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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

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I. Photosynthetic Parameters of Two Indonesian Soybean Top Varieties

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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

ABSTRACT

Each variety has its own photosynthetic parameters required to run crop growth model. The research is aimed at characterizing photosynthetic parameters particularly maximum photosynthesis and initial light use efficiency of two soybean varieties widely planted in Indonesia, *Dena-1* and *Anjasmoro* variety. Photosynthetic performances were measured in an experiment designed 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 µ mol (photon) m^{-2} s^{-1}. The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (Pgmax) of *Dena-1* is 45.64 µmol (CO_2) m^{-2} s^{-1}, while *Anjasmoro* variety is only 34.81 µmol (CO_2) m^{-2} s^{-1}. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 µmol (CO_2) $µmol^{-1}$ (photons) compare to Anjasmoro 0.058 µmol (CO_2) $µmol^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomycetes spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 µmol (photon) m^{-2} s^{-1} and higher at PAR above it.

KEYWORDS

Actinomycetes spp., crop model, light efficiency, light response curve, maximum photosynthesis.

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 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 (Strada and Unger, 2016; Gu et al., 2017). 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 (Baly, 1935; Farquhar, 1980; Yin and Struik, 2009). There are two important parameters in the photosynthetic light response curve, i.e.: maximum photosynthesis (Pmax), and initial light use efficiency, and in some cases is light compensation point. Pmax 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* variety is preferred by farmers because it is suitable for *tempe* and *tofu* industry as it has yellow grain color, relatively big bean size (14.8 g – 15.3 g per 100 grains), and high protein content (37 – 43 %) (Ginting et al., 2009; Krisnawati and Adie, 2017). Yellow and big grain soybean (> 13 g/100 grains) 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* variety also resistant to major disease in soybean such as leaf rust, and it is logging resistant (Mahdiannoor et al., 2017). Leaf rust of soybean, caused by *Phakopsora pachyrhizi* may cause yield loss of 40% to 80%.

Dena-1 variety was released in 2015 particularly as shaded tolerate 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

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tolerant to shading up to 50% of shading (Pratiwi and 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 enough photosynthate for reasonable yield.

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 28^1East 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. Therefore the experimental design was Factorial Design, in which soybean varieties as first factor that consist of Dena-1 variety (V1) and Anjasmoro vatiety (V2), and the second factor is density of *Actinomycetes spp* that consist of no *Actinomycetes spp* (A0), *Actinomycetes spp* with concentration of $1x10^3$ CFU mL^{-1} (A1), and *Actinomycetes spp* with concentration of $1x10^6$ CFU mL^{-1} (A2). Each treatment combination was repeated three times and therefore there were 18 experimental units or plots in total. The plot size is 3 m x 4 m, and the soybeans were sowed in August 20, 2017 in a row of 20 cm x 40 cm with 2 seeds per hole. However, the photosynthetic measurements were not following this experimental design, but were taken at two contrasting *Actinomycetes spp* treatments of two varieties, i.e. no *Actinomycetes* and $1x10^6$ CFU mL^{-1} *Actinomycetes* at Anjasmoro and Dena-1 varieties (W1A0, W1A2, W2A0, and W2A2).

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 cm x 3 cm, or $6m^2$. 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 µ mol (photon) m^2 s^{-1}. Environment conditions during experiments were as follows: air temperature – 25-27 ^oC; block and leaf temperature – 25-27 °C; air flow rate – 500 µmol $s^{–1}$; CO_2 concentration in sample cell – 380–400 µmol CO_2 $mol^{–1}$; 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 (Pn) (µmol CO2 $m^{–2}s^{–1}$), intercellular CO_2 concentration(Ci) (µmol CO_2 mol $air^{–1}$), and conductance to H2O (mol H2O m^{-2} s^{-1})

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

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RESULTS AND DISCUSSION

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

Maximum gross photosynthesis (Pgmax) of Dena-1 is 45.64 μmol (CO2) m^{-2} s^{-1}, while Anjasmoro variety is only 34.81 μmol (CO2) m^{-2} s^{-1} (Table 1). Along with high maximum photosynthesis, quantum yield at low light (initial light use efficiency) of Dena-1 variety is also higher which is 0.068 μmol (CO_2) μmol-1 (photons) compare to Anjasmoro 0.058 μmol (CO_2) μmol-1 (photons). Such a difference explains why Dena-1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety 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 (CO2) μmol-1 (photons)) than quantum yield of Anjasmoro variety (0.06 and 0.04 μmol (CO2) μmol-1 (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 variety is consistently higher at percentile 50 % all the way up to 95% than that of Anjasmoro variety. Light saturation point at 50% percentile of Dena-1 variety is 667 μmol (photons) m^{-2} s^{-1}, while Anjasmoro is 603 μmol (photons) m^{-2} s^{-1}. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 μmol (photons) m^{-2} s^{-1}, while Anjasmoro variety is 5,429 μmol (photons) m^{-2} s^{-1} (Table 2). High light saturation point indicates that Dena-1 varieties 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 variety 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 variety is higher than that of Anjasmoro at the beginning or at low light but then 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^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than Anjasmoro at PAR below 706 μmol (photon) m^{-2} s^{-1}, but it is the other way round at PAR above 706 μmol (photon) m^{-2} s^{-1}. Intial light use efficiency of Dena-1 variety is higher (0.096 μmol (CO_2) μmol^{-1} (photons)) than Anjasmoro variety (0.058 μmol (CO_2) μmol^{-1} (photons)). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 variety (33.03 μmol (CO_2) m^{-2} s^{-1}) then in Anjasmoro variety (48.77 μmol (CO_2) m^{-2} s^{-1}) (Table 1). This indicates that Anjasmoro variety responses better to *Actinomycetes spp* variety than Dena-1 variety such that additional nutrient from *Actinomycetes spp* can be converted well into increase in 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 variety than in Anjasmoro variety, i.e. 40 % (from 0.10 to 0.04) vs 17% (from 0.06 to 0.05).

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Actinomycetes spp. play an important role in soil nutrient cycling (Elliot and Lynch, 1995), solubilize inorganic phosphates (Ghorbani-Nasrabadi et al., 2013), hydrolyze phytate, a dominant form of organic P in soils (Ghorbani-Nasrabadi et al., 2012), and so improve the availability of nutrients (Bhatti et al., 2017) particularly phosphorus. Phosphorus (P) is required in many compounds in cells and organelles that are closely associated with energy transfer (Rychter and Rao, 2005). Anjasmoro variety seems response better than Dena-1 variety to *Actinomycetes spp* treatment such that more phosphorus is available for energy transfer in the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to accommodate light (PAR) increase. Mahdiannoor et al. (2017) reported that growth and yield responses of *Anjasmoro* variety are much higher than local soybean variety to bio-fertilizer application. Similar result was also found by Maysaroh (2018) that *Anjasmoro* variety responded better than *Dena-1* variety to NPK fertilizer in term of plant height, biomass weight, number of pods, weight of 100 seeds, and yield.

