



Effect of water supply on the water use-related physiological traits and yield of snap beans in dry seasons

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Abstract

Four snap bean varieties (*Phaseolus vulgaris* L.) with different pod type were grown under three water supply conditions (well-irrigated, water deficit, non-irrigated) to examine the stomatal resistance, stomatal density and leaf area index (LAI) and their relationship with the yield. The highest stomatal resistance of the leaves and the smallest LAI and harvest index concerning the pods were measured under non-irrigated growing conditions. During flowering and pod development, significant differences were found in stomatal density on both leaf surfaces between the green-podded and yellow-podded varieties under water deficiency. Under non-irrigated conditions, stomatal resistance measured during flowering had a large effect mainly on the individual pod yield. Under these conditions, close significant correlations were found between stomatal resistance and LAI and water use (WUc) during the generative period of plants and the pod weight per plant. Under moderate water deficiency, the stomatal resistance, adaxial stomatal density of the leaves, and LAI were more effective to evaluate the difference in the productivity of snap bean genotypes than those measurements in severe drought. WUc-related traits can be used for the selection of bean genotypes adapted to drought, while the difference in water use efficiency (WUEy) between the snap bean varieties is suitable to evaluate their productivity under deficit irrigation.

Introduction

The frequent occurrence of drought has significant effect on the productivity of legume crops. Climatic effects can be mitigated not only by irrigation, but also by the cultivated varieties that use water efficiently and tolerate drought stress (Köksal et al. 2008; Sezen et al. 2008; Nemeskéri et al. 2010,

2015a). Irrigation scheduling requires a more scientific basis including the estimation of crop water use, knowledge of the crop response to applied water amounts, to determine the timing of irrigation or assess the stress level of plants (Feres and Evans 2006). Over-irrigation negatively affects the generative growth due to the excess vegetative growth (Williams et al. 2010; Pires et al. 2011) and it reduces the yield processing quality (Çolak et al. 2015; Lahoz et al. 2016). Inadequate water supply such as partial root drying (PRD) and regulated deficit irrigation (RDI) results in a significant reduction of shoot and pod biomass (Wakrim et al. 2005) and leaf area index (Tangolar et al. 2015). In this condition, the total water used by transpiration was reduced by half, which has resulted in a substantial increase in plant water use efficiency (WUE) (Wakrim et al. 2005). In water scarce environments, the goal is to increase the water use efficiency of crops which can be approached by two ways. The first approach is to increase the adaptive capability of crops that increases the proportion of water that is transpired by the crops. The second one is to increase the crop's productivity to produce biomass and yield per unit of water transpired (Wallace 2000). Nevertheless, the crop response to the reduction of water use or yield depends on the degree

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of soil dryness, the crop characteristics and the timing of water deficiency (Webber et al. 2006).

The water use efficiency of plant species relates to the stomatal behaviour and stomatal density under limited water relations which determines their productivity (Hardy et al. 1995). A significant positive correlation was detected between the stomatal density and WUE, but this was negative between the stomatal aperture and WUE (Yang et al. 2004; Xu and Zhou 2008). Kanemasu and Tanner (1969) established that the number of stomata on the abaxial surface of leaf related to the leaf water potential and stomatal resistance. Although the stomatal density depends on several factors such as environmental conditions, leaf area and leaf position (Meidner and Mansfield 1969; Gay and Hurd 1975). Under drought conditions, plants reduce the water loss by stomatal closure. The soil drying triggers the synthesis of abscisic acid (ABA) in the root, then it is transported to the leaves where the rising ABA level induces stomatal closure (Saab et al. 1990; Davies and Zhang 1991; Sauter et al. 2002). Nevertheless, the transpiration and the atmospheric CO₂ diffusion into the intercellular space decrease due to the partial or total stomatal closure (Singh and Reddy 2011), which leads to the reduction of photosynthesis and the yield. Water deficit affects the growth of plants depending on their stage of development. Water stress occurring in the vegetative growth stage leads to short plants with small leaf area (Nielsen and Nelson 1998), while during generative stage, it causes flower drop and pod abortion (Boutraa and Sanders 2001; Young et al. 2004; Foolad 2005; Fang et al. 2010), resulting in a significant decrease in yield. During the generative stage, drought decreases the harvest index, i.e., the ratio of seed yield to total biomass (Shao et al. 2008).

In traditional breeding, harvest index has been used to select the genotypes which have good fertility under water deficit conditions. This selection process is sustained for long, because it is difficult to provide the reproduction of experimental and ecological conditions for the genotypes. The selection of promising genotypes can be efficiently used by not only one attribute, but by multivariate selection based on several parallel traits (Kozak 2010). Wnuk et al. (2013) suggested a visualisation technique and multiplicative model to reveal the relationships among grain yield, harvest index and biomass yield and to select among several genotypes under different environmental conditions.

Drought tolerance is a complex attribute of plants due to several physiological and biochemical processes operating simultaneously or consecutively. The changes in the physiological traits of genotypes in response to drought are different (Nemeskéri et al. 2015b), although their relationships can be a basis of the selection for genotypes with drought tolerance or good water use efficiency. Improvement of yield used by indirect selection based on physiological or biochemical measurement of photosynthetic

traits has been debated (Good 1986), however, this indirect selection is to be effective if the indirect traits have a high heritability and also have a high genetic correlation with the final interested traits (Scully et al. 1991). Despite past studies on the responses of legume species to water deficiency (Kamel et al. 2010; Nemeskéri et al. 2010; Zokaee-Khosroshahi et al. 2014), the knowledge of relationships between physiological traits related to water use, water use efficiency and productivity is rather incomplete.

The main goal of this study was to evaluate the effect of water deficit on the physiological traits determining the water use ability and productivity of snap bean genotypes. In addition, the objective was to examine which traits are suitable to test the adaptability of snap bean genotypes to drought.

Materials and methods

Plant material and experimental design

From 2011 to 2013, the physiological traits, water use and productivity of four snap bean varieties with green and yellow pods were investigated under different water regimes in a field experiment. The experiment was conducted at the Experimental Station of Centre of Agricultural Sciences, the University of Debrecen. The soil type was sandy loam containing 1.6% organic matter and the proportions of sand, silt and clay in the soil were 69, 22 and 9%, respectively. The field water capacity was 16.5% in the 0–30 cm layer of soil and total available water content was 120 mm/m. All varieties used in the experiments were dwarf beans; Serengeti and Pation varieties were investigated from the green-podded group and Carson and Maxidor beans represented the yellow-podded cultivars. The sowing of the varieties was carried out in random block design with three replications. The plots involved three rows which were 3 m long and 1.5 m wide. The following watering treatments were applied: $I_{1,0}$ —well-watered plots replenished with water lost to evapotranspiration, $I_{0,5}$ —water deficiency plots provided by half of irrigated dose of $I_{1,0}$ treatment and I_0 —non-irrigated plots corresponding to severe drought under natural precipitation conditions.

The dose of irrigation was determined by the daily weather data from a weather station located near the experimental site. The required meteorological parameters measured at the experimental site were the following: net radiation, relative humidity, temperature, wind speed. Input data was not specified for the different growth stages of snap bean, an average value was used for the whole vegetation period.

The estimation of reference evapotranspiration (ET_0) was carried out using the method described by Shuttleworth and Wallace (1985) where the basic equation was:

$$ET_0 = \frac{C_c \cdot ET_c + C_s \cdot ET_s}{\lambda} \text{ (mm day}^{-1}\text{)}, \quad (1)$$

where λ = heat of vaporization of water, value: 2.45 (MJ kg⁻¹), C_c = weight coefficient (canopy), C_s = weight coefficient (soil), ET_c = transpiration (mm day⁻¹), ET_s = evaporation (mm day⁻¹). Detailed calculation method for each parameter of the equation can be found in the study of Shuttleworth and Wallace (1985).

