Journal BiNET
Scientific Publication

Published with Open Access at Journal BiNET
Vol. 24, Issue 01: 1977-1989
Journal of Bioscience and Agriculture Research

Journal Home: www.journalbinet.com/jbar-journal.html

Reduced stomatal conductance and irradiance account for soybean [*Glycine max* (L.) Merrill] yield decline in maize-soybean intercrop

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Article received: 07.12.19; Revised: 26.03.20; First published online: 15 April 2020.

ABSTRACT

An increase in human population and urbanization has reduced availability of agricultural land making intercropping a system of choice amongst farmers with small land holdings. A study to determine the effect of soybean [Glycine max (L.) Merrill] and maize (Zea mays) intercropping on the interception of photosynthetically active radiation, stomatal conductance and yield of soybean was conducted in Siaya, Busia and Nakuru counties in Kenya during 2018 season. The experiment was laid out in a randomized complete block design (RCBD) and had three replicates. It had seven treatments; sole maize, sole soybean, within row intercropping, 1M:1S row pattern, 2M: 2S row pattern, 2M: 1S row pattern, 2M: 1S row pattern, and 1M:2S row pattern. Collected data were analyzed using analysis variance (ANOVA) using the linear mixed model for RCBD with a factorial treatment arrangement in the Genstat 18th edition. Soybean leaf chlorophyll content under intercropping was 21.16% more than chlorophyll content attained under sole cropping. Intercropping reduced soybean stomatal conductance, interception of photosynthetically active radiation and grain yield by 42.15, 78.88 and 83.85% respectively, compared to mono-cropping. Intercropping of maize and soybean was more productive than sole cropping and that maize was a more competitive crop than soybean in the mixture. Planting maize and soybean in 1M: 1S row pattern led to relatively higher soybean yields compared to other row patterns and is recommended for intercropping of the two crops in Kenya.

Key Words: *Intercropping, Nodulation, Photosynthesis, Row pattern and Sole cropping*

Cite Article: Mwamlima, L. H., Cheruiyot, E. K. and Ouma, J. P. (2020). Reduced stomatal conductance and irradiance account for soybean [*Glycine max* (L.) Merrill] yield decline in maize-soybean intercrop. Journal of Bioscience and Agriculture Research, 24(01), 1977-1989.
Crossref: https://doi.org/10.18801/jbar.240120.242

I. Introduction

Intercropping is the agricultural practice of cultivating two or more crops on the same piece of land at the same time (Malèzieux et al., 2009). Multiple cropping systems are estimated to account for 15-20% of world food production and the amount of land devoted to intercropping varies from 17 to 94% (Vandermeer, 1989; Altieri, 1999). In Kenya, soybean is mostly grown by smallholder farmers under intercropping with maize and newly planted sugarcane (Collombet, 2013). An increase in the human population and urbanization has reduced the availability of agricultural land, making intercropping a system of choice amongst farmers with small land holdings. Intercropping allows more efficient use of plant growth resources which include light, soil, water and mineral nutrients when component crops differ in peak demand and competitive ability (Szumigalski and Van Acker, 2008). Full canopy cover from component crops in intercropping helps reduce the impact of raindrops leading to a reduction in soil loss (Bybee-Finley and Ryan, 2018). Deep roots of component crops penetrate the soil and acquire water and mineral nutrients from deeper soil horizons while shallow roots hold the soil above ground thereby reducing runoff (Lithourgidis et al. 2012). Intercropping with legumes improves soil fertility using biological nitrogen fixation (BNF). After harvest, decaying plant biomass are sources of nitrogen and other nutrients upon mineralization for use by subsequent crops (Bybee-Finley and Ryan, 2018). Intercropping reduces risks of crop failure in areas prone to droughts and floods making it much less risky than monocropping (Eskandari, 2012). Intercropping reduces lodging of crops, thus minimizing disease, infections, mechanical damage and increases efficiency of light capture. Intercropping encourages crop diversification thereby reducing labour costs (Mousavi and Eskandari, 2011). For organic farming, intercropping helps to produce safe and nutritious food that help improve healthy living amongst consumers. Most important is the role intercropping plays in mitigating soil moisture loss through providing enough soil cover from crop canopies. Because of its biological, environmental and economic advantages, intercropping will continue to play important roles in improving production and productivity of marginal lands. While this is so, poorly planned intercropping system, coupled with inappropriate choice of cultivars, has the potential of reducing yields of the intercrops through increased competition for nutrients, water and light. Reduced light intensity which may arise from shading by a taller component of an intercrop has the potential to influence morphological and physiological processes of an understory crop species.

Previous studies have provided some insights into morphological and yield responses of soybean under intercropping with maize. Obtained results have often been contradictory and varied with location studies were conducted. Soybean and maize intercropping studies by Gong et al. (2015) and Kamara et al. (2017) reported high chlorophyll 'a' levels in soybean leaves under intercropping relative to sole soybean while the net photosynthesis rate was significantly reduced under intercropping. Photosynthetically active radiation reaching soybean leaves were significantly reduced by taller maize plants unlike in monocropping. Fan et al. (2018) reported that chlorophyll 'a' content, net photosynthesis rate and stomatal conductance in soybean grown under intercropping with maize was significantly lower compared to sole soybean both at vegetative (V5) and reproductive (R1) stages of soybean plant growth. The net photosynthesis rate varied with the spatial row arrangement with 2:2 row arrangement registering higher net photosynthesis rate compared to 1:1 row arrangement. Zhang et al. (2013) indicated that leaf chlorophyll content, net photosynthesis rate, stomatal conductance and transpiration rate in soybean intercropped with maize was higher compared to sole soybean at vegetative, flowering and pod filling stages of soybean. This calls for the need to continuously investigate and understand the functionalities of intercropping systems at physiological level which would help reduce potential impediments that may limit intercropping as a system of choice to improve crop yields. This study, therefore, determined the effect of soybean and maize intercropping on interception of photosynthetically active radiation, stomatal conductance and yield of soybean.

