Gas Exchange in Sweet Pepper (*Capsicum chinense* Jacq) under Different Light Conditions

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Abstract

Plants in the tropics are exposed to high radiation and consequently high temperature and evaporative demands throughout the year. Under these conditions, physiological processes and final yield may negatively affect crops. Responses of *C. chinense* to different light conditions were evaluated in open-field conditions. Two experiments were performed: In the first trial, *C. chinense* plants were grown under *Passiflora edulis* shade and under full sunlight. In the second, three light conditions (60 %, 40% and full sunlight) were assayed employing synthetic meshes. Microclimate measurements and gas exchange characteristics were evaluated. Partial shade resulted in lower VPD. Shade plants exhibited lower mean daily and total CO_2 assimilation rates compared to full sunlight plants. Partial shade induced lower stomatal aperture, regulated by light intensity; while the influence of VPD on stomata closure was less pronounced. The acclimation of sweet pepper to shade conditions was evident by lower chlorophyll Chl a/b concentrations.

Keywords: Light interception, Photosynthesis, Crop shading, Microclimate stress

1. Introduction

Variations in light intensity experienced by plants under open-field conditions can notably influence their photosynthetic activity. Therefore, any modification in the photosynthetic structure due to variations in light conditions (Osmond *et al*., 1999, Murchie et al., 2005) will also affect other metabolic processes such as growth and yield.

Within the genus *Capsicum*, the relationship between light intensity and flowering has only been evaluated under greenhouse conditions in *C. annuum*. A decrease of 60 to 90% of the radiation induced an increment in flower abscission (Aloni *et al.,* 1994) and a decrease in CO_2 assimilation rates which differed among cultivars (Aloni *et al*., 1996). The differences in CO_2 assimilation rates did not explain the differences in shade susceptibility for each cultivar, but rather the distribution of assimilates to flowers and their corresponding metabolism (Aloni *et al*., 1996). In the case of *C. annuum*, a functional decrease in photosystem II activity accompanied by an increase in accumulative exposure of photons has been observed. This trend is more pronounced in plants grown under low compared to high radiation conditions (Lee *et al.,* 1999).

To this date, the photosynthetic metabolism of *Capsicum* had not been evaluated in open-field conditions subjected to high radiations, typical of tropical regions, where plants frequently experience elevated leaf temperatures and accentuated differences in leaf to air water vapour pressure differences (VPD). The sum of these stress factors can contribute to a decrease in leaf conductance, which in turn can decrease the rates of CO_2 assimilation as well as induce reversible dynamic photoinhibition, all of which have been previously reported in different species (Lambers, *et al.,* 1998; Adams *et al*., 1999).

An attractive alternative for tropical field agriculture is to grow *Capsicum* species under shade conditions. Recently in Venezuela, Jaimez and Rada (2006) studied the effects of different shade conditions on the dynamics of flowering and fruit production of *C. chinense* growing under the shade of passion fruit vines (*P. edulis*), in the South of the Maracaibo Lake region (Venezuela). They did not find significant differences in either total number of flowers and fruits or yield. However, average fruit weight of shade plants was significantly greater. In a second experiment with shade levels (60%, 40% and full sunlight) they found significant higher yield differences for plants with 40% shade and full sunlight compared to plants with 60% shade.

Despite the detrimental effect shade may exert on gas exchange processes (Walters, 2005), shade conditions produced by a non-homogeneous cover probably offers a less stressful environment, thus improving or maintaining fruit production in a mixed crop, in which one of the cultivars establishes certain light conditions for the other (Da Matta, 2007). The shade produced by trees or other crops is characterized by light flecks with changing frequency and intensity during the course of the day. Therefore, it is evident that modifications of microclimatic conditions will affect processes such as photosynthesis and transpiration due to varying intensities of light flecks during the day. Even so, due to the heterogeneity of the canopy, a plant will receive sun flecks of varying light intensities. Partial shade under heterogeneous canopies can avoid an abrupt decrease in the available soil water content, compared to a soil exposed to full sunlight, especially during drought periods. Therefore, it is important to understand how changes in CO_2 assimilation and other metabolic processes under different light conditions are related to production parameters.

The purpose of the present study was to study the relationship between microclimate and gas exchange in *C. chinense* plants grown under varying light conditions. These light conditions were generated by a natural cover provided either by the canopy of *P. edulis* or by artificially modified covers employing different size meshes.

