Ethiop. J. Biol. Sci., **4(1): 11-25, 2005**

RESPONSES OF HARICOT BEAN (*PHASEOLUS VULGARIS* L.) TO MOISTURE AVAILABILITY AND TWO TEMPERATURE REGIMES

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ABSTRACT: Haricot bean (*Phaseolus vulgaris* L.) production is subjected to intermittent drought, which is often combined with various regimes of temperature in different agroecological regions. The objective of this investigation was to study effects of moisture availability on an indeterminate cultivar during three developmental phases and two temperature regimes. Eight factorial combinations of a wet and a dry soil moisture regime during the vegetative, flowering and seed filling phenological phases, at both 18 and 24°C constant temperature were used. Water stress significantly reduced flower bud number at the end of the vegetative and flowering phases. Flower bud number was similar for the two temperature regimes at the end of the vegetative phase, but there were more buds at the end of flowering at the higher temperature. The highest seed yield loss observed was 28% due to water stress during the seed filling phase followed by water stress during flowering. Stepwise multiple regression showed that moisture level during seed filling accounted for the largest portion of seed yield variation at both temperatures. However, moisture level during the vegetative phase was more important than during the flowering phase at 18°C, whilst the reverse was true at 24°C. Pod number per plant explained 81 and 52% of the variation in yield under 18 and 24°C, respectively. Despite a similar total biomass at both temperature regimes and a larger potential reproductive capacity at the higher temperature, seed yield was 18% lower at 24°C. Water use efficiency for seed yield was significantly reduced under high temperature.

Key words/phrases: *Phaseolus vulgaris*; Phenological phases; Temperature; Water stress; Yield; Yield components.

INTRODUCTION

Haricot bean is the most important pulse in the world (FAO, 2004). In Ethiopia, it is annually produced on about 209,000 hectares of land, ranking second among pulses (CACC, 2003). It is an important source of protein and energy in human diet in the tropics and sub-tropical developing countries, particularly in the Americas and eastern and southern Africa (Laing *et al.*, 1984). It is produced for its green pod and dry seed which are both edible. Moreover, haricot bean is an important understorey component crop in

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various intercropping systems throughout the world. In Ethiopia, it is grown either as a sole crop or intercropped with other crops like maize, sorghum, enset, coffee, sugar cane, cotton, sweet potato, etc. The crop is a major food and cash crop to the farmer and an important export commodity to the country.

Water stress is one of the most important factors limiting haricot bean production in many production areas. Sixty percent of haricot bean production in the world is grown under water stress making drought the second largest contributor, after disease, to yield reduction (Singh *et al.*, 1995). According to Laing *et al.* (1984), an examination of climate data for the 110 production areas in Latin America indicated that almost 60% of the crop experienced moderate to severe water deficits after flowering. This shows that haricot bean production under rain-fed conditions is limited by shortage of adequate moisture.

A substantial amount of haricot bean is produced in the drier regions of Ethiopia. In most haricot bean growing regions, rainfall is erratic in its distribution and the soil is often sandy with low moisture holding capacity (Belay Simane and Struik, 1993). The higher intensity of rainfall in such areas means that a considerable amount is lost as runoff. The large year-to-year variation in haricot bean yield in the Central Rift Valley area is attributed to periodic water stress as a result of poor distribution of rainfall (Ohlander, 1980). In Ethiopia, 67% of haricot bean production is exposed to moderate drought during flowering while 81% is subjected to moderate to severe water shortage during post-flowering growth stages (Wortmann *et al.*, 1998). In drought-prone lowland areas of central, eastern and southern Ethiopia, farmers use haricot bean in their risk aversion strategy (IAR, 1990). Availability of early maturing cultivars has made it a suitable substitute crop in case of crop failure due to drought while its canopy architecture and mode of assimilation have contributed for its choice as a component crop for intercropping.

