Influence of water-deficits on phenology, growth and dry-matter allocation in chickpea (Cicer arietinum)¹

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ABSTRACT

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Quantitative understanding of the response of phenology and crop growth to environmental factors is required to build yield-prediction models. Field experiments were conducted to study the influence of water-deficits on phenology, growth and dry-matter allocation in chickpea (Cicer arietinum L., cv. JG 74). The crop was subjected to increasing intensities of water deficits during both vegetative and reproductive phases by applying gradient irrigations. Durations of emergence to flowering (E-FL), flowering to beginning of pod-fill (FL-BPF), and beginning of pod-fill to physiological maturity (BPF-PM) were inversely correlated with normalized evapotranspiration-deficit (E_t -deficit) experienced by the crop during a growth period. In terms of thermal time (base temperature = 8°C, ceiling temperature = 30°C), the durations of E-FL, FL-BPF, and BPF-PM phases decreased by 4.5, 3.1, and 3.8°Cd for each mm kPa^{-1} of normalized E_t -deficit, respectively. Water-deficits prior to flowering decreased canopy development, light interception, and dry-matter production to the maximum extent compared with stress after flowering. Water-deficit prior to pod-initiation did not influence the allocation of dry-matter between leaves and branches, but water-deficit during the reproductive phase increased allocation to the reproductive organs. Normalized E_t -deficit of 1 mm kPa⁻¹ increased allocation to the pods by 0.75% of the biomass produced after pod-initiation and to the seeds by 0.52% of the biomass produced after BPF. It is concluded from this study that we need to consider the influence of water stress on phenology, growth and dry-matter allocation in chickpea in addition to other environmental factors affecting these processes.

INTRODUCTION

Chickpea is grown in ecologically diverse environments in India, the Mediterranean, eastern Africa, the Americas and Europe (Jodha and Subba Rao, 1987). It is cultivated almost exclusively on stored soil moisture during the

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post-rainy season in India, Pakistan and Nepal or during the winter, spring and summer month in the Mediterranean region (Saxena, 1984). In these environments, chickpea is subjected to varying photoperiod, temperature and moisture regimes, which can have a profound influence on phenology, growth and yield (Saxena, 1984). Therefore, to understand the adaptation of chickpea cultivars to these diverse environments, and to build crop-growth models of chickpea, it is essential to have a quantitative understanding of the phenological and growth responses of chickpea to these physical factors. Chickpea is a quantitative long-day plant, and both extended photoperiods and high temperatures have been reported to hasten vegetative and reproductive development (Summerfield et al., 1980, 1984). Although there are genotypic differences in the sensitivity of chickpea to photoperiod and temperature, the durations of both vegetative and reproductive phases decrease linearly with the increase in photoperiod and temperature (Summerfield et al., 1987). Chickpea is also reported to mature early under water stress (Khanna-Chopra and Sinha, 1987), but the influence of water deficits on vegetative and reproductive development and on growth and dry-matter partitioning have not been reported in a quantitative manner. In this paper, the influence of timing and degree of water-deficits on phenology, growth, and dry-matter allocation in chickpea is examined.

MATERIALS AND METHODS

Experiments were conducted during the post-rainy seasons of 1986 and 1987 on a Vertisol at the research farm of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) located at Patancheru (lat. 17°30'N; long. 78°16'E; alt. 549 m), Andhra Pradesh, India. The soil, classified as a fine montmorillonite isohyperthermic typic Pallustert, retains about 200 mm of plant-extractable water in the upper 1.5 m of soil profile.

Different degrees of water-deficits were created during the vegetative and reproductive growth phases of chickpea by applying gradient irrigations using the line-source irrigation technique (Hanks et al., 1976). The four main treatments were:

- I₁, gradient irrigation during all growth phases;
- I₂, gradient irrigation from emergence to 50% flowering, and uniform irrigation during other growth phases;
- I₃, gradient irrigation from 50% flowering to 50% beginning of pod-fill, and uniform irrigation during other growth phases; and
- I₄, gradient irrigation from 50% beginning of pod-fill to physiological maturity, and uniform irrigation during other growth phases.

