Journal of Tropical Plant Physiology 1(1) (2006): 27-44

ABNORMALITIES IN SWEET PEPPER (*CAPSICUM ANNUUM* L.) FLOWERS AND FRUITS INDUCED BY VARYING TEMPERATURES AND IRRADIANCE

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ABSTRACT

Environmental factors, in particular temperature, when in combination with irradiance imposed a predominant impact on reproductive growth and development in many horticultural crops, which severity of expression is dependable upon the existence of varietal differences. The aim of the paper is to describe the morphological expressions of the flowers and fruits of two varieties of *Capsicum annuum* L. (Blue Star-BS, a tropical selection; Bell Boy-BB, a temperate selection) exposed to varying temperature regimes (14, 20, 26 $\pm$ 3 °C) and irradiance levels (high, low irradiance). High irradiance of 3.8 MJ m^{-2} d^{-1} supported normal flower growth, which subsequently developed into normal fruit when exposed to higher temperature regimes (20 and 26 °C); whilst, low irradiance of 1.8 MJ m^{-2} d^{-1} did not seem to support sufficient biomass accumulation resulting in small, thin but still normal fruits. Low temperature at 14 °C, however, retarded flower and fruit growth and development, which could not be compensated by the increased irradiance. The flowers and ultimate fruits produced were abnormal with both varieties exhibited similar susceptibility towards the low temperature impact. Malformation occurred at early flower stage displaying large, flattened ovaries, either singly or doubly, with increased number of carpelloid petals being formed. The stigma was thicker and longer, extending out of the closed petals that seemed to stick together, whilst the style was also thickened and pointed. The presence of stamens was not significant due to its stout statue. Some carpelloid-like bodies appeared from the base of the developing flowers, and grew into abnormal thin fruit-like, shrunken and flattened organs, with seedless or seed deficient ovaries, and blunt ends caused by the inhibited style elongation. The malformed fruits were flattened registering lighter weight than the normal fruits. Anthesis was hampered and only occurred about 60 days after the first bud appearance stage. At higher temperature regimes and light condition, BS appeared to respond better in its fruit growth and development (weights and size) compared to BB, implying a broader base line trait in the former, hence a better choice for greenhouse cultivation.

Keywords: Sweet pepper, carpelloid organs, temperature-irradiance interactions, parthenocarpic fruits, flower and fruit abnormality

INTRODUCTION

Reproductive growth and development in sweet pepper are very sensitive to environmental factors, and problems of abnormal flower and fruit growth, and poor fruit set are common (Cochran 1924; Rylski & Spigelman 1982; Adam et al. 2001; Jaafar 2002). Temperature and irradiance have great influence on both early flower and fruit development (Kinet et al. 1985; Rylski & Spigelman 1982; Bakker 1989; Jaafar 2002). The optimum fruit set in sweet pepper was observed at 12-16 °C (Cochran 1936; 1938); however, the marketable yield obtained was low due to deformed fruits (Rylski 1986). According to Erwin (1932) and Kinet et al. (1985) infertility occurred due to poor pollen dehiscence and stigma receptivity, under low and high temperatures, respectively. Generally, the optimum temperature for pollen germination in pepper was 25 to 30 °C (Quagliotti 1979), whilst receptivity of stigma was higher at 17 °C mean temperature than at 22 °C (Cochran & Demsey 1966). There are varietal differences in the occurrence of anther dehiscence and stigma receptivity, and diurnal temperature appears to be the dominant factor. Pollen germination of cv. Tobasco (*C. frutescens*) for example occurs comparatively late in the day at 10 to 12 pm, germinates well even at 35 °C, and fairly at 40 °C. The dry and powdery pollen grains are extremely susceptible to even mild variations in temperature and humidity. They desiccate very rapidly under field condition and viability is very low under high temperature (Quagliotti 1979; Cochran & Dempsey 1966).

