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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

Rusnadi Padjung[*)], Elkawakib Syam'un and Nurlina Kasim

Department of Agronomy, Universitas Hasanuddin, Makassar, South Sulawesi, Indonesia

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*) Corresponding author:
E-mail: rusnadi2015@gmail.com

ABSTRACT

Each plant genotype has its own photosynthetic parameters required to run crop growth model. The research is aimed to characterize photosynthetic parameters particularly maximum photosynthesis and initial light use efficiency of two soybean varieties widely planted in Indonesia, Dena-1 and Anjasmoro. Photosynthetic performances were measured in a designed experiment to study the effect of *Actinomycetes* spp. on growth and yield of soybean. Photosynthesis was measured using an open chamber portable photosynthetic system (LI-6400), at variable Photosynthetically Active Radiation (PAR), i.e. 500; 1,000; 1,500; and 2,000 µmol (photon)/m^2/s. The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (P_{gmax}) of Dena-1 is 45.64 µmol (CO_2)/m^2/s, while Anjasmoro variety is only 34.81 µmol (CO_2)/m^2/s. Quantum yield at low light (initial light use efficiency) of Dena-1 is also higher with the value of 0.068 µmol (CO_2)/µmol(photons) compared to Anjasmoro that have 0.058 µmol (CO_2)/µmol (photons). Hence light response curve of Dena-1 variety is consistently higher than Anjasmoro. Under *Actinomycetes* spp. treatment the light response curve of Dena-1 is higher than Anjasmoro at PAR lower than 706 µmol (photon)/m^2/s and higher at PAR above it.

INTRODUCTION

Crop growth models require plant parameters associated to characteristic of a variety to run the model. As a new variety is developed, a set of plant parameters associated to the respected variety need to be characterized. Some of required parameters, particularly by detail crop models, are photosynthetic parameters. Radiation is a driving force for photosynthesis (Gu et al., 2017; Strada & Unger, 2016). Hence, the response of photosynthesis to change in radiation, or specifically Photosynthetic Photon Flux Density (PPFD) has a high significance in crop growth model. Such a response is well known as Photosynthetic Light Response Curve (Herrmann, Schwartz, & Johnson, 2020; Johnson & Murchie, 2011; Lobo et al., 2013). There are two important parameters in the photosynthetic light response curve, i.e.: maximum photosynthesis (P_{max}), and initial light use efficiency, and in some cases is light compensation point. P_{max} is a rate of photosynthesis by which increase in PPFD will no longer increasing photosynthesis rate; and initial light use efficiency is the slope of photosynthetic rate to light intensity at low light. These parameters are characterized in two new soybean varieties widely planted in Indonesia.

Anjasmoro and Dena-1 are two soybean varieties widely planted in Indonesia. Anjasmoro is preferred by farmers because it is suitable for *tempe* and *tofu* industry since it has yellow grain color, relatively big bean size, and high protein content (Isnaini, Rasyad, & Fianda, 2020; Krisnawati & Adie, 2017). Yellow and big grain soybean are good for *tempe* as it would give good color and high recovery of *tempe*. Of about 2.4 million ton per year soybean demand in Indonesia, 83.7% are used for *tempe* and *tofu*. In addition to its good quality grain, Anjasmoro also resistant to major disease

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in soybean such as leaf rust, and it is also logging resistant (Mahdiannoor, Istiqomah, & Syahbudin, 2017). Leaf rust of soybean, caused by *Phakopsora pachyrhizi* may cause yield loss up to 40 to 80%.