Main plots (18 m \times 18 m) were placed along the line-source in such a way that the amount of water applied progressively decreased with increasing distance from the sprinkler pipeline. In 1986, the main plots were divided into

three equal subplots $(6m \times 18 \text{ m})$ to which three plant population levels (20, 30 and 40 plants m⁻²) were randomly assigned. Before sowing, nitrogen at 20 kg ha⁻¹ and phosphorous at 18 kg ha⁻¹ (as diammonium phosphate) were uniformly applied. Chickpea (cv. JG 74) was sown on 30 October and emerged on 7 November 1986. Spacing between rows was 0.3 m, and within-row spacing varied according to the level of plant population in a subtreatment.

The 1987-season experiment was laid out in the same fashion as in the 1986 season, and the irrigation treatments were also the same. There were no subtreatments in 1987. Chickpea (cv. JG 74) was sown on 28 October 1987 and emerged on 5 November. The experiment had a plant population of 30 plants m⁻², and the remaining crop management was the same as in 1986. Treatments in both experiments were replicated three times.

Uniform irrigations with perforated pipes and gradient irrigations with the line-source were given at approximately 10-day intervals. Until complete ground cover, the amount of irrigation applied by the perforated pipes equalled available soil water-deficit in the root zone, as determined by neutron probe. Later, the amount applied equalled 75% of cumulative open-pan evaporation minus rainfall (if any) since the previous irrigation. Each gradient irrigation was applied in such a way that the area around the neutron-probe tube nearest to the line-source pipeline was brought to field capacity, and beyond that point the irrigation amount decreased to the minimum. Amount of irrigation re-

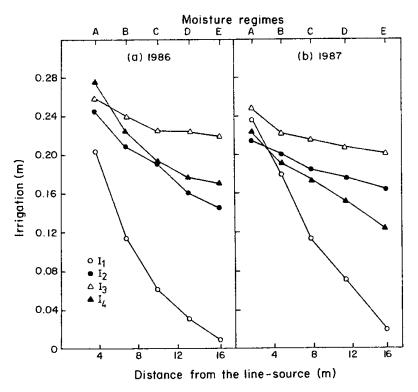


Fig. 1. Amounts of irrigation given to different treatments in the (a) 1986 and (b) 1987 seasons. For irrigation treatments I_1 to I_4 , see text.

ceived near each access tube was recorded using catch-cans. Total amount of irrigation given to the four treatments is presented in Fig. 1.

SOIL WATER MONITORING

To monitor changes in soil water content, neutron-probe access tubes were installed in each plot at 3.6, 3.8, 10.0, 13.2 and 16.4 m from the line-source in 1986 and at 1.8, 4.8, 7.8, 11.4 and 15.6 m in 1987. These five locations in each plot were designated respectively as A, B, C, D and E moisture regimes (Fig. 1). Neutron probe (Didcot Instruments¹, Wallingford, Great Britain) readings were taken every week at 0.15-m depth intervals from 0.3 m to 1.5 m soil depth. Soil moisture in the 0-0.1-m and 0.1-0.22-m layers was determined by gravimetry. Evapotranspiration (E_t) by the crop was calculated by the water-balance method:

$$E_{\mathrm{T}} = p + I + \Delta M - R - D \tag{1}$$

where: E_{t} , evapotranspiration; p, rainfall; I, irrigation; ΔM , change in soil moisture content; R, surface runoff; and D, deep drainage.

All the plots were diked to prevent runoff, and the irrigation applied did not exceed soil water-deficit or water loss from the crop. Therefore, R and D were considered negligible to calculate evapotranspiration during both seasons, except for a short period in 1987 when 240 mm of rain fell during the first 22 days after sowing. Therefore, $E_{\rm t}$ by the crop from emergence to 50% flowering in 1987 was estimated by the water-balance model of Ritchie (1972) using leaf-area index, potential evapotranspiration, and water-retention characteristics of the soil as input. After 50% flowering, $E_{\rm t}$ was calculated using the neutron-probe data. Evapotranspiration-deficit ($E_{\rm t}$ -deficit) experienced by the crop in each treatment and moisture regime was calculated as the difference between the maximum evapotranspiration observed in the well-watered treatment (moisture regime A of the I_4 treatment, Table 2) and the actual evapotranspiration during a growth period.

