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Leaf area development, dry weight accumulation and solar energy conversion efficiencies of *Phaseolus vulgaris* L. under different soil moisture levels near Nairobi, Kenya

M.M. Muniafu[1*], J.N.M. Macharia[1], C.J. Stigter[2], G.L. Coulson[3]

(1. Department of Botany, University of Nairobi, Nairobi, Kenya; 2. TTMI-Project, Department of Meteorology, Wageningen Agricultural University, Duivendaal 2, 6701 AP Wageningen, Netherlands; 3. TTMI-Project, Department of Botany, University of Nairobi, Kenya)

Abstract: Leaf area development, dry weight accumulation and solar energy conversion efficiencies of *Phaseolus vulgaris* L. cv GLP-2 under two soil moisture levels in two contrasting seasons near Nairobi, Kenya were investigated. The experiment confirms that dry weights and yields of *Phaseolus vulgaris* are limited by a drought induced decrease in leaf area, leading to less radiation interception as a source for assimilation. However, photosynthetic efficiency in *Phaseolus vulgaris* also appears to decrease and to contribute to these effects. Finally, an even larger decreases of economic efficiency as obtained in the second season, where stress lasted much later into the season, reveals that such a drought also limits considerably the partitioning and translocation of assimilates to the seeds of *Phaseolus vulgaris*. The efficiencies obtained are in line with the better literature data for other crops.

Key words: economic efficiency; *Phaseolus vulgaris* L.; photosynthetic efficiency; radiation absorption/interception; tube solarimeters

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Introduction

Kenya's high population growth rate has created pressure on the high potential areas. This has resulted in the migration of people to uncultivated "marginal" lands which make up about 80% of the country and are predominantly of low agricultural productivity (Hornetz, 1990). These lands are also characterized by low erratic rainfall (below 500 mm annually) with frequent dry spells and high evaporation (Hjort, 1976).

Crops which are ecologically adapted to these arid and semi-arid areas therefore need to be introduced, especially since agricultural practices such as irrigation have limitations in that they are too costly for small scale farmers to both afford and maintain. They may also lead to an increased soil salinity as well as a loss of fresh water resources with time (Simpson, 1981). This calls for evaluation of certain ecophysiological properties of the crops such as their response to water stress. In the experiment, leaf area development, dry weight accumulation and solar energy conversion efficiency of the common dry bean, *Phaseolus vulgaris* L. cv GLP-2, were compared under low and high water treatments respectively, in two contrasting growing seasons.

1 Materials and methods

Seeds of *Phaseolus vulgaris* L. cv GLP-2, previously dressed with Malathion dust to protect them against beanfly, were sown near Nairobi, Kenya on 21/12/89 [11/6/90]** under a strip plot design with two treatments of water, high and low. Each treatment consisted of three replicate plots measuring 4m by 17m separated by a path 0.5m wide. The seeds were planted at a spacing of 10 cm by 30 cm in numbers and arrangements which allowed for sampling by a destructive method and for the measurement of radiation. Diammonium phosphate (DAP) fertilizer

* Present address: Department of Botany, Egerton University, P.O. Box 536, Njoro, Kenya. ** Figures between brackets apply to the second season

was applied at a rate of 100 kg/hm^2.

Irrigation water was supplied when needed by means of a line source sprinkler system with the sprinklers on 2m risers. This provided a water gradient with the amount of water decreasing with an increasing distance from the line. The replicate plots for the high water treatment were 0.5m from the line while those for the low water treatment were 10m away. Attacks from beanfly and fungi were controlled by a fortnightly application of *dimethoate* and *dithane* M-45, respectively, from emergence through to flowering. Data on daily precipitation, temperature and evaporation were obtained from a meteorological station about 100m from the experimental site.

Soil moisture measurements were made once a week using the gravimetric method. The soil samples were excavated by the use of an auger at depths of 0—10 cm and 20—30 cm starting 39 DAS [17DAS]. This was extended to include 40—50 cm as the roots grew deeper.