Dena-1 variety was released in 2015 particularly as shaded tolerant variety. In addition to some good characters such as yellow color, big grain, high protein content, and resistant to leaf rust, Dena-1 variety also tolerant up to 50% shading (Pratiwi & Artari, 2018). Hence, it is suitable for intercropping with young high estate crops, such as coconut, oil palm, and rubber. With large plantation area of those estate crops Indonesia, expansion of soybean crop to plantation area is promising. Dena-1 variety, along with Dena-2 variety as well, are considered as varieties suitable to be intercropped with young trees at community forest (Abidin, 2015)

Characterizing photosynthetic parameters of Dena-1 variety is also important to understand the physiological trait underlying the capacity of the variety to tolerate shading. More importantly, it will give physiological explanation up to which light condition this variety produce sufficient photosynthate for reasonable yield. Comparing the physiological trait of Dena-1 with that of Anjasmoro provides better understanding of why these varieties response differently to shading.

MATERIALS AND METHODS

The experiment was conducted in Tarowang farm, owned by a smallholder farmer in Tarowang village, district of Takalar, South Sulawesi province, Indonesia from August to November 2017. Tarowang is located at 119^0 28^1 East and 5^0 39^1 South with altitude of 15 m above sea level.

Photosynthetic performances were measured in an experiment designed to study the effect of *Actinomycetes* spp. on growth and yield of soybean. The experimental design was Factorial Design, in which soybean varieties as first factor that consist of Dena-1 (V1) and Anjasmoro (V2), and the second factor is *Actinomycetes* spp. application that consist of no *Actinomycetes* spp. (A0), and *Actinomycetes* spp. with concentration of 1 x 10^6 CFU/ml (A1). Each treatment combination was repeated three times and therefore there were 12 experimental units or plots in total. The plot size is 3 x 4 m, and two seeds per hole of soybeans were sowed in August 20, 2017 in a row of 20 x 40 cm.

The photosynthetic measurement was taken in October 15, 2017 using an open chamber portable photosynthetic system (LI-6400, LI-COR, Inc., Logan, NE, USA). Mature leaf exposed to full sunlight was flipped to the chamber. The size of the chamber used, or the area of leaf flipped in the chamber, is 2 x 3 cm, or 6 cm^2. To develop a light response curve, the photosynthesis was measured at variable Photosynthetically Active Radiation (PAR), i.e. 500; 1,000; 1,500; and 2,000 μmol (photon)/m^2/s. Environment conditions during experiments were as follows: air temperature 25-27^{o}C; block and leaf temperature 25-27°C; air flow rate 500 *µmol*/s; CO_2 concentration in sample cell 380–400 *µmol* CO_2 / mol; and relative humidity in sample cell 56-70%. The measurements are repeated three times (once for each experimental unit). In each replication the system run for 5 second, and the data were registered every second, and therefore there are 15 data set available for each PAR level, or 60 data set for all replications and PAR levels. The parameters used are photosynthetic rate (P_n) (*µmol* CO_2/m^2/s), intercellular CO_2 concentration (Ci) (*µmol* CO_2/mol air), and conductance to H_2O (mol H_2O/m^2/s)

The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel to fit it to the model suggested by Lobo et al. (2013). The Solver function fit the function by finding the least sum of square difference between data and model.

RESULTS AND DISCUSSION

Photosynthetic light response curves of Anjasmoro and Dena-1 varieties are shown in Fig. 1. Under normal condition or no *Actinomycetes* the curve of Dena-1 variety is higher than that of Anjasmoro (Fig. 1a). This indicates that Dena-1 responses better than Anjasmoro to light, as it has higher initial light use efficiency as well as higher maximum photosynthesis.