Inadequate moisture supply affects the physiology of crop growth and its dry matter production. Various types of responses are encountered when plants are subjected to water stress. The types of responses vary depending on the magnitude and duration of the stress and the phase of plant development (Acosta Gallegos and Shibata, 1989). Several studies have been conducted to determine the effect of water stress on haricot bean growth and productivity (Maurer *et al.*, 1968; Dubetz and Mahalle, 1969; Stoker 1973; Acosta Gallegos and Shibata, 1989; Nielson and Nelson, 1998). However, there is dissimilarity in the reported results. Some workers found no effect by water stress during the vegetative phase on yield (Nielson and Nelson, 1998), others reported yield reduction as a result of water stress during the vegetative phase (Stoker 1973; Acosta Gallegos and Shibata, 1989). Some reported the highest yield loss from drought during flowering (Stoker 1973; Nielson and Nelson, 1998). These differences may have resulted due to differences in the degree, duration and monitoring of stress, after-effects of impacts in earlier phases, growth habit (determinate versus indeterminate) and soil and climatic factors.

Haricot bean is a warm season crop with an optimum average growth temperature between 16 and 24°C (Kay, 1979). Under field conditions, the crop is exposed to different levels of various climatic factors simultaneously in diverse agroecological regions. Moisture and temperature are among the most important climatic variables. Drought stress is a complex combination of stresses because of both water deficit and high temperature (Craufurd *et al.*, 1999). It is difficult to differentiate the separate effects of water stress and temperature under field conditions. This necessitates the use of controlled growth environments. However, there are few reports dealing with the effect of moisture supply in combination with temperature regimes.

Improvement of productivity through optimization of irrigation and/or rainfall in water-limited regions requires understanding the relative sensitivities and responses of the various phenological phases to water stress on a target crop. The efficiency of irrigation could be improved by identifying sensitive developmental phases. A well-timed irrigation at the right growth phase could enhance water use efficiency. So far, few studies have been made to investigate effects of drought on adapted haricot bean cultivars of the country under controlled conditions.

The objectives of this investigation were (1) to study the effect of water stress in different growth phases on seed yield and its components, (2) to investigate the effects of temperature regime on productivity and water use efficiency, and (3) to examine the possible interactions among phenological phases and the effect of temperature in modifying the sensitivity response to water stress.

MATERIALS AND METHODS

Seeds of the cultivar Red Wolaita, obtained from the Institute of Agricultural Research, Awassa Centre, were used in this experiment. It is a popular indeterminate cultivar from southern Ethiopia with medium seed size. An indeterminate cultivar is one in which the main axis continues indefinitely with a vegetative growing point (Ojehomon and Morgan, 1969). The experiment was conducted from January 20 to April 22, 1999 in a phytotron at the Agricultural University of Norway. Plastic pots of 14 cm diameter x 17 cm height were filled with a greenhouse soil made of peat, clay and sand with contents of about 60, 15 and 25%, respectively. One gram complete fertilizer containing 14:4:21:2:2.4% of NPKMgS and micronutrients (Fe, Mn, Cu, Zn, B, Mo) and 15 g $CaCO_3$ was added per kg of soil. In order to make root washing convenient the soil was sieved with a 4 mm screen. Five seeds were sown in each pot and the pots stayed in a greenhouse until eight days after germination. Plants were thinned to two seedlings per pot one week after germination and transferred to the phytotron.

The experiment was designed with eight factorial combinations of a wet (W) and a dry (D) soil moisture regime during each of three phenological phases: vegetative, flowering and seed filling. All eight combinations were used at both 18 and 24°C constant temperatures (Table 1).

Table 1 Treatments of the experiment for each temperature regime.

	Growth phases				Growth phases		
	Vegetative	Flowering	Seed filling		Vegetative	Flowering	Seed filling
1	W	W	W	5	D	W	W
2	W	W	D	6	D	W	D
3	W	D	W	7	D	D	W
4	W	D	D	8	D	D	D

W, wet; D, dry

The pots were assigned at random to each moisture treatment. Day lit growth rooms with supplemental artificial light (120 µmol m^{-2} s^{-1} for 10 hrs) provided from metal-halide lamps were used. A vapour pressure deficit of 0.53 kPa was kept at both temperature regimes.