Photosynthetically active radiation (PAR) transmitted by the crop was obtained from 29 DAS [21 DAS], as the difference between the outputs of a pair of Delta-T tube solarimeters placed NE/SW across the rows of the plants. One of these was unfiltered, measuring global radiation (GR) from 0.35—2.5 μm while the other was filtered and measured near infra-red radiation between 0.75—2.5μm. Each replicate plot had two such pairs of tube solarimeters. Their placement made sure that earlier identified problems with N/S mounted tubes (Mungai, 1992) did not occur. This was also independently verified using a line quantum sensor, while problems with the filters were accounted for (Mungai, 1992).

The PAR and GR intercepted were therefore taken as the difference between the output of a similar pair placed 1m above the crop and that of the solarimeters within the crop. PAR absorbed was calculated by subtracting the proportion of PAR reflected, which was taken as a constant value of 0.05 over the whole season (Monteith, 1990). The radiation measurements were integrated for seven day periods and coincided with the sampling of plants for dry weight.

Three plants were sampled weekly as from 28 DAS [29 DAS] in a predetermined random pattern with as much of the roots as possible being recovered. Leaf area was measured immediately, using a leaf area meter (LI-COR 3100), and the plants were then oven dried at 60℃ to a constant dry weight. Harvesting was done at 89 DAS from half of each replicate plot (using an improved technique at 103 DAS were a representative area of 10 m^2 was used from each replicate plot). The moisture content of the seeds in this latter season was determined after mixing samples of the sub-plots of each treatment and oven drying at 60℃ for 24 hours. The values obtained were used to correct the values of yield to what they would have been at the accepted storage moisture content of 10%. To test for significant differences between the two treatments, analysis of variance (ANOVA) was used for the soil moisture and leaf area values while, due to smaller sample sizes, the *t*-test was used for the dry weight and PAR absorbed values. To "smoothen" out the wide scatter of dry weight values, observations for each replicate plot were fitted using the second order polynomial (Hunt, 1982). Details are given in Muniafu (Muniafu, 1991).

Photosynthetic efficiency, *e*, was estimated as a regression of the dry matter accumulated over the growing season upon the cumulative GR intercepted and PAR absorbed over the same time period (Muniafu, 1991). The values obtained were also converted into dimensionless energy terms (expressed as percentages) by assuming a dry matter energy content of 17.5 kJ/g (Cooper, 1975). The economic efficiency was calculated using only the economically important part of the plant (i.e. the final dry seed) as the ratio of the final seed per unit of surface to the total GR intercepted and to the PAR absorbed over the season over that surface. Those data were also again expressed as a dimensionless energy term.

2 Results

The high and low water treatments received relatively high amounts in the first season: 699.6 and 421.5 mm water respectively, with rainfall contributing 309.5 mm to these totals. In January, the high water treatment (305.2 mm) received slightly more than twice the 139.9 mm received by the low water treatment. In February the two treatments got 179.5 and 66.7 mm respectively while in March both received 214.9 mm of rainfall, from which the low water treatment plants recovered (Muniafu, 1991). Reference evapotranspiration (Et_0) over the season was 329.3 mm and the mean maximum and minimum temperatures were 25.1℃ and 13.5℃. For the second, contrasting season the two treatments received only 255.7 and 123.8 mm respectively. Of these amounts, rainfall supplied 41.4 mm. In July the high water treatment got 158.1 mm and the low water treatment 85.6 mm while in August the two treatments got 90.8 and 31.4 mm respectively. September contributed 6.8 mm rainfall. Et_0 was 210.8 mm over the season while the mean maximum and minimum temperatures were 21.8℃ and 11.1℃. The altitude was about 1000m.

The soil moisture contents at the three measured depths are shown in Table 1. There were significant differences ($p < 0.05$) between treatments at most depths and days at which measurements were taken from 33 to 69 DAS (except for day 37) [from 37 DAS onwards (except for day 51)]. In the first season the March rainfall restored all soil moisture.

