Effects of Water Stress on the Reproductive Development of *Sorghum vulgare* Pers.

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EFFECTS OF WATER STRESS ON THE REPRODUCTIVE DEVELOPMENT OF *SORGHUM VULGARE* PERS.

SUMMARY

Sorghum vulgare plants were subjected to various droughting treatments, followed by rewatering, around the time of floral initiation. The consequences, particularly in respect of leaf numbers, time of initiation, and early inflorescence development, were observed.

Severe water stress caused cessation of morphological changes, vegetative and reproductive.

Plants droughted early resumed vegetative growth on rewatering and flowered at a slightly reduced leaf number.

Later drought allowed the more vegetatively advanced plants to accomplish the early changes of the floral transition without visible change. Rewatering led to immediate floral development without further leaf initiation.

The floral apex may develop at a water stress sufficient to prevent leaf expansion.

INTRODUCTION

Differentiation of the floral apex in sorghum occurs at an early stage of vegetative growth and at the expense of further leaf initiation. Consequently, water stress early in the life of the plant may not only affect growth directly, but in other ways through an influence on reproductive behaviour.

Although it is commonly believed that low soil moisture affects flowering, there is, as Hagan *et al.* (1957) have pointed out, little exact information. The data of these authors, together with that of Phillis (1956) and Alvim (1960) for various crops, suggest influences both on initiation and subsequent development of the floral structures. Scott (1956) discusses the belief that under adverse soil-moisture conditions, grasses seed at the expense of leaf production. On the other hand, Phillis (1956) claims that under moisture stress, sorghums remain vegetative, producing leaf nodes until favourable moisture conditions cause the apex to become reproductive. He regards as part of its drought adaptation the ability of sorghum to enter the reproductive phase only when sufficient moisture is available to ensure some seed production. These latter ideas were based on field observations which did not include examination of apices and the relationship of drought conditions, both in degree and timing, to floral differentiation and subsequent development. The present study was undertaken to provide more precise information.

MATERIALS AND METHODS

Sorghum vulgare (cv. Saccaline) was grown in the glasshouse in pots containing 6.5 kg of black earth at field capacity and, before floral initiation, exposed to various droughting treatments. Two plants were grown in each pot, one being removed at an earlier sampling and the other left for later observations.

Three replicate plants were sampled from each treatment at 2-day intervals prior to initiation, and at longer intervals thereafter until floral emergence. Plants were dissected and the initiation and subsequent growth in length of the inflorescence followed. Plant height to uppermost emergent leaf base, and number of emergent leaves, were recorded for all plants in each treatment at regular intervals.

RESULTS

Experiment I. The effect of increasing duration of wilting

Pots were watered to field capacity at sowing, and the control plants were maintained at adequate water levels throughout. Watering was restricted in the other pots to cause wilting just prior to the normal time of floral differentiation. Wilting durations of 2, 3, and 4 weeks were imposed. Small additions of water were given during these periods to prevent death of the plants, which however always remained wilted. The design was a randomized block, with sufficient plants in each treatment to allow fifteen sampling occasions, leaving thirty plants to flower.

Height increment and leaf emergence show that the plants in all droughting treatments suffered from water stress about a week before actually wilting, when the first observations were made. Height growth virtually ceased until rewatering, and emergence of leaves was affected in a similar way (Fig. 1). The first floral differentiations were observed in the control plants on the 24th day, when there were six fully emergent leaves, and were completed on the 26th day, without further leaf emergence. Wilting had begun in the other plants on the 25th day, initiations were first seen on the 26th and completed on the 28th. These plants had only five emergent leaves and remained at this stage, except for a gain of one leaf in the 2-week-drought plants,

TABLE 1

THE EFFECT OF INCREASING DURATIONS OF WATER STRESS ON PLANT HEIGHT, STEM DIAMETER, LEAF NUMBER, TIME TO FLOWER EMERGENCE, AND SEED NUMBER PER HEAD

Treatment	Plant Height (cm)	Stem Diameter (mm)	Number of Leaves	Time to 50% Flowering (days)	Number of Seeds per Head
Control	84	9.0	12	64	1,300
2 weeks' wilting	74	7.4	11	74	830
3 weeks' wilting	78	6.1	11	88	1,190
4 weeks' wilting	78	4.7	11	94	1,340
	Not Significant	LSD. (1%) = 1.3			Not Significant