While temperature plays a predominant role in pepper fruit set, temperature also affects the early development stages of flower into the final size and shape of pepper fruit (Rylski 1986). The existence of inter-specific differences may also influence crop sensitivity and responses to the effects of temperature and irradiance, and their interactions on flower and fruit development, and the final yield (Rudich et al. 1977; Rylski 1986; Bakker 1989; Jaafar 2002). Understanding the varietal preferences of each cultivar, may help in better choice of cultivar or variety for different cultivation sites.

The paper described the morphological changes during the stages of flower development and fruit growth of tropical and temperate varieties of *C. annuum* as influenced by the interactions of temperature and irradiance, particularly at pre- and post-anthesis and fruit set stages. It also observed the ultimate fruit formation.

MATERIALS AND METHODS

Two F_1 hybrid varieties of sweet pepper (*C. annuum* L.) were raised in pots in controlled environment glasshouses at the University of Nottingham. A tropical hybrid variety Blue Star (BS) was purchased from the Know-You Seeds Co. Ltd. Taiwan, and Bell Boy (BB), a temperate selection from Breeders' Seeds Ltd, Lancaster, UK.

Propagation and seedling management

Seeds of F_1 hybrid varieties were sown in flat trays containing Levington Universal Compost F2 (Fison's Horticulture Ltd, Ipswich) and placed on a germination bed heated at 24 °C. Ambient temperature was maintained between 20 °C and 22 °C. Six days after emergence, uniform seedlings with fully expanded cotyledons were pricked out into 3.5-litre pots containing Levington M2 potting compost. The pots were placed on benches in a glasshouse under natural glasshouse lighting conditions and mean daily temperature at 20 $\pm$ 3 °C until they reached the third pair of true leaf stage ($\geq$1 cm), after which treatments were imposed. A standard nutrient solution containing Vitafeed NPK 214 (16:8:32; $N:P_2O_5:K_2O$) was applied through a fertigation system at a concentration of 0.5 µl litre^{-1} every morning throughout the growing period to maintain optimum growth. Pesticide spraying at manufacturer's recommended concentration was applied when necessary. Pesticide *Torque* (fenbutatin oxide at 50% w/w by Zeneca) and *Pirimor* (pirimicarb at 50 % w w^{-1} by I.C.I.) were used fortnightly at a concentration of 5 g litre^{-1} of water to control red spider mites and aphids, respectively, whilst thrips were controlled using *Hostaquicks* (heptanophos by Hoechst) and *Decis* (deltamethrin by Hoechst) at a concentration of 7.0-7.5 ml litre^{-1} of water.

Experimental design and treatments

Two varieties, three temperature regimes and two irradiance levels were arranged in a 3-factorial Randomized Complete Block Design (RCBD) with four replicates. Varietal responses to differing temperatures and irradiance combinations were examined on morphological changes of the developing flowers to fruit set, with special interest on the induction of abnormal characteristics. Three daily mean temperature treatments at 26, 20 and 14 $\pm$ 3 °C were set up prior which the temperature regime within the glasshouse was set to the required values and allowed to stabilize one week before commencing treatments. Air temperature was measured at plant height using screened and aspirated "PT - 100" sensors and the values were recorded by a "Squirrel" Data Logger (Grant Instruments Cambridge Ltd, Cambridge, UK) at 30 min intervals. The ventilation system operated to reduce and to increase the temperatures, when reaching the respective above and below the set temperatures.

Two irradiance levels used were the high irradiance (HI) treatment comprised the incident radiation received within the glasshouse and also referred to as the control; and the low irradiance (LI) treatment achieved by suspending 50% shade green Rokolene netting (Rokolene KDA, Rokocontainers, Nottingham, UK) above and around the plants. In both treatments, supplemented lighting from 400 W high pressure sodium lamps (SON/T) was used to provide an additional total radiation of approximately 5.4 MJ m^{-2} ($\approx$ 2.5 MJ m^{-2} PAR; 400 - 700 nm) between 0500 h and 2300 h, apart from the natural incident glasshouse radiation received. Daily radiation receipts were measured at plant height using tube solarimeters (Green & Deuchar 1985) that had been calibrated against a Kipp Solarimeter

(Delta-T Devices, Cambridge, UK) and values were recorded using a Campbell CR10 data Logger (Campbell Scientific Inc., Shepshed, UK) at 60 min intervals. The experiment was designed as a 3 x 2 x 2 factorial in RCBD with 4 replicates, which contained 16 plants each. For every parameter studied, eight treatment samples were randomly selected from each replicate.