2. Materials and Methods

The present study was carried out in Alberto Adriani County, State of Merida, Venezuela (8^o, 32' N, 7 ^{o}37' W) at an altitude of 130 m. This region presents a mean annual precipitation of 1822 mm and a mean annual temperature of 27.9 $^\circ$C (data obtained from the Venezuelan Ministry of Environment and Renewable Natural Resources). Average monthly maximum and minimum temperatures registered during the study period oscillated between 33 and 35 ^{o}C and 19 and 23 ^{o}C, respectively (Data obtained from the Venezuelan Air Force Meteorological Station, El Aeropuerto- El Vigia). The soil was classified as a Fluventic Eutropepts, isohypertermic, and well drained (Kijeweski *et al.,* 1981). The chemical-physical analysis of the soil is shown on table 1. The cultivar employed during this study was *Pepón* which is grown in Eastern Venezuela. Jaimez (2006) gives an extensive characterization of this cultivar, while the design of both experiments mentioned ahead are described in detail by Jaimez & Rada (2006).

First Trial: *C. chinense* grown under the shade of *P. edulis.*

In this first experiment, seedlings of the cultivar Pepón were transplanted to the field 50 days after sowing (das), 1 m between plants and 1.5 m between rows. *P. edulis* vines were transplanted 65 days earlier at a distance of 12 m. Stems and branches of passion fruit plants were extended on a wire mesh which gradually provided shade to a certain group of plants. This procedure created two treatments: Plants growing in shade and plants exposed to full sunlight. Four plots for each light condition were established randomly. Each plot contained 7 plants.

Second trial: *C. chinense* grown under artificial shade.

In this second experiment, 60 days after the transplant (dat) of the Pepón seedlings, artificial shade was created employing different size meshes. In this case, three light conditions were evaluated: partial (40%), heavy (60%) and full exposure (100 %) to sunlight. Plots with 10 plants were established randomly with 3 replications for each light condition.

Gas exchange measurements

CO_2 assimilation (A), leaf conductance (Gs) and transpiration (E) measurements were carried out during periods of flowering and fruit production in both trials. First trial measurements were performed on sweet pepper plants every two and half hours at 114, 124 and 170 dat. While for the second trial these were carried out at 115, 135 and 157 dat. Measurements were performed on the second and/or third leaf, from the apex, on 4 plants in each plot for each trial, using a portable open gas exchange system (LCA4, ADC, United Kingdom). Integration of daily CO_2 assimilation curves were carried out according to Rada *et al.* (1996) in order to obtain total daily CO_2 assimilation (A_{tot}). Instant water use efficiency (WUE), defined as A/E, was estimated for all daily courses. Microclimatic variables were recorded simultaneously. Photosynthetic photon flux density (PPFD) was measured with a built-in quantum sensor incorporated into the leaf chamber. Leaf and air temperatures (4 for each treatment) were measured with chromel-alumel thermocouples (36 gauge) and relative humidity with a digital hygrometer (Extech Instruments, model 407445. United States). From these temperatures and relative humidities, leaf-air water vapour pressure differences (VPD) were determined through the equation:

$$\mathrm{VPD} = \rho_{\mathrm{leaf}} - (\rho_{\mathrm{air}} * \mathrm{RH}/100),$$

where ρ_{leaf} and ρ_{air} correspond to the saturation water vapour pressure at the given leaf and air temperatures, respectively, and RH to relative humidity (Pearcy et al., 1989).

Chlorophyll content

Several leaves, positioned among the first five nodes starting at the apex, were collected in the field, their area was determined in the laboratory and then macerated in acetone (100%) according to Arnon (1949) and Lichtenthaler and Wellburn (1983). Chlorophyll content was measured at 662 and 645 nm using a spectrophotometer (spectronic 20). Chlorophyll "a" and "b" contents were estimated using equations given by Lichtenthaler and Wellburn (1983):

$$\mathrm{Chl\ a} = 11.75\ A_{662} - 2.35\ A_{645}$$

$$\mathrm{Chl\ b} = 18.61\ A_{645} - 3.96\ A_{662},$$

where A_{645} and A_{662} are the absorbencies measured at 645 and 662 nm, respectively.

Differences in all variables were determined by analysis of variance (ANOVA) and Tukey's test was used to compare the effect of light intensities.