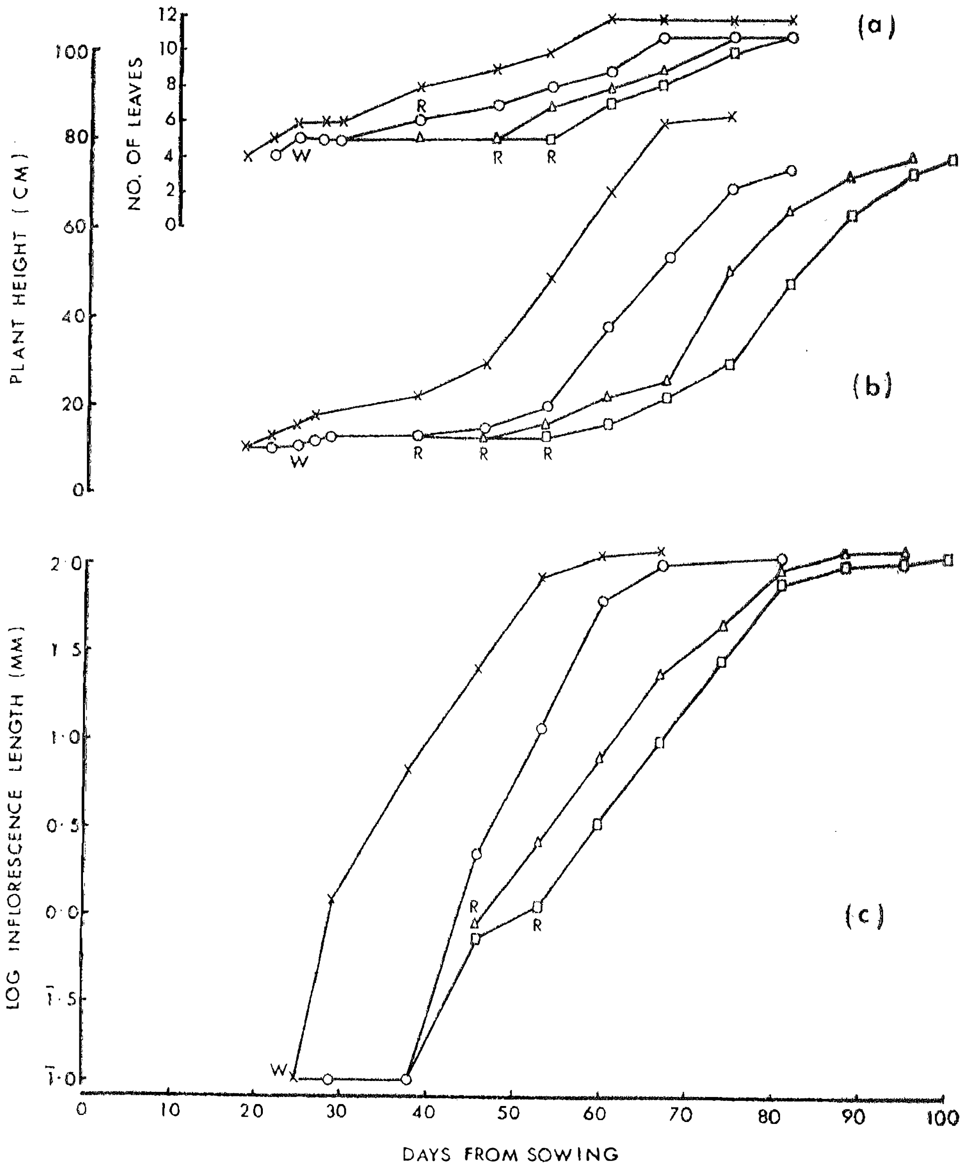

FIG. 1.—Experiment 1. Effect of increasing duration of wilting on (a) number of emergent leaves, (b) plant height, and (c) inflorescence length. X, control; O, 2 weeks' wilting; △, 3 weeks' wilting; □, 4 weeks' wilting; W, onset of wilting; and R, time of rewatering.

until rewatered. At floral emergence the control plants had a mean leaf number of twelve, compared with only eleven in the droughted. Therefore water stress, applied immediately prior to and during the floral differentiation period, reduced the number of leaves and delayed initiation slightly.

Adequately watered plants, in keeping with their greater node number and probably their continued expansion of both stem and leaf sheaths, were taller at initiation (Fig. 1) and remained so at flowering (Table 1), although the difference is not significant. The stem diameter of droughted plants decreased significantly with increasing duration of wilting.

Inflorescences of control plants elongated rapidly from the time of differentiation and, in the 2-week-drought plants, immediately on rewatering. The others however commenced elongation prior to full rewatering, probably due to the small applications of water made to keep the plants alive. Emergence of flowers was delayed by periods corresponding fairly closely to the duration of drought, viz. delays of 10, 24, and 30 days for 14, 21, and 28 days drought (Table 1). The rate of extension after rewatering was therefore little influenced by the previous drought history. Final inflorescence length is also independent of the earlier delays, and this is reflected in the number of seeds set per head (Table 1).