Crop phenology

The crop was observed every alternate day to record crop development in each treatment. The growth stages recorded were emergence (E), flowering (FL), pod-initiation (PI), beginning of pod fill (BPF) and physiological maturity (PM). The crop was assumed to have reached a particular growth stage when at least 50% of the plants had shown that stage of development. Ther-

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TABLE 1

Monthly mean values of various climatic elements during the 1986 and 1987 seasons, as observed in the meteorological observatory about 500 m away from the experimental plot

Month	Year	Total rainfall (mm)	Temp. (°C)		Open pan	Solar radiation (MJ m ⁻² day ⁻¹)	Sunshine
			Max. (°C)	Min. (°C)	evaporation (mm day ⁻¹)	(MJ m day)	(h)
Nov.	1986	36.8	29.9	17.2	4.8	16.1	8.8
	1987	240.0	27.5	18.0	3.6	13.6	6.1
Dec.	1986	6.3	28.5	15.3	5.0	15.5	9.3
	1987	0.8	26.9	14.2	3.8	15.1	8.5
Jan.	1987	4.4	28.6	15.0	5.1	17.1	9.6
	1988	0.0	28.4	14.1	4.6	16.9	9.7
Feb.	1987	0.0	30.6	15.6	7.7	18.8	10.5
	1988	4.0	32.0	17.4	6.1	17.5	9.8

TABLE 2

Cumulative maximum $E_{\rm t}$ ($E_{\rm t_{max}}$) and mean saturation deficit of air (Δe) for different growth phases of chickpea during the 1986 and 1987 seasons

Growth phase	$E_{\rm t_{max}} ({ m mm})^{\rm a}$	$E_{l_{max}}$ (mm) ^a		
	1986	1987	1986	1987
E-FL	158	122	2.5	1.7
FL-BPF	86	96	2.0	1.8
BPF-PM	182	173	2.5	2.7
Total	426	391		

^aAs observed in moisture regime A of the I_4 treatment.

mal time (°Cd) required for each phenological event was calculated from the daily maximum ($T_{\rm max}$) and minimum air temperatures ($T_{\rm min}$) recorded in the meteorological observatory located about 500 m away from the experimental plot. The relation used was:

Thermal time (°Cd) =
$$(T_{\text{max}} - T_{\text{min}})/2 - T_{\text{b}}$$
 (2)

where T_b is the base temperature taken as 8°C for chickpea development (Huda and Virmani, 1987). On days when $T_{\rm max}$ was greater than 30°C, it was taken as 30°C. The degree-days thus calculated were summed over days to arrive at thermal-time requirements of different growth phases.

^bAs recorded in the meteorological observatory at 14:14 h.

Radiation interception

To determine radiation interception by the crop canopy, incoming PAR (photosynthetically active radiation) was measured twice a week with a line-quantum sensor (LI-COR, Lincoln, NE, U.S.A.) both at the surface and below the crop canopy and recorded on a polycorder (Omni-data, Logan, UT, U.S.A.). To eliminate the effect of solar altitude on PAR interception, the measurements were confined to the mid-day period. These observations were taken in A, C and E moisture regimes of all treatments.

Growth analysis

Ten plants from 0.30-m² area each were harvested at weekly intervals from A, C and E moisture regimes of all treatments. Plant components such as leaves, stems including branches, and pods were separated and oven-dried at 60°C to constant weight. Before drying, the leaf area of each sample was determined using a LI-COR leaf-area meter. Later, all plant components were weighed and pods threshed to determine seed weight. The weight of flowers was negligible, and thus ignored in the growth analysis.