Beside the limitation by 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 variety has higher conductance (2.28 mol H_2O m^{-2} s^{-1}) than Anjasmoro variety (2.09 mol H_2O m^{-2} s^{-1}) and it increases faster with the increase of PAR from 500 to 2,000 μmol (photon) m^{-2} s^{-1}. Along with this increase, internal CO_2 concentration in Dena 1 variety decreae at a rate slower than in Anjasmoro variety (Table 2). This indicates that stomata of Dena 1 variety is more resilient to keep the internal CO_2 concentration higher than Anjasmoro variety as a demand for CO_2 increase

It has been known widely that light affect stomatal opening, and so leaf conductance. The effect of light to the stomatal response is mainly`through a direct response and is only a small extent through change in intercellular CO2 concentration (Sharkey, and Raschke, 1981). Sharkey and Raschke (1981) demonstrated a high difference on stomatal response to light between *Xanthium stumarium* L., *Gossypium hirsutum* L., *Phaseolis vulgaris* L., and *Perilla frutescens* (L.), Britt. McAusland et al. (2016) also reported a significant variation in the rapidity of stomatal responses amongst species to light change. For soybean, Bunce (2016) found 15 cultivars differed significantly in stomatal conductance.

Unlike at normal condition, under *Actinomycetes spp*. treatment, the decrease in internal CO_2 concentration due to light increase in Dena 1 variety is faster than Anjasmoro. This is brought about by high response of Anjasmoro variety to *Actinomicetes spp.* than Dena 1 variety. As discussed earlier, Anjasmoro variety responses better to soil fertilization than Dena 1 variety.

CONCLUSIONS

Initial light use efficiency and maximum photosynthesis of Dena 1 variety is 0.068 μmol (CO2) μmol^{-1} (photons) and 45.64 μmol (CO2) m^{-2} s^{-1} respectively. while Anjasmoro variety is 0.068 μmol (CO2) μmol^{-1} (photons) and 34.81 μmol (CO2) m^{-2} s^{-1} respectively. High initial light use efficiency of Dena-1 could be one of the reasons that made Dena 1 variety tolerant to shading. Responses of stomatal conductance and internal CO_2 concentration to light is higher in Anjasmoro than in Dena 1 variety.

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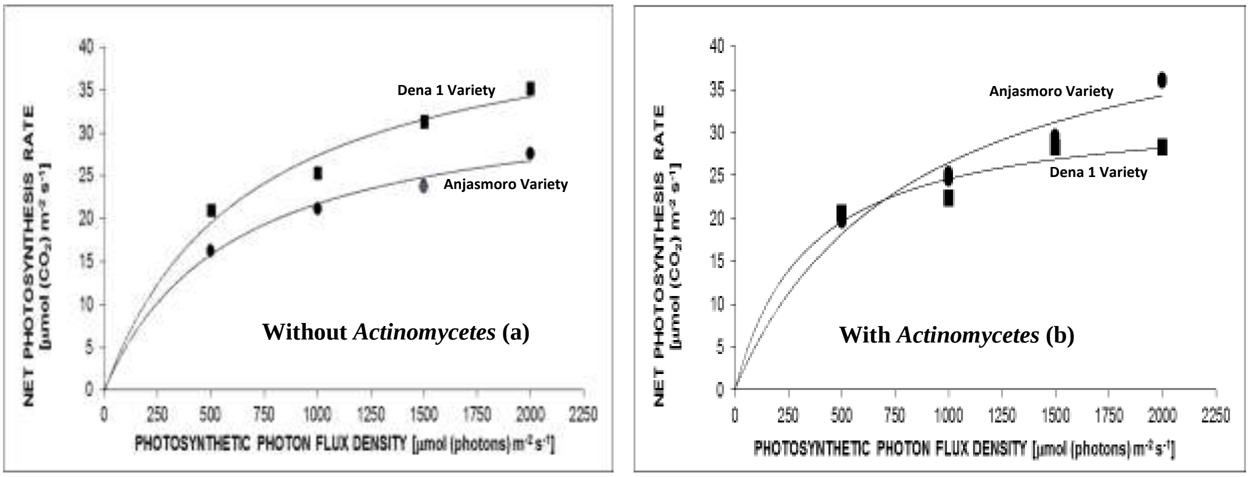

Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

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The following are the editable graph for Figure 1.