Flower and fruit development

Periodic observations and description on the sweet pepper flowers were carried out from bud emergence to anthesis and fruit set (15 days after reaching anthesis; Jaafar et al. 1994). Subsequently, fruit growth and development were documented at the end of the experiment (65 days after start of treatment). The parameters used in the pictorial descriptions of the developing flowers were the easiness of flowering progress to anthesis and fruit set, flower and ovary size and shape, presence of carpelloid bodies, shape of stigma and style, petals numbers and flower stalk thickness. Destructive analysis was carried out to determine the biomass of mature fruits, lobe numbers and fruit sizes (length and breadth). The developed fruit parameters were carried out to complement the descriptive analyses made as the result of varietal responses to differing temperatures and irradiance. Overall observations on malformation of the developing flowers were also noted to ascertain the influence of micro-climate and their interacting factors on ultimate fruit development.

Statistical analysis

Data were analyzed using the analysis of variance (ANOVA), which provided the means for all variables measured.

RESULTS

Observations carried out on both the developing flowers and fruits described the effects of varying temperatures and irradiance on the malformation of the growing reproductive organs (Tables 1 and 2). During the experiment, plants under HI received about 250 MJ m^{-2} cumulative irradiance (3.8 MJ m^{-2} d^{-1}), whilst under LI, it was 119 MJ m^{-2} (1.8 MJ m^{-2} d^{-1}), about 48 % lower irradiance received than that received from the HI condition.

Flower and early fruit growth and development

The effects of temperature and irradiance on the growth and development of flowers and early fruits were examined. The flowers and early fruits developed from plants grown at 14 °C were completely abnormal regardless of varietal differences or irradiance levels. Subsequently, increased number of capelloid petals was observed in the abnormal organs (Figure 1). Normal flower growth and development, however, occurred especially in the highest temperature regime (27 °C), which finally developed into normal mature fruits.

Table 1. Significance of temperature, irradiance and varietal effects on fruit fresh and dry weight in *Capsicum annuum* L.

Source / Variable	Fruit fresh weight (g)	Fruit dry weight (g)	Fruit size (cm) Length	Fruit size (cm) Breadth	Carpelloid petals (No.)	Lobe No. /fruit
Temperature	**	**	**	**	**	ns
Irradiance	**	**	*	**	ns	**
Variety	**	**	**	**	ns	**
Temp * IRR	**	**	**	**	ns	ns
Var * IRR	**	ns	ns	*	ns	ns
Var * Temp	**	ns	**	*	ns	**
Temp * IRR * Var	ns	ns	ns	ns	ns	ns

ns, not significant at 5%; **, significant at 1%
Temp = temperature; IRR = irradiance; Var = variety

Table 2. Effects of interaction between temperatures, irradiance and varieties on fresh and dry biomass and fruit size of *Capsicum annuum* L. F_1 varieties Blue Star and Bell Boy.

Source	FR Fresh Wt (g)		FR Dry Wt (g)		Fruit Length (cm)		Fruit breadth (cm)		Lobe No./fruit	
Temp*IRR	100%	50%	100%	50%	100%	50%	100%	50%	100%	50%
14	16.4	10.6	3.2	2.6	34.6	36.9	41.7	30.7	3.4	2.8
20	61.9	32.4	7.1	4.2	61.2	70.8	58.6	40.8	3.5	2.9
26	72.9	27.7	5.8	3.6	70.7	65.5	68.9	38.5	3.3	2.8
Temp*Var	BS	BB	BS	BB	BS	BB	BS	BB	BS	BB
14	16.7	10.3	3.1	2.7	41.7	29.8	37.9	34.5	3.5	2.7
20	54.5	39.8	5.9	5.3	78.5	53.5	50.9	48.5	3.1	3.3
26	63.6	37.1	5.1	4.3	82.9	53.3	61.8	45.6	3.1	3.0
Var*IRR	100%	50%	100%	50%	100%	50%	100%	50%	100%	50%
BB	39.4	18.7	5.0	3.1	44.2	46.9	50.4	35.3	3.3	2.8
BS	61.4	28.4	5.7	3.8	66.8	68.6	62.3	38.0	1.2	2.9