RESULTS AND DISCUSSION

Total rainfall during November was greater in 1987 (240 mm) than in 1986 (36.8 mm; Table 1). This decreased both maximum and minimum temperatures during November and December 1987. Rainfall in December, January and February was negligible during both seasons. Open-pan evaporation, sunshine duration and solar radiation per day were generally lower in 1987 than in 1986. This resulted in lower saturation vapour pressure deficit of the air (Δe) and lower maximum E_t by the crop prior to flowering (Table 2) in 1987 compared with 1986. Total seasonal E_t as observed in moisture regime A of the I_A treatment was 426 mm in 1986 and 391 mm in 1987.

Because there was no yield response to different levels of plant population studied in 1986, all data on plant, soil and microclimatic observations were averaged over sub-treatments for further analysis.

Phenology

Water-deficits during both the vegetative and reproductive phases hastened crop development and thus decreased their duration (Fig. 2). Normalized E_t -deficit, which is defined as the maximum E_t minus actual E_t observed during a growth phase and divided by the mean saturation deficit (Δe) of air, was used as an index to reflect the magnitude of water-deficit experienced by the crop. Duration of emergence (E) to flowering (FL) was inversely corre-

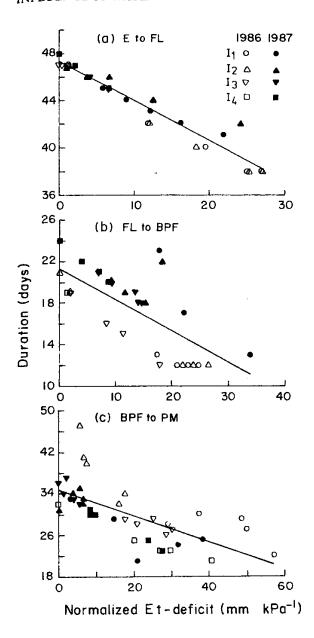


Fig. 2. Relation to normalized E_t -deficit with the duration of (a) E-FL, (b) FL-BPF, and (c) BPF-PM. For a: Y = 47.3 - 0.34X, RSE=0.72, $r^2 = 0.95$, P < 0.01; for b: Y = 21.2 - 0.30X, RSE=2.6, $r^2 = 0.51$, P < 0.01; for c: Y = 34.7 - 0.25X, RSE=4.2, $r^2 = 0.47$, P < 0.01.

lated $(r^2=0.95, P<0.01)$ with normalized E_t -deficit (Fig. 2a). Extremely stressed chickpea took ten days less to reach FL compared with well-watered chickpea, and the duration of E-FL decreased at the rate of 0.34 days mm⁻¹ kPa of normalized E_t -deficit. Similarly, the durations of FL to beginning of pod-fill (BPF) and BPF to physiological maturity (PM) decreased with increase in normalized E_t -deficit (Fig. 2b,c), and 1 mm kPa⁻¹ of normalized E_t -deficit was equivalent to 0.30 and 0.25 day decrease in the duration of respective phases. Maximum reduction in the duration of the reproductive phase was 22 days. When the duration of both vegetative and reproductive phases was expressed on a thermal time (°Cd) basis and correlated with normalized E_t -deficit, the correlations did not improve significantly (Fig. 3).

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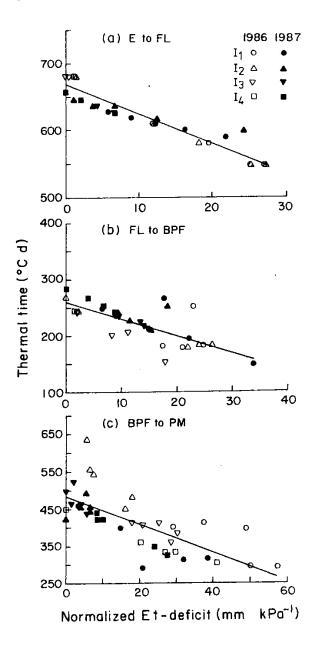


Fig. 3. Relation of normalized E_t -deficit with the thermal time requirement for (a) E-FL, (b) FL-BPF, and (c) BPF-PM. For a: Y=669.5-4.5X, RSE=14.2, $r^2=0.89$, P<0.01; for b: Y=259.3+3.1X, RSE=23.7, $r^2=0.57$, P<0.01; for c: Y=485.1-3.8X, RSE=53.6, $r^2=0.55$, P<0.01.