Figure 1.a. Without Actinomycetes

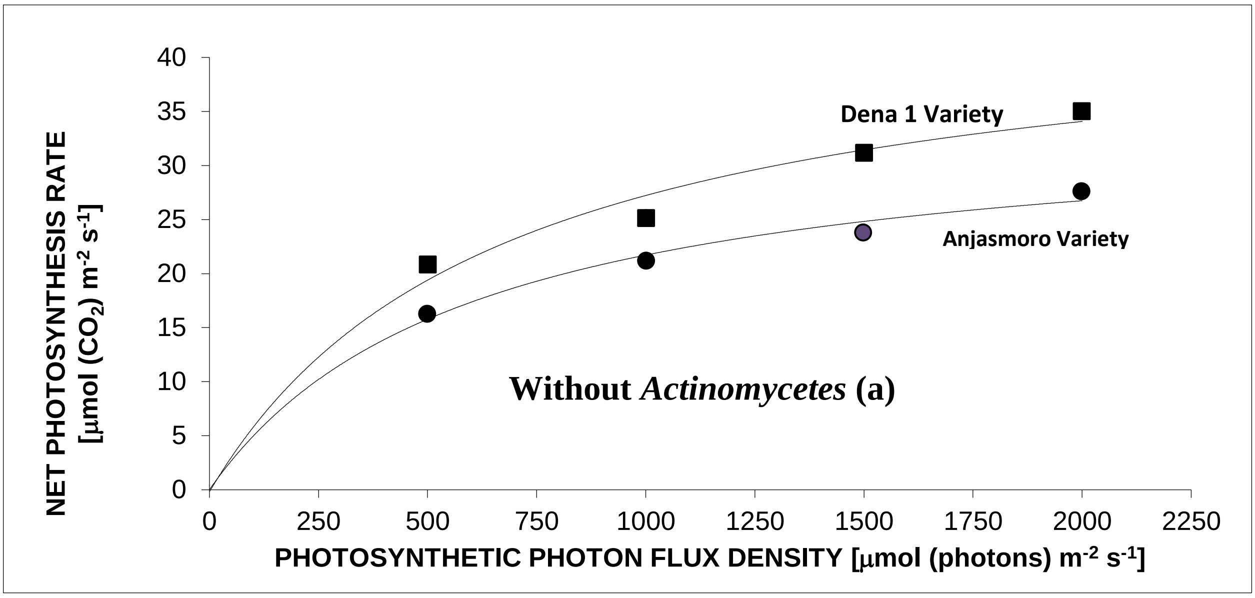

Figure 1.b . With Actinomycetes

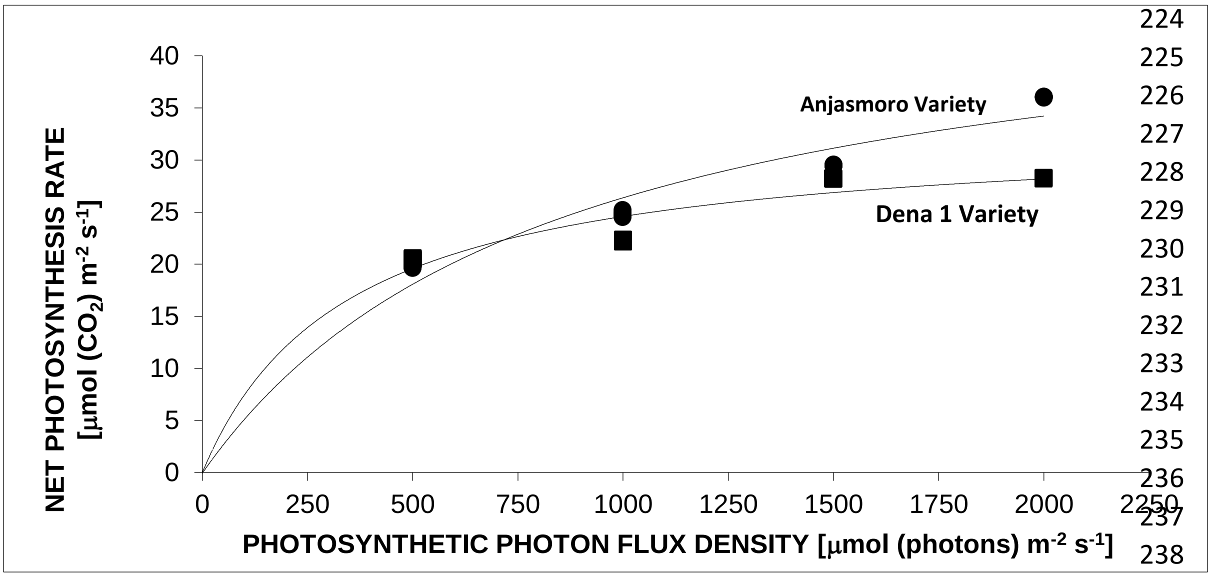

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Table 1. Light response curve related parameters of Dena 1 and Anjasmoro varieties with and without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjamoro – no Actinomycetes, Dena-1 – Actinomycetes, Anjasmoro - Actinomycetes.

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) m^{-2} s^{-1})	(µmol (CO_2) $µmol^{-1}$ (photons))	(µmol photons) m^{-2} s^{-1})	(µmol (photons) m^{-2} s^{-1})	(µmol (photons) m^{-2} s-1)	(µmol (photons) m^{-2} s^{-1})	(µmol (CO_2) m^{-2} s^{-1})	(µmol (CO_2) $µmol^{-1}$ (photons))	(µmol (CO_2) $µmol^{-1}$ (photons))
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 H2O and Intercellular CO2 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 $m^{-2}s^{-1}$				Intercellular CO_2 Concentration µmol CO_2 mol^{-1}			
	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

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We have reached a decision regarding your submission to AGRIVITA, Journal of Agricultural Science, "Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties".

Our decision is to: revision required (from reviewer 1)

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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

ABSTRACT

Each variety has its own photosynthetic parameters required to run crop growth model. The research is aimed at characterizing photosynthetic parameters particularly maximum photosynthesis and initial light use efficiency of two soybean varieties widely planted in Indonesia, *Dena-1* and *Anjasmoro* variety. Photosynthetic performances were measured in an experiment designed 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 µ mol (photon) m^{-2} s^{-1}. The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (Pgmax) of *Dena-1* is 45.64 µmol (CO_2) m^{-2} s^{-1}, while *Anjasmoro* variety is only 34.81 µmol (CO_2) m^{-2} s^{-1}. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 µmol (CO_2) $µmol^{-1}$ (photons) compare to Anjasmoro 0.058 µmol (CO_2) $µmol^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomycetes spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 µmol (photon) m^{-2} s^{-1} and higher at PAR above it.

KEYWORDS

Actinomycetes spp., crop model, light efficiency, light response curve, maximum photosynthesis.

The red ones, must be revised

INTRODUCTION (Use new reff., less than 10 years)

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 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 (Strada and Unger, 2016; Gu et al., 2017). 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 (Baly, 1935; Farquhar, 1980; Yin and Struik, 2009). There are two important parameters in the photosynthetic light response curve, i.e.: maximum photosynthesis (Pmax), and initial light use efficiency, and in some cases is light compensation point. Pmax 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* variety is preferred by farmers because it is suitable for *tempe* and *tofu* industry as it has yellow grain color, relatively big bean size (14.8 g – 15.3 g per 100 grains), and high protein content (37 – 43 %) (Ginting et al., 2009; Krisnawati and Adie, 2017). Yellow and big grain soybean (> 13 g/100 grains) 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* variety also resistant to major disease in soybean such as leaf rust, and it is logging resistant (Mahdiannoor et al., 2017). Leaf rust of soybean, caused by *Phakopsora pachyrhizi* may cause yield loss of 40% to 80%.

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Dena-1 variety was released in 2015 particularly as shaded tolerate 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 to shading up to 50% of shading (Pratiwi and 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 enough photosynthate for reasonable yield.

The objective of this research?? Do you want to compare between varieties? Or just studying of parameters?

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 28^1East 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. Therefore the experimental design was Factorial Design, in which soybean varieties as first factor that consist of Dena-1 variety (V1) and Anjasmoro vatiety (V2), and the second factor is density of *Actinomycetes spp* that consist of no *Actinomycetes spp* (A0), *Actinomycetes spp* with concentration of $1x10^3$ CFU mL^{-1} (A1), and *Actinomycetes spp* with concentration of $1x10^6$ CFU mL^{-1} (A2). Each treatment combination was repeated three times and therefore there were 18 experimental units or plots in total. The plot size is 3 m x 4 m, and the soybeans were sowed in August 20, 2017 in a row of 20 cm x 40 cm with 2 seeds per hole. However, the photosynthetic measurements were not following this experimental design, but were taken at two contrasting *Actinomycetes spp* treatments of two varieties, i.e. no *Actinomycetes* and $1x10^6$ CFU mL^{-1} *Actinomycetes* at Anjasmoro and Dena-1 varieties (W1A0, W1A2, W2A0, and W2A2).

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 cm x 3 cm, or $6m^2$. 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 µ mol (photon) m^2 s^{-1}. Environment conditions during experiments were as follows: air temperature – 25-27 ºC; block and leaf temperature – 25-27 °C; air flow rate – 500 µmol s^{-1}; CO_2 concentration in sample cell – 380–400 µmol CO_2 mol^{-1}; 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 (Pn) (µmol CO2 $m^{-2}s^{-1}$), intercellular CO_2 concentration(Ci) (µmol CO_2 mol air^{-1}), and conductance to H2O (mol H2O m^{-2} s^{-1})

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

RESULTS AND DISCUSSION (Use new reff., less than 10 years)

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

Maximum gross photosynthesis (Pgmax) of Dena-1 is 45.64 µmol (CO2) m^{-2} s^{-1}, while Anjasmoro variety is only 34.81 µmol (CO2) m^{-2} s^{-1} (Table 1). Along with high maximum photosynthesis, quantum yield at low light (initial light use efficiency) of Dena-1 variety is also higher which is 0.068 µmol (CO_2) µmol-1 (photons) compare to Anjasmoro 0.058 µmol (CO_2) µmol-1 (photons). Such a difference explains why Dena-1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety 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 (CO2) µmol-1 (photons)) than quantum yield of Anjasmoro variety (0.06 and 0.04 µmol (CO2) µmol-1 (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 variety is consistently higher at percentile 50 % all the way up to 95% than that of Anjasmoro variety. Light saturation point at 50% percentile of Dena-1 variety is 667 µmol (photons) m^{-2} s^{-1}, while Anjasmoro is 603 µmol (photons) m^{-2} s^{-1}. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 µmol (photons) m^{-2} s^{-1}, while Anjasmoro variety is 5,429 µmol (photons) m^{-2} s^{-1} (Table 2). High light saturation point indicates that Dena-1 varieties 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 variety 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 variety is higher than that of Anjasmoro at the beginning or at low light but then 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^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than Anjasmoro at PAR below 706 µmol (photon) m^{-2} s^{-1}, but it is the other way round at PAR above 706 µmol (photon) m^{-2} s^{-1}. Intial light use efficiency of Dena-1 variety is higher (0.096 µmol (CO_2) $µmol^{-1}$ (photons)) than Anjasmoro variety (0.058 µmol (CO_2) $µmol^{-1}$ (photons)). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 variety (33.03 µmol (CO_2) m^{-2} s^{-1}) then in Anjasmoro variety (48.77 µmol (CO_2) m^{-2} s^{-1}) (Table 1). This indicates that Anjasmoro variety responses better to *Actinomycetes spp* variety than Dena-1 variety such that additional nutrient from *Actinomycetes spp* can be converted well into increase in 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