The actual evapotranspiration was calculated with the water budget and irrigation decision support model by FAO which is based on the following equation:

$$ET_{c,adj} = (K_s \times K_{cb}, K_e) \times ET_0, \quad (2)$$

where $ET_{c,adj}$ represents the actual crop evapotranspiration (mm day⁻¹), ET_0 the reference evapotranspiration (mm day⁻¹), K_s the transpiration-reduction (stress), K_{cb} the basal crop coefficient to describe plant transpiration and K_e is the soil water evaporation coefficient, respectively. The values of K_s , K_{cb} and K_e as well as the calculation methods of each coefficient were used as described by Allen et al. (1998). The calculation of the required irrigation water was carried out on the basis of the actual evapotranspiration. The accumulated water loss was recharged with irrigation in every 5 days

for each treatment. Drip irrigation was applied prior to flowering and during pod setting depending on the years. In 2011 and 2012, the water supply provided by irrigation was almost the same during the whole growth of plants (Table 1), but it was different during the developmental stages of plants in the different years (Fig. 1). The soil moisture content was measured with Campbell CS616 water content reflectometers at 30 and 60 cm depth. The measurements of soil temperature were carried out with Campbell 107 thermistor probe at 10 cm depth. During the developmental stages of snap beans, soil moisture content given by volumetric water content ($v\%$) was represented in Table 2. At the 6-leaf stage, ten plants were selected and tagged to measure the stomatal resistance and stomatal density in each plot.

Stomatal resistance and density

Stomatal resistance was measured on the middle leaf of the shoot of the selected plants using an AP4 porometer (Delta T-Devices Ltd, England). During the development of beans, the measurements were made four times: between 10:00 and 15:00 h at the 6-leaf stage (BF1) corresponding to about 14 days before flowering, green bud stage, i.e., 7 days before flowering (BF2), during flowering (F) and pod development (P) periods.

The determination of stomatal density was performed simultaneously after the measurement of stomatal resistance.

Table 1 Available water for the snap bean varieties from sowing to harvest

Years	Precipitation (mm)	Irrigation (mm)		Total water (mm)		
		$I_{0.5}$	$I_{1.0}$	I_0	$I_{0.5}$	$I_{1.0}$
2011	128.0	39.9	79.8	128.0	167.9	207.8
2012	159.4	43.5	87.0	159.4	202.9	246.4
2013	138.8	19.7	39.4	138.8	158.5	178.2

^a $I_{1.0}$ =regularly irrigated, $I_{0.5}$ =moderate water deficit, I_0 =non-irrigated, serious dry conditions

Fig. 1 Meteorological data during the growth stages of snap beans. I from sowing to emergence, II from emergence to flowering, III during flowering period, IV from flowering to pods setting, V from pod development to harvesting from 2011 to 2013. T_{min} the minimum temperature, T_{max} maximum temperature

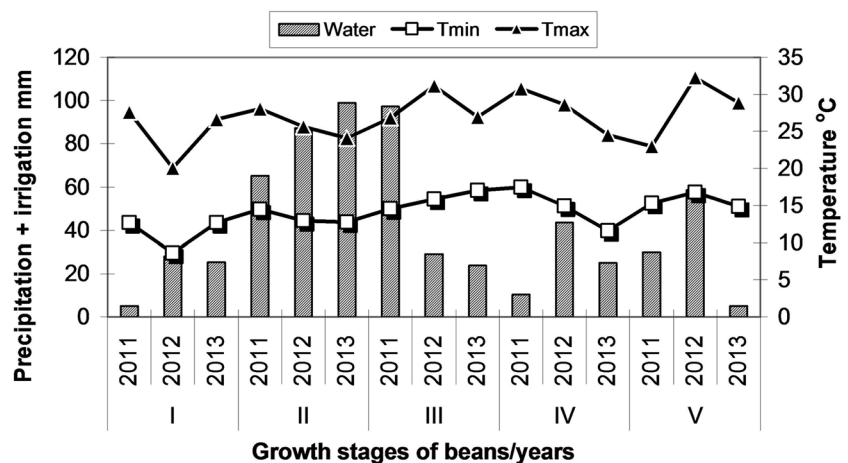


Table 2 Temperature (*T*) soil moisture content and relative humidity (RH) during the growth of snap beans

Stage	Years	RH%	Soil, <i>T</i> (°C)	Soil moisture 0–30 cm (v %)	Soil moisture 30–60 cm (v %)
Sowing to emergence	2011	62.94	16.54	26.0	25.7
	2012	74.79	15.71	33.1	34.4
	2013	67.18	19.15	22.7	18.9
Emergence to flowering	2011	64.15	17.88	25.0	26.8
	2012	70.90	17.78	35.5	33.4
	2013	75.85	18.50	31.3	24.9
During flowering	2011	71.42	17.60	25.5	29.6
	2012	68.67	19.56	39.7	36.8
	2013	76.55	22.30	26.5	20.2
Pod setting	2011	68.37	21.48	33.6	37.2
	2012	67.06	19.21	33.6	27.6
	2013	71.20	18.92	27.1	23.4
During pod development	2011	84.27	18.87	35.8	39.4
	2012	63.55	21.19	28.3	24.1
	2013	67.53	20.63	24.8	21.9

All values represented an average during the stage

Three of the middle leaves were harvested from the selected plants of each variety in every water treatment to determine the number and size of stomata as described by Nemeskéri et al. (2015b). Stomatal density is expressed by the number of stomata per square mm and the size of stomata was given in microns.

LAI

The leaf area index (LAI) representing the growth intensity of canopy was measured by a LAI-2000 Plant Canopy Analyzer (LI-COR Inc., USA). The measurements were made between 10:00 and 15:00 h during the development of beans to investigate the relationship between the LAI and stomatal traits. The dates of LAI measurements were the same as described for that of stomatal resistance.

Water use efficiency and harvest index

The selected plants were harvested separately to determine the number and weight of pods per plant. Other plants harvested from the plots were separated to pods and shoot and weighed. The yield was classified into two groups; quality 1 group contained the normal formed well-coloured and healthy pods for canning processing and quality 2 group involved the abnormal formed curved diseased pods and pod initiations.

Water use or water consumption coefficient was expressed by the ratio of amount of water during generative period (i.e., from flowering to harvest) to unit pod yield. It was calculated by the following equation:

$$WU_c = \frac{\text{water (m}^3 \text{ ha}^{-1}\text{)}}{\text{green pod (kg ha}^{-1}\text{)}},$$

where the amount of water included precipitation and irrigation water.

The water use efficiency (WUE) referred to the green pod's yield was calculated as follows:

$$WUE_y = \frac{\text{Yield (kg ha}^{-1}\text{)}}{ET_{c,adj} \text{ (mm)}},$$

where the $ET_{c,adj}$ presented the crop evapotranspiration from sowing to harvest. $ET_{c,adj}$ was calculated in regularly irrigated ($I_{1,0}$), deficit irrigated ($I_{0,5}$) and severely water stress treatment (I_0) used by Eq. 2.

Harvest index (HI) expressed by the ratio of green pod yield to biomass yield was calculated as follows:

$$HI = \frac{\text{green pod (kg)}}{\text{biomass (kg)}}.$$

Statistical analysis

Statistical differences among the treatments and varieties were determined by analysis of variance (ANOVA) using SPSS 13.0 for Windows. The means of each treatment were compared by Duncan's multiple range test at $P < 0.05$. Regression analysis was used to reveal the relationships among the stomatal resistance, stomatal density in the leaf, LAI and pod yield in different stages of development. Linear, logarithmic, hyperbolic, power and exponential regression

analysis were carried out and the most appropriate regression equation based on the highest correlation coefficient (r) and significant P level was defined.

Results

Beans require between 200 and 400 mm of rainfall during growth and development (Broughton et al. 2003); however, on the basis of total available water shown in Table 1, the weather was moderately dry during the year 2011 and severely dry in 2013. The available water from the precipitation and irrigation was satisfactory for the plants until flowering in all years (Fig. 1). The distribution of natural precipitation varied by year during different growth stages of beans; the weather was wet during flowering in 2011, while it was dry in 2012 and 2013. In dry years (2011 and 2013), during flowering, the moisture content was 25.5 and 26.5% at 30 cm depth of the soil, while it was 39.7% in 2012 (Table 2). There was also difference in the distribution of precipitation during pod setting and development periods (Fig. 1). In 2011, the high temperature (T_{\max}) associated with little precipitation and low relative humidity (68%) during pod setting when the soil water content was 33.6% at a 30 cm depths of the soil (Fig. 1; Table 2). In 2013, during pod setting and pod development period, the soil moisture content was low; 27.1% and 24.8% at 30 cm depth and 23.4 and 21.9% at 60 cm depth of the soil, respectively (Table 2). These soil moisture contents associated with relatively high soil and air temperatures during pod development affected the water use of snap beans.