3. Results

Daily courses of microclimatic variables and gas exchange

The shade provided by *P. edulis* increased progressively during the trial. Due to the non-homogeneous shade to which *C. chinense* plants were subjected, mean incident PPFD received by the aerial parts of the plants was approximately 700 µmol m^{-2} s^{-1}. The partial shade produced corresponded to an approximate 30% decrease of total PPFD (Table 2). VPD during morning and noon hours was higher in plants grown under full sunlight; however, in the afternoon the values were similar in both light and shade treatments. Mean daily VPD was significantly higher under full sunlight conditions (2.3 KPa) (Table 2).

Gs responded linearly and positively with increases in VPD ($R^2 = 0.50$) (Figure 1a) in shade plants; in contrast, full sunlight plants showed a slight tendency to decrease Gs as VPD increased. Mean daily Gs under both light conditions were similar (Table 2). A also varied according to light conditions. Nevertheless, plants grown under partial shade of passion fruit reached maximum rates of 13.8 µmol m^{-2} s^{-1}, whereas full sunlight plants reached 18 µmolm^{-2} s^{-1}. Mean A_{max} rates (7.4 µmol m^{-2} s^{-}1) for shade plants represented 52% of the average A_{max} presented by full sunlight plants. Partial shade produced a 23% decrease ($p<0.05$) in the rates of A_{tot} (table 2). E was similar for both light conditions. Full sunlight plants showed higher water use efficiencies (WUE) (Table 2).

In the second experiment, PPFD reached 2000 µmol m^{-2} s^{-1} at noon in plants growing in full sunlight. Under 40% shade, it ranged from 1100 to 1250 µmol m^{-2} s^{-1} and for 60 % shade, it remained below 800 µmol m^{-2} s^{-1}. These differences affected VPD; with highest values obtained in plants growing in full sunlight during most of the day. In the case of the two mesh-induced shade treatments, maximum VPD did not reach 2 KPa, compared to 2.5 KPa for the passion fruit shade treatment. These values suggest that the passion fruit shade allows for higher quantities of light flecks to be intercepted by *C. chinese* plants (Table 2 and 3).

Similar to the first trial, Gs increased linearly with VPD increments ($R^2 = 0.42$) in shade treatments. In contrast, plants growing in full sunlight showed a negative linearly tendency in Gs as VPD increased (Figure 1b). Daily Gs averages were similar ($p < 0.05$) for plants grown in full sunlight when compared to plants grown under 40 % shade. Nevertheless, plants grown under 60 % shade showed a significantly lower Gs (approximately 33%) ($p <0.05$) (Table 3). Gs for full sunlight plants reached values ranging between 300 and 350 mmol m^{-2} s^{-1} under maximum PPFD (approximately 2000 µmol m^{-2} s^{-1}). Plants maintained under 40 % shade presented values of approximately 350 mmol m^{-2} s^{-1}, whereas maximum Gs values for plants under 60% shade remained below 300 mmol m^{-2} s^{-1}.

Average A_{max} for plants grown in full sunlight was significantly higher compared to the other treatments (Table 3). Mean A_{tot} for plants under 40% and 60 % shade were 15 % and 25% lower, respectively, compared to full sunlight plants. Mean E reached values of 4.4 mmol m^{-2} s^{-1} in full sunlight plants, and 3.7 and 2.6 mmol $m^{-2}s^{-1}$ in plants grown under 40% and 60 % shade, respectively. Full sunlight exposure also implied a higher daily average E which decreased as shade increased. Significant differences were found between plants in full sunlight and plants under 60% shade (Table 3).

Pepón cultivar presented a maximum mean CO_2 assimilation rate of 14 µmol m^{-2} s^{-1}, with PPFD between 1700-1850 µmol m^{-2} s^{-1} (Figure 2). Leaf conductance of partially shaded plants increased as light increased, reaching a plateau above 1100 µmol photons m^{-2} s^{-1} (Figure 3).The light compensation point occurred at a PPFD of 98 µmol m^{-2} s^{-1}. Chlorophyll a and b concentrations and chla:b exhibited a tendency to decrease as the percentage of shade increased (Table 4).