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point (I_c) to I_{200} is much higher in Dena-1 variety than in Anjasmoro variety, 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 (Elliot and Lynch, 1995), solubilize inorganic phosphates (Ghorbani-Nasrabadi et al., 2013), hydrolyze phytate, a dominant form of organic P in soils (Ghorbani-Nasrabadi et al., 2012), and so improve the availability of nutrients (Bhatti et al., 2017) particularly phosphorus. Phosphorus (P) is required in many compounds in cells and organelles that are closely associated with energy transfer (Rychter and Rao, 2005). Anjasmoro variety seems response better than Dena-1 variety to *Actinomycetes spp* treatment such that more phosphorus is available for energy transfer in the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to accommodate light (PAR) increase. Mahdiannoor et al. (2017) reported that growth and yield responses of *Anjasmoro* variety are much higher than local soybean variety to bio-fertilizer application. Similar result was also found by Maysaroh (2018) that *Anjasmoro* variety responded better than *Dena-1* variety to NPK fertilizer in term of plant height, biomass weight, number of pods, weight of 100 seeds, and yield.

Beside the limitation by 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 variety has higher conductance (2.28 mol H_2O m^{-2} s^{-1}) than Anjasmoro variety (2.09 mol H_2O m^{-2} s^{-1}) and it increases faster with the increase of PAR from 500 to 2,000 µmol (photon) m^{-2} s^{-1}. Along with this increase, internal CO_2 concentration in Dena 1 variety decreae at a rate slower than in Anjasmoro variety (Table 2). This indicates that stomata of Dena 1 variety is more resilient to keep the internal CO_2 concentration higher than Anjasmoro variety as a demand for CO_2 increase

It has been known widely that light affect stomatal opening, and so leaf conductance. The effect of light to the stomatal response is mainly`through a direct response and is only a small extent through change in intercellular CO2 concentration (Sharkey, and Raschke, 1981). Sharkey and Raschke (1981) demonstrated a high difference on stomatal response to light between *Xanthium stumarium* L., *Gossypium hirsutum* L., *Phaseolis vulgaris* L., and *Perilla frutescens* (L.), Britt. McAusland et al. (2016) also reported a significant variation in the rapidity of stomatal responses amongst species to light change. For soybean, Bunce (2016) found 15 cultivars differed significantly in stomatal conductance.

Unlike at normal condition, under *Actinomycetes spp*. treatment, the decrease in internal CO_2 concentration due to light increase in Dena 1 variety is faster than Anjasmoro. This is brought about by high response of Anjasmoro variety to *Actinomicetes spp.* than Dena 1 variety. As discussed earlier, Anjasmoro variety responses better to soil fertilization than Dena 1 variety.

CONCLUSIONS

Initial light use efficiency and maximum photosynthesis of Dena 1 variety is 0.068 µmol (CO2) $µmol^{-1}$ (photons) and 45.64 µmol (CO2) m^{-2} s^{-1} respectively. while Anjasmoro variety is 0.068 µmol (CO2) $µmol^{-1}$ (photons) and 34.81 µmol (CO2) m^{-2} s^{-1} respectively. High initial light use efficiency of Dena-1 could be one of the reasons that made Dena 1 variety tolerant to shading. Responses of stomatal conductance and internal CO_2 concentration to light is higher in Anjasmoro than in Dena 1 variety.

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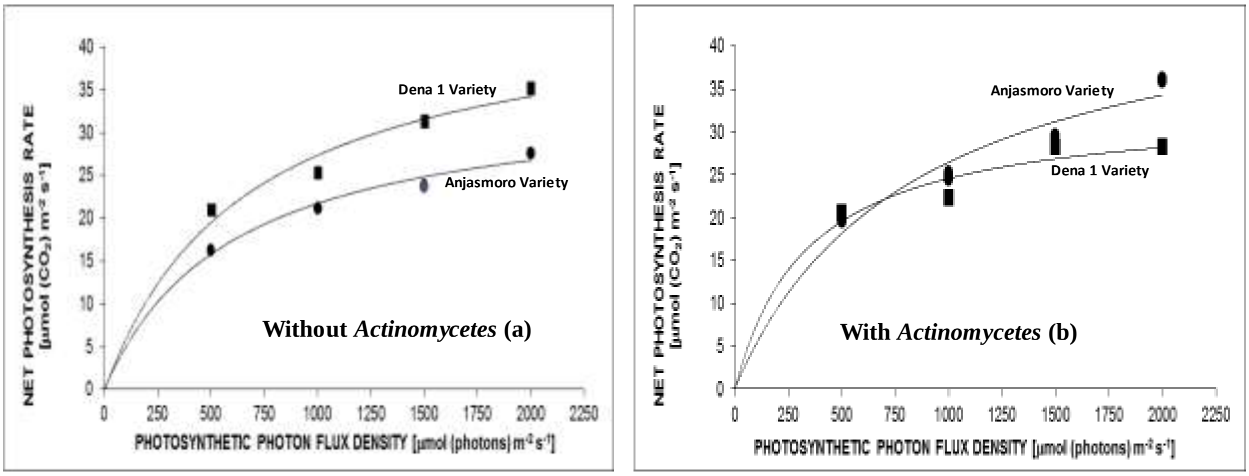

Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

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The following are the editable graph for Figure 1.