Experiment II. The effect of time of onset of wilting

In this experiment the effect of a constant duration of wilting applied at different stages prior to initiation was studied. In addition to control plants, three droughting treatments were applied, viz. wilted from day 15 until day 21, from day 19 to day 25, and day 27 to day 35 (early, intermediate, and late drought respectively). There were twenty sampling occasions during the growing period and thirty plants were allowed to flower.

Again, water stress effects were apparent before wilting, as shown by reduced height growth, while during wilting height increment and leaf emergence ceased (Fig. 2).

Water stress delayed floral initiation, and morphological change at the apex occurred only after supply had been restored. Irrespective of age when wilting was imposed, all plants differentiated floral apices between days 34 and 37, compared with 23 to 26 days for control plants (Fig. 2). Although the late drought plants were wilted only after the normal time of floral initiation, increasing water stress leading up to wilting sufficed to prevent the transition.

Mean leaf number was reduced as the onset of water stress approached the normal time of floral initiation. As in the previous experiment, reduction in node number was accompanied by a reduction in mean plant height at flowering (Table 2).

The time of floral emergence was delayed by about the same period (corresponding very approximately to the length of drought) in all wilting treatments, probably because of the similar duration of all three.

Inflorescences in all treatments elongated at a similar rate and attained the same final sizes (Fig. 2).

TABLE 2

THE EFFECT OF WILTING PERIODS ON FINAL PLANT HEIGHT, LEAF NUMBER, AND TIME TO FLOWER EMERGENCE

Drought Period	Plant Height (cm)	Number of Leaves	Time to 50% Flowering (days)
Nil	117	14.8	58
Day 15—Day 21	112	14.1	68
Day 19—Day 25	108	13.8	68
Day 27—Day 35	104	13.2	65

DISCUSSION

The changes at the apex depend on the interaction of two factors; firstly whether or not there is sufficient vegetative development to allow the formation of a floral stimulus, and secondly the extent to which water stress may prevent changes occurring. In the second experiment early drought stopped growth before the plants had grown sufficiently, and these plants remained vegetative, returning to leaf initiation after rewatering. During the development of the floral stimulus, leaf initiation continued and ceased only when the apex became floral. Therefore, more leaves were produced than in plants exposed to late drought which had already attained the critical stage.