The same method of FAO was used for the calculation of ETc_{adj} values of the three different treatments as shown in Eq. 2. The sole difference between the treatments was the irrigation water input. This was zero for water stressed treatment, the amount of water lost by evapotranspiration for the well-watered treatment as well as half of the evapotranspiration for the water deficiency treatment. The total water transpired by the crop differed during generative stages, depending on the years and water supply conditions. During flowering, the amount of transpired water was 37 and 64% higher in the deficit irrigation ($I_{0.5}$) as well as regularly irrigated treatments ($I_{1.0}$) in comparison with the non-irrigated one in 2011, but this was significantly larger in 2013 (Fig. 2). Nevertheless, during pod development, the crop evapotranspiration (ETc) was higher in the irrigated treatments ($I_{1.0}$, $I_{0.5}$) than rainfed (control) one in 2012, while the difference in ETc between the irrigated and rainfed treatments was lower in 2013 and no change was detected in ETc between the different water supply conditions in 2011 (Fig. 2).

The extent of water use efficiency of the varieties depended on the climate of year and the crop

evapotranspiration. All varieties grown without irrigation had lower $WUEy$ than under optimal water supply condition (Table 3). Under non-irrigated condition (I_0), there was a greater water use (WUc) during the generative period for almost all varieties which indicated that the large part of available water was used for the transpiration rather than for the pod production, as a consequence the $WUEy$ was low. In drought years (2011 and 2013), Serengeti bean variety utilized most efficiently the deficit irrigation ($I_{0.5}$), its $WUEy$ did not change significantly in comparison with the regularly irrigated plants, while the $WUEy$ of the others changed depending on the crop year.

Stomatal characteristics

Weather conditions and/or water supply caused a change in stomatal traits; however, it was different during the stages of development of beans. Smaller sized and more stomata can be found on the lower epidermis (abaxial surface) of bean leaves than upper epidermis (adaxial surface). Stomatal size on the leaves did not change during the stages of development of beans; however, a small change in the size of stomata on the leaf of the varieties can be detected under different water supply. The green-podded Serengeti variety had smaller sized stomata on both abaxial and adaxial surfaces of the leaves in drought (20.1–25.3 μm) than under irrigated conditions. Contrary to the Serengeti variety, significant larger sized stomata were recorded on both surface of the leaf of the Carson and Maxidor varieties with yellow pods in drought (25.5–32.4 μm) than under irrigated condition (Fig. 3a, b).

Larger stomatal density on both surfaces of leaves and stomatal resistance were measured during the flowering period, than during pod development (Figs. 4, 5, 6a). During flowering and pod development, change in stomatal density on the abaxial surface of leaves of bean varieties was detected under different water supply conditions. The Serengeti variety already responded to moderate water deficiency ($I_{0.5}$) and showed a high stomatal density on the abaxial surface of leaves, in the Carson variety, this was only observed in severe drought (I_0), while no change was detected for the others (Fig. 4b, c). During flowering, under dry conditions (I_0 and $I_{0.5}$), significantly higher stomatal density was detected on adaxial surface of leaves of bean varieties than in irrigated plants, except for the Carson variety (Fig. 5b). Under these conditions, the yellow-podded Maxidor variety had by 27 and 35% more stomata on mm^2 of adaxial leaf surface in comparison with Carson variety. During pod development, the Serengeti variety with green pods responded intensely to severe drought (I_0) and moderate water deficiency ($I_{0.5}$) which is proved by the significantly higher stomatal density on the adaxial leaf surface

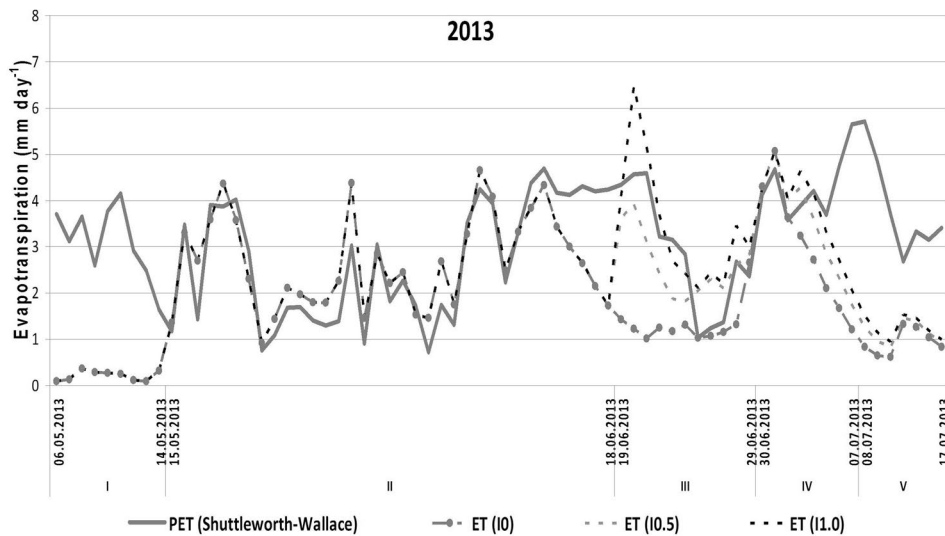
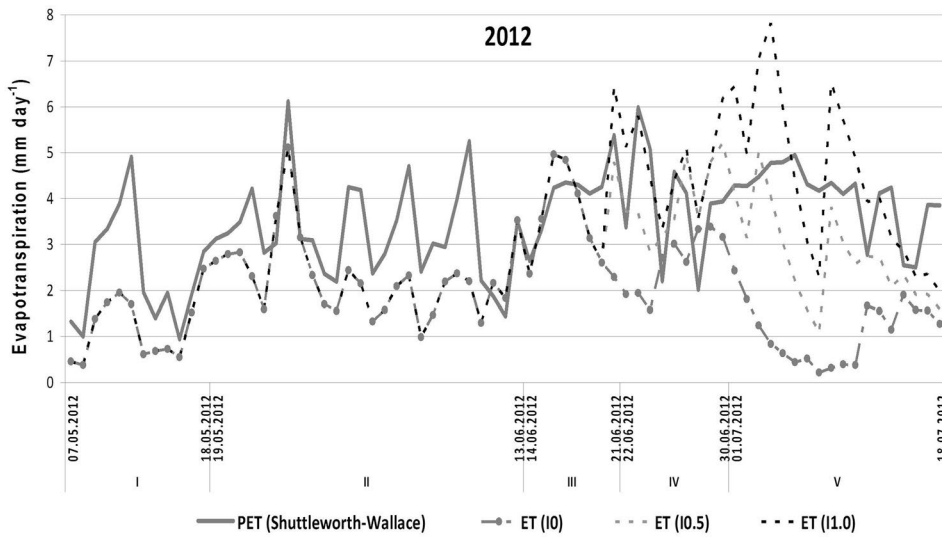
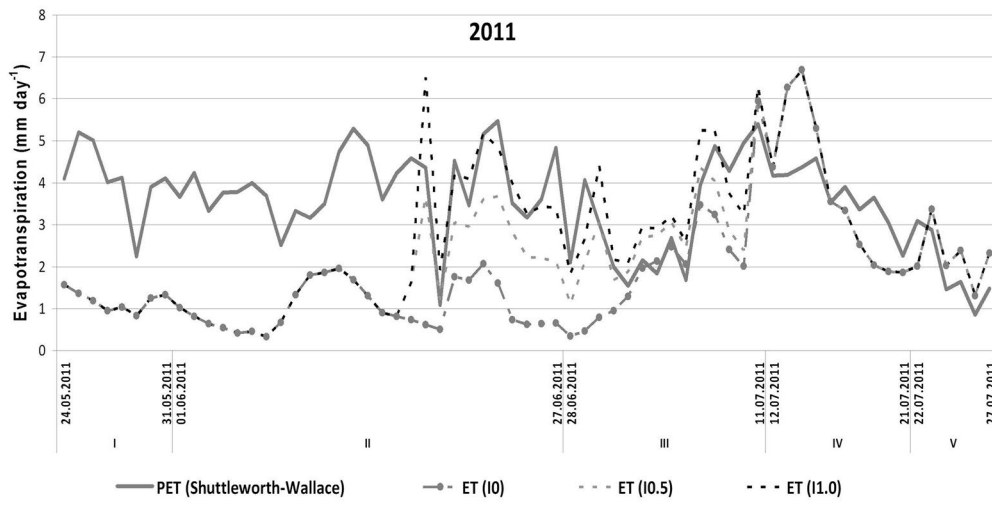


Fig. 2 Reference evapotranspiration (PET) and crop evapotranspiration (ETc adj) during the growth stages of snap beans under well-irrigated ($I_{1.0}$), water deficit ($I_{0.5}$) and non-irrigated (I_0) conditions. I from sowing to emergence, II from emergence to flowering, III during flowering period, IV from flowering to pods setting, V from pod development to harvesting from 2011 to 2013

in comparison with the irrigated plants (Fig. 5c). During this period, the response of yellow-podded bean varieties to drought concerning the adaxial stomatal density was different.