Moisture content of the pots was continuously monitored by a DL2e data logger with Theta probes (Delta-T-Devices Ltd, Cambridge, England). Four probes were used at each temperature regime, thus, with convenient pairs made during the seed filling phase. Watering was done manually and the amount recorded throughout. The cyclic water stress was imposed by withholding water until the moisture level reached a specified level. Wet treatments were kept above -0.025 MPa (above 85% of field capacity) while the dry treatments were allowed to fall to -1.25 MPa (28% of field capacity) soil water potential before rewatering. Upon rewatering pots were brought to field capacity. Evapotranspiration efficiency (ETE) and water use efficiency (WUE) were estimated by dividing total dry matter and seed yield by cumulative water used, respectively (Ehdaie and Waines, 1993). This implies that WUE consists of two components: ETE and harvest index.

The soil moisture retention curve of the potting soil was determined at the University's Department of Soil and Water Sciences by the pressure plate method at the beginning of the experiment (Fig. 1). Information on water use and growth duration is presented on Table 2.

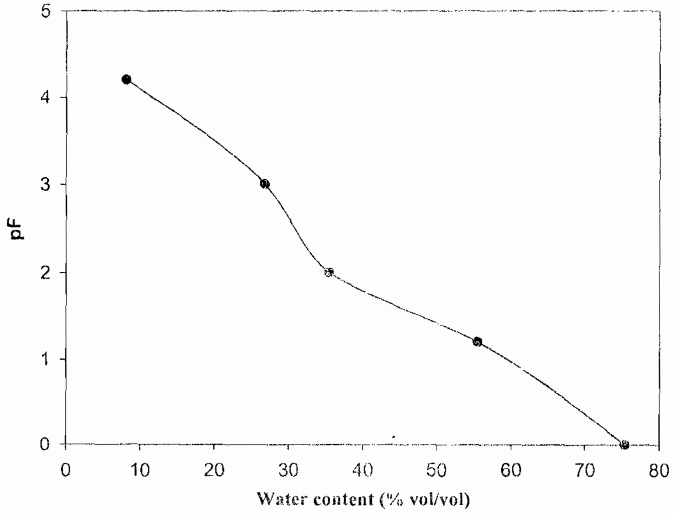

Fig. 1. Soil moisture retention curve of the soil used for the experiment. n = 4. pF is a measure of relative magnitude of the energy that binds H_2O in soil.

The phenological phases were determined as: (1) vegetative: emergence to first flowering by 50% of the plants, (2) flowering: commencement of flowering to full length first pod by 50% of the plants and (3) seed filling: start of full pod length to physiological maturity. A plant was deemed to have reached physiological maturity when the first pods by 50% of the plants turned black and loose to touch. The final harvest was made when the first pods were dry to touch. Due to the indeterminate nature of the cultivar, flowering and pod set occurred concurrently. Similarly in soybean, Egli *et al.* (1985) observed that pod development occurred rapidly after pollination and the pod reached its maximum size before any significant dry matter accumulation in the seeds.

Table 2 Amount of water (ml) used and duration (days) of phenological phases at two temperature regimes during the experiment (all parameters are per plant basis).

Treatment		Water use/ growth phase		Cumulative water use[b]		Duration/ growth phase	
		18°C	24°C	18°C	24°C	18°C	24°C
M_V	W	1676	1577	5762	6780		
	D	1114	977	4320	6265	29	20
M_F	W	1450	2122	5326	7338		
	D	1100	1242	4756	5708	18	13
M_{SF}	W	2637	3945	5335	7195		
	D	2050	2745	4747	5850	29	22
Mean				5041	6522		

[a] During the entire growth cycle; M_V, vegetative phase moisture level; M_F, flowering phase moisture level; M_{SF}, seed filling phase moisture level; W, wet; D, dry.

Samples were taken three times: At the end of vegetative phase, at the end of flowering phase and after ripening. At the first two samplings, three pots were harvested per treatment, while for the final, four to six pots were harvested. Seed yield and all the components were determined after oven drying at 70°C for 48 hours.