Normalized E_t -deficit of 1 mm kPa⁻¹ decreased the duration of E-FL by 4.5°Cd, of FL-BPF by 3.1°Cd, and of BPF-PM by 3.8°Cd (Fig. 3). These results on hastening of crop development with water stress are in line with those observed in other crops. For example, Done et al. (1984) observed that the durations of different growth phases of five sorghum cultivars decreased when water stress in the crop was imposed by increasing irrigation interval. Similarly, Angus and Moncur (1977) reported hastening of anthesis in wheat under mild stress, but delaying under severe stress. The mechanism of hastened development has been related to increase in leaf or canopy temperature (Slatyer, 1969; Sandhu and Horton, 1978) which accompanies water stress.

It is inferred from these results that we need to account for the influence of water-deficits on the development of chickpea, in addition to photoperiod and temperature, while assessing adaptation of a chickpea cultivar to different environments and in building chickpea phenology models.

Canopy development, radiation interception and dry-matter production

Although the observations on radiation interception, green leaf area index $(L_{\rm g})$ and growth analysis were taken at A, C and E moisture regimes of all treatments, the results have been presented only for the E level of moisture regime because the maximum treatment effects were observed at that level. Greater differences among treatments in canopy development were observed in 1986 than in 1987 because of 240 mm of rainfall during early crop growth in 1987 (Fig. 4). Water-deficits during all growth phases decreased foliage growth, but the reduction in foliage growth was greater when the crop was stressed prior to flowering (Fig. 4a,c). Maximum reduction in $L_{\rm g}$ occurred when the crop was continuously stressed throughout the season (I_1 treat-

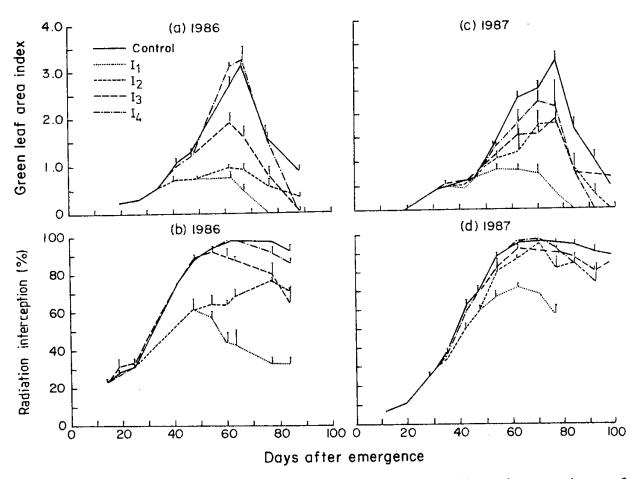


Fig. 4. Green-leaf-area index and radiation interception observed in moisture regime E of various treatments during 1986 (a and b) and 1987 (c and d) seasons. Control refers to the moisture regime A of the I_4 treatment. Vertical bars represent the standard error of the mean. For clarity, the standard errors have been omitted for the points which are too close to each other.

ment). Because chickpea is an indeterminate crop, and continues its vegetative growth during the reproductive period, water-deficits during the FL-BPF phase also decreased leaf-area growth. However, the reduction in $L_{\rm g}$ was less compared with when stress occurred prior to flowering. Reduction in $L_{\rm g}$ during pod-filling was primarily due to increase in leaf senescence caused by leaf fall or translocation of assimilates to the reproductive sinks. Decrease in $L_{\rm g}$ in each treatment caused corresponding reductions in radiation interception by the crop canopy (Fig. 4b,d) and total dry-matter production (Fig. 5a,b). Because of lesser water deficits in 1987, greater differences among treatments in radiation interception and dry-matter production were observed in 1986 than in 1987.