Figure 1.a. Without Actinomycetes

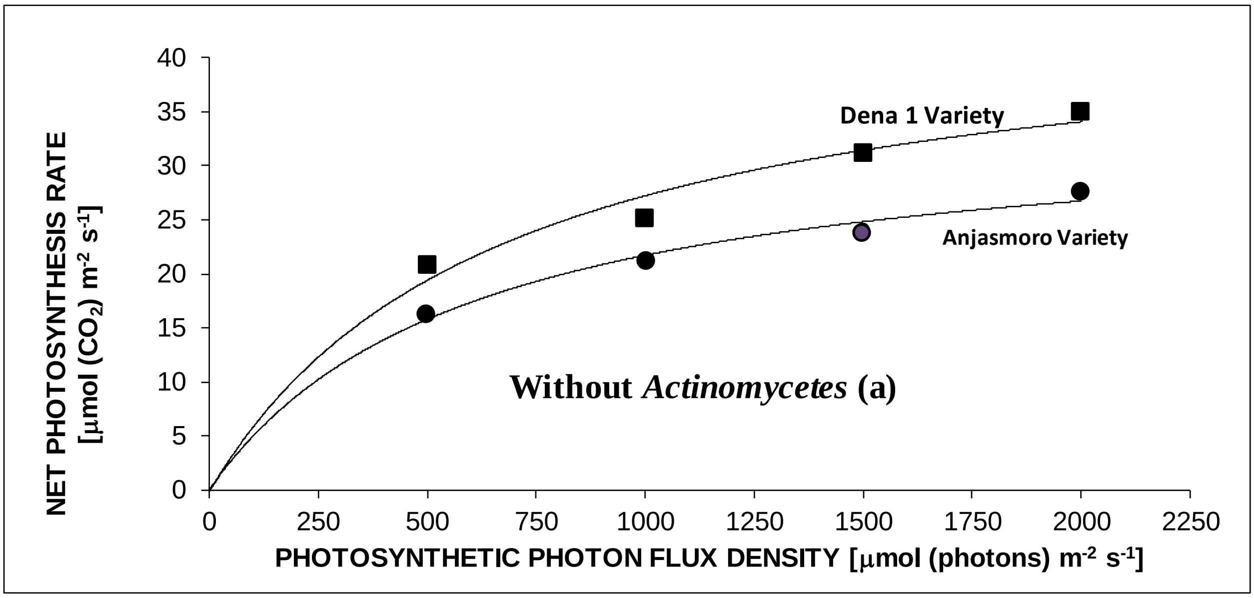

Figure 1.b . With Actinomycetes

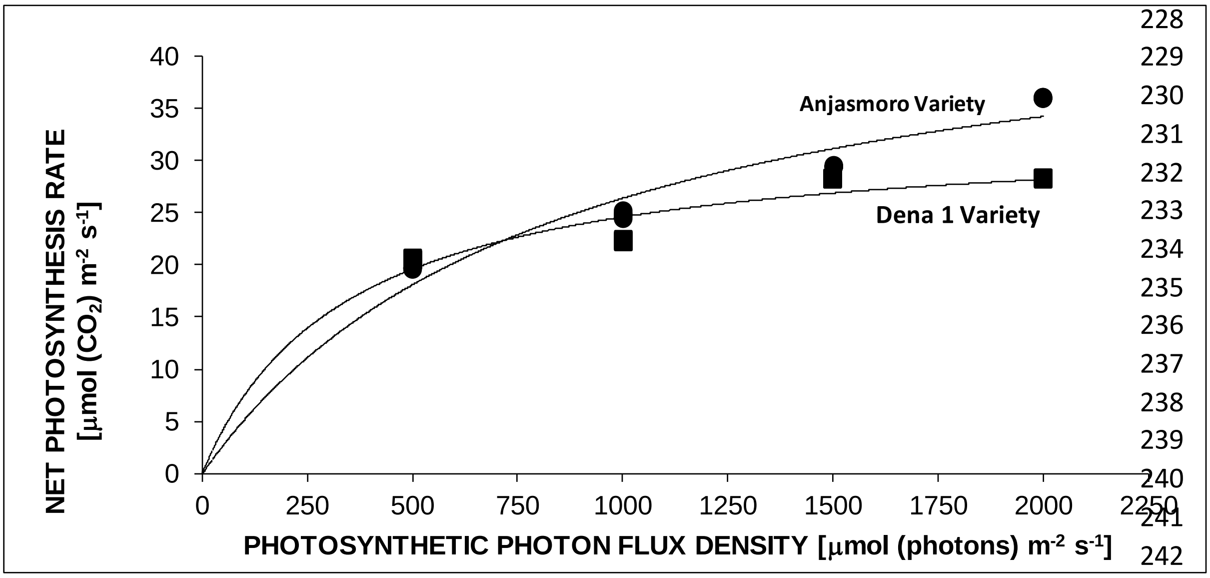

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Table 1. Light response curve related parameters of Dena 1 and Anjasmoro varieties with and without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjamoro – no Actinomycetes, Dena-1 – Actinomycetes, Anjasmoro - Actinomycetes.

Varieties and Actinomycetes Tratments	Standard Parameters: Maximum Photosynthesis P_{gmax} (µmol (CO_2) m^{-2} s^{-1})	Standard Parameters: quantum yield at I = 0 ϕ(Io) (µmol (CO_2) $µmol^{-1}$ (photons))	Light saturation point at: 50 percen-tile $I_{sat(50)}$ (µmol photons) m^{-2} s^{-1})	Light saturation point at: 85 percen-tile $I_{sat(85)}$ (µmol (photons) m^{-2} s^{-1})	Light saturation point at: 90 percen-tile $I_{sat(90)}$ (µmol (photons) m^{-2} s-1)	Light saturation point at: 95 Percent-tile $I_{sat(95)}$ (µmol (photons) m^{-2} s^{-1})	Light-saturated net CO_2 uptake PN(I_{max}) (µmol (CO_2) m^{-2} s^{-1})	Quantum yield at: light compensation point ϕ(Icomp) (µmol (CO_2) $µmol^{-1}$ (photons))	Quantum yield at: LCP to I = 200 ϕ(Ic-I200) (µmol (CO_2) $µmol^{-1}$ (photons))
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 H2O and Intercellular CO2 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 $m^{-2}s^{-1}$				Intercellular CO_2 Concentration µmol CO_2 mol^{-1}			
	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

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[AGRIVITA] Editor Decision

rusnadi padjung <rusnadi2015@gmail.com> 25 April 2021 08.33
Kepada: "Kuswanto Kuswanto, Prof." <kuswantoas@ub.ac.id>
Cc: Elkawakib Syam'un <elkawakibsyam@gmail.com>, Nurlina Kasim <nina_nurlina@yahoo.com>

Thank you for the decision and notification. I will make the revision accordingly and submit it back with-in two days.

Sincerely yours,

Rusnadi Padjung
[Kutipan teks disembunyikan]

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Gmail **rusnadi padjung <rusnadi2015@gmail.com>**

[AGRIVITA] Editor Decision

rusnadi padjung <rusnadi2015@gmail.com> 26 April 2021 09.49
Kepada: "Kuswanto Kuswanto, Prof." <kuswantoas@ub.ac.id>

Dear Prof.Kuswanto,

I am writing you to inform that I have submitted the revision of the manuscript entitled "Photosynthetic Paramaters of Two Indonesian Soybean
Top Varieties" through the Agrivita online manuscript management system this morning, Monday 26 April, 2021. I have revised the manuscript following reviewer comments and suggestions.

Looking forward to having the manuscript accepted.

Thank you very much.

Sincerely,

Rusnadi Padjung
[Kutipan teks disembunyikan]

Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

ABSTRACT

Each variety has its own photosynthetic parameters required to run crop growth model. The research is aimed at characterizing photosynthetic parameters particularly maximum photosynthesis and initial light use efficiency of two soybean varieties widely planted in Indonesia, *Dena-1* and *Anjasmoro* variety. Photosynthetic performances were measured in an experiment designed 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 µ mol (photon) m^{-2} s^{-1}. The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (Pgmax) of *Dena-1* is 45.64 µmol (CO_2) m^{-2} s^{-1}, while *Anjasmoro* variety is only 34.81 µmol (CO_2) m^{-2} s^{-1}. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 µmol (CO_2) $µmol^{-1}$ (photons) compare to Anjasmoro 0.058 µmol (CO_2) $µmol^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomycetes spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 µmol (photon) m^{-2} s^{-1} and higher at PAR above it.

KEYWORDS

Actinomycetes spp., crop model, light efficiency, light response curve, maximum photosynthesis.