Flower growth from both varieties was well supported by higher temperature regimes. Contrastingly, low temperature (14 °C) severely hampered flower growth from bud emergence to anthesis and fruit set in both the varieties to an extent, which could not be compensated for by high irradiance, resulting in the formation of high numbers of abnormal fruitlets. When the flowers finally opened (≅ 60 days after first bud appearance), abnormalities were distinctly observed in the flower parts, the petals, stamens and gynoecium. The fruits, which eventually developed, were also deformed and not of marketable quality. A very significant negative relationship also existed between temperature regime and formation of carpelloid petals (Figure 2; R2 = 0.8555). The sepals, however, were not affected.

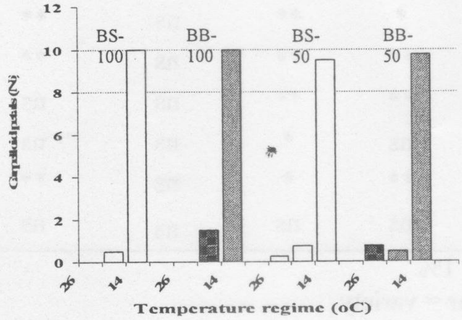


Figure 1. Temperature effect on inducing the formation of abnormal carpelloid petals.

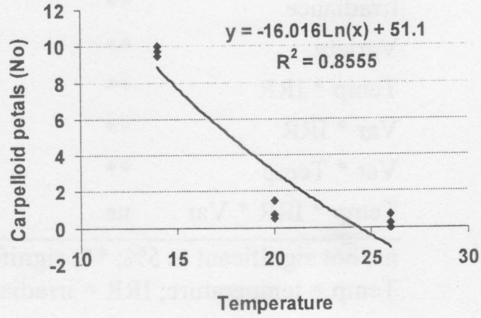


Figure 2. Relationship between the varying temperatures and incidence of carpelloid petals.

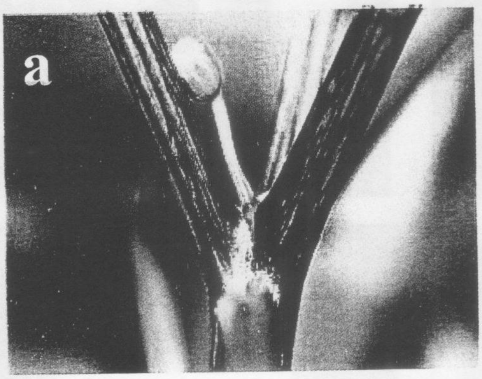
Visual description of the developing flower at pre- and post-anthesis

The impact of low temperature (14 °C) on abnormal flower growth and development is best described in a pictorial manner. Plate 1 illustrates the slow process of flower growth from emergence to anthesis, which took about 39 days compared to 18 days in normal flower growth. Anthesis is the opening of the flowers, and pre-anthesis is the time prior to flower blooming. At pre-anthesis, diameter of the growing bud and its stalk (Plate 1a) were observed to be thicker than that of the normal flower bud (Plate 2a). The flower bud also had thicker and longer stigma erected and extended outside the closed petals that seemed to adhere together inhibiting easy opening of the petals (Plate 1b). The process of anthesis was very slow, with petals opened one at a time (Plate 1c) vs. normal flower anthesis (Plate 2b). When anthesis finally occurred about 60 days after the third true leaf stage, a larger and thicker ovary with extended, thick stigma and some bodies like growth was exposed (Plate 1d). Meanwhile the presence of stamens was not significant as the latter were stout. Under low temperature of 14 °C, development of post-anthesis flowers into fruit set and harvestable fruits was very sluggish, as if the reproductive growth and development was not taking place at all unlike those growing flower buds under the high temperature regime (Plate 2, 3a).