II. Materials and Methods

Sites description: The experiment was conducted at three sites in Kenya; Siaya Agriculture Training Centre farm [0^{0}3' N; 34^{0}17' E; 1270 meters above sea level (m.a.s.l.)] in Siaya County, Busia prison farm (0^{0}45' N; 34^{0}25' E; 1253 m.a.s.l) in Busia County and at Egerton University agronomy teaching and research farm (0^{0}22' S; 35^{0}56' E; 2267 m.a.s.l.) in Nakuru County. All sites have a bimodal rainfall pattern with long rains from March to June and the short rains start from September to November. Mean temperatures for the sites in Siaya, Busia and Egerton University are 21^{0}C, 22^{0}C and 17^{0}C, respectively.

Experimental design and treatments: The experiment was laid out in a randomized complete block design (RCBD) with 3 replicates. There were five soybean and maize intercropping arrangements and two sole treatments of soybean and maize making a total of 7 treatments (Table 01). Gross plot sizes were 4.5 m long and 4 m wide (18 m^2) while net plot sizes were 3 m by 3 m (9 m^2). Maize rows were spaced at 75 cm apart while soybean rows were spaced at 45 cm for sole treatment, 37.5 cm apart for 1:1 and 2:1 treatments and 25 cm apart for 2:2 and 1:2 treatments. In the within row intercropping treatment, soybean was planted in-between maize hills.

Table 01. Description of experimental treatments

No.	Treatment
1	Sole soybean
2	Sole maize
3	Within row (soybean planted in-between maize stands in the same row)
4	1M:1S row ratio (1 row of maize followed by 1 row of soybean
5	2M: 2S row ratio (2 rows of maize followed by 2 rows of soybean.
6	2M:1S row ratio (2 rows of maize followed by 1 row of soybean)
7	1M:2S row ratio) 1 row of maize followed by 2 rows of soybean)

M = Maize; S = Soybean

Planting and crop management: Soybean cultivar DPSB 19 and Kenya Seed maize cultivar 513 were used in the experiment. Planting was done on 19th March 2018 in Siaya, 20th March 2018 in Busia and on 30th March 2018 at Egerton University. Soybean seed was inoculated with BIOFIX *(Bradyrhizobium japonicum)* inoculant strain USD 110 from Mea Limited–Kenya at the rate of 10 g kg^{-1} of seed prior to planting. For soybeans, triple super phosphate and muriate of potash fertilizers were used at the rates of 30 kg P_2O_5 ha^{-1} and 30 kg K_2O ha^{-1} respectively as basal dressing fertilizers. Soybean was planted at a within row spacing of 10 cm while maize was planted at a spacing of 25 cm between hills. Basal dressing of maize was done using 41 kg N ha^{-1}, 60 kg P_2O_5 ha^{-1} at planting and then top dressed with 60 kg N ha^{-1}. Fall armyworm (*Spodoptera frugiperda*) in maize was controlled using Lufemtron 50g per litre (Match 50 EC) at the rate of 25 milliliters in 20 liters of water. The application of insecticide was made twice, one at maize vegetative stage and the second at tasseling stage.

Data collection

Root nodulation: Total number of nodules per plant was assessed by counting number of nodules formed on five plants randomly selected in a net plot at 50% flowering stage.

Intercepted photosynthetically active radiation (% of incoming PAR): Intercepted photosynthetically active radiation (IPAR) was measured at soybean 50% flowering and 50% poding stages using an AccuPar Ceptometer (LP-80 PAR/LAI Decagon Devices, USA). For intercropped treatments, IPAR measurements were done on top of maize and soybean plants, and 10 cm above ground level. For sole treatments, IPAR was measured above and below canopies of maize and soybean crops. Intercepted photosynthetically radiation (IPAR) was determined as a percentage of incoming photosynthetically active radiation (PAR) using a modified formula by Purcell (2000).

$$IPAR\ (\%) = \left[1 - \left(\frac{PAR_b}{PAR_a}\right)\right] \times 100 \qquad \text{Eq. (1)}$$

Where,

$IPAR$ = intercepted photosynthetically active radiation (PAR);
PAR_a is PAR (μmol m^{-2} s^{-1}) measured above soybean canopy and
PAR_b is PAR (μmol m^{-2} s^{-1}) measured below soybean canopy

Chlorophyll content determination (Chlorophyll Content Index- CCI): Total leaf chlorophyll content was measured using chlorophyll meter (CCM-200-OPTI-Sciences, USA) on a third trifoliate leaf from the top of the plant at vegetative (V5) and 50% flowering stages. Three plants were measured in a net plot and measurements were done between 12.00-13.00 hours.

Measurement of stomatal conductance (mmol H_2O m^{-2}s^{-1}): Stomatal conductance was determined on three plants per plot at 50% flowering and 50% podding stages of soybean growth on the abaxial side of a middle leaflet of a third trifoliate leaf from the top of the plant using a steady state leaf porometer (SC1, Decagon Devices, USA). It was measured between 12.00 - 14.00 hours on sunny days (Mwamlima et al., 2019).

Determination of photosynthesis (µmol CO_2 m^{-2} s^{-1}) and transpiration (mmol H_2O m^{-2} s^{-1}) rates: Leaf photosynthesis and transpiration rates were determined on two plants per plot at 50% flowering stage of soybean on abaxial side of a middle leaflet of a third trifoliate leaf from the top of the plant. Photosynthesis and transpiration rates were measured between 12.00 - 14.00 hours during sunny days using a TPS-2 (V2.02-PP systems Inc., USA) portable photosynthesis system (Mwamlima et al., 2019).

Crop yield and yield components: Number of pods per plant was determined from an average number of pods borne on ten plants per treatment. Pod length was measured using a 30 cm ruler on 20 pods randomly picked from harvested pods in each treatment. Grain yield was from plants harvested from a net plot when pods had dried. Dried pods were then threshed, and grains separated. The weight of sun dried grains was adjusted to soybean storage moisture content of 12 % (Famurewa and Raji, 2011).

Productivity of intercropping: Intercropping productivity was assessed using land equivalent ratio (LER) equation below as described by Malèzieux et al. (2009).

$$LER = \frac{Y_{ia}}{Y_{sa}} + \frac{Y_{ib}}{Y_{sb}} \qquad \text{Eq. (2)}$$

Where,

LER = land equivalent ratio; Y_{ia} = intercrop yield of maize;
Y_{sa} = yield of sole maize; Y_{ib} = yield of intercrop soybean and
Y_{sb} = yield of sole soybean.