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 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 (Strada and Unger, 2016; Gu et al., 2017). 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 (Johnson and Murchie, 2011; Labo, et. al., 2013; Herrmann et al., 2020). There are two important parameters in the photosynthetic light response curve, i.e.: maximum photosynthesis (Pmax), and initial light use efficiency, and in some cases is light compensation point. Pmax 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* variety is preferred by farmers because it is suitable for *tempe* and *tofu* industry as it has yellow grain color, relatively big bean size, and high protein content (Isnaini et al., 2020; Krisnawati and 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* variety also resistant to major disease in soybean such as leaf rust, and it is logging resistant (Mahdiannoor et al., 2017). Leaf rust of soybean, caused by *Phakopsora pachyrhizi* may cause yield loss of 40% to 80%.

Dena-1 variety was released in 2015 particularly as shaded tolerate 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 to shading up to 50% of shading (Pratiwi and Artari, 2018). Hence, it is suitable for intercropping with

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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 enough 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 28^1East 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. Therefore the experimental design was Factorial Design, in which soybean varieties as first factor that consist of Dena-1 variety (V1) and Anjasmoro vatiety (V2), and the second factor is density of *Actinomycetes spp* that consist of no *Actinomycetes spp* (A0), *Actinomycetes spp* with concentration of $1x10^3$ CFU mL^{-1} (A1), and *Actinomycetes spp* with concentration of $1x10^6$ CFU mL^{-1} (A2). Each treatment combination was repeated three times and therefore there were 18 experimental units or plots in total. The plot size is 3 m x 4 m, and the soybeans were sowed in August 20, 2017 in a row of 20 cm x 40 cm with 2 seeds per hole. However, the photosynthetic measurements were not following this experimental design, but were taken at two contrasting *Actinomycetes spp* treatments of two varieties, i.e. no *Actinomycetes* and $1x10^6$ CFU mL^{-1} *Actinomycetes* at Anjasmoro and Dena-1 varieties (W1A0, W1A2, W2A0, and W2A2).

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 cm x 3 cm, or $6m^2$. 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 µ mol (photon) m^2 s^{-1}. Environment conditions during experiments were as follows: air temperature – 25-27 ºC; block and leaf temperature – 25-27 °C; air flow rate – 500 µmol $s^{–1}$; CO_2 concentration in sample cell – 380–400 µmol CO_2 $mol^{–1}$; 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 (Pn) (µmol CO2 $m^{–2}s^{–1}$), intercellular CO_2 concentration(Ci) (µmol CO_2 mol $air^{–1}$), and conductance to H2O (mol H2O m^{-2} s^{-1})

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

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RESULTS AND DISCUSSION

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

Maximum gross photosynthesis (Pgmax) of Dena-1 is 45.64 μmol (CO2) m^{-2} s^{-1}, while Anjasmoro variety is only 34.81 μmol (CO2) m^{-2} s^{-1} (Table 1). Along with high maximum photosynthesis, quantum yield at low light (initial light use efficiency) of Dena-1 variety is also higher which is 0.068 μmol (CO_2) μmol-1 (photons) compare to Anjasmoro 0.058 μmol (CO_2) μmol-1 (photons). Such a difference explains why Dena-1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety 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 (CO2) μmol-1 (photons)) than quantum yield of Anjasmoro variety (0.06 and 0.04 μmol (CO2) μmol-1 (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 variety is consistently higher at percentile 50 % all the way up to 95% than that of Anjasmoro variety. Light saturation point at 50% percentile of Dena-1 variety is 667 μmol (photons) m^{-2} s^{-1}, while Anjasmoro is 603 μmol (photons) m^{-2} s^{-1}. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 μmol (photons) m^{-2} s^{-1}, while Anjasmoro variety is 5,429 μmol (photons) m^{-2} s^{-1} (Table 2). High light saturation point indicates that Dena-1 varieties 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 variety 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 variety is higher than that of Anjasmoro at the beginning or at low light but then 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^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than Anjasmoro at PAR below 706 μmol (photon) m^{-2} s^{-1}, but it is the other way round at PAR above 706 μmol (photon) m^{-2} s^{-1}. Intial light use efficiency of Dena-1 variety is higher (0.096 μmol (CO_2) $μmol^{-1}$ (photons)) than Anjasmoro variety (0.058 μmol (CO_2) $μmol^{-1}$ (photons)). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 variety (33.03 μmol (CO_2) m^{-2} s^{-1}) then in Anjasmoro variety (48.77 μmol (CO_2) m^{-2} s^{-1}) (Table 1). This indicates that Anjasmoro variety responses better to *Actinomycetes spp* variety than Dena-1 variety such that additional nutrient from *Actinomycetes spp* can be converted well into increase in 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 variety than in Anjasmoro variety, i.e. 40 % (from 0.10 to 0.04) vs 17% (from 0.06 to 0.05).

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Actinomycetes spp. play an important role in soil nutrient cycling (Bhatti et al., 2017), solubilize inorganic phosphates (Ghorbani-Nasrabadi et al., 2013), hydrolyze phytate, a dominant form of organic P in soils (Ghorbani-Nasrabadi et al., 2012), and so improve the availability of nutrients (Hozzein et al., 2019) particularly phosphorus. Phosphorus (P) is required in many compounds in cells and organelles that are closely associated with energy transfer (Carstensen et al., 2018). Anjasmoro variety seems response better than Dena-1 variety to *Actinomycetes spp* treatment such that more phosphorus is available for energy transfer in the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to accommodate light (PAR) increase. Mahdiannoor et al. (2017) reported that growth and yield responses of *Anjasmoro* variety are much higher than local soybean variety to bio-fertilizer application. Similar result was also found by Timotiwu et al. (2020) that *Anjasmoro* variety responded better than *Dena-1* variety to NPK fertilizer in term of plant height, biomass weight, number of pods, weight of 100 seeds, and yield.

Beside the limitation by 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 variety has higher conductance (2.28 mol H_2O m^{-2} s^{-1}) than Anjasmoro variety (2.09 mol H_2O m^{-2} s^{-1}) and it increases faster with the increase of PAR from 500 to 2,000 µmol (photon) m^{-2} s^{-1}. Along with this increase, internal CO_2 concentration in Dena 1 variety decreae at a rate slower than in Anjasmoro variety (Table 2). This indicates that stomata of Dena 1 variety is more resilient to keep the internal CO_2 concentration higher than Anjasmoro variety as a demand for CO_2 increase

It has been known widely that light affect stomatal opening, and so leaf conductance. The effect of light to the stomatal response occurs in two ways. The first one is through decrease in intercellular CO_2 concentration due to increase in photosynthesis, and the second is through direct activation of guard cells (Driesen et al., 2020). McAusland et al. (2016) also reported a significant variation in the rapidity of stomatal responses amongst species to light change. For soybean, Bunce (2016) found 15 cultivars differed significantly in stomatal conductance.

Unlike at normal condition, under *Actinomycetes spp*. treatment, the decrease in internal CO_2 concentration due to light increase in Dena 1 variety is faster than Anjasmoro. This is brought about by high response of Anjasmoro variety to *Actinomicetes spp.* than Dena 1 variety. As discussed earlier, Anjasmoro variety responses better to soil fertilization than Dena 1 variety.