The data were analysed using the General Linear Model of the Statistical Analysis System (SAS, release 6.12). Hypotheses for all the parameters from the final harvest were tested against the pooled three and four factor interactions, $T(M_V{*}M_F{*}M_{SF})$, used as an error term. Thus, the analytical model was:

$$Y = \mu + b_1M_V + b_2M_F + b_3M_V{*}M_F + b_4\,M_{SF} + b_5M_V{*}M_{SF} + b_6M_F{*}M_{SF} + b_7T + b_8M_V{*}T + b_9M_F{*}T + b_{10}M_{SF}{*}T + b_{11}T(M_V{*}M_F{*}M_{SF}) + \epsilon$$

where: T, temperature; M_V, M_F, M_{SF} designate soil moisture levels during the vegetative, flowering and seed filling phases, respectively.

Recordings at the end of the vegetative and flowering phases were analysed by similar models using interactions with pots as an error term.

RESULTS

Reproductive Development

The effect of temperature on the number of flower buds produced was not significant at the end of the vegetative phase (Fig. 2A). Nevertheless, the higher temperature significantly increased the number of flower buds at the end of the flowering phase ($p < 0.01$). Compared to the end of the vegetative phase, number of flower buds increased at the end of the flowering phase by 65% at 18°C and by 96% at 24°C. The plants produced nearly similar reproductive dry matter under the two temperature regimes (Fig. 2B). Water stress significantly reduced the number of flower buds both at the end of vegetative ($p < 0.01$) and flowering ($p < 0.05$) phases (Fig. 3A). On the other hand, significantly higher amount of reproductive dry matter was produced by the dry moisture treatments during the vegetative ($p < 0.01$) and flowering ($p < 0.05$) phases (Fig. 3B).

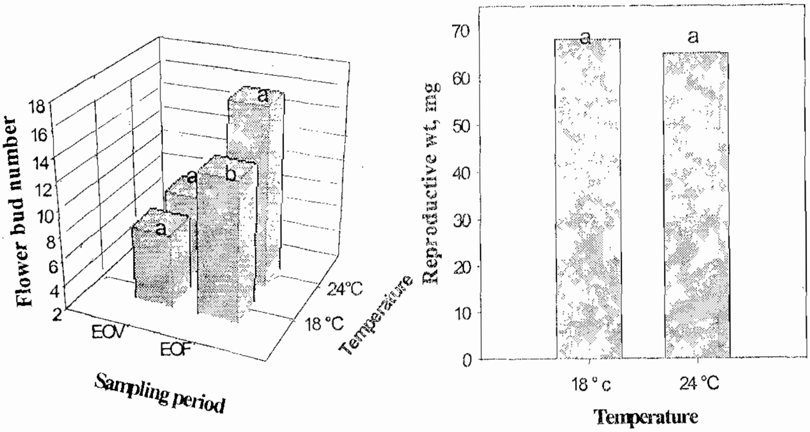

Fig. 2. The effect of temperature on (A) the number of flower buds at the end of the vegetative and flowering phases and (B) on reproductive weight at the end of the flowering phase. EOV, end of vegetative phase; EOF, end of flowering phase. Bars with similar lower case letters (a, b) indicate there is no significance difference in the number of flower buds, and vice versa.

Seed Yield and its Components

Seed yield

Seed yield was significantly influenced by all treatments, though moisture level during the vegetative phase barely passed the 5 percent level ($P = 0.060$; Table 3). Yield at 18°C was 18% higher than that at 24°C. Since the total biomass produced at the two temperatures were similar, this was a result of a higher harvest index (Table 3 versus 7). Yield reduction was 14, 17, and 29% for water stress during the vegetative, flowering and seed filling phases, respectively. Under both temperatures, the largest effect of water stress was during the seed-filling phase: 30% at 18°C and 26% at 24°C (Table 4). Statistically significant interactions between temperature and moisture level of different phases were not found for seed yield, but important tendencies were evident (Table 4). Also, a stepwise regression analysis showed the magnitude of explained variation associated with water stress during the two phases to differ between the two temperature regimes (Table 5). Relative yield reduction for water stress (Table 4), partial R^2 and yield loss per unit of water deficit (Table 5) showed that at 18°C water deficit during the vegetative phase accounted for a larger part than stress during flowering while the reverse was true for 24°C. Water stress during the seed filling phase accounted for a similar proportion of the variation at 18 and 24°C even though the relative yield and pod number reduction was higher at 18°C.