Leaf area increased with time for both treatments to a maximum of about 2200 and 1500 cm^2 per plant respectively for the high and low water treatments between days 49 and 70 (77 for low water treatment)[to about 1900 and 1000 cm^2 per plant between days 64 (57 for low treatment) and 85 for the two treatments respectively]. The leaf area of the plants in the low water treatment was significantly lower than that of the high water treatment from 28 to 70 DAS (excluding day 42) throughout the season starting day 29. In the first season the March rainfall benefitted the low water treatment till day 77.

The PAR absorbed by the plants as a percentage of that available increased to a maximum at 49 DAS (between 57 and 64 DAS; Fig. 1), coinciding with the start of the period with maximum leaf area. The differences in the amount of PAR absorbed between the two treatments were statistically significant ($p < 0.05$) throughout most of the second season (Fig. 1). For the first season the absorbed PAR was always lower in the low water treatment but differences were statistically significant only between 49 and 63 DAS, during maximum leaf area. Values of the GR intercepted in each replicate plot also clearly show that more radiation was intercepted in the high water than in the low water treatment, though the difference again was much smaller in season one (Table 2).

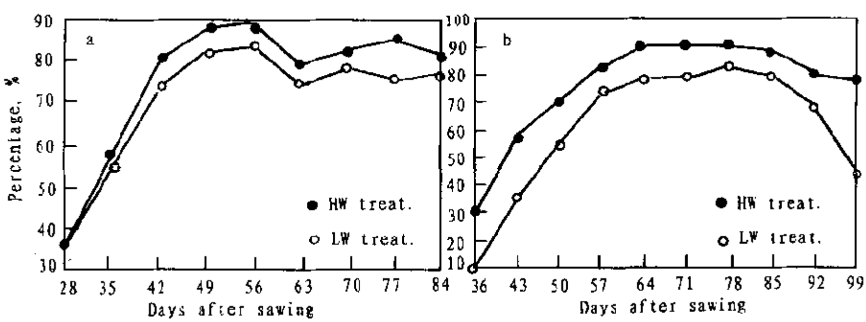

Fig. 1 Percentage PAR absorbed for both treatments

a. season 1; b. season 2

Table 1 Soil moisture content (%) for the two treatments

	DAS	Depth, cm	HW treat., $\bar{x}$	S.E	LW treat., $\bar{x}$	S.E	F_{value}	$F_{0.05}$ d.f 1,4 (1,10)
Season 1	25	10	35.8	0.87	34.3	2.77	0.3ns	(7.71)
		30	43.6	4.00	39.5	0.93	1.5ns	4.96
	33	10	37.3	2.06	30.6	0.39	9.2*	4.96
		30	41.7	1.36	32.5	1.17	31.5*	4.96
	37	10	31.2	1.70	30.3	0.72	0.2ns	4.96
		30	37.5	2.41	32.1	1.10	4.1ns	4.96
	45	10	31.1	0.68	29.2	1.63	15.3*	4.96
		30	36.6	0.68	32.6	0.62	23.0*	4.96
		50	40.5	0.68	35.6	0.54	17.7*	4.96
	61	10	37.7	1.20	27.3	0.84	76.1*	(7.71)
		30	36.6	0.04	27.7	0.98	126.5*	(7.71)
		50	39.3	1.07	28.3	0.90	93.6*	(7.71)
	69	10	36.8	0.48	30.1	0.43	169.9*	(7.71)
		30	38.0	0.48	32.0	1.24	30.7*	(7.71)
		50	40.1	0.27	33.7	0.57	154.2*	(7.71)
	DAS	Depth, cm	HW treat., $\bar{x}$	S.E	LW treat., $\bar{x}$	S.E	F_{value}	$F_{0.05}$ d.f (1,8)
Season 2	16	10	34.8	1.00	33.0	1.38	1.7ns	5.32
		30	36.5	1.12	32.2	1.35	4.9ns	5.32
	23	10	36.3	1.57	31.2	2.14	5.0ns	5.32
		30	35.9	2.04	34.9	1.20	2.0ns	5.32
	30	10	36.3	0.79	31.3	0.59	4.2ns	5.32
		30	35.9	1.76	34.1	1.11	4.0	5.32
	37	10	37.4	0.79	31.3	0.59	38.8*	5.32
		30	41.0	0.34	32.5	1.01	81.3*	5.32
	44	10	33.9	0.84	31.1	0.44	15.0*	5.32