Competitive ratio (CR) as a measure of competition between crop species was determined using the equation below as described by Dhima et al. (2007).

$$CR_{maize} = \frac{LER_{maize}}{LER_{soybean}} \times \frac{Z_{lm}}{Z_{ml}} \qquad \text{Eq. (3)}$$

$$CR_{soybean} = \frac{LER_{soybean}}{LER_{maize}} \times \frac{Z_{ml}}{Z_{lm}} \qquad \text{Eq. (4)}$$

Where,

CR_{maize} = competitive ratio for maize;
$CR_{soybean}$ = competitive ratio for soybean;
LER_{maize} = land equivalent ratio for maize;
$LER_{soybean}$ = land equivalent ratio for soybean;
Z_{lm} and Z_{ml} = proportions of soybean and maize in the mixture.

Statistical analysis: Data obtained were checked for the fulfillment of analysis of variance (ANOVA) assumption of normality by using Shapiro-Wilk normality test in Genstat release 18. Data that did not conform to the ANOVA assumption of normality were transformed using log base 10 [log 10(x+c)]before analysis. Data were then subjected to ANOVA using the linear mixed model for RCBD in Genstat (Restricted Maximum Likelihood-REML).

III. Results and Discussion

Intercepted photosynthetically active radiation: Intercepted photosynthetically active radiation (IPAR) by soybean plants at 50% flowering stage significantly (p=0.001) varied with spatial row arrangement and sites. At 50% pod development stage, IPAR significantly (p=0.001) changed with row pattern (Figure 01). The highest IPAR at both growth stages was under sole soybean treatment. While within row intercropping of maize and soybean had the lowest IPAR at 50% flowering, all other intercropping treatments had a non-significant difference. Except for sole soybean treatment which had the highest IPAR at 50% podding stage, all intercropping treatments had a uniform interception of photosynthetically active radiation. Intercepted photosynthetically active radiation at 50% pod development stage was the highest in Busia (34.34 µmol m^2 s^{-1}) followed by Siaya (22.28 µmol m^2 s^{-1}) and low at Egerton University (15.37 µmol m^2 s^{-1}).

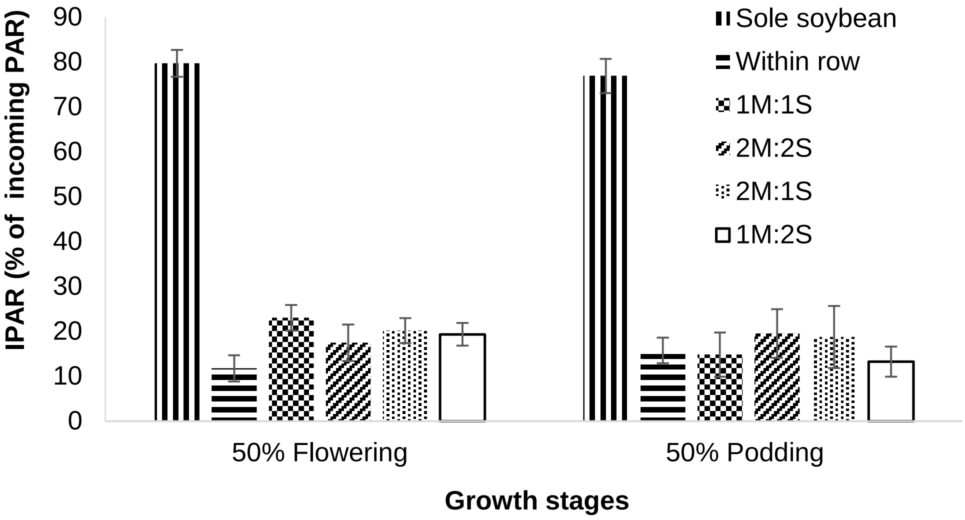

Figure 01. Effect of maize and soybean intercropping on intercepted photosynthetically active radiation (IPAR) by soybean canopy. Vertical bars represent standard error, values significantly different at p=0.001.

Chlorophyll content: The interaction of spatial row arrangement and sites had a significant effect on soybean leaf chlorophyll content at 50% flowering (p=0.001) and 50% pod development (p=0.05) stages (Table 02). The highest leaf chlorophyll content at 50% flowering was under 2M: 2S treatment at Egerton University while sole soybean treatment in Busia had the lowest chlorophyll content index. At 50% pod development stage, the highest chlorophyll content was under 2M:1S treatment in Siaya while the least chlorophyll content was under 2M:1S treatment in Busia. Overall, leaf chlorophyll content under intercropping treatments was 21.16% more than leaf chlorophyll content registered under sole soybean treatment.

Table 02. Effect of maize and soybean intercropping on soybean leaf chlorophyll content

Treatments	Soybean leaf chlorophyll content (CCI)							
	50% Flowering stage				50% Podding stage			
	Busia	EU	Siaya	Mean	Busia	EU	Siaya	Mean
Sole soybean	28.49	33.65	38.23	33.46	42.85	39.90	39.54	40.76
Within row	46.05	56.59	34.79	45.81	49.60	46.87	48.55	48.34
1M:1S	49.76	55.10	34.04	46.30	38.37	49.91	47.14	45.14
2M:2S	43.73	59.40	36.84	46.66	46.50	44.92	46.47	45.98
2M:1S	44.49	55.18	36.80	45.49	37.98	48.55	58.21	48.25
1M:2S	46.15	55.48	37.15	46.26	45.55	47.86	46.68	46.70
Mean	43.11	52.56	36.31		43.48	46.34	47.76	
	p-value	SED	CV%		p-value	SED	CV%	
Row pattern	<0.001	2.169			0.047	2.484		
Site	<0.001	1.534			0.059	1.756		
Interaction	<0.001	3.758	10.1		0.021	4.302	11.5	

SED = Standard error of difference of means; CV = Coefficient of variation; M = maize row; S = soybean row; CCI = Chlorophyll content index; EU = Egerton University.

Stomatal conductance: Stomatal conductance significantly varied with the interaction of spatial row arrangement and sites at 50% flowering (p=0.01) and 50% pod development (p=0.001) stages (Table 03). The highest stomatal conductance was registered under sole soybean treatment in Busia at both growth stages. Within row intercropping treatment at Egerton University had the lowest stomatal conductance at 50% flowering stage while 2M:2S treatment in Busia had the lowest stomatal conductance level at 50% pod development stage.