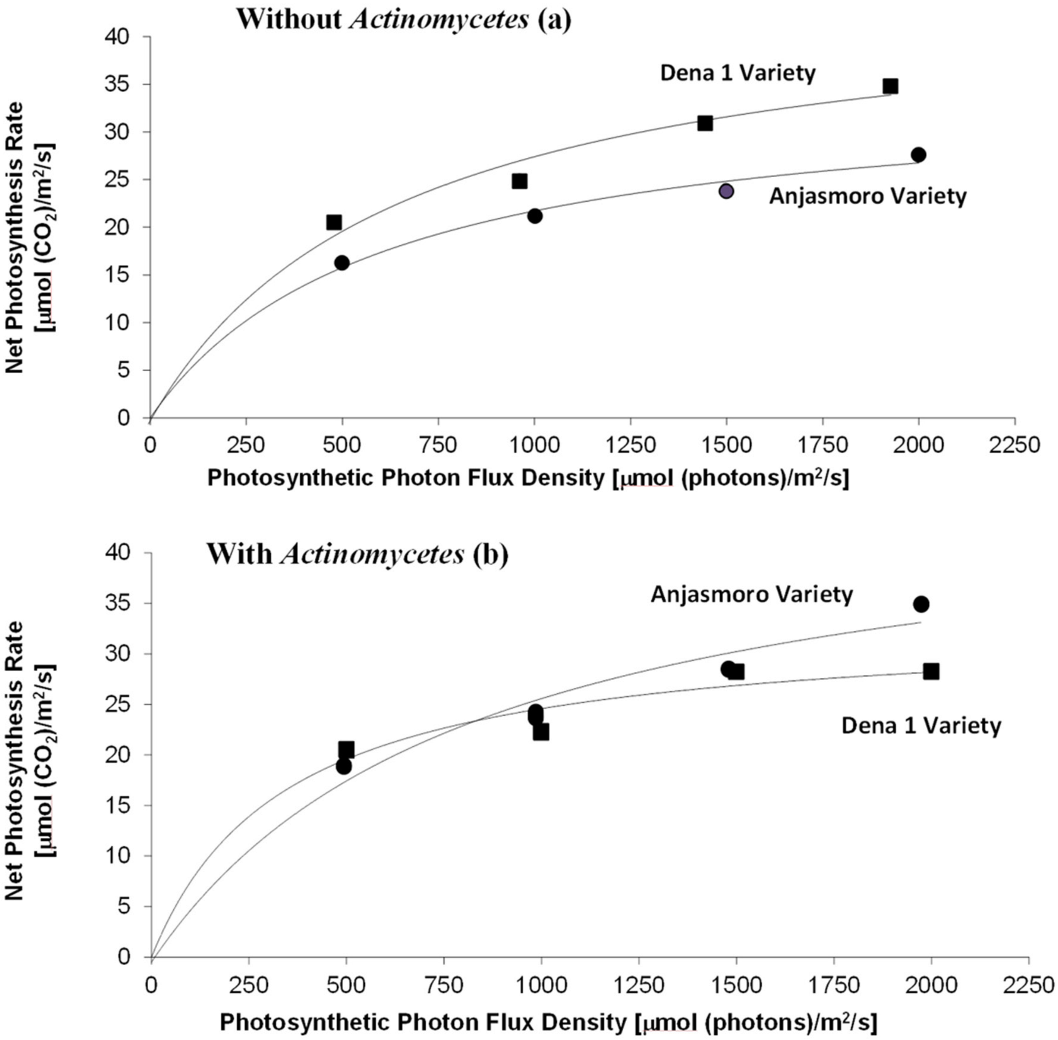

Fig. 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under *Actinomycetes* spp. treatment (b)