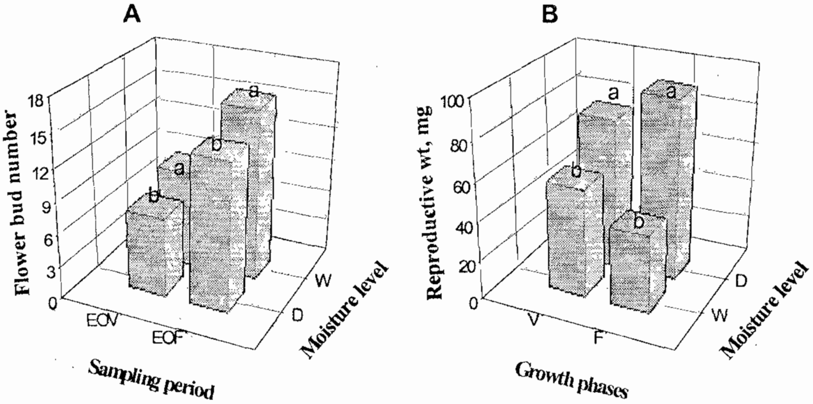

Fig. 3. The effect of moisture level on (A) the number of flower buds at the end of the vegetative and flowering phases and (B) on reproductive dry weight at the end of the flowering phase. V, vegetative phase; F, flowering phase. Bars with similar lower case letters (a, b) indicate there is no significance difference in the number of flower buds, and vice versa.

Yield components

Pod number per plant: It was significantly reduced by water stress at all phases (Table 3). The largest reduction of 20% was observed when water was withheld during flowering. The relative loss in pod number due to water stress during the vegetative and seed-filling phases was greater at 18 than at 24°C (Table 4). On the other hand, the loss due to drought during flowering out-ranked the other phases at 24°C. It was observed that pods with 6-9.5 cm length, which had commenced the seed-filling phase, were aborted at 18°C when exposed to terminal water stress.

Seed number per pod: A significant reduction in seed number per pod occurred due to water stress during seed filling and at a higher temperature (Table 3).

Seed weight: Temperature did not significantly affect seed weight (Table 3). Water stress during flowering significantly increased seed weight while water stress during seed filling significantly reduced it (Table 3).

Table 3 Effects of moisture level during the vegetative (M_V), flowering (M_F) and seed filling (M_{SF}) phase and temperature (T) on seed yield and yield components of haricot bean.

Treatment		Yield^a plant^{-1} (g)	Relative reduction (%)	Pod No. plant^{-1}	Seed No. pod^{-1}	100 seed wt (g)
T	18°C	6.47a		4.2a	5.5a	27.33a
	24°C	5.29b	18.2	4.6a	4.2b	26.77a
M_V	W	6.38a		4.7a	4.8a	26.84a
	D	5.48a	14.1	4.1b	4.9a	27.26a
M_F	W	6.42a		4.9a	4.9a	26.55a
	D	5.34b	16.8	3.9b	4.8a	27.56b
M_{SF}	W	6.87a		4.8a	5.1a	28.20a
	D	4.89b	28.8	4.1b	4.6b	25.90b

^{a} given as dry matter. Treatment means with the same lower case letter (a, b) are not significantly different at 5% level; W, wet; D, dry; n = 48; error df = 5.

Table 4 Comparisons of seed yield and pod number per plant of haricot bean at two temperature regimes as influenced by moisture level during the vegetative (M_V), flowering (M_F) and seed filling (M_{SF}) phases.