Table 03. Effect of maize and soybean intercropping on soybean stomatal conductance

Treatments	Soybean stomatal conductance (mmol H_2O m^{-2} s^{-1})							
	50% Flowering stage				50% Podding stage			
	Busia	EU	Siaya	Mean	Busia	EU	Siaya	Mean
Sole soybean	75.6	51.2	62.0	62.9	91.0	48.1	71.9	70.6
Within row	53.0	25.3	71.9	50.1	33.6	24.7	60.6	39.6
1M:1S	62.6	41.8	69.1	57.8	52.0	39.9	64.5	52.1
2M:2S	47.6	32.1	49.8	43.2	23.1	24.1	47.0	31.4
2M:1S	68.1	43.9	63.2	58.4	43.2	33.2	52.0	42.8
1M:2S	42.2	37.8	57.5	45.8	39.5	25.5	49.9	38.3
Mean	58.2	38.7	62.2		47.2	32.6	57.7	
p-value		SED	CV%		p-value	SED	CV%	
Row pattern	<0.001	3.61			<0.001	3.84		
Site	<0.001	2.55			<0.001	2.71		
Interaction	0.005	6.25	14.40		<0.001	6.65	17.8	

SED = Standard error of difference of means; CV = Coefficient of variation; M = maize row; S = soybean row; EU = Egerton University.

Photosynthetic rate: Sole soybean treatment had the highest (p=0.05) photosynthesis rate compared to all intercropping treatments (Figure 02). Amongst intercropping treatments, 2M: 1S planting pattern had the lowest photosynthesis rate which corresponded to a 75.29% reduction compared to sole soybean treatment Planting 2 rows of soybean in between maize rows (2M:2S and 1M:2S) had higher photosynthetic rates than other intercropping treatments.

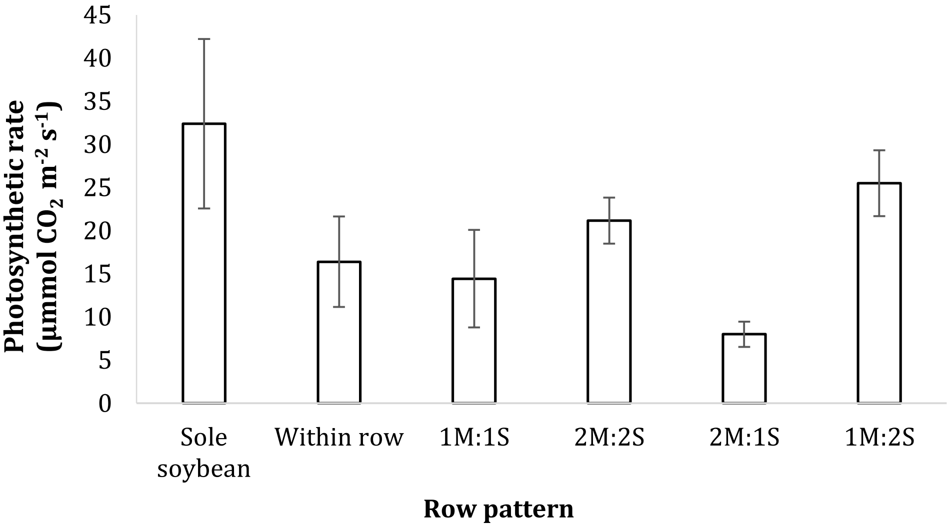

Figure 02. Effect of maize and soybean intercropping on soybean photosynthetic rate at 50% flowering stage. Vertical bars represent standard error, values significantly different at p=0.05.

Transpiration rate: Intercropping of maize and soybean in 2M:2S, 2M:1S and 1M:2S row arrangements reduced (p=0.05) soybean transpiration rate relative to mono-cropped soybean (Figure 03). Transpiration rate was not significantly different amongst intercropping treatments. There was a mean transpiration rate reduction of 41.80% under intercropping compared to sole soybean at 50% flowering stage.

Nodulation: Spatial row arrangement and sites had significant (p=0.001) independent influence on number of nodules per plant (Figure 04). Manuscript soybean registered the highest number of nodules per plant, though not significantly different from number of nodules formed under 1M:1S and 2M:1S treatments. Within row intercropping had the lowest number of nodules per plant compared to all other treatments. Across sites, Siaya recorded the highest number of nodules per plant (50.13) while mean number of nodules per plant between Egerton University (26.21) and Busia (16.56) were statistically at par.

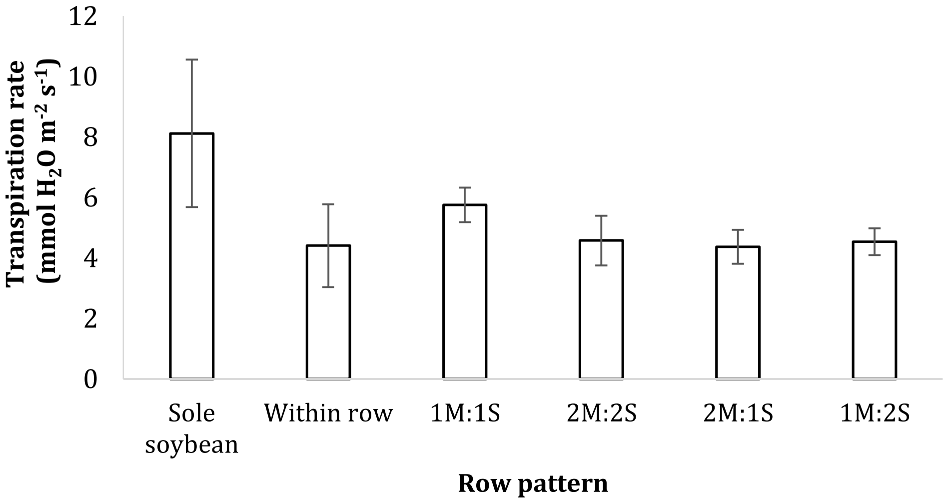

Figure 03. Effect of maize and soybean intercropping on soybean transpiration rate at 50% flowering stage. Vertical bars represent standard error, values significantly different at p=0.05.