4. Discussion

Daily mean PPFD under the cover provided by passion fruit vines represented a 56% of total global sunlight, which does not necessarily constitute the total amount of incident PPFD for all of the *C. chinense* plants, due to the irregular arrangement of passion fruit stems and leaves. The heterogeneity of the passion fruit shade demonstrates that light conditions can vary depending on the sun's orientation and the arrangement of leaves and branches. Partial shade provided by passion fruit vines modified the amount of incident sunlight producing light flecks which varied from 200 to 700 µmol m^{-2} s^{-1} for a particular time of day (Jaimez & Rada, 2006). While in the case of the synthetic meshes, fluctuations in the intensity of the light flecks varied consistently between 200 and 300 µmol m^{-2} s^{-1}.

Plant exposure to different light conditions produced changes in stomatal sensitivity to VPD. Under shade conditions, a VPD above 2 KPa did not influence stomatal closure notably due to lower light inputs. In contrast, similar VPD values induced stomatal closure in full sunlight plants. A negative linear relationship between these two variables has also been reported by Pérez (2002) for Pepón cultivar grown in the same region under non-shade conditions. These results are probably a consequence of higher leaf temperatures and probably lower soil water availability experienced by non-shade plants. However, stomatal closure was not severe enough to induce a drastic decrease in transpiration rates. On the contrary, despite these environmental conditions, stomatal conductance remained higher in the majority of plants at all hours when compared to *C. chinense* plants cultivated under passion fruit shade. It seems that under normal field conditions, partial shade induces lower stomatal aperture regulated by light intensity. Under these conditions the influence of high VPD on stomatal opening is less pronounced.

It is evident that a partial shade above 40% is adequate since it does not reduce significantly CO_2 assimilation rates in *C. chinense*, whereas a 60 % shade decreases significantly CO_2 assimilation, and in turn decreases fruit production as indicated by Jaimez and Rada (2006). Bhatt *et al.* (2006) also found lower CO_2 assimilation rates and leaf conductances with decreasing light intensity in tropical grasses and legumes. Mixed cropping systems with *C. chinense* under shade of other species can be used in tropical regions where air temperatures reach values between 32-37 °C. CO_2 assimilation rates do not decrease severely and do not have a negative influence on yield. In spite of higher CO_2 assimilation rates, plants under full sunlight can reach leaf temperatures above 36 °C during periods of high radiation. Such temperatures may produce the abortion of flowers or small fruits (Jaimez and Rada, 2006; Aloni *et al*., 1994) or can affect metabolic processes in the photosynthetic machinery. Elad *et al.* (2007) and Medany *et al.* (2008) obtained higher yields for C. *annuum* under net covers compared to plants grown in open fields. It seems that species of Capsicum grown under partial shade can produce higher yields. Maximun CO_2 assimilation rates are achieved between 1500-1600 µmol m^{-2} s^{-1} (Jaimez *et al*., 2005) which also suggests that species of Capsicum may be photoinhibited.

Leaf conductance was reduced under 60 % shade resulting in lower E. However, plants under 40% shade exhibited similar leaf conductances to those of full sunlight. This can be attributed to limitations on maximum stomata aperture by the high VPD under non shade conditions.

Chlorophyll content

Johnson *et al.* (1993a,b) emphasize that there is no correlation between chlorophyll or chl a/b and the habitat from which a species derives. However, these authors admit a referential relative shade tolerance value that separate sun species, due to a more elevated chl a/b which is related to a lower concentration of chlorophyll a under shade conditions. These tendencies have also been observed in *Inga* species (Matsubara *et al*., 2005), rice (Murchie *et al*., 2005), and two climbing species *Stephania japonica* and *Smilax australis* (Adams *et al*., 1999), as well as in a few other crops such as mustard, spinach and peas (Anderson *et al*., 1988). The changes in the concentrations of these components demonstrate the functional plasticity of *C. chinense* to sun and shade conditions. Walters (2005) established that the relation chl a/b is an accurate indicator of acclimation capacity in plants, and in the case of *C. chinense* apparently three months of partial shade are sufficient to induce changes in the structure of the photosynthetic components and to the acclimation to fluctuations in incident light. This change is accompanied by a significantly higher specific leaf area shown by plants grown under partial shade (Jaimez and Rada, 2005).