Maximum gross photosynthesis (P_{gmax}) of Dena-1 is 45.64 *µmol* (CO_2)/m^2/s, while Anjasmoro variety is only 34.81 *µmol* (CO_2)/m^2/s (Table 1). Reported maximum net photosynthesis (P_{nmax}) of other soybean varieties are 28.8 *µmol* (CO_2) /m^2/s (Yao et al., 2017), 29.9 *µmol* (CO_2)/m^2/s (Zhang, Hu, Luo, Chow, & Zhang, 2011), and 34.8 *µmol* (CO_2)/m^2/s (Sakoda, Tanaka, Long, & Shiraiwa, 2016). Net photosynthesis (P_n) is gross photosynthesis (P_g) minus dark respiration (R_d). The values of dark respiration are 3.19 *µmol* (CO_2)/m^2/s (Yao et al., 2017), and 6.72 *µmol* (CO_2)/m^2/s (Zhang, Hu, Luo, Chow, & Zhang, 2011). Along with high maximum photosynthesis, quantum yield at low light (initial light use efficiency) of Dena-1 variety is also higher with the value of 0.068 *µmol* (CO_2)/*µmol* (photons) compared to Anjasmoro 0.058 *µmol* (CO_2)/*µmol* (photons). Both Yao et al. (2017) and Zhang, Hu, Luo, Chow, & Zhang (2011) reported a similar quantum yield of soybean at 0.053 *µmol* (CO_2)/*µmol* (photons). Such a difference in P_{gmax} and quantum yield between Dena-1 and Anjasmoro indicate Dena-1 is more tolerant to shading than Anjasmoro. As reported by Pratiwi & Artari (2018), Dena-1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 both at light compensation point (ϕ(Icomp)) and at light between compensation point to 200 (ϕ(Ic-I200)) is higher (0.07 and 0.05 *µmol* (CO_2)/*µmol* (photons)) than quantum yield of Anjasmoro (0.06 and 0.04 *µmol* (CO_2)/*µmol* (photons)) (Table 1). In another word, photosynthesis at Dena-1 variety still occurs at acceptable rate even under low light or under shading.

Along with high maximum gross photosynthesis, initial light use efficiency, and quantum yield, the light saturation point of Dena-1 is consistently higher at percentile 50 % all the way up to 95% than that of Anjasmoro. Light saturation point at 50% percentile of Dena-1 variety is 667 *µmol* (photons)/m^2/s, while Anjasmoro is 603 *µmol* (photons)/m^2/s. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 *µmol* (photons)/m^2/s, while Anjasmoro is 5,429 *µmol* (photons)/m^2/s (Table 2). High light saturation point indicates that Dena-1 is not only tolerant to shading but also tolerant to high light. In another word, increase in light intensity can be accommodated by Dena-1 due to high capacity of its photosynthetic apparatus.

The photosynthetic light response curves of these two varieties change under Actinomycetes treatment. Under such condition the curve of Dena-1 is higher than that of Anjasmoro at the beginning or at low light. As light increase, the quantum yield is decreasing at a rate faster in Dena-1 than in Anjasmoro such that Dena-1 curve is surpassed by Anjasmoro curve at PAR 706 µmol (photon)/m^2/s (Figure 1b). In another word, the photosynthetic light-response curve of Dena-1 is higher than Anjasmoro at PAR below 706 µmol (photon)/m^2/s, but it is the other way round at PAR above 706 µmol (photon)/m^2/s. Initial light use efficiency of Dena-1 is higher (0.096 µmol (CO_2)/µmol (photons)) than Anjasmoro (0.058 µmol (CO_2)/µmol (photons)). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 (33.03 µmol (CO_2)/m^2/s) then in Anjasmoro (48.77 µmol (CO_2)/m^2/s) (Table 1). This indicates that Anjasmoro responses better to *Actinomycetes* spp. than Dena-1. The better response includes the conversion of additional nutrient from *Actinomycetes* spp. into the increase of the capacity of photosynthetic apparatus. With an increase in capacity of photosynthetic apparatus, photosynthesis rate increases along with increase in light, and so increase in light saturation point, and maximum photosynthesis (Table 1). Hence, the rate of decrease in quantum yield from light compensation point (I_c) to I_{200} is much higher in Dena-1 than in Anjasmoro, i.e. 40 % (from 0.10 to 0.04) vs 17% (from 0.06 to 0.05).