Treatment		Seed yield plant^{-1} (g)		Relative reduction (%)		Pod No. plant^{-1}		Relative reduction (%)	
		18°C	24°C	18°C	24°C	18°C	24°C	18°C	24°C
M_V	W	7.4±0.58	5.4±0.39			4.7±0.31	4.9±0.26		
	D	5.5±0.30	5.2±0.30	25.7	3.7	3.7±0.17	4.4±0.21	21.3	10.2
M_F	W	7.0±0.51	5.8±0.30			4.6±0.25	5.0±0.24		
	D	6.1±0.52	4.6±0.38	12.8	20.6	3.8±0.28	4.0±0.10	17.4	40.0
M_{SF}	W	7.6±0.49	6.1±0.33			4.7±0.29	4.8±0.22		
	D	5.3±0.25	4.5±0.18	30.2	26.2	3.7±0.19	4.4±0.26	21.3	8.3

Each value is mean of 12 samples ± standard error of the mean; seed yield is given as dry matter; W, wet; D, dry.

Table 5 Parameter estimates and coefficients of determination from a stepwise multiple regression analysis to partition seed yield (g/plant) variation into main effect components of water deficit (mm) during three phenological phases.

Variable	18°C		24°C		Pooled	
	Parameter estimate	Partial R^2	Parameter estimate	Partial R^2	Parameter estimate	Partial R^2
Intercept	9.08		6.64		7.70	
Vegetative	-3.22	0.25***		NS	-1.60	0.09 ***
Flowering	-2.93	0.08 *	-1.28	0.22 **	-1.60	0.12 ***
Seed filling	-4.05	0.43 **	-1.31	0.43 ***	-1.89	0.38 ***
Model		0.76		0.65		0.59

NS, not significant; n = 24 for each temperature regime; n = 48 for pooled; α level for inclusion in the model ≤ 0.05; *, **, ***indicate significance at 0.05, 0.01 and 0.001probability levels, respectively.

Relation Between Seed Yield and its Components

A stepwise multiple regression analysis of seed yield per plant in relation to yield components showed that pod number was strongly correlated with yield at both temperature regimes. It explained 81 and 52% of the variation in seed yield at 18 and 24°C, respectively (Table 6). Seed weight was more important to yield than number of seeds per pod at 18°C but totally it ranked third among the tested components. A major contribution from seed number per pod was found at 24°C and in the pooled data. The importance of seed weight under the low temperature may be related to the shortening of seed growth duration due to terminal stress, which reduced the seed filling phase by four out of 29 days.

Table 6 Stepwise multiple regression analysis of contributions of pod number per plant, seed number per pod, and seed weight to variation in seed yield per plant in haricot bean.

Variable	18°C		24°C		Pooled	
	Parameter estimate	Partial R^2	Parameter estimate	Partial R^2	Parameter estimate	Partial R^2
Intercept	-12.67		-7.73		-10.44	
Pod No plant^{-1}	1.40	0.82***	1.07	0.52***	1.27	0.46 ***
Seed No pod^{-1}	1.22	0.04 **	1.12	0.35 ***	1.24	0.42 ***
Seed wt	0.23	0.08 ***	0.12	0.04 **	0.17	0.04 ***
Model		0.94				0.92

n = 24 for each temperature regime; n = 48 for pooled; α level for inclusion in the model ≤ 0.05;
*, **, ***, indicate significance at 0.05, 0.01 and 0.001 probability levels, respectively.

Days to Maturity

The temperature rise from 18 to 24°C reduced number of days from emergence to maturity by three weeks (Table 7). Also, water stress during the seed-filling phase significantly reduced the maturity period. However, the response was not similar for the two temperature regimes.

Table 7 Effects of moisture level during the vegetative (M_V), flowering (M_F) and seed filling (M_{SF}) phases and temperature (T) on physiological maturity (PM), total dry matter (TDM), harvest index (HI), evapotranspiration efficiency (ETE) and water use efficiency (WUE) of haricot bean.