Figure 4 represents a conceptual scheme that links the various physiological processes that influence production in *C. chinense* under different light conditions. *C. chinense* responds quickly to different shades and the major variable conditions indicative of acclimation are decreased chl a/b levels (Walters, 2005). Under the conditions of this study, any type of shade given by another plant, not just the evaluated *P.edulis*; will involve an environment where VPD will be lower than in conditions of full exposure to full sunlight and will reduce stress, especially during maximum radiation periods. Depending on the extent of light reduction, this may have two different impacts on yield. Light reductions greater than 40 % will result in approximately 30% reductions in CO_2 assimilation due to the lack of light to maintain high rates of electron transfer and NADPH generation coupled to the process of reduction of CO_2 in the Calvin cycle. This leads to an approximate 26 % reduction in fruit production (Jaimez and Rada, 2006). When light input is reduced by less than 40 %, it does not significantly limit the photosynthetic process and fruit production is maintained at a similar level compared to that of full sunlight plants. It is important to point out that sun flecks that enter through the branches and leaves of passion fruit vines create a very dynamic environment for *Capsicum* plants underneath. Even maximum light intensities may be recorded for very short time periods as sun flecks in plants under 30-40% shade.

Higher rates of photosynthesis were observed in daily averages and overall terms in *C. chinense* cultivated under open field conditions. On the other hand, transpiration is not as efficient in decreasing leaf temperature to optimal settings for photosynthesis in moments of high PPFD. Consequently, leaf temperatures reach higher values which may have negative impacts on enzymatic processes or increase photorespiration and decrease CO_2 assimilation rates while PPFD remains high. There is evidence that high leaf temperatures induce loss of flowers and small fruits in *C. annuum* (Aloni *et al.*, 1994) and therefore decreases fruit production. *C. chinense* also has a similar behavior, but flower loss is not high enough to produce significant falls in fruit production.

It seems that in this species high light has a more serious effect upon fruit development. Jaimez and Rada (2006) show that light conditions do not affect the dynamics or the amount of mature flowers. However larger fruits were obtained under shade conditions.

In conclusion, partial shade in environments with average temperatures above 32 ^{o}C create an environment characterized by lower VPD and constant changes in incident light intensity for *C. chinense*. Under these conditions this species shows both physiological (decrease chl a/b) acclimation mechanisms. Even though A decreases slightly in partially shaded plants, yields are similar to those of plants grown in full sunlight. Partial shade induces lower stomata aperture as it is regulated by light intensity. Under partial shade the effect of high VPD on aperture of stomata is less pronounced.

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Table 1. Texture and chemical composition of the soil in the area of El Vigia, Venezuela

Depth (cm)	**S %**	**L %**	**C %**	**Texture**	**OC %**	**N %**	**P ppm**	**K ppm**	**Mg ppm**	**Na ppm**	**Ca ppm**
0-20	53.6	38.6	6.8	Fa	0.35	0.06	38	97.5	70	42.1	309

S: sand, L: lime, C: clay, OC: organic carbon

Table 2. Mean of Photosynthetic photon flux density (PPFD, µmol m^{-2} s^{-1}); transpiration (E, mmol m^{-2} s^{-1}); CO_2 assimilation (A, µmol m^{-2} s^{-1}); maximum CO_2 assimilation ($A_{max,}$ µmol m^{-2} s^{-1}); leaf conductance (Gs, mmolm^{-2}s^{-1}); leaf temperature (Tf, ^{o}C); leaf-air vapour pressure difference (VPD, kPa); total CO_2 assimilation (A_{tot}, mmol m^{-2}), water use efficiency (WUE, µmol mmol^{-1}) of *C. chinense* plants fully exposed to sunlight and shaded under passion fruit. Standard errors are given in parentheses. Data include measurements of three days.

Light condition	**PPFD**	**E**	**A**	**A_{max}**	**Gs**	**Tf**	**DPV**	**A_{tot}**	**WUE**
Full sunlight	1234^{a}*(230.3)	4.3 (0.6)	8.5^{a} (1.5)	14.2^{a}(0.3)	232.6 (21)	33.6 (1.1)	2.3^{a}(0.2)	205.4^{a} (14.3)	2.0^{a}(0.3)
Shaded	702^{b}80.3)	3.9 (0.6)	5.1^{b} (1.0)	7.4^{b}(0.8)	246.4 (32)	31.7 (1.8)	1.7^{b}(0.1)	157.1^{b} (27.3)	1.3^{b}(0.1)

* Values in each column with different letters are significantly different (Tukey test $p < 0.05$).