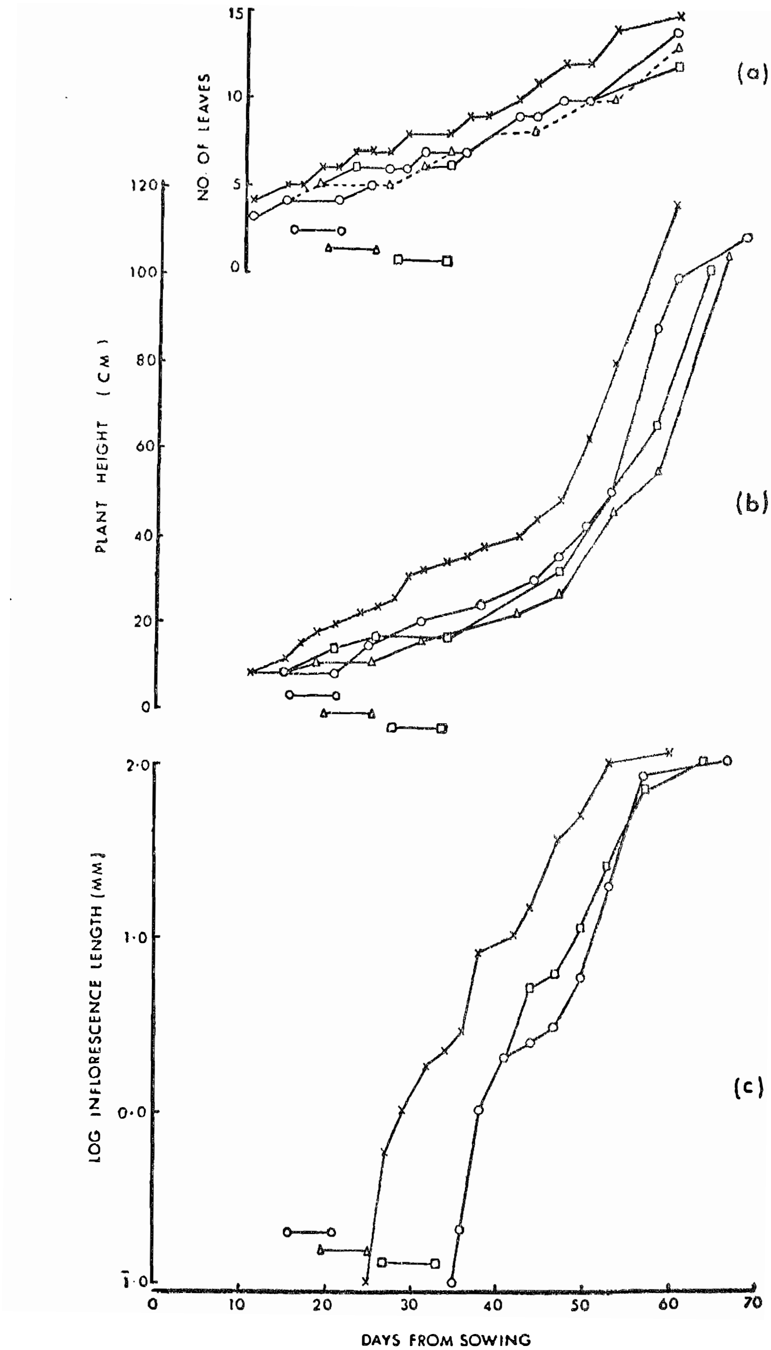

FIG. 2.—Experiment 2. Effect of time of onset of wilting on (a) number of emergent leaves, (b) plant height, and (c) inflorescence length. X, control; ○, wilted from day 15 to day 21; △, day 19 to day 25; □, day 27 to day 33. ○—○, △—△, and □—□, wilting periods. In (c), △ follows very closely the line for ○.

In these latter plants, notwithstanding the cessation of growth which prevented leaf initiation, the floral stimulus developed, and on rewatering the morphological changes of floral initiation occurred without further leaf initiation. In the early drought plants there was a cessation of progress towards ripeness to flower, whereas with late drought the delay was in the morphological changes which follow the perception of the flowering stimulus. The constant length of the delays in each treatment, although on different processes, led to a similar retardation of the appearance of a floral apex in each case. Therefore all plants exposed to water stress differentiated flowers at the same time, although leaf numbers varied according to the time of droughting.

In the first experiment, the various durations of droughting were all imposed at the one age, very close to floral initiation by the controls, although again height increments and leaf emergence reveal earlier water deficits. All drought treatments were comparable with the late drought of the second experiment. Vegetative development was adequate for the formation of the floral stimulus at the same time as in the controls, but leaf production ceased, resulting in a reduced leaf number. Evidently the small additions of water to the droughted plants sufficed to allow, with a slight delay of about 2 days, the visible transition to a floral apex and some subsequent elongation of this structure. Meyer & Anderson (1952, p. 260), Kramer (1959), and Gwynne (1960) draw attention to the ability of apical tissue to obtain water at the expense of older tissue, and Wilson (1948) showed that stem tips of tomatoes continued growth when the stem was shrinking under a water deficit. Increasing duration of drought in this experiment had no effect on initiation and leaf number, as all relevant changes were completed early in the period. However, duration of stress influenced subsequent development of the structures initiated. Leaf and flower emergence and plant height increment were delayed, although the constant node number led to constant final leaf numbers and heights. The greater height of control plants is due to the higher number of nodes. Likewise in Experiment II, heights follow node numbers, but the delay in floral emergence, which was the same for all droughting treatments, corresponds to the delay in initiation. This is in contrast to Experiment I, in which the delay was due to varying post-initiation dormancy resulting from the varying duration of drought.

The reproductive behaviour in these two experiments agrees with earlier views that both initiation and subsequent floral development can be affected by drought. Drought, prior to initiation, exerts an influence before wilting. In the pre-"ripeness to flower" stage, water stress leads to apical dormancy as judged by external observation, and the restoration of water supply leads to a resumption of leaf production. With drought at later stages, the floral stimulus may develop while the apex is dormant in respect of leaf initiation, and while leaf expansion and internode extension have ceased. The morphological change to a floral structure and its subsequent growth may occur while the plant is still wilted.

Phillis' (1956) observation that droughted plants produce additional leaves is only understandable in the case of water stress less severe than those employed here. Unpublished results show that at the usual ages of floral initiation in *Sorghum vulgare* plant survival below wilting point, without water additions, is less than 2 weeks. Plants could perhaps remain near wilting point, continuing leaf initiation without sufficient vegetative development for floral initiation. If leaf area is the facet of vegetative development which is important, the progressive death of leaf tissue might keep plants vegetative. There is also the possibility that prolonged retardation could carry plants which are normally sown before midsummer into longer days which in turn leads to greater leaf number (Quinby & Martin, 1954, and unpublished data of the present investigations).

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