Treatment		PM (Days)	TDM (g)	HI (%)	ETE (g kg^{-1})	WUE (g kg^{-1})
T	18°C	87a	15.52a	41a	3.03a	1.27a
	24°C	66b	14.83a	35b	2.29b	0.81b
M_V	W	77a	16.90a	39a	2.72a	1.03a
	D	76a	13.60b	37a	2.60a	1.05a
M_F	W	76a	16.28a	39a	2.60a	1.05a
	D	76a	14.21b	37a	2.71a	1.03a
M_{SF}	W	77a	17.65a	39a	2.87a	1.14a
	D	75b	12.91b	38a	2.44b	0.94b

Treatment means with the same letter are not significantly different at 5% level;
W, wet; D, dry; n = 48; error df = 5. Figures with similar lower case letters (a, b) indicate there is no significance difference, and vice versa.

Water stress reduced maturity period at 18°C, but was without an apparent effect at 24°C. This explains the significant T x M_{SF} interaction (P = 0.009). The enhanced rate of maturation due to water stress during seed filling was associated with severe senescence at 18°C. At 24°C, severe senescence may have been avoided by new vegetative growth and lower seed set, which entails a lower demand for nitrogen. Drought during the vegetative or the flowering phases did not significantly affect maturity period.

Water Use and Water Use Efficiency (WUE)

Total water use was increased by 29% at 24°C compared to that at 18°C. Water use efficiency was significantly reduced by water stress during the seed-filling phase and by the higher temperature (Table 7). Evapotranspiration efficiency (ETE) has followed a similar trend, indicating that both components, ETE and harvest index, have contributed to WUE. At the higher temperature the plants needed 57% more water to produce the same amount of seed.

DISCUSSION

Water stress during the vegetative and flowering phases affected the potential reproductive capacity by reducing the number of flower buds on the main stem. The low temperature also showed a similar effect at the end of the flowering period. These effects might be attributed to the associated effect of water stress and temperature on the number of internodes produced and plant height. Reproductive capacity is directly related to number of internodes produced, for species like *P. vulgaris*, which produce flowers in their leaf axils. Water stress tends to produce stunted plants by limiting internode number and length through its effect on cell multiplication and elongation. Also, the number of internodes and length of the stem increase with rise in temperature between the base and optimum temperatures especially for indeterminate genotypes (Squire, 1990). As the number of flower buds was well above the number of pods produced, it is understandable that water stress did not cause yield loss via reduced flower buds.

In spite of the larger reproductive capacity, the higher temperature gave a lower seed yield. The mechanism of yield reduction at the higher temperature was associated with low number of seeds per pod. Yield reduction at high temperatures was also reported in faba bean (*Vicia faba* L.), associated with reduced seed number per pod and reduced pod number per shoot (Skjelvåg, 1981) and in groundnut mediated by reductions in pod number per plant, seed number per pod, and seed weight (Talwar *et al.*, 1999). In haricot bean, it has been indicated that reproductive growth predominates under cool climates while vegetative growth predominates under warm climate (Masaya and White, 1991). Moreover, Konsens *et al.* (1991) have shown that raising the night temperature from 17 to 27°C strongly reduced pod production, mature pod size and seeds per pod while increase in day temperature had a smaller effect. Pod and seed number reduction in haricot bean due to high temperature is caused by increased abscission of flower buds, flowers and young pods and by the failure of fertilization and seed development (Ofir *et al.*, 1993). Reduction of reproductive growth at the higher temperature favoured formation of alternate vegetative sinks, which was observed in the lower harvest index at 24°C.

The seed filling phase was the most susceptible to water stress at both temperature regimes when comparisons are made based on entire phases and yield loss per unit of water deficit. However, there was a tendency indicating that the vegetative phase was more sensitive than the flowering stage at 18°C while the flowering stage was more sensitive at 24°C. This could be due to the limited subsequent growth leading to inadequate leaf area and, thus, insufficient assimilate to reproductive structures at the lower temperature. More number of internodes and leaves were produced after the end of the vegetative phase at the higher temperature (data not shown). On the other hand, a relatively greater yield reduction at 24°C from water stress at flowering might be due to an increased abortion aggravated by high temperature. There is inconsistency among works regarding the plant's sensitivity to water stress during different phenological phases. The way the plants responded to water stress at different temperatures, in addition to factors like differences in intensity, duration of stress, and growth habit used in different studies, may give a basis to explain some of the discrepancy.