Table 3. Mean photosynthetic photon flux density (PPFD, µmol m^{-2} s^{-1}); transpiration (E, mmol m^{-2} s^{-1}); CO_2 assimilation (A, µmol m^{-2} s^{-1}); maximum mean CO_2 assimilation ($A_{max,}$ µmol m^{-2} s^{-1}); leaf conductance (Gs, mmolm^{-2}s^{-1}); leaf temperature (Tf, ^{o}C); leaf-air vapour pressure difference (VPD, kPa); total CO_2 assimilation (A_{tot}, mmol m^{-2}); water use efficiency (WUE, µmol mmol^{-1}) for *C. chinense* plants exposed to full sunlight and under two different light conditions (40 and 60 % shade). Standard errors are given in parentheses

Shade %	**PP$\boxed{\text{FD}}$**	**E**	**A**	**A_{max}**	**Gs**	**Tf**	**DPV**	**A_{tot}**	**WUE**
Full sunlight	1519^{a}*(77.0)	4.39^{a} (0.9)	9.6^{a} (1.2)	13.1^{a} (1.1)	252^{a} (16)	34.11^{a}(0.1)	2.21^{a} (0.1)	244^{a} (38)	2.2(0.3)
40	931^{b}(26.1)	3.72^{a} (0.5)	8.2^{ab}(1.2)	9.40^{b} (1.3)	250^{a} (28)	32.6^{b} (0.3)	1.64^{b} (0.1)	209^{ab} (50)	2.2(0.2)
60	593^{c}(19.4)	2.64^{b} (0.23)	6.6^{a} (0.69)	8.98^{b}(1.1)	171^{b} (12)	32.08^{c} (0.23)	1.48^{b} (0.01)	190^{b} (18)	2.5(0.3)

* Values in each column with different letters are significantly different (Tukey test $p < 0.05$).

Table 4. a and b Chlorophyll concentration (µmol chlorophyll m^{-2}).

in *C. chinense* under three light conditions. Standard errors are given in parentheses.

% shade	**Chl a**	**Chl b**	**Chl a/b**	**Chl a+b**
Full sunlight	263^{a}*(9.5)	194(18.5)	1.39(0.09)	457(20.2)
40	207^{b}(8.6)	188 (15.8)	1.11(0.08)	395 (21.2)
60	197^{b} (8.1)	172(4.2)	1.14(0.04)	369(9.3)

* Values in each column with different letters are significantly different (Tukey test $p < 0.05$).

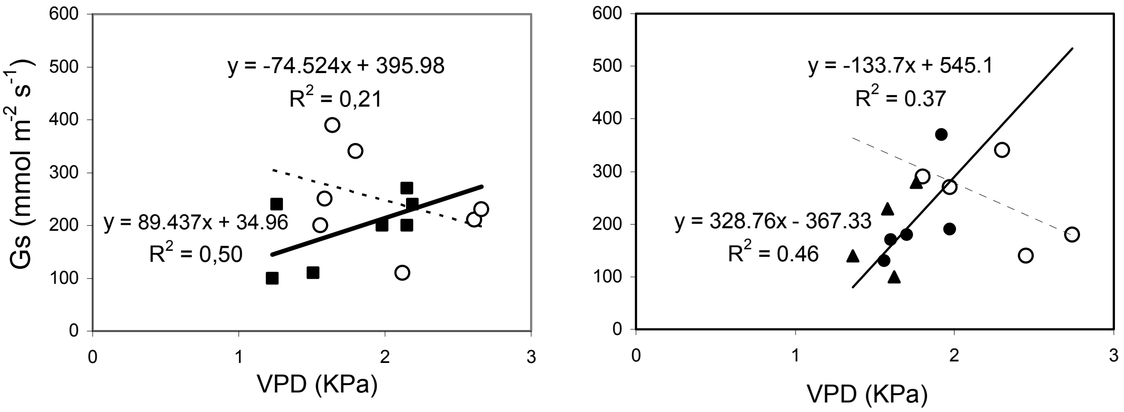

Figure 1. Relationship between VPD and Gs in *C. chinense* plants exposed to full sunlight (○), under the shade of a *P. edulis* (■), and under the shade of 40% (●) and 60% (▲) meshes. Dashed lines correspond to full sunlight plants, solid lines to shaded plants.