Plate 1. Stages in the abnormal development of primary flowers exposed under low temperature treatment (14 °C) regardless of variety or irradiance level. Note (arrows) the (a) presence of thick ovary, extended stigma outside the petals and thick petiole; (b) flower petals seemed to stick together, prohibiting anthesis from taking place, causing the thick ovary and stigma to stick out of the thick petals; (c) slow opening of the petals during anthesis exposing the thick stigma and ovary; (d) occurrence of complete anthesis at ≅ 60 days after first appearance of the true leaf stage, exposing the thick stigma and ovary.

Visual description of the developing flowers at fruit set stage

Developing flower buds at 15 d after anthesis was considered to have reached the fruit set stage (Jaafar 2002), and the period between anthesis and fruit set stage was considered as the post-anthesis stage. Normal flower from the 26 °C-HI treatment experienced a steady post-anthesis growth stage into fruit set, exhibiting the normal small sized ovary, with significantly longer stamens than the stigma (Plate 2b). The flowers had 4 - 6 well-shaped petals (Plate 3a). However, flowers at fruit set stage exposed to continuous low temperature treatment produced larger single (Plate 3c), and sometimes double ovaries with blunt ends caused by the inhibited style elongation probably due to slow growing of the style (Plate 3b, 3c). The petals were were observed to be larger and thicker with higher petal numbers than normal flowers between nine and 13 (Plate 3b, 3c, 3d *vs* Plate 3a). The flower was extended from the thicker flower stalk. Carpelloid bodies were also noticed attached to the deformed fruitlets (Plate 3d).



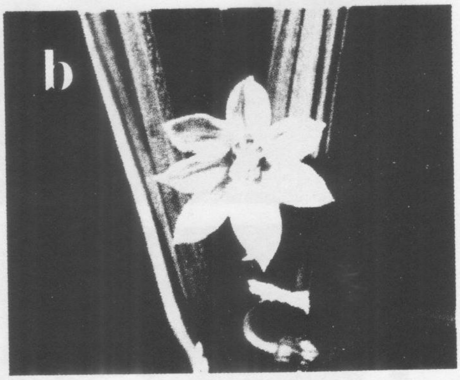
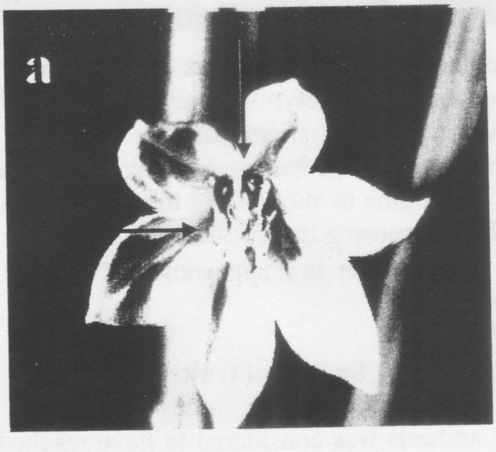


Plate 2. Development of normal primary flower from the 26 °C treatment at bud stage (a), and reaching complete anthesis at 28-30 days after the third true leaf stage (b). Note the normal petiole size and the presence of normal flower parts (stigma, anthers, ovary and petals).



3a: Normal sweet pepper flower from the 26 °C treatment at anthesis. Note the normal size of the ovary, stigma and stamens (arrows).

Plate 5. Abnormal fruit formation from the 14 °C treatment for Blue Star (a) and Bell Boy (b) varieties compared to normal fruit formation from the 26 °C treatment for Blue Star (c) and Bell Boy (d) varieties. Note the occurrence of inhibited thickened style elongation in both varieties under 14 °C treatment giving rise to pointed fruit ends with thick showy stigma (arrows).