The largest difference in the stomatal resistance in the leaves between the varieties was established both during flowering and pod development periods under non-irrigated condition (Fig. 6b, c). In severe drought (I_0), during flowering, the Carson variety had the highest stomatal resistance (3.0 s cm^{-1}) and Maxidor variety showed the smallest one (2.3 s cm^{-1}) of the yellow-podded groups. Under this condition, during pod development of Carson variety, the extent of stomatal resistance was decreased by 25% compared to that of flowering stages, while it was less decreased (13%) for the Maxidor variety. During flowering and pod development periods, no significant difference was found in the stomatal resistance of Paton and Serengeti varieties with green pods under water deficiency (Fig. 6b, c).

Leaf area index

The changes in the leaf area index (LAI) express the intensity of growth of plants under different growing conditions. Under water deficiency ($I_{0.5}$), the growth of the plant is retarded. Under this condition, the LAI was lower than that of irrigated plants ($I_{1.0}$); however, its extent of retardation depends on the weather of crop years. The canopy of beans increased progressively during the stages of development; the increase in LAI was intense for all varieties until flowering, subsequently during pod development the extent of increases depended on the varieties (Fig. 7a) and water supply. Under severe drought condition (I_0), during flowering, the leaf area of Maxidor and Carson varieties with yellow pods decreased by 28.1 and 35.0% in comparison with the irrigated plants, while the extent of decrease was larger (47.7 and 48.1%, respectively) for the green-podded Serengeti and Paton varieties. A significant difference in LAI among the varieties can be detected under water deficiency ($I_{0.5}$) when the LAI changed from 1.5 to 2.4 during flowering, but it ranged from 2.2 to 3.8 LAI during pod development period (Fig. 7b, c).

Relationships between stomatal characteristics and WUc and yield

The most sensitive phase of development in snap beans is the flowering, when drought determines the yield. Therefore,

the relationships between stomatal characteristics, water use and yield have been tested in this stage of development. Under dry conditions (I_0 and $I_{0.5}$), there was no correlation between the stomatal density on abaxial surface and stomatal resistance of the bean leaves. Nevertheless, a high stomatal density on the adaxial surface of leaf was related to low stomatal resistance ($r=0.5896$, $P<0.1$) only in the driest year (2013) under non-irrigated condition. In this condition, the increase in the stomata number on adaxial surface of leaf was related to the increasing pod weight per plant, but the extent of increase varied by the crop year. In dry years (2011 and 2013), under non-irrigated condition, the stomatal resistance measured during flowering correlated with the LAI and water use (WUc) measured during the generative period and influenced significantly the pod weight per plant (Table 4). During this period, the significant close correlation between the stomatal resistance and crop biomass can be originated in the change in stomatal resistance after flowering (Fig. 6c). During pod development, the stomatal resistance decreased significantly in comparison with the flowering stage thus it contributed to an increase in the crop biomass. In dry years, the LAI had great affect on the yield and WUEy of bean grown under non-irrigated condition which was confirmed by the correlations shown in Table 4.

Under water deficiency ($I_{0.5}$) using deficit irrigation, a significant close correlation between the stomata number on the adaxial leaf surface and LAI, depending on the crop year, was recorded (Table 5). On the basis of correlations, a higher stomata density on upper epidermis (adaxial surface) of leaf was associated with a low LAI which could be attributed to the decrease in the size of the leaf, therefore, more stomata could be found on its unit surface regulating effectively the transpiration. In dry years (2011 and 2013), the stomatal density on the adaxial surface of leaf measured during flowering affected significantly the water use (WUc), the individual yield represented by pod weight per plant as well as the yield and WUEy of beans grown under water deficit condition ($I_{0.5}$). Nevertheless, the stomatal resistance had a more important role in the yield of beans grown in moderate water deficiency ($I_{0.5}$) than those in severe drought (I_0). It was confirmed by the correlations between the stomatal resistance and LAI and water use (WUc), although the extent of seasonal drought influenced the expected yield of snap beans (Table 5). Closer correlation between the crop evapotranspiration (ETc) measured during flowering and water use (WUc) during generative period was detected under severe drought (I_0) than water deficit condition ($I_{0.5}$) using deficit irrigation. Under severe drought (I_0), the water use (WUc) significantly determined the individual yield as the pod weight per plant ($r=-0.6494$, $r=-0.6125$), while its influence depended on the crop years under moderate drought ($I_{0.5}$) ($r=0.7313$, $r=0.5617$). Nevertheless, the

Table 3 Crop evapotranspiration (ETc), water use (WUc) and water use efficiency (WUEy) during growth of snap beans under different water supply conditions

Variety	Water supply ^a	2011					2012					2013				
		Total water ^b (mm)	ETc (mm)	WUc (m ³ kg ⁻¹)	WUEy (kg h ⁻¹ mm ⁻¹)	Total water ^b (mm)	ETc (mm)	WUc (m ³ kg ⁻¹)	WUEy (kg h ⁻¹ mm ⁻¹)	Total water ^b (mm)	ETc (mm)	WUc (m ³ kg ⁻¹)	WUEy (kg h ⁻¹ mm ⁻¹)			
Green-podded																
Serengeti	<i>I</i> _{1.0}	202.7	171.45	175.82	54.13	218.4	228.14	118.0	48.76	153.0	171.81	101.11	43.16			
	<i>I</i> _{0.5}	162.9	150.29	155.94	52.61	174.9	188.44	126.58	36.77	133.3	159.90	72.16	47.92			
	<i>I</i> ₀	123.0	121.75	334.54	20.48	131.4	145.18	207.90	14.64	113.6	140.31	100.94	25.14			
Pation	<i>I</i> _{1.0}	194.4	165.98	97.06	100.24	218.2	221.51	164.34	32.27	153.0	183.96	117.97	34.55			
	<i>I</i> _{0.5}	154.5	144.82	85.93	99.08	174.7	183.03	90.01	44.86	133.3	161.63	251.78	13.58			
	<i>I</i> ₀	114.6	116.28	202.13	35.48	131.2	140.77	508.36	3.08	113.6	175.39	200.22	10.25			
Yellow-podded																
Carson	<i>I</i> _{1.0}	172.8	160.25	130.47	74.02	206.2	207.58	98.84	60.94	153.0	164.54	132.76	47.92			
	<i>I</i> _{0.5}	132.9	139.09	149.95	55.09	162.7	173.16	100.01	47.07	133.3	153.21	118.73	27.54			
	<i>I</i> ₀	93.0	110.55	701.59	9.68	119.2	134.50	99.89	28.28	113.6	134.56	68.27	33.10			
Maxidor	<i>I</i> _{1.0}	150.1	165.98	721.16	12.93	199.2	207.58	276.77	20.40	153.0	166.54	53.56	84.01			
	<i>I</i> _{0.5}	132.4	144.82	667.82	11.70	159.2	173.16	147.16	28.93	133.3	154.99	54.28	65.72			
	<i>I</i> ₀	114.6	116.28	595.71	10.83	119.2	134.50	547.10	4.10	113.6	135.83	48.78	54.73			

^a*I*_{1.0} = regularly irrigated, *I*_{0.5} = moderate water deficit, *I*₀ = non-irrigated, severe dry conditions seen in "Materials and methods"^bPrecipitation + irrigation WUc = water use from flowering to harvest