		30	34.6	1.26	32.6	0.62	2.3ns	5.32
	51	10	28.5	0.57	29.1	0.98	0.4ns	5.32
		30	32.9	1.35	29.7	0.73	4.4ns	5.32
		50	35.9	1.57	31.3	1.16	6.7ns	5.32
	58	10	33.7	0.70	27.2	0.99	36.0*	5.32
		30	35.8	1.12	31.1	0.54	16.3*	5.32
		50	38.2	1.43	31.4	0.58	20.0*	5.32
	65	10	30.3	0.59	26.6	0.59	26.4*	5.32
		30	31.9	0.50	30.0	0.49	19.2*	5.32
		50	31.6	0.56	29.2	0.58	9.3*	5.32
	72	10	33.8	0.64	27.1	0.68	51.4*	5.32
		30	35.8	0.44	29.4	0.63	65.3*	5.32
		50	36.7	0.42	28.9	1.37	35.2*	5.32
	79	10	30.5	0.85	26.0	0.46	21.3*	5.32
		30	32.5	0.83	29.0	0.53	34.1*	5.32
		50	32.7	0.84	27.5	0.31	4.6ns	5.32
	86	10	35.3	0.61	32.3	1.29	5.0ns	5.32
		30	36.5	0.42	32.4	0.92	16.4*	5.32
		50	38.8	0.64	30.2	0.58	224.5*	5.32

*: Significant difference at 5% level; ns: Not significant

Plants from the high water treatment generally accumulated more dry weight than those from the low water treatment in both seasons (Fig. 2). The scatter most likely resulted from the small sample size used in this study, which aimed at not removing more than 5% of the total population. In spite of this wide scatter between replicates of the same treatment for the observed values, the fitted data (Fig. 2) show clear difference in dry weight values between the high and low water treatments. This must be due to the fact that drought reduces the amount of assimilate accumulated as dry weight. The mean final seed-weight for high and low water treatment and the mean yields were was given in Table 3. These figures represent a drop of 20% and 40% in yield in the low water treatment of the first and second season respectively.

Table 2 Global radiation (GR) intercepted (MJ/m^2) for the two treatments

	Week	High water treatment Replicates				Low water treatment Replicates			
		1	2	3	x	1	2	3	$\bar{x}$
Season 1	4	50.6	48.2	37.5	45.5	42.3	51.3	31.9	41.7
	5	67.2	81.3	83.5	77.3	74.3	73.8	65.6	75.1
	6	103.0	111.7	116.9	110.5	103.6	100.3	97.0	100.3
	7	120.5	130.2	134.0	128.2	115.3	121.1	114.7	117.0
	8	128.5	131.3	130.8	130.2	118.1	118.8	110.5	115.8
	9	88.4	100.6	97.6	95.5	86.2	83.9	79.8	83.3
	10	94.0	99.0	100.2	97.7	91.0	90.4	77.4	86.3
	11	92.4	91.5	91.0	90.6	83.2	82.3	71.6	79.0
	12	104.7	109.0	100.4	104.7	94.8	95.7	91.7	94.1
Season 2	5	28.0	27.0	26.2	27.1	7.6	8.4	9.0	8.3
	6	43.1	41.4	30.1	38.2	16.8	21.1	21.2	19.7
	7	74.9	65.2	55.5	65.2	34.4	44.2	42.3	40.3
	8	49.5	45.2	39.0	44.6	26.5	34.7	36.9	32.7
	9	58.3	56.1	52.0	55.5	34.8	45.0	46.6	42.1
	10	73.2	68.9	68.9	70.3	44.4	57.5	58.2	53.4
	11	50.9	49.3	49.9	50.0	33.6	41.5	42.9	39.3
	12	94.0	94.0	92.9	93.6	56.7	57.6	73.2	62.9
	13	87.2	95.0	92.0	91.4	50.0	59.9	70.3	60.1
	14	86.9	88.8	91.1	88.9	37.5	44.5	51.9	44.6