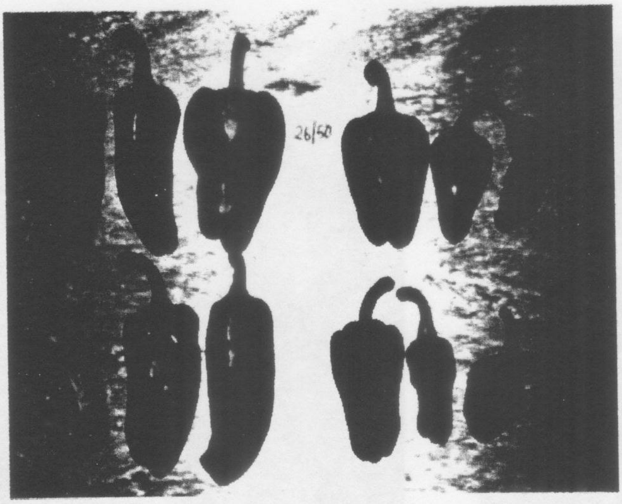


Plate 6. Small, thinned fruits developed under high temperature (26 °C) and low irradiance level, signifying reduced biomass production under low irradiance and possible increased respiration due to the high temperature.

Fruit weight

The interaction between temperature and irradiance imposed very profound impact of fresh and dry fruit biomass (Tables 1, 2) although impact of varietal responses at either varying temperatures or irradiance was only observed with fresh biomass (Figure 4). Under high temperature (26 °C)-HI condition, fruit fetched the highest fresh weight (72.9 g; $p \leq 0.05$), whilst highest fruit dry biomass (7.05 g; $p \leq 0.05$) was produced in the intermediate temperature (20 °C) regime exposed under HI (Table 2). Under LI, the fruits registered lighter weights, and had relatively thin walls when exposed under high temperature (Table 2; Plate 6).

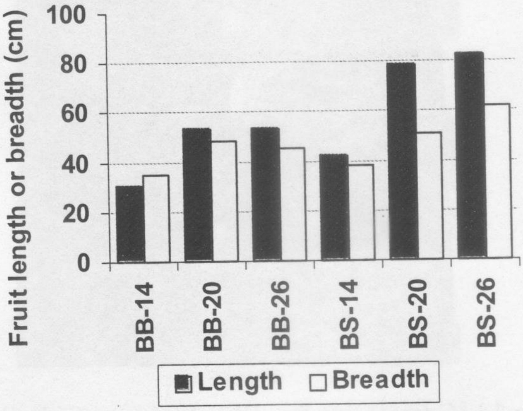


Figure 3. Varietal responses to varying temperatures on fruit size (length and breadth).

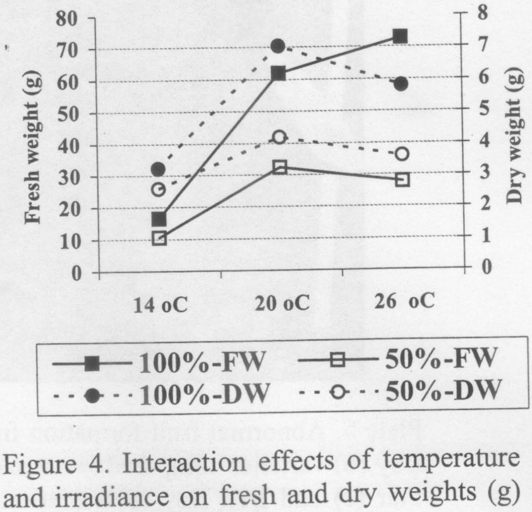


Figure 4. Interaction effects of temperature and irradiance on fresh and dry weights (g) of Blue Star and Bell Boy varieties.