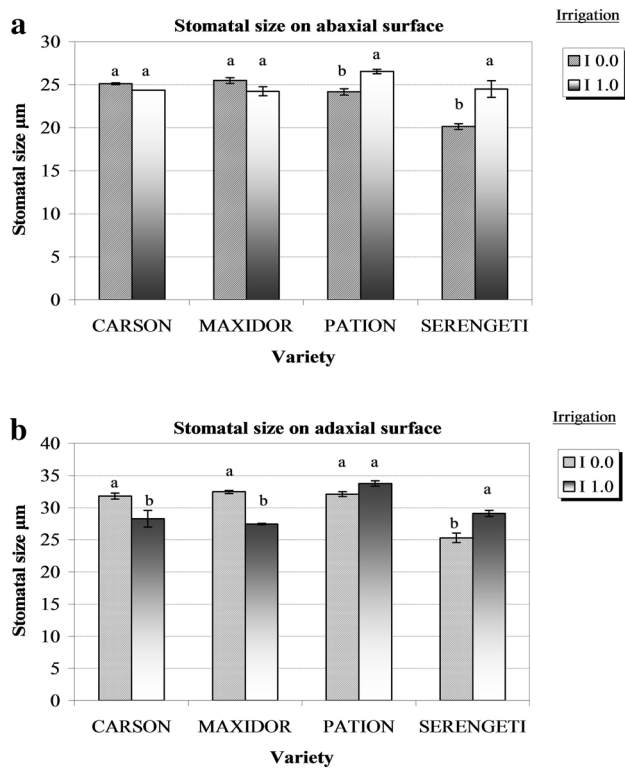


Fig. 3 Changes in stomatal size on abaxial surface (a) and adaxial surface (b) of leaves under irrigated ($I_{1.0}$) and non-irrigated ($I_{0.0}$) conditions. The data presented the average of 3 years \pm SD. Mean values followed by the different letters are significantly different at the $P < 0.05$ level. $I_{1.0}$ =regularly irrigated I_0 =non-irrigated conditions

water use (WUc) influenced significantly the productivity and WUEy of snap beans (Tables 4, 5).

The stomatal behaviour regulating the circulation of water and CO_2 inside the cells influences indirectly the photosynthetic activity of the plants. Nevertheless, the extent of water shortage occurring during flowering or pod development periods of snap beans affected differently the stomatal function and the size of canopy (LAI) which provided the development of yield. A further analysis of the relationships between the physiological traits, LAI and yield tended to suggest the traits useful for the selection of snap bean genotypes with improved WUEy. A close significant correlation between the stomatal resistance and LAI could be shown both during flowering and pod development stages of snap beans grown under water deficiency in dry years (2011 and 2013). On the basis of correlations shown in Table 4, the expected yield of beans can be predicted using physiological traits of plant measured during flowering. It was established that in a very dry year (2013) under severe drought (I_0) during flowering, when stomatal resistance is high (3.0 s cm^{-1}), the canopy is relatively small (1.9 LAI) then the expected yield may be 2.1 t ha^{-1} and WUEy is low. Under moderate water deficiency ($I_{0.5}$), during the flowering period, if

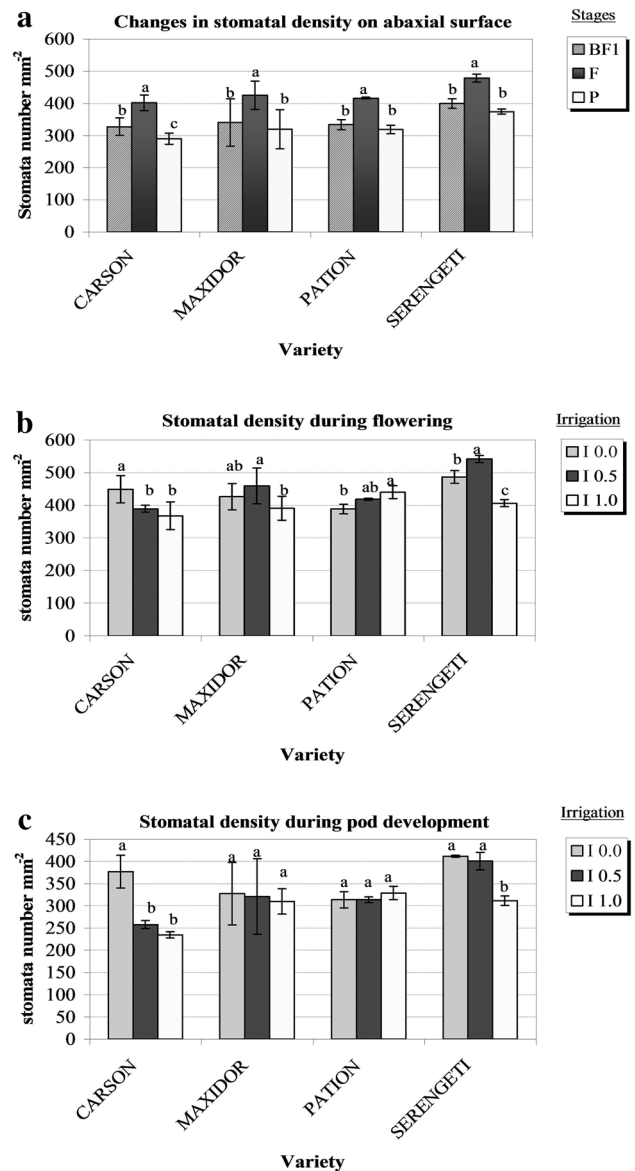


Fig. 4 Changes in number of abaxial stomata under growth phases (BF1 before flowering, F during flowering, P pod development) (a) and during flowering (b) and pod development (c) at different water supply in dry years. The data presented the average of 3 years \pm SD. Mean values followed by the different letters are significantly different at the $P < 0.05$ level. $I_{1.0}$ =regularly irrigated, $I_{0.5}$ =moderate water deficit, I_0 =non-irrigated, severe dry conditions

the stomatal resistance of leaf is low (e.g., 1.3 s cm^{-1}) and related to a larger size of canopy (3.4 LAI) then the expected yield, depending on the crop year, may be 6.1 or 9.0 t ha^{-1} based on the correlations shown in Table 5. During flowering, independent of the water supply, the LAI showed significant close correlation with the water consumption of plants and yield. It can be said that under unsatisfactory water conditions ($I_{0.5}$), both during flowering and pod development a low stomatal resistance associated with moderate

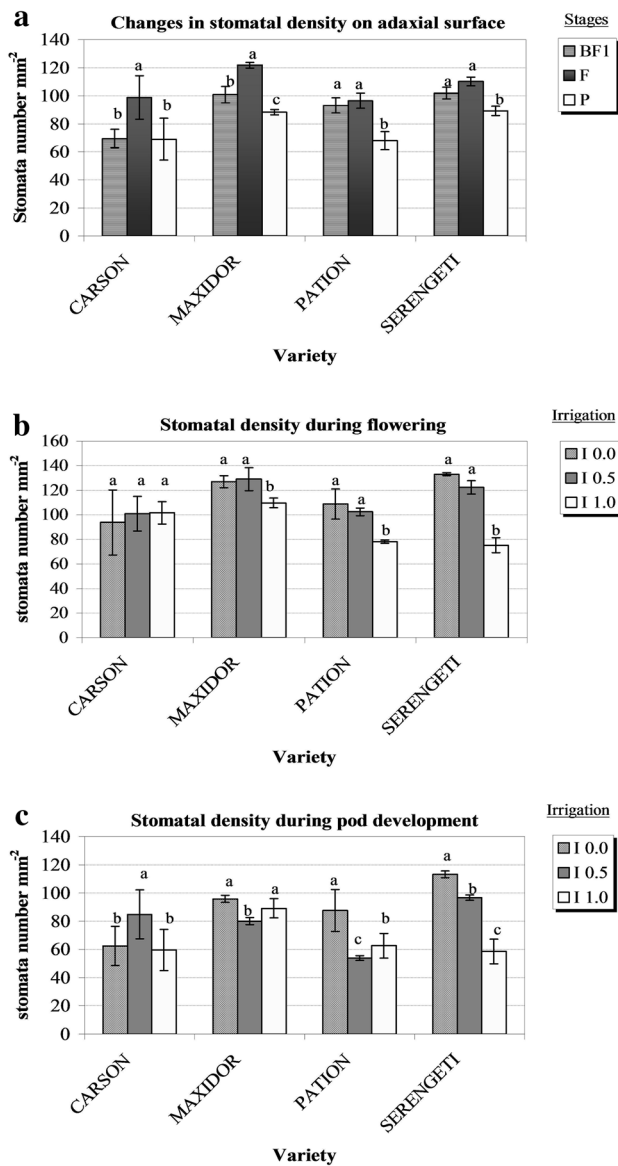


Fig. 5 Changes in number of adaxial stomata under growth phases (BF1 before flowering, F during flowering, P pod development) (a) and during flowering (b) and pod development (c) at different water supply in dry years. The data presented the average of 3 years \pm SD. Mean values followed by the different letters are significantly different at the $P < 0.05$ level. $I_{1.0}$ =regularly irrigated, $I_{0.5}$ =moderate water deficit, I_0 =non-irrigated, severe dry conditions

size of canopy (e.g., 2.0 LAI) can contribute to the increase in WUEy of the snap bean varieties.