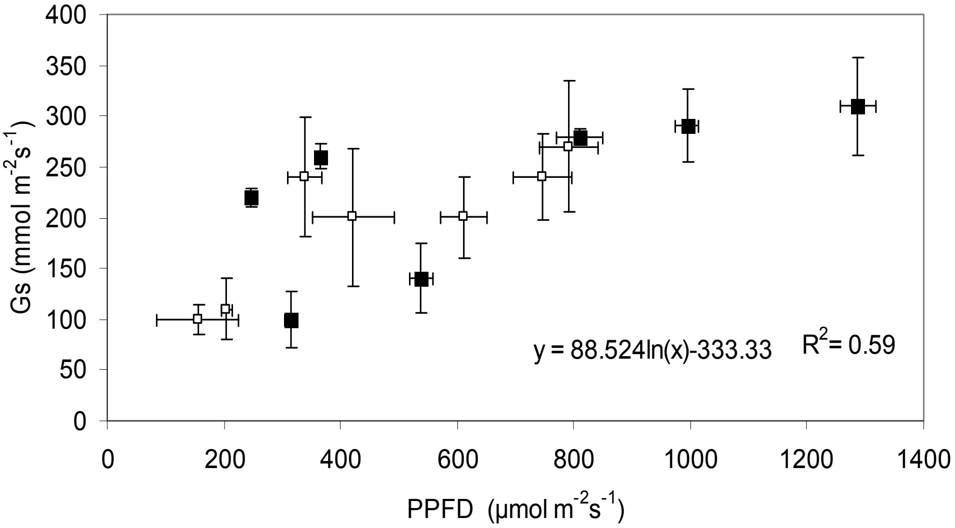

Figure 2. Relationship between PPFD and CO_2 assimilation for *C. chinense* under full sunlight: Full sunlight trial 1(Δ), full sunlight trial 2 (○); and shade: shade of *P. edulis* (■), shade of mesh 40 % (●) and 60 % (▼). Each point corresponds to the mean of 15 measurements. A=13.5*-97.8+ PPFD /97.8+554.1+PPFD, R^2=0.68.

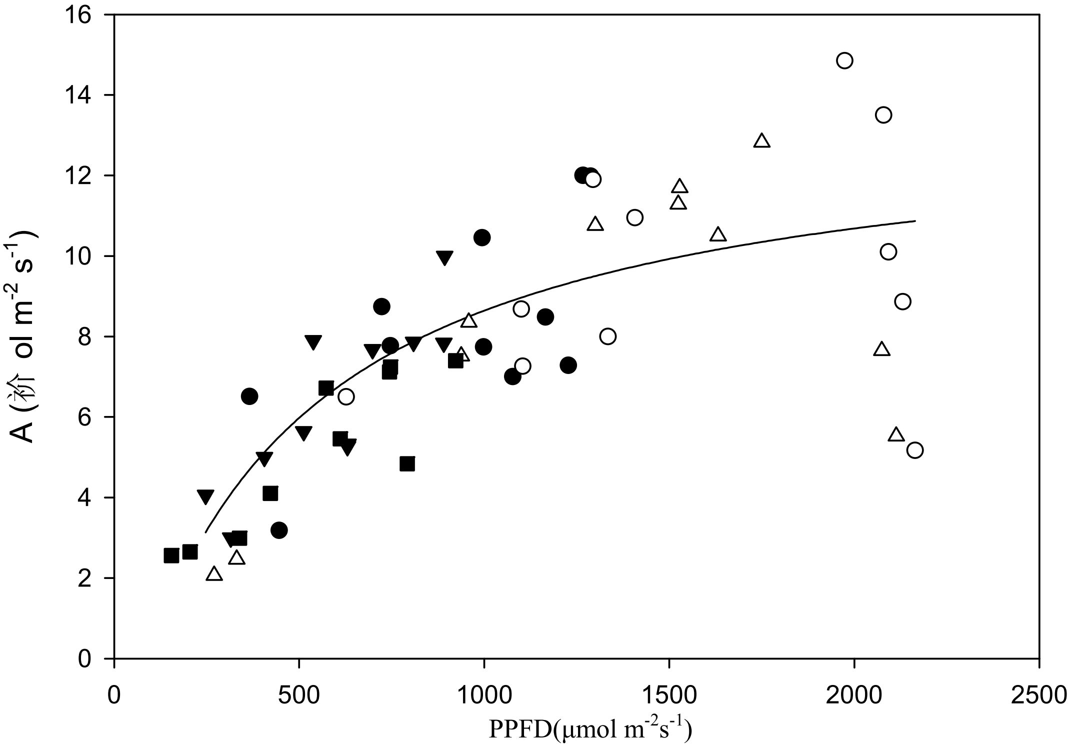

Figure 3. Effect of PPFD on Gs in *C. chinense* plants under shade of *P. edulis* (○) and under artificial shade of synthetic meshes (●). Bars are standard errors.