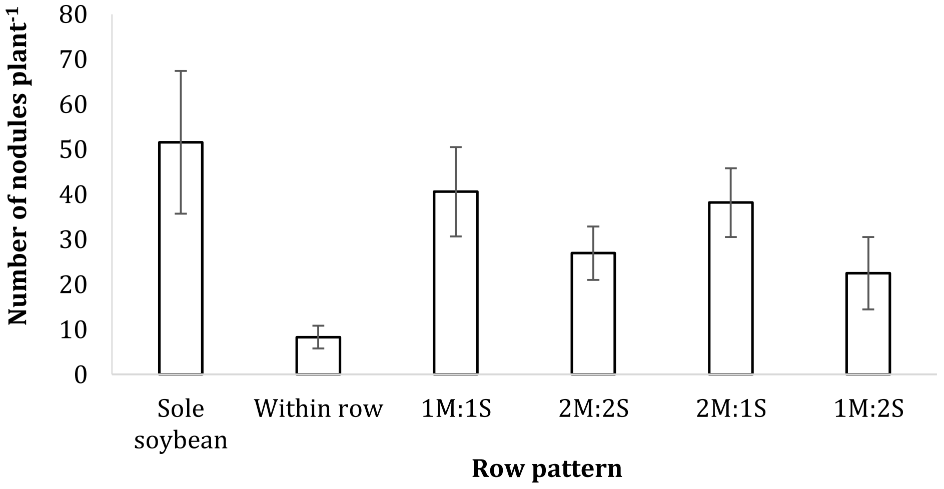

Figure 04. Effect of maize and soybean intercropping on soybean nodulation. Vertical bars represent standard error, values significantly different at p=0.001.

Number of pods: The interaction of spatial row arrangement and sites significantly (p=0.001) influenced number of soybean pods per plant (Table 04). Sole cropping treatment in Siaya had more pods per plant followed by sole soybean treatment in Busia and then sole treatment at Egerton University. The fewest pods per plant were obtained in Siaya under 2M: 1S treatment.

Table 04. Effect of maize and soybean intercropping on number of soybean pods per plant

Treatments	Number of pods plant $^{-1}$			
	Busia	Egerton	Siaya	Mean
Sole soybean	50.89	47.40	79.44	58.43
Within row	28.15	21.42	20.29	23.17
1M:1S	34.85	26.38	30.57	30.50
2M:2S	25.35	20.50	23.06	22.92
2M:1S	36.01	29.31	17.56	27.06
1M:2S	20.94	20.74	23.63	21.75
Mean	32.02	26.95	29.89	
	p-value	SED	CV%	
Row pattern	<0.001	0.265		
Site	0.055	0.188		
Interaction	<0.001	0.459	10.3	

SED = Standard error of difference of means; CV = Coefficient of variation; M = maize row; S = soybean row.

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Pod length: Soybean pod length was significantly (p=0.001) dependent on spatial row arrangement (Figure 05) and sites. Sole soybean had the longest pods compared to all other treatments though not significantly different from 1M:1S and 2M:1S treatments. On the other hand, within row intercropping had the shortest pods. Planting one row of soybean in-between maize rows (1M:1S and 2M:1S) relatively increased soybean pod length though not significantly different from pod lengths attained from 1M:2S and 2M: 2S row patterns. Across sites, the longest (3.77 cm) and the shortest (3.58 cm) pod lengths were registered in Busia and Egerton University, respectively.

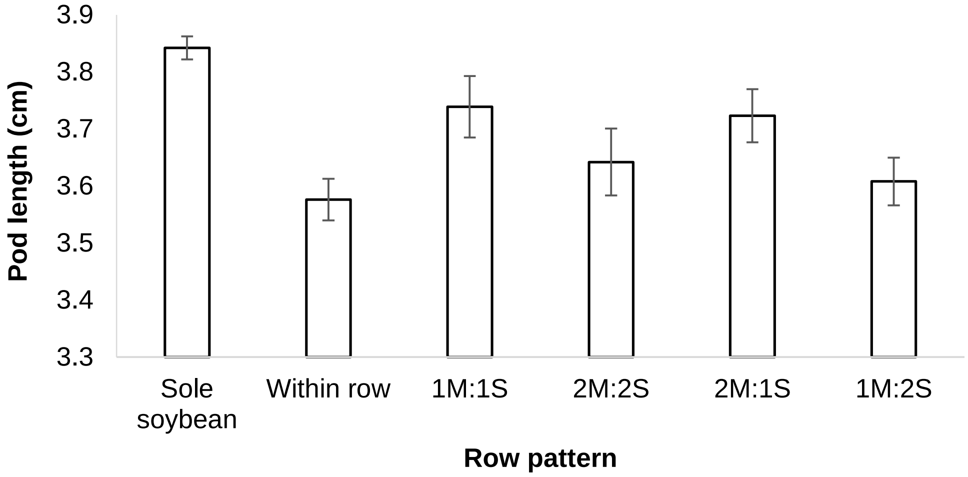

Figure 05. Effect of maize and soybean intercropping on soybean pod length. Vertical bars represent standard error, values significantly different at p=0.001.

Grain yield: The interaction of spatial row arrangement and sites had significant (p=0.01) influence on soybean grain yield (Table 05). Sole soybean treatment had the highest grain yield at all sites with grain yield being significantly higher at Siaya. Within row intercropping treatment at Egerton University had the lowest yields. Overall, there was 83.85% soybean yield reduction under intercropping compared to sole cropping.

Table 05. Effect of maize and soybean intercropping on soybean grain yield

Treatments	Soybean grain yield (Kg ha^{-1})			
	Busia	**Egerton**	**Siaya**	**Mean**
Sole soybean	1767	1450	2600	1910
Within row	310	80	237	195
1M:1S	714	339	479	499
2M:2S	667	241	672	503
2M:1S	428	136	240	254
1M:2S	540	217	450	389
Mean	667	320	633	
	p-value	SED	CV%	
Row pattern	<0.001	1.228		
Site	<0.001	0.868		
Interaction	0.004	2.126	11.3	

SED = Standard error of difference of means; CV = Coefficient of variation; M = maize row; S = soybean row.

Intercropping productivity: Results in Table 06 show that total land equivalent ratio values were more than unity indicating that intercropping was more productive than monocropping. Maize had higher partial land equivalent ratio values compared to soybean. Higher LER value of 1.28 for 1M: 1S and 1M: 2S row patterns indicate that 28% (0.28 hectare) more land area would be need by monocropping to equal productivity of intercropping. Relatedly, competitive ratio (CR) index values indicate that intercropped maize registered higher CR values in all row patterns compared to soybean.