Table 3 Yields for the two treatments

		High water treatment Replicates				Low water treatment Replicates			
		1	2	3	$\bar{x}$	1	2	3	$\bar{x}$
Season 1	Seed weight per plant, g	16.8	16.4	14.1	15.8	13.9	12.1	12.7	12.9
	Tons per hectare	2.7	2.6	3.2	2.8	2.4	2.3	1.8	2.2
Season 2	Seed weight per plant, g	15.0	15.3	15.3	15.2	8.4	7.7	9.0	8.4
	Tons per hectare	3.5	2.8	3.5	3.3	1.7	1.8	2.1	1.9

Based on either the intercepted GR or absorbed PAR, the photosynthetic efficiency of conversion of light energy to plant dry matter (e) decreased by 20% in plants of the low water treatment in both seasons. For the fitted data, based on GR, average e was 1.6 and 1.3 g/MJ (1.7 and 1.3 g/MJ) and on the basis of PAR, it was 2.8 and 2.4 g/MJ (3.1 and 2.5 g/MJ) for the high and low water treatments respectively (Table 4). These figures correspond to 4.9% and 4.1% (5.4% and 4.3%) efficiency of solar energy (PAR) conversion to plant dry weight. The economic efficiencies on the bases of both GR and PAR for the first season were 0.6 ± 0.04 and 0.5 ± 0.0 g/MJ respectively 1.0 ± 0.1 and 0.8 ± 0.1 g/MJ for high and low water treatment [0.7 ± 0.04 and 0.6 ± 0.04 g/MJ respectively 1.3 ± 0.04 and 0.9 ± 0.1 g/MJ] (Table 5). Expressed as a dimensionless percentage, with PAR as the basis, e was $1.8\% \pm 0.07$ and $1.5\% \pm 0.1$ ($2.2\% \pm 0.04$ and $1.0\% \pm 0.1$) for the high and low water treatments respectively, representing

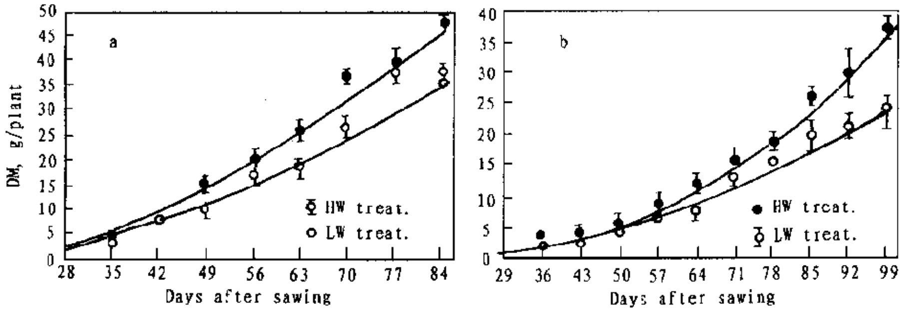

Fig. 2 Dry matter (g/plant) for both treatments
lines: fitted values; points: observed values with $S.E.$ bars

a decrease in the economic efficiency of about 20% and 50% for these seasons respectively (Muniafu, 1991).