In drought years, the deficit irrigation ($I_{0.5}$) gave inadequate water supply for the growth of pods in bean plants during flowering. The extent of canopy, the size and density of stomata influenced both the transpiration and water use during the generative period (WUC) and water use efficiency in green pods (WUEy). Under drought and non-irrigated conditions (I_0) when the extent of stomatal resistance in

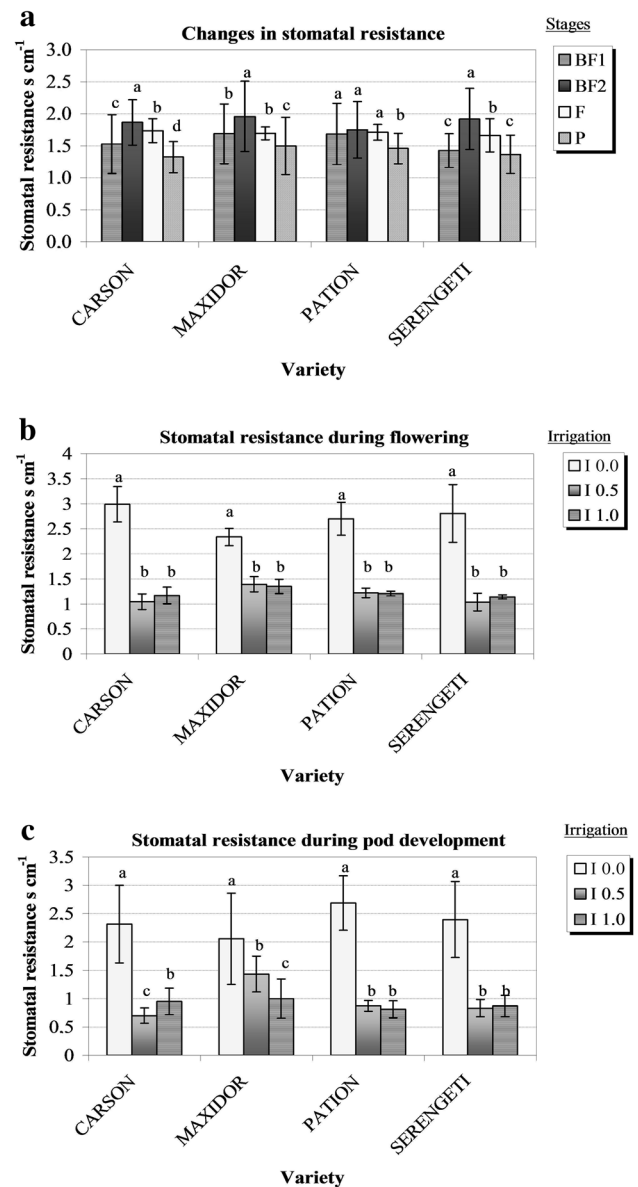


Fig. 6 Changes in stomatal resistance under growth phases (BF1 and BF2 before flowering, F during flowering, P pod development) (a) and during flowering (b) and pod development (c) at different water supply in dry years. The data presented the average of 3 years \pm SE. Mean values followed by the different letters are significantly different at the $P < 0.05$ level. $I_{1.0}$ =regularly irrigated, $I_{0.5}$ =moderate water deficit, I_0 =non-irrigated, severe dry conditions

the bean leaves was high then the pod yield, green biomass and harvest index (HI) decreased (Table 6). Nevertheless, the differences between the bean varieties could be better demonstrated under moderate water deficit ($I_{0.5}$) than those grown under non-irrigated severe dry conditions (I_0). Deficit irrigation ($I_{0.5}$) decreased the leaf canopy of the plants in comparison with the irrigated ones. Under these growing conditions, the smaller size and greater number of stomata on the both leaf surfaces could compensate the loss of water

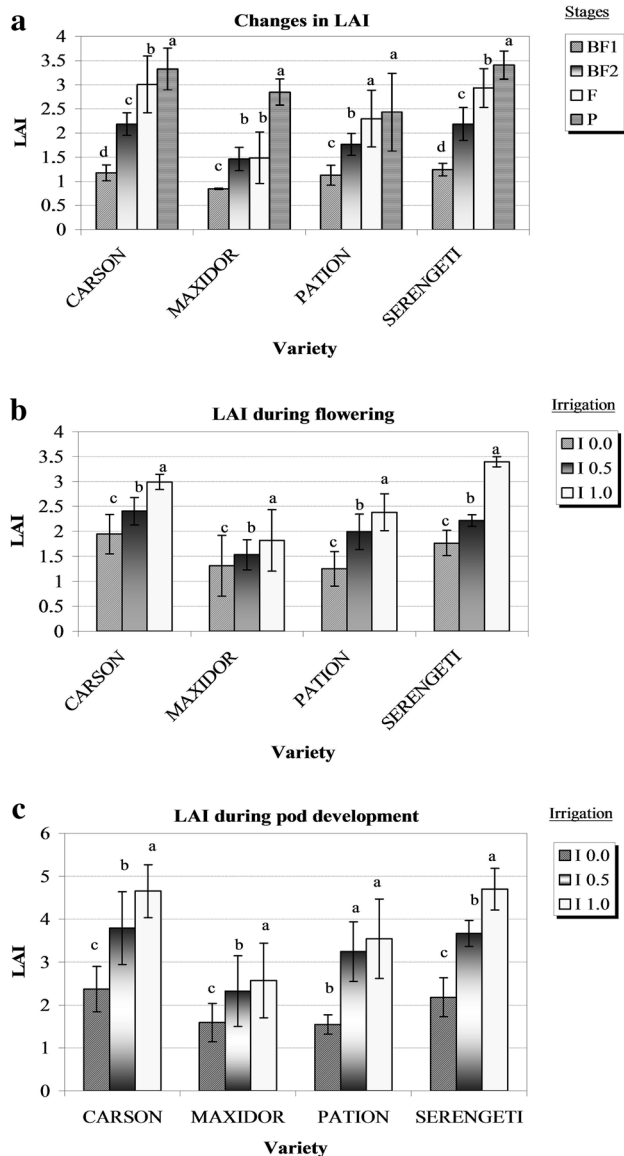


Fig. 7 Changes in LAI under growth phases (BF1 and BF2 before flowering, F during flowering, P pod development) (a) and during flowering (b) and pod development (c) at different water supply in dry years. The data presented the average of 3 years \pm SD. Mean values followed by the different letters are significantly different at the $P < 0.05$ level. $I_{1.0}$ = regularly irrigated, $I_{0.5}$ = moderate water deficit, I_0 = non-irrigated, severe dry conditions

in the plants thus the reduction of yield was also moderated and values of HI and WUEy were improved as observed in Serengeti bean variety with green pods (Fig. 3; Table 6). The larger size and number of stomata on the adaxial leaf surface and large LAI value induced more intensive transpiration of plants that resulted in restrictions of water availability for the yield production thus the yield and WUEy decreased as we observed for Carson variety with yellow pods (Fig. 3; Tables 3, 6). Under moderate water deficiency, using deficit irrigation ($I_{0.5}$), the amount of fully developed pods of the

bean varieties decreased by 20% compared to the irrigated plants except in the Carson variety, however, that of abnormal pods remained high. Under these conditions, the difference in the productivity between the varieties could be detected more effectively by WUEy than by HI. The range of water deficit tolerance based on the stomatal traits relating to the water use (WUC) and the water use efficiency (WUEy) was Serengeti > Patton > Maxidor > Carson varieties (Table 6).