Abnormally developed fruits under low temperature (14 °C) registered lower fresh and dry weights (78% and 49%, respectively) compared to those produced under the highest temperature regime. They were considerably small and flattened regardless of irradiance levels, registering lowest per fruit fresh and dry biomass (respectively 13.5 g and 2.9 g; Table 2). The fruits observed were also parthenocarpic, that is seedless and seed-deficient. The fresh and dry weights of both varieties tested were lowest when exposed to the lowest temperature regime compared to the normally developed fruits (Figure 5). Variety BS recorded the highest fresh weight when exposed under highest temperature regime (26 °C; Plate 5b, 5c), but highest dry weight by BS was achieved at 20 °C.

Fruit size

Temperature seemed to impose greater influence on fruit size, particularly fruit expansion (Table 1; Figure 3). Under low temperature regime, observation revealed that abnormal fruits with almost flat fruit appearance registering a relatively wider fruit circumference than fruit length (36.2 cm vs. 35.7 cm) from both the HI and LI levels (Plates 4a, 4b). Occurrence of inhibited style elongation in both varieties under low temperature (14 °C) treatment was also observed, and to some degrees gave rise to thickened fruits ends or with thick, showy and incomplete stigma development. In contrast, normal fruits in the higher temperature regimes (20, 26 °C) registered significantly longer (66.0 – 68.1 cm) than wider (49.7 – 53.7 cm) fruits (Table 2), giving rise to longer fruit size of higher market value (Plates 4c, 4d) without any formation of pointed ends. Formation of lobes in both varieties were sensitive to low temperature (Table 2). Less number of lobes in BB was formed under low tempearture (14 °C) whilst a contrasting effect was observed in variety BS resulting in highest number of lobes (3.5 vs. 2.7 lobes). Normal number of lobes were formed under the intermediate and high temperature regimes in both pepper varieties.

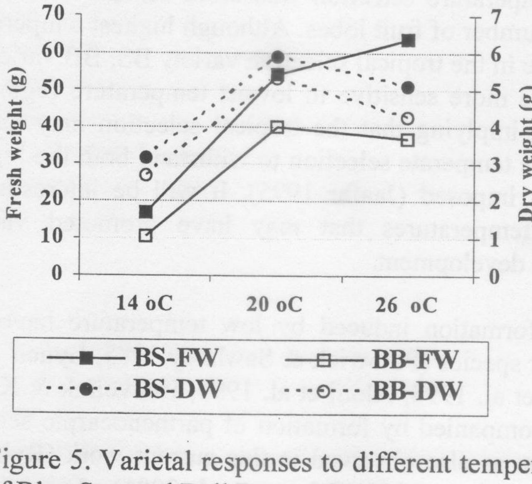


Figure 5. Varietal responses to different temperatures on fresh and dry weights (g) of Blue Star and Bell Boy varieties.

DISCUSSION

Results presented showed that temperature regime when combined with irradiance strongly influenced the growth and development of flowers and fruits of *C. annuum* L. plants. Whilst varieties responded positively to HI when exposed under high temperature regime either to enhance flower growth to fruit set, as observed in the present work, or negatively to LI which ended flower growth abruptly in high abscission (Jaafar 2002), low temperature (14 °C) imposed a very pronounced effect on reproductive growth and development to retain flowers to fruit-set that no HI could compensate for the distorted effect of the reduced temperature on fruit formation. Low temperature also hampered the reproductive growth from bud emergence to anthesis and finally to maturity stage. It also induced various abnormalities in petals, stamen and gynoecium development, flower and fruit shape although the development of sepal was spared.

