensitivity of crop yield to water deficit at different stages of growth have not considered that the rate of increase and level of stress will vary with plant development. In the present study the well adapted dryland plants appeared to be less sensitive to water stress during grain formation than the less well adapted D and WD treatment plants, even though these plants had received water at a much later stage. The well adapted behaviour of the dryland plants is illustrated again by the grain mass. These plants reduced the potential grain sink size mainly by producing fewer heads so that approximately 9 000 grains per m^2 developed. These grains were reasonably well filled. The WD treatment, despite some apparent grain abortion, still had 12 000 grains per m^2 which, with the rapidly increasing water deficit and consequent loss of leaves, were poorly filled.

Conclusions

It has been shown that the simple measurement of leaf growth in the field is a sensitive indicator of the effects of environmental variables. Provided a plant is well supplied with water and nutrients, leaf growth is highly responsive to diurnal changes in temperature. When a water deficit occurs and temperatures are not limiting, growth during the day will be limited by low turgor pressures. The response of leaf growth to water deficit is very quickly reflected by measuring leaf area.

The rate of increase and severity of water deficits can affect the timing of phenological events and the result of these events. The slow imposition of stress allows the plant to adapt so that it may appear to be less sensitive to a given water deficit than a plant which has had little chance to be conditioned. Mild water stress after differentiation can cause a "speed-up" in the rate of phasic development. A severe stress, however, may cause a "slow-down" in phasic development. For a given variety, stress can alter the time of phenological events such as anthesis by two to four days. Tracing phenological development and analysing grain yield can produce considerable information about the timing of water stress. Once differentiation has occurred the potential yield for any particular head is almost fixed. Thereafter, yield may be decreased through poor fertilization, grain abortion and a lack of grain filling. The potential yield of the dryland plants was affected at an early developmental stage because of reduced head numbers. The potential yield of the other two drying treatments remained relatively high since grain numbers per unit area were higher (this, despite some grain abortion) but the potential failed to be realised because of the rapid increase in the rate of leaf senescence.

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