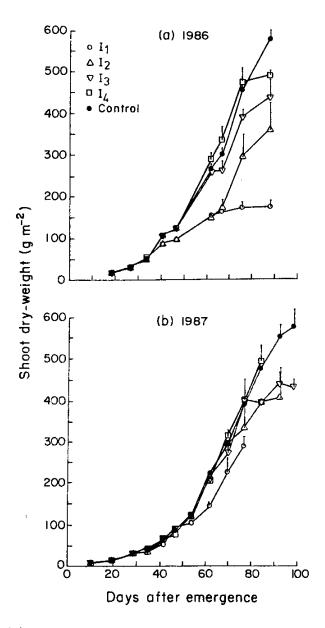


Fig. 5. Total shoot dry-weight observed in moisture regime E of various treatments during (a) 1986 and (b) 1987 seasons. Control refers of the moisture regime A of the I_4 treatment. Standard errors as in Fig. 4.

Dry-matter allocation

Leaves, stems (main stem plus branches), roots and nodules are the major sinks for the assimilates produced prior to the initiation of pods. The results showed that timing of water stress had no influence on relative allocation to leaves and stems up to the pod-initiation (PI) stage. Of the total above-ground biomass produced up to PI, 48-51% was allocated to leaves and the remaining to the stems (Fig. 6a,b).

Because chickpea is an indeterminate crop, dry-matter allocation to the vegetative parts continues even during the reproductive phase, thus competing for assimilates with the reproductive organs. As the pods grow, the assimilate allocation to the vegetative parts decreases, and finally some assimilates

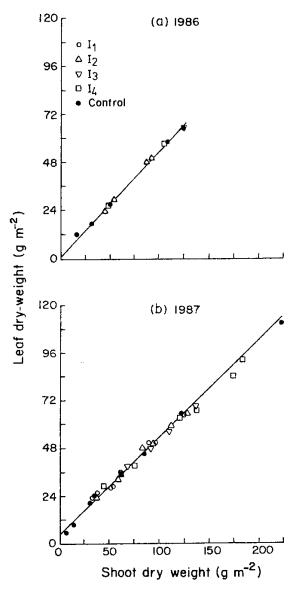


Fig. 6. Increase in leaf dry-weight with the increase in total shoot dry-weight up to PI during (a) 1986 and (b) 1987 seasons. For a: Y=2.01+0.51X, RSE=1.01, $r^2=0.99$, P<0.01; for b: Y=3.94+0.84X, RSE=1.79, $r^2=0.99$, P<0.01.

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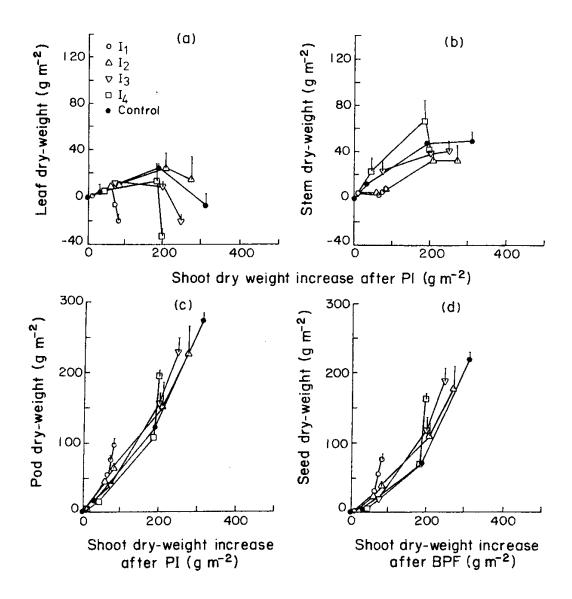


Fig. 7. Accumulation of dry-matter in (a) leaf, (b), stem and (c) pod in relation to increase in shoot dry-weight after PI and (d) seed in relation to increase in shoot dry-weight after BPF during 1986. Standard errors as in Fig. 4.