CONCLUSIONS

Initial light use efficiency and maximum photosynthesis of Dena 1 variety is 0.068 µmol (CO2) $µmol^{-1}$ (photons) and 45.64 µmol (CO2) m^{-2} s^{-1} respectively. while Anjasmoro variety is 0.068 µmol (CO2) $µmol^{-1}$ (photons) and 34.81 µmol (CO2) m^{-2} s^{-1} respectively. High initial light use efficiency of Dena-1 could be one of the reasons that made Dena 1 variety tolerant to shading. Responses of stomatal conductance and internal CO_2 concentration to light is higher in Anjasmoro than in Dena 1 variety.

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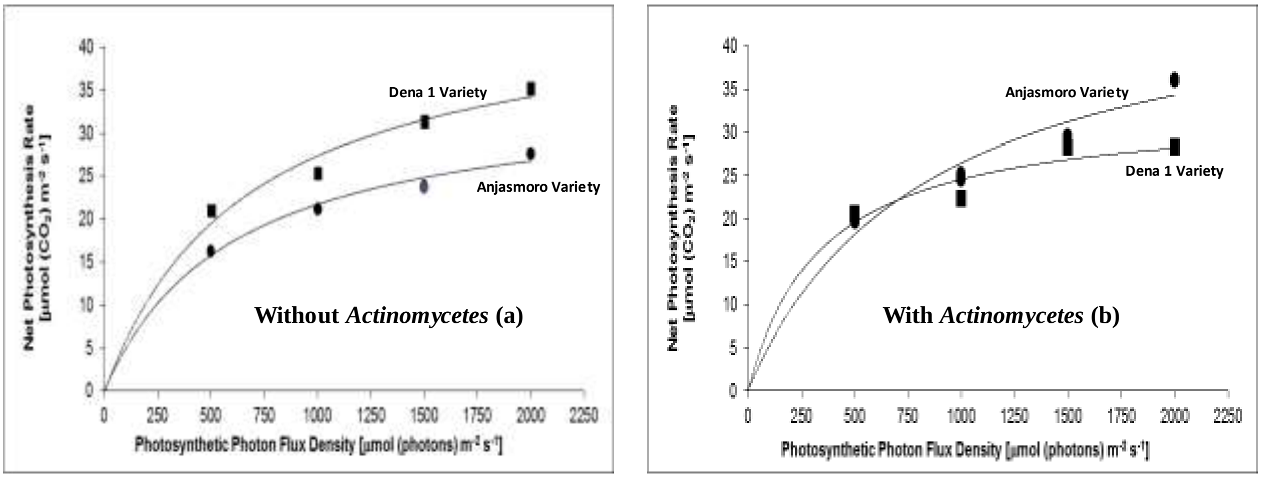

Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

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The following are the editable graph for Figure 1.

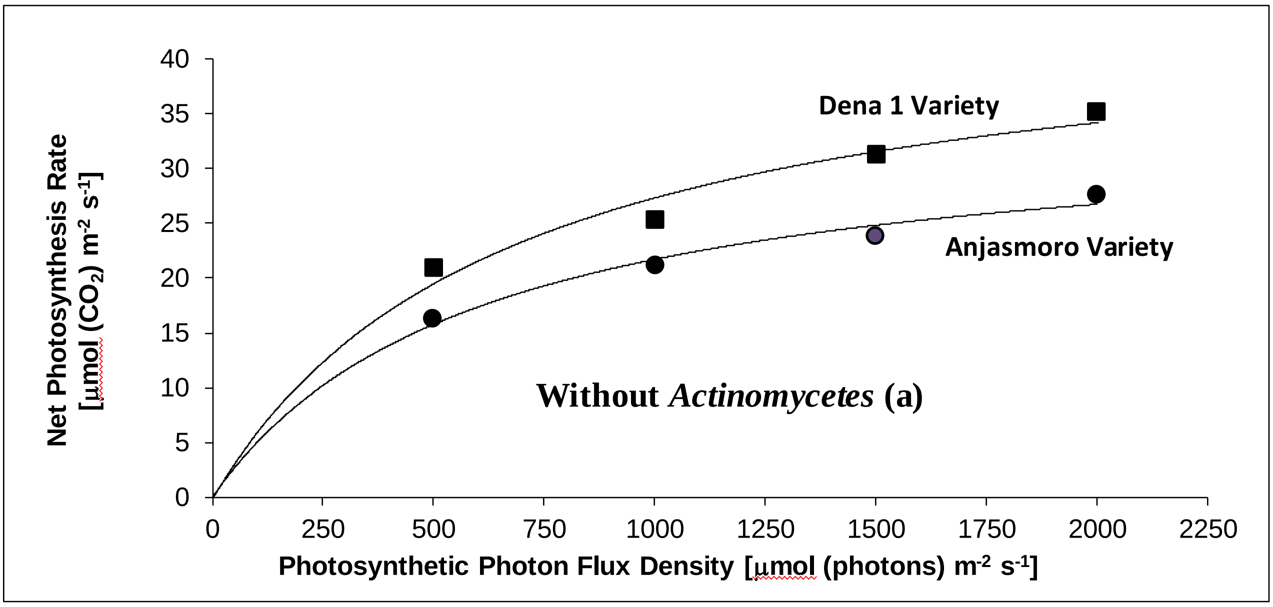

Figure 1.a. Without Actinomycetes

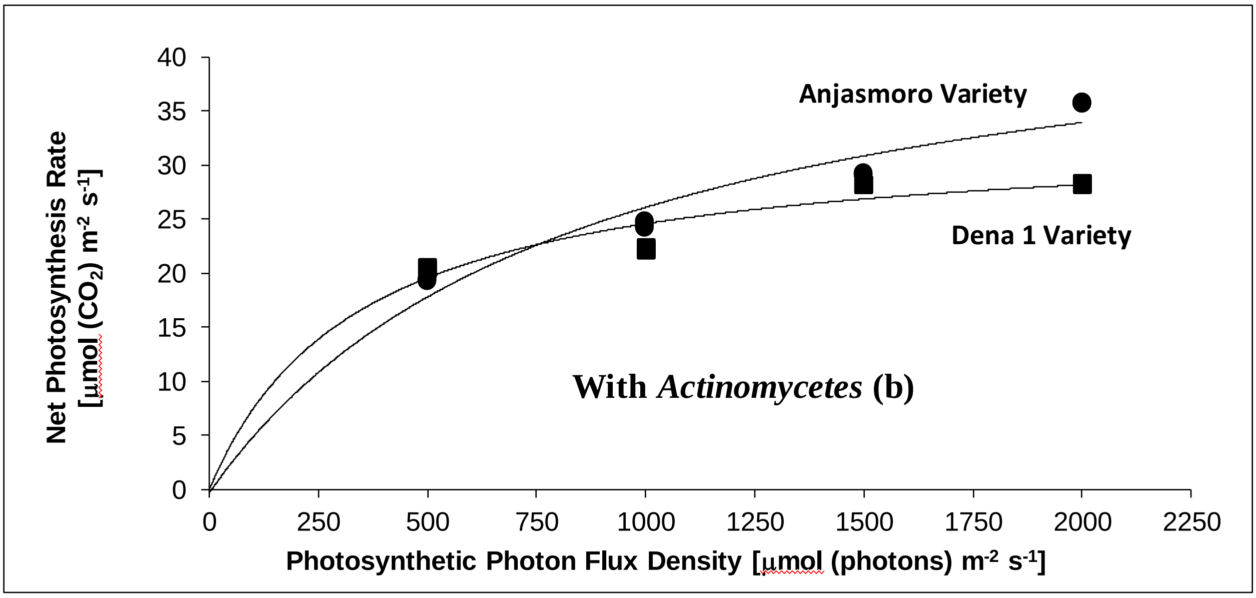

Figure 1.b . With Actinomycetes

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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) m^{-2} s^{-1})	(µmol (CO_2) µmol^{-1} (photons))	(µmol photons) m^{-2} s^{-1})	(µmol (photons) m^{-2} s^{-1})	(µmol (photons) m^{-2} s-1)	(µmol (photons) m^{-2} s^{-1})	(µmol (CO_2) m^{-2} s^{-1})	(µmol (CO_2) µmol^{-1} (photons))	(µmol (CO_2) µmol^{-1} (photons))
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 H2O and Intercellular CO2 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 $m^{-2}s^{-1}$				Intercellular CO_2 Concentration µmol CO_2 mol^{-1}			
	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