Table 06. Land equivalent and competitive ratios of intercropping systems

Row pattern	$PLER_{soybean}$	$PLER_{Maize}$	$Total_{LER}$	CR_{maize}	$CR_{soybean}$
Within row	0.10	1.06	1.16	8.48	0.12
1M:1S	0.26	1.02	1.28	1.96	0.51
2M:2S	0.26	1.00	1.27	1.92	0.52
2M:1S	0.13	0.99	1.12	2.51	0.40
1M:2S	0.20	1.08	1.28	5.4	1.54

PLER= Partial land equivalent ratio; LER= land equivalent ratio, CR = Competitive ratio.

Intercropping maize and soybean led to a significant reduction in soybean yield. This observation is attributed to reduced stomatal conductance, IPAR, photosynthetic rate, transpiration and soybean nodulation which concurs with observations by Zhang et al. (2013); Gong et al. (2015); Tsujimoto et al. (2015); Kamara et al. (2017) and Fan et al. (2018). Crop yield is influenced principally by photoassimilates synthesis and partitioning by plants (Campillo, 2012) which has also been demonstrated in this study. Intercropped soybean had low stomatal conductance which could have limited diffusion of carbon dioxide for photosynthesis. This was further exacerbated by reduced light reaching soybean canopy. Soybean under maize received about 25% of incoming PAR which means that understory soybean experienced reduced capacity to synthesize photoassimilates to support both growth and yield formation (Mõttus et al., 2012). Shading also leads to changes in red/infrared ratio through plant canopies, which affect the structure of chloroplasts, carbohydrate portioning to cells and photosynthetic efficiency (Kasperbauer, 1987). Low red/infrared light in plant canopies has also been reported to reduce branching, which is an important component of increased grain yield (Casal, 2013). As a shade avoidance mechanism, soybean plants under intercropping treatments were taller than in sole cropping. This indicates that soybean plants under shade invested internally available resources to increase height to optimize light interception and utilization by photosynthesis. This, however, was at the expense of the reproductive growth of soybean plants leading to reductions in pod development and yield.

Soybean plant growth and yield depend on a source-strength by the photosynthetic capacity of plants (Basuchaudhuri, 2016). For optimum crop yields, crop plants require stomata to open so that carbon dioxide can pass through mesophyll cells to chloroplasts for photosynthesis to take place (Roche, 2015). Unlike in C_4 plants where stomatal conductance has minimal effect on photosynthesis, the maximum rate of stomatal conductance in C_3 plants optimizes photosynthesis and thus contributing to increased crop yields (Hetherington and Woodward, 2003; Panda, 2011). Higher levels of stomatal conductance also lead to evaporative cooling of plants, which contributes to reductions in flower and fruit abortions (Lu et al., 1994). Variations in stomatal conductance in C_3 plants has also been linked to optimization of radiation use efficiency which is a critical component for increased soybean yields (Reynolds and Pfeiffer, 2000; Condon et al., 2008). The results of this study have however shown that intercropping maize and soybean reduced stomatal conductance of understory soybean by 31.16% compared to sole soybean. Reduction in stomatal conductance ought to have therefore contributed to low soybean yield due to either compromised intake of carbon dioxide for optimization of photosynthetic process or increased flower and pod abortions.

Plants grown under shade conditions optimize light interception for photosynthesis by increasing chlorophyll content (Wittmann et al., 2001). Increases in chlorophyll content, however, means that plants are reallocating nitrogen from Calvin cycle enzymes and investing in chlorophyll biosynthesis leading to a reduction in nitrogen use efficiency of plant growth and productivity (Zhu et al., 2007). Under increased chlorophyll content, interception of PAR occurs by the adaxial chloroplasts causing light limitation on the abaxial side of the leaf (Slattery et al., 2017). This creates within leaf variations in photosynthesis which limits the efficiency of photosynthesis (Oguchi et al., 2011). Compromised photosynthetic rate leads to a reduction in the production of assimilate required for plant growth and pod development. Shading also results in increased biosynthesis of chlorophyll 'b' at the expense of chlorophyll 'a' (Shao et al., 2014). Considering that chlorophyll 'a' is a major photosynthetic pigment (Scheer, 1991), reduction in its biosynthesis may contribute to reduced photosynthetic rate in shaded plants with a resultant negative effect on plant growth and yield.

Nitrogen is a critical element for plant growth as it is an important constituent of amino acids and proteins, purine and pyrimidine in nucleic acids (Bloom, 2015). Nitrogen is also an important constituent of chlorophyll formation (Leghari et al., 2016). It is estimated that between 50-70% of nitrogen requirements for soybean growth is attained through biological nitrogen fixation (Ohyama et al., 2017). It is therefore evident that realization of increased soybean yields is dependent on good nodulation. It has however been observed from the results of this study that intercropping maize and soybean reduced soybean nodulation by about 47.0% relative to sole soybean. Reduced nodulation under intercropping could have emanated from an inadequate supply of assimilates from photosynthesis to support symbiotic association with rhizobia for nodule development (Basuchaudhuri, 2016). This could have resulted in low biological nitrogen fixation to sustain soybean reproductive growth leading to reduction in soybean grain yield. Overall, intercropped maize had a higher partial land equivalent ratio and competitive ratio than soybean, which indicates that maize had a competitive advantage over soybean. This is line with observations by Yilmaz et al. (2008) and Khonde et al. (2018) who reported competitive advantage of maize over soybean and cowpea when grown in a mixture.

IV. Conclusion

Maize and soybean intercropping reduces soybean stomatal conductance, IPAR, photosynthetic rate and root nodulation which leads to reductions in the number of pods per plant and grain yield. Planting maize and soybean in 1M: 1S and 2M: 2S row patterns led to relatively higher soybean yields compared to other row patterns. The 1M:1S row pattern is however recommended for intercropping of maize and soybean due to reduced crowdedness of plants and therefore allow farmers to work with reduced impediments compared to 2M:2S row pattern.

Acknowledgement

The study was conducted with financial assistance from the Malawi Government through a World Bank funded Agricultural Productivity Programme for Southern Africa (APPSA). Logistical assistance offered by Egerton University during the implementation of the study is sincerely appreciated.

Conflict of interest disclosure

Authors declare that no conflict of interest exists on the funding of the study and writing of the manuscript.