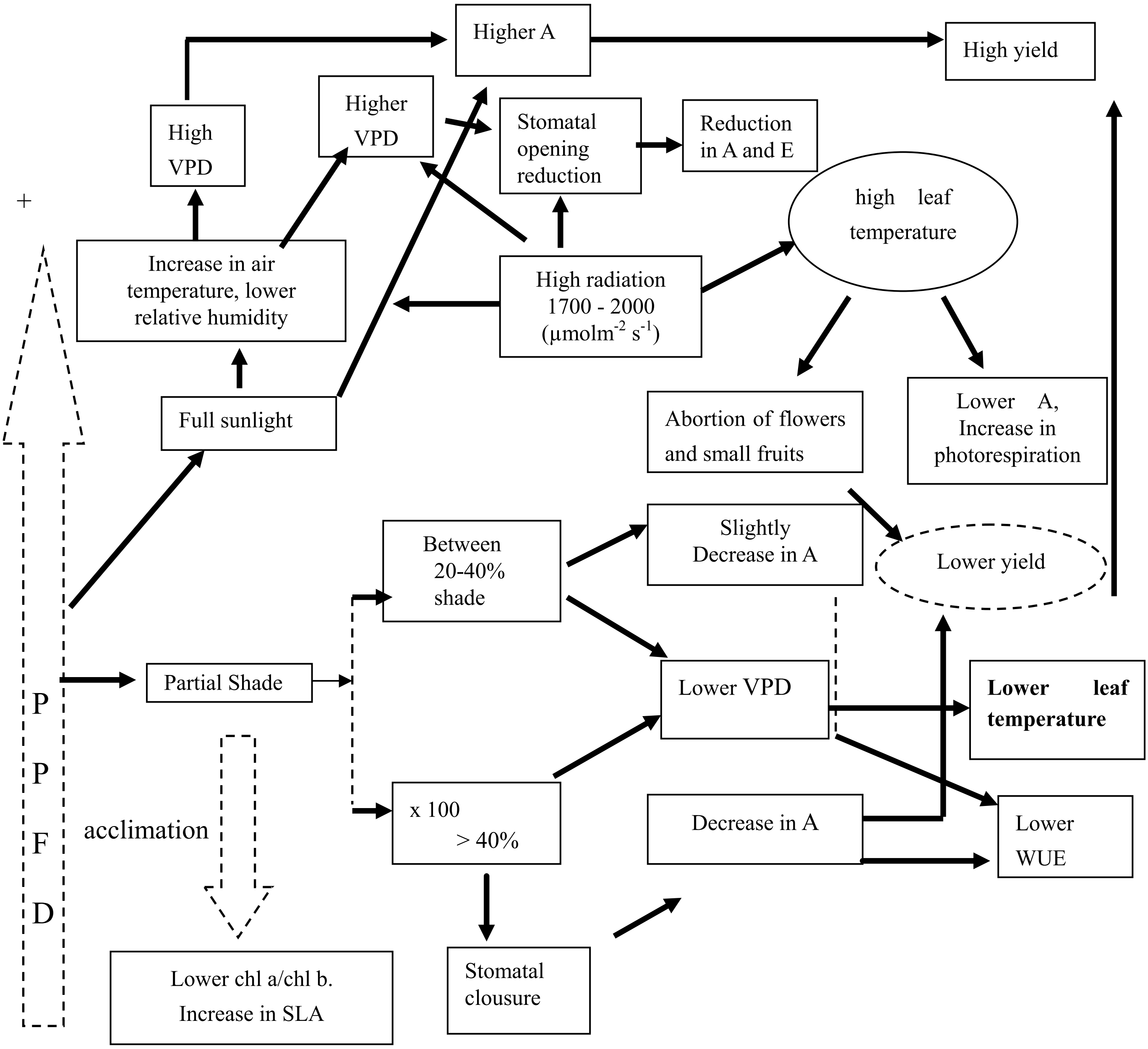

Figure 4. Effects of different light conditions on different components of the microclimate and its consequences on morphological and physiological processes in *C. chinense*.