Actinomycetes spp. play an important role in soil nutrient cycling (Bhatti, Haq, & Bhat, 2017), inorganic phosphates solubilizing (Ghorbani-Nasrabadi, Greiner, Alikhani, Hamedi, & Yakhchali, 2013; Pragya, Yasmin, & Anshula, 2012; Saif, Khan, Zaidi, & Ahmad, 2014), phytate hydrolyzing, a dominant form of organic P in soils (Ghorbani-Nasrabadi, Greiner, Alikhani, & Hamedi, 2012; Schneider, Cade-Menun, Lynch, & Voroney, 2016), and so improvement of nutrients availability (AbdElgawad et al., 2020; Hozzein et al., 2019) particularly phosphorus. *Actinomycetes* spp. is not only increasing the availability of phosphorus, but also nitrogen (AbdElgawad et al., 2020). Janati et al. (2021) also reported the importance of microbial P bio-solubilization such as *Actinomycetes* spp. as a pathway for improving biological nitrogen fixation (BNF) in grain legumes via P solubilizing microorganisms (PSM) and P solubilizing bacteria (PSB).

Increase the availability of phosphorus and nitrogen in the soil may increase crop growth and yield (Amule, Sirothiya, Rawat, & Mishra, 2018; Sahur, Ala, Patandjengi, & Syam'un, 2018; Soe, Bhromsiri, Karladee, & Yamakawa, 2012). Crop response to available nutrient, however, differs among species. Mahdiannoor, Istiqomah, & Syahbudin (2017) reported that growth and yield responses of Anjasmoro are much higher than local soybean variety to bio-fertilizer application. Similar result was also reported by Timotiwu, Nurmiaty, Pramono, & Maysaroh (2020) that Anjasmoro responded better than Dena-1 to NPK fertilizer in term of plant height, biomass weight, number of pods, weight of 100 seeds, and yield. Research by AbdElgawad et al. (2020) may explain such a different in responses. They found that all tested legumes (soybean, kidney bean, chickpea, lentil, and pea crops) increase in its chlorophyll a and b content after enrichment with biologically active *Actinomycetes* spp. isolates. They further found that different plants responded differently to the same isolate. In relation to photosynthesis, phosphorus play an important role in energy transfer (Carstensen et al., 2018; Meng et al., 2021). Unfortunately, under P deficiency, P is allocated more to roots than to leaves (Muhammad, Abdullah, Saud, Shaharuddin, & Isa, 2021). An implication of this is that leaves and physiological processes occurring in leaves such as photosynthesis suffers more than other parts and physiological processes in the plants under deficient P. Anjasmoro seems to response better than Dena-1 to *Actinomycetes* spp. treatment such that the more chlorophylls are available, energy transfers are more efficient in the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to accommodate light (PAR) increase.

Table 1. Light response curve related parameters of Dena-1 and Anjasmoro varieties with and without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjamoro – no Actinomycetes, Dena-1 – Actinomycetes, Anjasmoro - Actinomycetes.

Varieties and Actinomycetes Tratments	Standard Parameters		Light saturation point at				Light-saturated net CO_2 uptake	Quantum yield at	
	Maximum Photosynthesis	Quantum yield at I = 0	50 percen-tile	85 percen-tile	90 percen-tile	95 Percent-tile		Light compensation point	LCP to I = 200
	P_{gmax}	ϕ(Io)	$I_{sat(50)}$	$I_{sat(85)}$	$I_{sat(90)}$	$I_{sat(95)}$	PN (I_{max})	ϕ(Icomp)	ϕ(Ic-I200)
	(μmol (CO_2)/m²/s)	(μmol (CO_2) /μmol (photons))	(μmol photons)/ m²/s)	(μmol (photons)/ m²/s)	(μmol (photons)/ m²/s)	(μmol (photons)/ m²/s)	(μmol (CO_2) / m²/s)	(μmol (CO_2)/ μmol (photons))	(μmol (CO_2)/ μmol (pho-tons))
Anjasmoro – No Actinomycetes	34.81	0.058	603.26	3,418.47	5,429.33	11,461.92	26.59	0.06	0.04
Dena-1 – No Actinomycetes	45.64	0.068	667.17	3,780.66	6,004.57	12,676.32	34.01	0.07	0.05
Anjasmoro - Actinomycetes	48.77	0.058	843.63	4,780.60	7,592.71	16,029.06	34.04	0.06	0.05
Dena-1 – with Actinomycetes	33.03	0.096	343.41	1,945.97	3,090.66	6,524.73	28.09	0.10	0.06