produced prior to PI may also be translocated to pods, as observed in other legumes (Khanna-Chopra and Sinha, 1987; Saxena, 1984). Water stress during all growth phases increased allocation to pods and seeds, although greater proportions of assimilates were allocated when the crop was stressed after flowering or when raised completely without irrigation (Fig. 7c,d; Fig. 8c,d). Plots of data on the changes in leaf and stem weights against total biomass gain after PI show that greater loss occured in leaf weight than in stem weight at the end of season. Because all the fallen leaves were collected to determine total leaf weight, these results mean that most of the translocation of assimilates to pods and seeds occurred from the leaves rather than stems. Some translocation from stems or branches may also occur when the crop is severly stressed. Because of greater water-deficits in 1986, relatively greater translocation was observed in 1986 than in 1987 (Figs. 7a, 8a). Of the total biomass

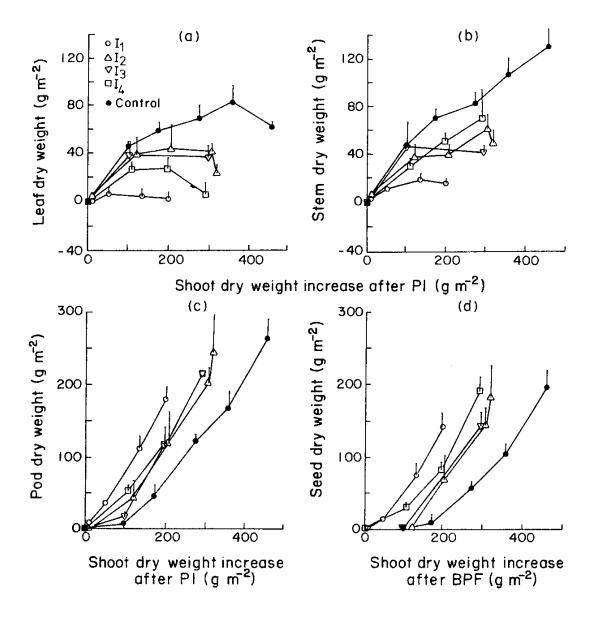
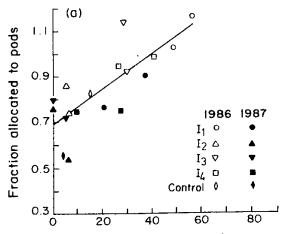
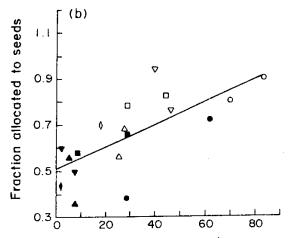


Fig. 8. Accumulation of dry-matter in (a) leaf, (b) stem and (c) pod in relation to increase in shoot dry-weight after PI; (d) seed in relation to increase in shoot dry-weight after BPF during 1987. Standard errors as in Fig. 4.

gain after PI, allocation to pods and seeds was directly proportional to the intensity of water stress experienced by the crop during pod and seed growth (Fig. 9). Allocation to pods increased from 0.64 to 1.15 among treatments at the rate of 0.0075 fractional increase per mm kPa⁻¹ of normalized E_t -deficit (Fig. 9a). These results also suggest that, over the season, about 15% of the assimilates produced prior to PI were translocated to pods. This is comparable to the 20% translocation to pods reported by Saxena (1984). Allocation to seeds increased from 0.50 to 0.95 among treatments at the rate of 0.0052 fractional increase per mm kPa⁻¹ of normalized E_T -deficit (Fig. 9b). These changes in assimilate allocation to different plant organs due to water-deficit suggest that we need to consider the influence of water stress on partitioning of dry-matter while building models of chickpea growth and development.



Normalized ET-deficit (mm kPa-1) from PI to PM



Normalized ET-deficit (mm kPa⁻¹) from BPF to PM

Fig. 9. Relation of normalized E_t -deficit with fractional allocation (a) to pods of the shoot drymatter produced after PI and (b) to seeds of the shoot dry-matter produced after BPF. For a: Y=0.69+0.0075X, RSE=0.11, $r^2=0.59$, P<0.01; for b: Y=0.50+0.0052X, RSE=0.13, $r^2=0.51$, P<0.01. Standard errors as in Fig. 4.

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