V. References

[1]. Altieri, A. (1999). The ecological role of biodiversity in agro ecosystems. Agriculture Ecosystem and Environment, 74, 19-31.

[2]. Basuchaudhuri, P. (2016). Source-sink relationship in soybean. Indian Journal of Plant Science, 5, 19-25.

[3]. Bloom, A. J. (2015). The increasing importance of distinguishing among plant nitrogen sources. Current Opinion in Plant Biology, 25, 10-16. https://doi.org/10.1016/j.pbi.2015.03.002

[4]. Bybee-Finley, K. and Ryan, M. (2018). Advancing intercropping research and practices in industrialized agricultural landscapes. Agriculture, 8, 1-24. https://doi.org/10.3390/agriculture8060080

[5]. Campillo, C., Fortes, R. and Del Henar Prieto, M. (2012). Solar radiation effect on crops. In Babatunde, E. B. (Ed.), Solar radiation, InTech, 152-185. Retrieved March 10, 2019 from http://www.intechopen.com/books/solar-radiation/solar-radiation-effect-on-crop-production.

[6]. Casal, J. J. (2013). Canopy light signals and crop yield in sickness and in health. ISRN Agronomy, 1-16. https://dx.doi.org/10.1155/2013/650439

[7]. Collombet, R. N. (2013). Investigating soybean market situation in Western Kenya: constraints and opportunities for smallholder producers. Wageningen University, 1-43.

[8]. Condon, A. G., Reynolds, M. P., Brennan, J., van Ginkel, M., Trethowan, R., Rebetzke, G. J., Bonnett, D. G., Richards, R. A. and Farquhar, G. D. (2008). Stomatal aperture related traits and yield potential in bread wheat. *In*: Reynolds, P. M., Pietragalla, J. and Brown, H. J. (Eds.), International Symposium on Wheat Yield Potential: Challenges to International Wheat Breeding, CIMMYT, Mexico.

[9]. Dhima, K. V., Lithourgidis, A. A., Vasilakoglou, I. B. and Dordas, C. A. (2007). Competition indices of common vetch and cereal intercrops in two seeding ratio. Field Crops Research, 100, 249-256. https://doi.org/10.1016/j.fcr.2006.07.008

[10]. Eskandari, H. (2012). Intercropping of maize *(Zea mays)* with cowpea *(Vigna sinensis)* and mungbean *(Vigna radiata)*: effect of complementarity of intercrop components on resource consumption, dry matter production and legume forage quality. Journal of Basic and Applied Scientific Research, 2, 355-360.

[11]. Famurewa, J. A. V. and Raji, A. O. (2011). Effect of drying methods on physic-chemical properties of soyflour. African Journal of Biotechnology, 10, 5015-5019. https://doi.org/10.5897/AJB10.998

[12]. Fan, Y., Chen, J., Cheng, Y., Raza, M. A., Wu, X., Wang, Z., Liu, Q., Wang, R., Wang, X., Yong, T., Liu, W., Liu, J., Du, J., Shu, K., Yang, W. and Liu, W. (2018). Effect of shading and light recovery on the growth, leaf structure, and photosynthetic performance of soybean in a maize-soybean relay-strip intercropping system. PloSOne, 13, e0198159. https://doi.org/10.1371/journal.pone.0198159

[13]. Gong, W. Z., Jiang, C. D., Wu, Y. S., Chen, H. H., Liu, W. Y. and Yang, W. Y. (2015). Tolerance vs. avoidance: two strategies of soybean (*Glycine max*) seedlings in response to shade in intercropping. Photosynthetica, 53, 259-268. https://doi.org/10.1007/s11099-015-0103-8

[14]. Hetherington, A. M. and Woodward, F. I. (2003). The role of stomata in sensing and driving environmental change. Nature, 424, 901–908. https://doi.org/10.1038/nature01843

[15]. Kamara, A. Y., Tofa, A. I., Ademulegun, T., Solomon, R., Shehu, H., Kamai, N. and Omoigui, L. (2017). Maize–soybean intercropping for sustainable intensification of cereal–legume cropping systems in northern Nigeria. Experimental Agriculture, 1-15. https://doi.org/10.1017/S001447971700056

[16]. Kasperbauer, M. J. (1987). Far-red light reflection from green leaves and effects on phytochrome-mediated assimilate partitioning under field conditions. Plant Physiology, 85, 350-354.

[17]. Khonde, P., Tshiabukole, K., Kankolongo, M., Hauser, S., Djamba, M., Vumilia, K. and Nkongolo, K. (2018). Evaluation of Yield and Competition Indices for Intercropped Eight Maize Varieties, Soybean and Cowpea in the Zone of Savanna of South-West RD Congo. Open Access Library Journal, 5, e3746. https://doi.org/10.4236/oalib.1103746

[18]. Leghari, S. J., Wahocho, N. A., Leghari, G. M., Hafeezlaghari, A., Bhabhan, G. M., Talpur, K. H., Bhutto, T. A. and Wahocho, S. A. (2016). Role of nitrogen in plant growth and development: A review. Advances in Environmental Biology, 10, 209-218.

[19]. Lithourgidis, A. S., Dordas, C. A., Damalas, C. A. and Vlachostergios, D. N. (2011). Annual intercrops: an alternative pathway for sustainable agriculture. Australian Journal of Crop Science, 5, 396-410.

[20]. Lu, Z. M., Radin, J. W., Turcotte, E. L., Percy, R. and Zeiger, E. (1994). High yields in advanced lines of Pima cotton are associated with higher stomatal conductance, reduced leaf-area and lower leaf temperature. Physiologia Plantarum, 92, 266–272.

[21]. Malèzieux, E., Crozat, Y., Dupraz, C., Laurans, M., Makowski, D., Ozier-Lafontaine, H., Rapidel, B., De Tourdonnet, S. and Valantin-Morison, M. (2009). Mixing plant species in cropping systems: concepts, tools and models. A review. Agronomy for Sustainable Development, 29, 43-62. https://doi.org/10.1051/agro:2007057

[22]. Mõttus, M., Sulev, M., Baret, F., Lopez-Lozano, R. and Reinart, A. (2012). Photosynthetically Active Radiation: Measurement and Modelling. Retrieved August 24, 2019 from https://www.researchgate.net/publication/281510241.