Table 2. Conductance to H_2O and Intercellular CO_2 concentration of Dena and Anjasmoro varieties with and without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjamoro – no Actinomycetes, Dena-1 – Actinomycetes, Anjasmoro – Actinomycetes at variable PAR

Varieties - Actinomycetes Tratments	Conductance to H_2O mol H_2O m^2/s				Intercellular CO_2 Concentration µmol CO_2 /mol			
	PAR 500	PAR 1,000	PAR 1,500	PAR 2,000	PAR 500	PAR 1,000	PAR 1,500	PAR 2,000
Anjasmoro – No Actinomycetes	2.09	3.52	2.29	3.01	316	314	295	286
Dena-1 – No Actinomycetes	2.28	2.70	3.50	3.00	327	318	315	305
Anjasmoro - Actinomycetes	3.92	3.46	3.82	4.08	323	312	301	294
Dena-1 – with Actinomycetes	2.90	1.59	2.34	1.72	321	306	299	292

Beside the limitation of chlorophyll availability and energy transfer, photosynthesis at high light is apparently also limited by the availability of CO_2 as can be indicated by conductance to H_2O and internal CO_2 concentration. Under normal condition or no Actinomycetes treatment, Dena 1 has higher conductance (2.28 mol $H_2O/m^2/s$) than Anjasmoro (2.09 mol $H_2O/m^2/s$) and it increases faster with the increase of PAR from 500 to 2,000 µmol (photon)/m^2/s. Along with this increase, internal CO_2 concentration in Dena 1 decrease at a slower rate than in Anjasmoro (Table 2). This indicates that stomata of Dena 1 is more resilient to keep the internal CO_2 concentration higher than Anjasmoro when the demand for CO_2 increase.

It has been known widely that light affect stomatal opening, and so leaf conductance. The effect of light intensity to the stomatal response occurs in two ways. The first is through the decrease of intercellular CO_2 concentration due to increase in photosynthesis (Eyland, van Wesemael, Lawson, & Carpentier, 2021), and the second is through direct activation of guard cells (Driesen, Van den Ende, De Proft, & Saeys, 2020; Elhaddad, Hunt, Sloan, & Gray, 2014; Ye et al., 2020). Unlike at normal condition, under *Actinomycetes* spp. treatment, the decrease in internal CO_2 concentration due to light increase in Dena 1 is faster than Anjasmoro. Limitation in availability of internal CO_2 at high light can be overcome by *Actinomycetes* spp. in Anjasmoro. A significant variation in the rapidity of stomatal responses amongst species to light change is existed (McAusland et al., 2016). For soybean, Bunce (2016) found 15 cultivars differed significantly in stomatal conductance. Variation in rapidity of stomatal responses to light could be altered by application of *Actinomycetes* spp.

CONCLUSION

Initial light use efficiency and maximum photosynthesis of Dena-1 is 0.068 µmol (CO_2)/µmol (photons) and 45.64 µmol (CO_2)/m^2/s, respectively. While, Anjasmoro is 0.068 µmol (CO_2)/µmol (photons) and 34.81 µmol (CO_2)/m^2/s, respectively. High initial light use efficiency of Dena-1 could be one of the reasons that Dena 1 is tolerant to shading. Application of *Actinomycetes* spp. alters light response curve such that photosynthesis rate of Anjasmoro is higher than Dena-1 at PAR above 706 µmol (photon)/m^2/s and consequently, maximum photosynthesis (P_{max}) of Anjasmoro is also higher than Dena-1, i.e. 48.77 and 33.03 µmol (CO_2)/m^2/s, respectively. Such alteration could be brought about by higher increase in the capacity of photosynthetic apparatus of Anjasmoro than in Dena-1 under *Actinomycetes* spp. treatment.

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