Low temperature (14 °C) used in this work might have decreased the pollen viability and germinability of both varieties allowing poor or no fertilization, and ultimately forming parthenocarpic fruits (Polowick & Sawhney 1985; Aloni et al. 1999; Adams et al. 2001). Aloni et al. (1999) also suggested that flower abnormality under low temperature was partly controlled by the source-sink relationship that increased assimilates translocation to flower buds under low night-time temperature (12 °C) subsequently caused deformation of fruits. According to Rylski (1978), there exist varietal differences in susceptibility to various fruits malformations induced by adverse temperatures, which was also observed in tomato. However, in this study varietal differences in susceptibility of BS and BB to low temperatures did not occur, expressing in equal and total fruit malformation in both varieties at all flower levels although the number of fruit lobes and fruit length were governed by varietal exposure to different temperatures regimes. BS being a tropical selection seemed to response positively to lowest temperature giving rise to highest number of lobes, whilst BB being a temperature selection was more sensitive to lowest temperature resulting in lowest number of fruit lobes. Although highest temperature regime produced longest fruit size in the tropical selection variety BS, BB variety of temperate selection seemed to be more sensitive to lowest temperature regime to exhibit the shortest fruit length, implying that the tropical selection may have a broader temperature base than the temperate selection to withstand both the highest and lowest temperature regimes imposed (Jaafar 1995). It will be interesting to further examine the baseline temperatures that may have promoted varietal differences in pepper growth and development.

Flowers and fruits malformation induced by low temperature have also been studied in tomato and other species (Polowick & Sawhney 1985; Lynch 1990; Shuff & Thomas 1993; Lozano et al. 1998; Aloni et al. 1999; Heuvelink & Korner 2001). Subsequently, it was accompanied by formation of parthenocarpic seedless fruits, or seed-deficient condition as also observed in this current work (Rylski & Spigelman 1982; Polowick & Sawhney 1985; Adams et al. 2001). According to Rylski (1986) seedless fruits were accompanied with various degree of malformation in fruit shape. The seedless or seed-deficient small fruits produced under low temperature (15 °C) were also highly correlated with fruit weight (Rylski 1973), which remained lighter due to the small and flattened shape (Rylski 1986). The latter shape was also promoted by low night temperature in combination with high light intensity to produced fruits with diameter wider than the fruit length (Rylski & Spigelman 1982) giving rise to abnormally flattened fruits. Under high temperature regimes, normal fruits with longer than wider shape were produced as observed in the present work.

In the present work, abnormal developing flowers and fruits were also observed to produce larger flower buds and ovaries than normal flowers and fruits. Flower stalks were thicker and longer, and the individual flowers produced many more petals than normal flowers. A highly malformed style-like structure also appeared as curved protrusions at tip of the ovary. Similar morphological malformation in pepper flower parts and fruits occurred in the female sterilized plants causing deformity of the pistil (Wilson et al. 1982). Bergh and Lippert (1964) suggested that the action of some female sterile genes could be attributed to induce physiological changes, which modified the course of development of both floral and vegetative organs. In tomatoes, fruit deformation stemmed from low temperature condition during flower development also consisted of aberrations at the blossom end, either navel-like or scar-like (Rylski 1978). Similar malformation was observed in both varieties of *C. annuum* L., Blue Star and Bell Boy, under low temperature where the incompletely closed, navel-like blossom ends appeared, which were also frequently scarred regardless of the irradiance levels. The current work also corroborates the finding by Sawhney (1981) who observed carpel-like organs located around the pistil, which developed into small fruits at the side of the main central fruits from GA-induced feminization of stamens which ranged from the production of a few ovules to complete transformation of a stamen into a carpel with ovary, style, and stigma. However, these fruits from the extra carpels were distinctively deformed in shape and seedless.

Fruits malformation was not necessary the result of an absence of seeds (Rylski 1974). Abnormality could also be rooted by the environmental condition, in particular the temperature. The same temperature condition, which caused the infertility, also caused malformation in the shape of the ovary at its initial stages of flower development, thus resulting in abnormal fruits that were flat. Flat fruit originated from a flat ovary, and thickening of the style thus became an integral part of the abnormal fruit (Rylski 1986). Regardless of irradiance and varietal differences, both BS and BB exhibited similar malformation of the fruits implying a total influence of the temperature on fruit formation in which both varieties were sensitive to low temperature of 14 °C. Choice of any one variety even though from a temperate selection for growing under such climatic condition is not economic due to unmarketable harvest. With increasing temperature though, better reproductive growth responses were observed in variety BS than variety BB, indicating of a broader base line traits for BS, hence a better choice for greenhouse cultivation under tropical and fluctuating climatic condition.

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