The importance of different yield components to seed yield per plant as related to water stress varied with each phenological phase. Whether a particular environmental stress promotes a predominance of source limitation or sink limitation may well depend on the timing and severity of stress (Hay and Walker, 1989). Seed yield reduction due to water stress during the vegetative phase resulted from reduction in number of pods per plant. Reduction in the number of pods per plant was also responsible for the yield loss from the flowering phase water stress. Comparable results were reported in haricot bean (Acosta Gallegos and Shibata, 1989; Nielsen and Nelson, 1998). However, plants partially compensated for the loss from flowering drought by producing heavier grains. This may suggest that the loss in seed yield from water stress during flowering could be due to sink limitation. The increase in seed weight by the flowering phase water stress could be associated with the concomitant decline in number of pods per plant. This allowed fewer seeds to compete for assimilate during the terminal phase.

Yield loss from seed filling water stress was caused by contributions of all the yield components. Nielsen and Nelson (1998) observed seed weight reductions, but did not find pod and seed number reductions from terminal water stress. The reduction in seed weight during terminal water stress may be ascribed to both reduced seed growth rate and shortened seed growth duration. In soybean, Meckel *et al.* (1984) observed that water stress affected seed size more by shortening seed growth duration than by reducing seed growth rate. Our result showed that while both mechanisms were important at the lower temperature, reduced seed growth rate was responsible for seed weight loss at the higher temperature. The higher sensitivity of the seed filling phase to water stress might be attributed to the inability of the plant to make further adjustment, involvement of many yield components which subsequently were negatively affected, and the susceptibility of aged leaves to increased rate of senescence.

Both evapotranspiration efficiency and WUE were reduced by water stress and high temperature. These results are in agreement with those of Nielsen and Nelson (1998) who observed that ETE was reduced by water stress and high temperature in haricot bean. Also, Craufurd *et al.* (1999) observed a similar effect for temperature in groundnut though the effect for water stress was the opposite. A number of reasons could be attributed to the fact that WUE was superior at the lower temperature. A larger amount of water use may be due to increased transpiration. Moss (1963) reported a steady increase of stomatal aperture and transpiration when maize was grown at temperatures of 14 to 40 °C under a similar vapour pressure deficit. Also, it is reported that high night temperature enhanced stomatal aperture during the daytime (Zelitch, 1963). Another possible reason for reduced WUE is low dry matter production as a result of higher respiratory loss at high night temperatures. The third reason could be the lower harvest index for 24°C, which was 35% against 41% for 18°C. Similarly, Talwar *et al.* (1999) from a comparison of 35/30 and 25/25°C day/night temperatures have showed that higher temperature increased shoot growth but reduced final reproductive biomass leading to a lower harvest index. Higher rate of evaporation from the soil surface especially at the initial stages of wetting may also contribute to the elevated water use and low WUE at the higher temperature.

CONCLUSION

The study showed that water stress at any development phase of this indeterminate cultivar caused reduction in seed yield per plant even though the magnitude of reduction varied considerably. Terminal water stress caused the largest yield reduction at both temperature regimes. The lower end of the optimum temperature range for haricot bean appeared to be more productive for seed yield. This implied that within the given range of adaptation, medium to high altitudes could be more productive than lower altitudes. Both the higher seed yield and the lower water use contributed to greater water use efficiency under the lower temperature. The evidence seems to suggest that water supply during the early growth period may be important to establish adequate plant size under the lower temperature. This is because of a more restricted vegetative growth after the end of the vegetative phase at this temperature. Significant interactions for grain yield among soil moisture levels at various developmental phases were not observed. However, there were indications of interactions for seed yield between temperature and moisture levels during various phases. There is a need to consider the effect of temperature on water relations and sensitivity of phases further over a wider range of temperature regimes.

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