Table 4 Photosynthetic efficiency (by regression) expressed in g/MJ (with intercepted GR and absorbed PAR as a basis) and as a dimensionless *e* (%) (with absorbed PAR as a basis) for the two treatments

		High water treatment Replicates					Low water treatment Replicates				
		1	2	3	$\bar{x}$	$S.E$	1	2	3	$\bar{x}$	$S.E$
Season 1	Fitted data, GR	1.7	1.6	1.4	1.6	0.1	1.3	1.1	1.6	1.3	0.2
	Observed data, GR	1.6	1.7	1.5	1.7	0.1	1.7	1.5	1.6	1.6	0.1
	Fitted data, PAR	2.9	2.8	2.7	2.8	0.1	2.4	1.9	2.8	2.4	0.3
	Observed data, PAR	3.2	3.1	2.9	3.1	0.1	2.9	2.6	3.1	2.9	0.2
	Fitted data, %	5.1	4.9	4.7	4.9	0.1	4.2	3.3	4.9	4.1	0.5
	Observed data, %	5.6	5.4	5.1	5.4	0.2	5.1	4.6	5.4	5.0	0.3
Season 2	Fitted data, GR	1.7	1.7	1.8	1.7	0.1	1.3	1.1	1.6	1.3	0.1
	Observed data, GR	1.6	1.6	2.0	1.7	0.2	1.7	1.5	1.6	1.6	0.1
	Fitted data, PAR	3.0	3.0	3.2	3.1	0.1	2.4	2.5	2.4	2.5	0.1
	Observed data, PAR	3.2	3.2	3.4	3.3	0.2	2.3	2.4	2.9	2.5	0.2
	Fitted data, %	5.3	5.3	5.6	5.4	0.1	4.2	4.4	4.2	4.3	0.4
	Observed data, %	5.6	5.6	6.0	5.7	0.2	4.0	4.2	4.9	4.4	0.3

Table 5 Economic efficiency expressed in g/MJ (with intercepted GR and absorbed PAR as a basis) and as a dimensionless *e* (%) (with absorbed PAR as a basis), for the two treatments

		High water treatment Replicates					Low water treatment Replicates				
		1	2	3	$\bar{x}$	$S.E$	1	2	3	$\bar{x}$	$S.E$
Season 1	$GR_{int.}$	0.6	0.6	0.5	0.6	0.04	0.5	0.5	0.5	0.5	0.0
	$PAR_{abs.}$	1.1	1.0	0.9	1.0	0.1	0.9	0.8	0.9	0.8	0.1
	%, $PAR_{abs.}$	1.9	1.8	1.6	1.8	0.07	1.6	1.4	1.6	1.5	0.1
Season 2	$GR_{int.}$	0.7	0.7	0.8	0.7	0.07	0.6	0.5	0.6	0.6	0.04
	$PAR_{abs.}$	1.2	1.3	1.3	1.3	0.04	0.9	0.8	1.0	0.9	0.1
	%, $PAR_{abs.}$	2.1	2.2	2.2	2.2	0.04	1.1	0.9	1.1	1.0	0.1

3 Discussion

Soil moisture fluctuated, be it more pronouncedly for the high water treatment, depending on irrigation (Table 1) but was between the field capacity and the permanent wilting point as measured for this soil in the laboratory by Lenga (Lenga, 1979). In both seasons, but more frequently in the second one, soil moisture content of the low water treatment actually fell below the permanent wilting percentage in a number of days. This may reflect the unreliability of laboratory measurements as indicators of soil water relations, since the field capacity and the permanent wilting point depend on the soil profile and structure (Kramer, 1983). The high water treatment fell to 50%—70% (40%—50%) of the total water available before each irrigation while the low water treatment was before irrigation at 0%—30% (0%—20%) of the available soil water.