[23]. Mousavi, S. R. and Eskandari, H. (2011). A general overview on intercropping and its advantages in agriculture. Journal of Applied Environmental and Biological Sciences, 1, 482-486.

[24]. Mwamlima, L. H., Ouma, J. P. and Cheruiyot, E. K. (2019). Physiological response of soybean [*Glycine max* (L) Merrill to soil moisture stress. African Journal of Agricultural Research, 14, 725-735. https://doi.org/10.5897/AJAR2019.13961

[25]. Oguchi, R., Douwstra, P., Fujita, T., Chow, W. S. and Terashima, I. (2011). Intra leaf gradients of photoinhibition induced by different colour lights: implications for the dual mechanisms of photoinhibition and for application of conventional chlorophyll fluorometers. New Phytologist, 191, 146-159. https://doi.org/10.1111/j.1469-8137.2011.03669.x

[26]. Ohyama, T., Tewari, K., Ishikawa, S., Tanaka, K., Kamiyama, S., Ono, Y., Sato, T., Hatano, S., Ohtake, N., Sueyoshi, K., Hasegawa, H., Sato, T., Tanabata, S., Nagumo, Y., Fijita, Y. and Takahash, Y. (2017). Role of nitrogen on growth and seed yield of soybean and a new fertilization technique to promote nitrogen fixation and seed yield. In *Soybean*-The basis of yield, biomass and productivity. InTech, 154-185. https://dx.doi.org/10.5772/66743

[27]. Panda, D. (2011). Diurnal variation in gas exchange and chlorophyll fluorescence in rice leaves: the cause for mid-day depression in CO_2 photosynthetic rate. Journal of Stress Physiology and Biochemistry, 7, 175–186.

[28]. Purcell, L. C. (2000). Soybean canopy coverage and light interception measurements using digital imagery. Crop Science, 40, 834-837. https://doi.org/10.2135/cropsci2000.403834x

[29]. Reynolds, M. P. and Pfeiffer, W. H. (2000). Applying physiological strategies to improve yield potential. In: Royo, C., Nachit, M., Di Fonzo, N. and Araus, J. L. (Eds.), Durum wheat improvement in the Mediterranean region: New challenges. Options Mediterranéennes, 40, 95-103.

[30]. Roche, D. (2015). Stomatal conductance is essential for higher yield potential of C3 crops. Critical Reviews in Plant Science, 34, 429-453. https://doi.org/10.1080/07352689.2015.1023677

[31]. Scheer, H. (1991). Structure and occurrence of chlorophylls. Retrieved June 21, 2019 from https://pdfs.semanticscholar.org/85e1/9da78897244a742c6bb8b214e075781cfd6b.pdf.

[32]. Shao, Q., Wang, H., Guo, H., Zhou, A., Huang, Y., Sun, Y. and Li, M. (2014). Effects of shade treatments on photosynthetic characteristics, chloroplast ultrastructure and physiology of *Anoectochilus roxburghii*. PloseOne, 9, e85996. https://doi.org.10.1371/journal.pone.0085996

[33]. Slattery, R. A., VanLoocke, A., Bernacchi, C. J., Zhu, X. and Ort, D. R. (2017). Photosynthesis, light use efficiency, and yield reduced-chlorophyll soybean mutants in field conditions. Frontiers in Plant Science, 8, 549. https://doi.org/10.3389/fpls.2017.00549

[34]. Szumigalski, A. R. and Van Acker, R. C. (2008). Intercropping: land equivalent ratios, light interception and water use in annual intercrops in the presence or absence In Crop herbicides. Agronomy Journal, 100, 1145-1154. https://doi.org/10.2134/agronj2006.0343

[35]. Tsujimoto, J. A., Pedro, G., Boina, M. V., Murracama, O., Ito, S., Tobita, T., Oya, C., Cuambe, C. E. and Martinho, C. (2015). Performance of maize-soybean intercropping under various N application rates and soil moisture conditions in Northern Mozambique. Plant Production Science, 18, 365-376. https://doi.org/10.1626/pps.18.365

[36]. Vandermeer, J. H. (1989). The Ecology of Intercropping. Cambridge, England: Cambridge University Press.

[37]. Wittmann, C., Aschan, G. and Pfanz, H. (2001). Leaf and twig photosynthesis of young beech (*Fagus sylvatica*) and aspen *(Populus tremula)* trees grown under different light regime. Basic and Applied Ecology, 2, 145-154. https://doi.org/10.1078/1439-1791-00047

[38]. Yilmaz, S., Atak, M. and Erayman, M. (2008). Identification of Advantages of Maize-Legume Intercropping over Solitary Cropping through Competition Indices in the East Mediterranean Region. Turkish Journal of Agriculture and Forestry, 32, 111-119.

[39]. Zhang, X., Huang, G., Bian, X. and Zhao, Q. (2013). Effects of root interaction and nitrogen fertilization on the chlorophyll content, root activity, photosynthetic characteristics of intercropped soybean and microbial quantity in the rhizosphere. Plant, Soil and Environment, 59, 80-88.

[40]. Zhu, X. G., De Sturler, E. and Long, S. P. (2007). Optimizing the distribution of resources between enzymes of carbon metabolism can dramatically increase photosynthetic rate: a numerical simulation using an evolutionary algorithm. Plant Physiology, 155, 513-526. https://doi.org/10.1104/pp.107.103713

HOW TO CITE THIS ARTICLE?

Crossref: https://doi.org/10.18801/jbar.240120.242

MLA

Mwamlima et al. "Reduced stomatal conductance and irradiance account for soybean [*Glycine max* (L.) Merrill] yield decline in maize-soybean intercrop." Journal of Bioscience and Agriculture Research, 24(01) (2020): 1977-1989.

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Chicago

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Harvard

Mwamlima, L. H., Cheruiyot, E. K. and Ouma, J. P. 2020. Reduced stomatal conductance and irradiance account for soybean [*Glycine max* (L.) Merrill] yield decline in maize-soybean intercrop. Journal of Bioscience and Agriculture Research, 24(01), pp. 1977-1989.

Vancouver

Mwamlima LH., Cheruiyot EK. and Ouma, JP. Reduced stomatal conductance and irradiance account for soybean [*Glycine max* (K.) Merrill] yield decline in maize-soybean intercrop. 2020 April 24(01): 1977-1989.