Discussion

Insufficient water during the vegetative period has less impact on final yield (Loveys et al. 2004), however, the water shortages that occurred during flowering and pod setting significantly decreased the yield of snap beans. Kirda (2002) also established that soybean yield decreased proportionately more where evapotranspiration deficiency occurred during flowering and pod development rather than during vegetative growth. Water stress tolerance of plants is realised by different defence mechanisms against drought. The first response of plant is to reduce the water loss by stomata closure under water deficit conditions. Closing stomata decreased the transpiration rate (Singh and Reddy 2011) and photosynthetic rate (Yang et al. 2004). However, the size and number of stomata on the leaves has an important role in the water balance of the plants. The distribution of stomata on the leaf surface is variable by species; the stomata occur only on abaxial surface of leaves for sour cherry (Ferdinand et al. 2000) and apple (Nemeskéri et al. 2009), while some others such as tomato (Gay and Hurd 1975) green bean (Kanemasu and Tanner 1969) and pea (Yang et al. 2004) have stomata on both leaf surfaces. Our findings showed that the stomatal density on the lower (abaxial) surface of leaves was significantly higher than on the upper epidermis; however, its change significantly depended on variety and water supply. Others (Makbul et al. 2011) also detected more stomata on the upper epidermis of leaves of plants grown under water stress conditions than that of unstressed plants. The difference among the bean varieties was recorded by the size and number of stomata on upper (adaxial) surface of leaf under non-irrigated conditions. Under this condition, the size of stomata on adaxial surface of leaf of the green-podded varieties was smaller by 5–12%, but more of them were found than that on irrigated plants. The yellow-podded varieties had 13–18% larger sized stomata on adaxial leaf surfaces of plants exposed to drought, but their number did not change significantly in comparison with the irrigated ones. Contrary to the report of Kanemasu and Tanner (1969), no correlation between the number of stomata on the abaxial surface of leaf and stomatal resistance was found. However, it was established that the stomatal density on the adaxial surface of leaf

Table 4 Correlation coefficients and significant levels between physiological and productive traits of snap beans under non-irrigated (I_0) condition during flowering

Characters	Years	ETc (mm)	LAI	WUc	Pod weight (g plant ⁻¹)	Yield (t ha ⁻¹)	Biomass (t ha ⁻¹)	WUEy (kg h ⁻¹ mm ⁻¹)
Stomatal resistance (s cm ⁻¹)	2011	0.5671 [†]	0.6906 [†]	0.8197**	0.7864**	0.4851	0.5367 [†]	0.5592
	2012	0.3364	0.2650	0.2160	0.2556	0.0564	0.1327	-0.1533
	2013	0.4111	0.7962*	0.6819 [†]	0.7804**	0.8646**	0.8803**	0.8728**
Abaxial stomatal density (no. × mm ²)	2011	-0.3242	0.2057	0.3303	0.3038	-0.2348	0.3138	-0.2912
	2012	-0.1333	0.5709 [†]	-0.4976 [†]	-0.2700	0.4325	-0.2964	0.4162
	2013	0.5253 [†]	0.1916	0.5685 [†]	0.4760	-0.5109	-0.5923 [†]	0.5091
Adaxial stomatal density (no. × mm ²)	2011	0.3097	0.3079	0.4378	0.5871*	0.5950	0.8308***	0.5592
	2012	0.4049	0.2062	-0.3577	0.4317	0.3376	0.1313	0.3549
	2013	0.5342	-0.6726*	0.4607	0.9694***	0.4581	0.6219	0.5610
ETc (mm)	2011	-	0.6173*	0.5766*	0.3209	0.7063*	0.6151	0.7049
	2012	-	0.6923 [†]	0.7171*	0.4388	0.5723	0.6486 [†]	0.5488
	2013	-	-0.2950	0.1951	0.3309	0.3090	0.2502	0.1898
LAI	2011	-	-	-0.5257 [†]	0.2554	0.5330 [†]	-0.2298	0.7587**
	2012	-	-	-0.8816***	0.4376	0.8111**	0.7771**	0.8034**
	2013	-	-	0.6281*	0.8395*	0.9287**	0.9679***	0.8842**
WUc	2011	-	-	-	-0.6494*	-0.9995***	0.6940*	0.9553***
	2012	-	-	-	0.2963	0.9915***	0.9113***	0.9950***
	2013	-	-	-	-0.6125*	0.9996***	0.9556***	0.9905***

WUEy water use efficiency referred to green pod's yield, ETc cumulative crop evapotranspiration during flowering, WUc water use from flowering to harvest

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; [†] $P < 0.1$

Table 5 Correlation coefficients and significant levels between physiological and productive traits of snap beans grown under water deficiency ($I_{0.5}$) during flowering

Characters	Years	ETc	LAI	WUc	Pod weight (g plant ⁻¹)	Yield (t ha ⁻¹)	Biomass (t ha ⁻¹)	WUEy (kg h ⁻¹ mm ⁻¹)
Stomatal resistance (s cm ⁻¹)	2011	-0.558 [†]	-0.6888*	0.8249**	0.4477	-0.6913*	0.8004**	-0.6867*
	2012	0.0837	0.5874	0.7498*	0.3608	0.7548*	0.7443*	0.7186*
	2013	0.4117	-0.7733**	0.7556 [†]	0.7663*	0.7028 [†]	0.7974*	0.7068 [†]
Abaxial stomatal density (no. × mm ²)	2011	-0.3972	0.2946	0.2691	0.7273*	0.5567	0.2968	0.5743
	2012	0.2623	0.6837 [†]	0.3234	0.8157**	0.3553	0.4264	0.3862
	2013	0.1497	-0.3904	0.4352	0.7908**	0.5456	0.4576	0.5266
Adaxial stomatal density (no. × mm ²)	2011	0.3235	-0.6382*	0.6393 [†]	0.6701*	0.7279*	0.5191	0.7414*
	2012	0.3928	0.2384	0.2276	0.3303	0.2777	0.1533	0.3140
	2013	0.3652	-0.7019*	0.8813***	-0.6542*	-0.9069***	-0.8764***	0.9092**
ETc	2011	-	-0.4008	0.4384	-0.5507 [†]	-0.4606	0.5848*	-0.4378
	2012	-	0.2960	0.1146	0.6506 [†]	0.2425	0.2863	0.2097
	2013	-	-0.2161	0.1100	0.3460	-0.1534	-0.1079	-0.0575
LAI	2011	-	-	0.9810***	-0.2535	0.8833***	0.8259***	0.8872***
	2012	-	-	0.8040**	0.5072 [†]	0.8169**	0.9077***	0.8233**
	2013	-	-	0.9683***	0.5045	0.9691***	0.9478***	0.9663***
WUc	2011	-	-	-	0.7313**	0.9999***	0.9491***	-0.9999***
	2012	-	-	-	0.2275	0.9830***	0.9468***	-0.9843***
	2013	-	-	-	0.5617 [†]	0.9985***	-0.9886***	0.9993***

WUEy water use efficiency referred to green pod's yield, ETc cumulative crop evapotranspiration during flowering, WUc water use from flowering to harvest

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; [†] $P < 0.1$

Table 6 Stomatal characteristics, LAI, yield and WUE of snap bean varieties during the growth under different water supply conditions

Variety	Water supply ^a	Stomatal density 1 (no. × mm ²)	Stomatal density 2 (no. × mm ²)	Stomatal resistance (s cm ⁻¹)	LAI	Yield (t ha ⁻¹)	Yield category		Biomass (t ha ⁻¹)	HI	WUE _y (kg h ⁻¹ mm ⁻¹)
							Quality 1 ^b (t ha ⁻¹)	Quality 2 (t ha ⁻¹)			
Green-podded											
Serengeti	<i>I</i> _{1.0}	362	70	1.17 d	3.10 a	9.61 a	8.19 b	1.42 a	32.49 a	0.310 a	48.68
	<i>I</i> _{0.5}	451*	108*	1.11 d	2.27 b*	7.40 a	6.24 b	1.16 a	26.56 a	0.306 a	45.77
	<i>I</i> ₀	439*	124*	2.59 a*	1.82 c*	2.61 c*	1.90 c*	0.71 b*	14.54 c*	0.186 c*	20.09
Patton	<i>I</i> _{1.0}	382	74	1.29 d	2.39 b	10.19 a	9.28 a	0.91 a	29.09 a	0.342 a	55.68
	<i>I</i> _{0.5}	351	76	1.34 d	2.07 b	9.01 a	7.86 b*	1.15 a	25.54 a	0.348 a	52.51
	<i>I</i> ₀	335	107*	2.65 a*	1.27 c*	2.15 c*	1.53 c*	0.62 b*	9.75 c*	0.190 c*	16.27
Yellow-podded											
Carson	<i>I</i> _{1.0}	300	73	1.28 d	2.91 a	11.16 a	10.04 a	1.12 a	32.15 a	0.350 a	60.96
	<i>I</i> _{0.5}	311	86*	1.05 e*	2.39 b*	6.98 b*	5.87 b*	1.11 a	22.97 b*	0.302 a	43.23
	<i>I</i> ₀	409*	79	2.66 a*	1.88 c*	2.94 c*	2.25 c*	0.69 b*	12.09 c*	0.222 b*	23.69
Maxidor	<i>I</i> _{1.0}	334	97	1.58 c	1.55 c	6.79 b	6.06 b	0.74 b	23.26 b	0.270 b	39.11
	<i>I</i> _{0.5}	383*	104*	1.67 c	1.47 c	5.63 b	4.87 c*	0.76 b	19.23 c*	0.280 b	35.45
	<i>I</i> ₀	368*	109*	2.26 b*	1.37 c	2.94 c*	2.27 c*	0.67 b	14.32 c*	0.166 c*	23.22