The leaf area development and the maximum leaf area attained in both seasons are in agreement with those of others in a range of plants under water stress. These include Maurer *et al.* (Maurer, 1969) working on *Phaseolus vulgaris* under five water treatment levels, Sobrado and Turner (Sobrado, 1983) who obtained significantly smaller leaves for sunflower plants under drought stress and Aggarwal and Sinha (Aggarwal, 1987) in wheat. Leaf area and leaf area duration are important determinants of yield (Yoshida, 1972). A large leaf area leads to an increased dry matter production (Fig. 2) through an increased interception of radiation (Fig. 1). However, after the attainment of complete canopy cover, mutual leaf shading causes a decrease in the mean photosynthetic rate per unit leaf area (Thiagarajah, 1981). As a result of reduced leaf area, the low water treatment plants absorbed less radiation compared to the high water treatment plants (Fig. 1). This obviously confirms that yields were limited by drought induced decrease in leaf area development, that leads to a reduction in the amount of absorbed radiation and hence a "source limitation". Similar observations have been noted in many other plants (Puckridge, 1971; Biscoe, 1975; Kanemasu, 1975; Victor, 1979; Macharia, 1988).

Zelitch (Zelitch, 1982) stated that the yield of small grain cereal crops is closely related to the leaf area duration after flowering. Woolhouse (Woolhouse, 1981) has also reviewed literature which shows a high correlation between the leaf area, leaf area duration after ear emergence and grain yield in wheat. Such cases, in which main water shortages occurred somewhat late in the season, we have here with equally convincing results (Muniafu, 1991). The lower seed weight of beans under low water treatment in this study indeed will in part be a results of reduced leaf area.

The plant photosynthetic efficiency is a reflection of the efficiency with which trapped radiant energy is converted into dry matter. The decrease in this efficiency that was observed in the low water treatment for both seasons (Table 4) indicates that drought not only limits the amount of light energy trapped through a decrease in leaf area but that the efficiency by which the absorbed energy is converted to dry matter is also reduced. This efficiency was 20% lower in droughted plants than in the high water treatment plants in both seasons. It confirms that the rate of CO_2 assimilation under non-limiting light may be depressed through disfunctions within the photosynthetic apparatus (Newton, 1981; Thakur, 1981). The larger decrease in the economic than in the photosynthetic efficiency (50% against 20% as obtained in season tow) confirms that in addition to reduced photosynthetic processes, severe drought that lasts late into the season may also limit the partitioning and translocation of assimilates to the sinks, including the seed (Zelitch, 1982).

The mean values for *e* obtained in this study on the basis of global radiation intercepted fall within the range of 1.2—1.7 g/MJ given by Russell *et al.* (Russell, 1989). Those based on absorbed PAR were as expected slightly less than double those based on GR intercepted (Russell, 1989; Muniafu, 1991). In terms of a dimensionless energy, the practical maximum efficiency for solar energy (PAR) conversion to organic compounds for C_3 plants is given as 5% to 6% (Jesch, 1981). Beadle and Long (Beadle, 1985) give values of 5.8%, 5.8% and 6% for maize, rice and sorghum, respectively. The values obtained for the high water treatment plants in this study compare well with these values in other plants, while drought decreased the photosynthetic efficiency. Our careful radiation measurements certainly contributed to these results.

4 Conclusion

Phaseolus vulgaris L. cv GLP-2 was grown near Nairobi, Kenya, in two plots over two seasons, from January to March and from July to September 1990. A line source sprinkler system was used so that the two plots received different amounts of water. On a weekly basis, the soil moisture was significantly different between treatments, at almost all the three depths measured, from 33 days after sowing (DAS) to 69 DAS for the first season and from 37 DAS to the end for the second season. Leaf area, amounts of intercepted GR and absorbed PAR as well as dry weight accumulation were, on the whole, significantly lower in the low water treatment than in the high water treatment for both seasons. Seed yield and both photosynthetic and economic efficiencies of the low water treatments therefore all decreased by about 20% in the first season and by about 40%, 20% and 50% respectively in the second season.

Solar radiation observations with tube solarimeters were taken with special care. Quantification of these effects is necessary to screen crops for their suitability under the rain fed semi-arid conditions of Kenya.

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