The data presented the average of three dry years. Values in each column having different letters are significantly different at $P < 0.05$ level using Duncan's multiple range test

*Significantly different from the $I_{1.0}$ at the $P < 0.05$ level

^a $I_{1.0}$ = regularly irrigated, $I_{0.5}$ = moderate water deficit, I_0 = non-irrigated, serious dry conditions seen in "Materials and methods"

^bQuality 1 = pods for processing, Quality 2 = abnormal pods, stomatal density 1 = abaxial surface of leaf, stomatal density 2 = adaxial surface of leaf, LAI = leaf area index, HI = harvest index calculated for pod, WUE_y = water use efficiency referred to green pod's yield

measured during flowering influenced considerably the yield per plant under both moderate and severe dry conditions.

Silva et al. (2014) reported that chickpea varieties responded differently to supplemental irrigation, but the water use efficiency depended on the year and the genotype. However, the plants responded to water deficit by various ways in their different stages of development. The stomatal resistance has been found too high during flowering, but its extent was significantly changed by the weather and water supply conditions (Nemeskéri et al. 2015b). The question could be raised whether the measurements of physiological traits related to the water consumption of plant, WUEy or harvest index are suitable to evaluate the productivity of snap bean genotypes and which of them can be used to select genotypes with good water use efficiency. Under drought, stomatal conductance for water and CO₂ decreases by the closing of stomata (Singh and Reddy 2011) in fact, the stomatal resistance increases. A high stomatal resistance moderating the transpiration impedes with photosynthesis in the leaves thereby the development of plant canopy decreases, thus they are not able to develop a high yield. The findings revealed that during flowering, the extent of stomatal resistance influenced significantly the water use and indirectly the yield production in particular during severely dry condition. During this period, the number of stomata on the adaxial surface of leaf correlated with the stomatal resistance only under severe drought (I_0), however, both stomata density on adaxial leaf surface and stomatal resistance affected mainly the individual yield (i.e., pod weight per plant) in dry years (2011 and 2013) that was confirmed by the correlations shown in Table 4. Under severe drought, when a high stomatal resistance (3.0 s cm^{-1}) is related to a smaller leaf canopy (LAI) during flowering and if this relation persists into pod development then a low productivity of bean can be expected. The decrease in not only leaf canopy but in the chlorophyll content of the leaves occurred when the stomatal resistance exceeded 3.5 s cm^{-1} during the flowering of snap bean (data not shown). As a consequence of decreasing leaf canopy the water loss decreased due to the large number of stomata controlling the transpiration; however, the increasing stomatal resistance resulted in a low utilization of water for the pod's development which lead to the decrease in the yield of snap beans under severe dry conditions (Table 6).

Deficit irrigation is used to reduce the water consumption, increase water use efficiency (M'hamed et al. 2015). However, this requires precise knowledge of crop response to available water, because the drought tolerance varies by the variety and stage of the growth. The results showed that in severely dry years, using deficit irrigation ($I_{0.5}$), the productivity and water use efficiency of bean varieties could be improved if they had a low stomatal resistance in the leaf during flowering and pod development. According to Medrano et al. (2015), the water use efficiency (WUE) can

be measured at different scales ranging from the instantaneous measurements including the stomatal conductance and transpiration on the leaf to more integrated ones at the whole plant and crop levels. They debate that clear relationship exists between the WUE on leaf and whole plant level; however, our findings revealed a strong relationship between the WU on leaf level presented by the stomatal resistance measured during flowering period and whole plant level (WUc) measured during generative period (Tables 4, 5) which influenced significantly the pod weight per plant and biomass production under different water supply conditions. Under moderate water deficit ($I_{0.5}$) during flowering the stomatal resistance was low, and ranged from 1.0 to 1.4 s cm^{-1} (Fig. 6), however, the increase in stomatal resistance up to 1.3 s cm^{-1} associated with decreasing LAI that influenced the water use during generative period (WUc). On the basis of correlations shown in Table 5, under moderate water deficit conditions ($I_{0.5}$), a low stomatal resistance measured during flowering facilitated for the canopy development and equilibrated the water circulation for the plants, hence the expected yield of snap beans can be large (9.0 t ha^{-1}). Nevertheless, the strength and trend of the correlations between the stomatal resistance and expected yield of snap beans can be affected by the WUc and seasonal drought.

However, the prediction of yield based on the measurement during flowering can be modified when the translocation of photosynthates from the green biomass to reproductive parts of the plants changes during pod development. This progress is influenced by the weather conditions particularly the water relations and the maturity of the varieties. Harvest index is an important trait for the improvement of yield of genotypes during breeding. The increase in harvest index is also considered to increase the water use efficiency (Passioura 2004). Under drought, the harvest index was higher for some plant species; therefore, it was found to be a useful trait in the selection of drought sensitive or tolerant breeding lines (Aggarwal et al. 1986; Sánchez et al. 2001; Mounce et al. 2016) and genotypes with large seed yield, respectively (Foulkes et al. 2007). Contrary to these statements, the results showed that harvest index (HI) referred to pods was low in drought and there was no significant difference in HI between the snap bean varieties (Table 6). Scully et al. (1991) found a high genetic correlation between the yield and biomass ($r=0.86$), but the harvest index had a low correlation with the yield ($r=0.42$). Thus, the progress of selection to produce high productive genotypes based on HI will probably be slow. Others (Lovelli et al. 2007) established that the yield response coefficient to water (K_y), as a proportional factor between the related productivity loss and the related evapotranspiration reduction, is an important factor to determine the crop tolerance to water stress and it can be used for irrigation scheduling. Under conditions of scarce water supply and drought, deficit irrigation can lead

to great economic gains for some crops, but this requires precise knowledge of crop response to water (Kirda 2002). The expectation of use of deficit irrigation is that any yield reduction will be insignificant compared with that of other irrigation practices. Those varieties responding to water deficit ($I_{0.5}$) with a small reduction in yield and WUEy in comparison with the optimal water supply are suitable for the cultivation with deficit irrigation. The green-podded snap bean varieties had higher water deficit tolerance based on the stomatal traits relating to the water use and the water use efficiency than yellow-podded bean varieties (Table 6). The findings demonstrate that during the flowering period, the stomatal resistance and stomatal density on adaxial surface of bean leaves determined the individual pod yield (i.e., pod weight per plant) with 60% reliability under non-irrigated conditions, hence these traits can be used to select genotypes in drought, although the development of canopy and biomass of the genotype should be also taken into consideration. This is confirmed by the close significant correlation between the LAI measured during the flowering period and pod yield and green biomass yield, respectively. The results also confirm that the water use (WUc) related traits and WUEy are favourable in the evaluation of the differences in the productivity of bean genotypes grown under moderate water deficit conditions.

Conclusions

The findings revealed that the stomatal traits related to the water use (WUc) during the generative period of plant and LAI influenced the water use efficiency (WUEy) of snap beans grown under different water supply conditions. During flowering and pod development periods, stomatal resistance was significantly high for the snap bean varieties grown in non-irrigated, dry conditions. The stomatal resistance measured during flowering had a large effect mainly on the individual pod yield (i.e., pod weight per plant) of the varieties grown under non-irrigated condition. In severe drought, during the flowering period, the high stomatal resistance relating to a low canopy (LAI) resulted in a low yield of snap beans. Under this condition, the correlation between the stomatal resistance and pod weight expressed by pod weight per plant gives the basis of selection for high productive plants. Under moderate water deficit, the water use (WUc) related traits including stomatal resistance, the size and number of stomata on the adaxial surface of leaf and LAI jointly are more suitable for the evaluation of the difference in productivity of bean varieties than those during severely dry condition. WUc-related traits can be used for the selection of genotypes adapted to drought, while the difference in water use efficiency (WUEy) between the snap bean varieties is

more suitable for the evaluation of their productivity under deficit irrigation.

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