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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

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Dear Prof Maghfoer,

Thank you for the suggestion for revision to my manuscript entitled
Photosynthetic Parameters of Two Indonesian Soybean Top Varieties.

Following your suggestion, I have revised the manuscript and uploaded into
'manuscript management system of the journal' on April 25th.

Looking forward to having further decision from you.

Sincerely,

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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

ABSTRACT

Each variety has its own photosynthetic parameters required to run crop growth model. The research is aimed at characterizing photosynthetic parameters particularly maximum photosynthesis and initial light use efficiency of two soybean varieties widely planted in Indonesia, *Dena-1* and *Anjasmoro* variety. Photosynthetic performances were measured in an experiment designed 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 µ mol (photon) m^{-2} s^{-1}. The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (Pgmax) of *Dena-1* is 45.64 µmol (CO_2) m^{-2} s^{-1}, while *Anjasmoro* variety is only 34.81 µmol (CO_2) m^{-2} s^{-1}. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 µmol (CO_2) $µmol^{-1}$ (photons) compare to Anjasmoro 0.058 µmol (CO_2) $µmol^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomycetes spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 µmol (photon) m^{-2} s^{-1} and higher at PAR above it.

KEYWORDS

Actinomycetes spp., crop model, light efficiency, light response curve, maximum photosynthesis.

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 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 (Strada and Unger, 2016; Gu et al., 2017). 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 (Johnson and Murchie, 2011; Labo, et. al., 2013; Herrmann et al., 2020). There are two important parameters in the photosynthetic light response curve, i.e.: maximum photosynthesis (Pmax), and initial light use efficiency, and in some cases is light compensation point. Pmax 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.

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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 28^1East 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. Therefore the experimental design was Factorial Design, in which soybean varieties as first factor that consist of Dena-1 variety (V1) and Anjasmoro vatiety (V2), and the second factor is density of *Actinomycetes spp* that consist of no *Actinomycetes spp* (A0), *Actinomycetes spp* with concentration of $1x10^3$ CFU mL^{-1} (A1), and *Actinomycetes spp* with concentration of $1x10^6$ CFU mL^{-1} (A2). Each treatment combination was repeated three times and therefore there were 18 experimental units or plots in total. The plot size is 3 m x 4 m, and the soybeans were sowed in August 20, 2017 in a row of 20 cm x 40 cm with 2 seeds per hole. However, the photosynthetic measurements were not following this experimental design, but were taken at two contrasting *Actinomycetes spp* treatments of two varieties, i.e. no *Actinomycetes* and $1x10^6$ CFU mL^{-1} *Actinomycetes* at Anjasmoro and Dena-1 varieties (W1A0, W1A2, W2A0, and W2A2).

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 cm x 3 cm, or $6m^2$. 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 µ mol (photon) m^2 s^{-1}. Environment conditions during experiments were as follows: air temperature – 25-27 ^oC; block and leaf temperature – 25-27 °C; air flow rate – 500 µmol $s^{–1}$; CO_2 concentration in sample cell – 380–400 µmol CO_2 $mol^{–1}$; 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 (Pn) (µmol CO2 $m^{–2}s^{–1}$), intercellular CO_2 concentration(Ci) (µmol CO_2 mol $air^{–1}$), and conductance to H2O (mol H2O m^{-2} s^{-1})

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

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RESULTS AND DISCUSSION

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

Maximum gross photosynthesis (Pgmax) of Dena-1 is 45.64 μmol (CO2) m^{-2} s^{-1}, while Anjasmoro variety is only 34.81 μmol (CO2) m^{-2} s^{-1} (Table 1). Along with high maximum photosynthesis, quantum yield at low light (initial light use efficiency) of Dena-1 variety is also higher which is 0.068 μmol (CO_2) μmol-1 (photons) compare to Anjasmoro 0.058 μmol (CO_2) μmol-1 (photons). Such a difference explains why Dena-1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety 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 (CO2) μmol-1 (photons)) than quantum yield of Anjasmoro variety (0.06 and 0.04 μmol (CO2) μmol-1 (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 variety is consistently higher at percentile 50 % all the way up to 95% than that of Anjasmoro variety. Light saturation point at 50% percentile of Dena-1 variety is 667 μmol (photons) m^{-2} s^{-1}, while Anjasmoro is 603 μmol (photons) m^{-2} s^{-1}. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 μmol (photons) m^{-2} s^{-1}, while Anjasmoro variety is 5,429 μmol (photons) m^{-2} s^{-1} (Table 2). High light saturation point indicates that Dena-1 varieties 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 variety 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 variety is higher than that of Anjasmoro at the beginning or at low light but then 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^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than Anjasmoro at PAR below 706 μmol (photon) m^{-2} s^{-1}, but it is the other way round at PAR above 706 μmol (photon) m^{-2} s^{-1}. Intial light use efficiency of Dena-1 variety is higher (0.096 μmol (CO_2) $μmol^{-1}$ (photons)) than Anjasmoro variety (0.058 μmol (CO_2) $μmol^{-1}$ (photons)). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 variety (33.03 μmol (CO_2) m^{-2} s^{-1}) then in Anjasmoro variety (48.77 μmol (CO_2) m^{-2} s^{-1}) (Table 1). This indicates that Anjasmoro variety responses better to *Actinomycetes spp* variety than Dena-1 variety such that additional nutrient from *Actinomycetes spp* can be converted well into increase in 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 variety than in Anjasmoro variety, i.e. 40 % (from 0.10 to 0.04) vs 17% (from 0.06 to 0.05).

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Actinomycetes spp. play an important role in soil nutrient cycling (Bhatti et al., 2017), solubilize inorganic phosphates (Ghorbani-Nasrabadi et al., 2013), hydrolyze phytate, a dominant form of organic P in soils (Ghorbani-Nasrabadi et al., 2012), and so improve the availability of nutrients (Hozzein et al., 2019) particularly phosphorus. Phosphorus (P) is required in many compounds in cells and organelles that are closely associated with energy transfer (Carstensen et al., 2018). Anjasmoro variety seems response better than Dena-1 variety to *Actinomycetes spp* treatment such that more phosphorus is available for energy transfer in the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to accommodate light (PAR) increase. Mahdiannoor et al. (2017) reported that growth and yield responses of *Anjasmoro* variety are much higher than local soybean variety to bio-fertilizer application. Similar result was also found by Timotiwu et al. (2020) that *Anjasmoro* variety responded better than *Dena-1* variety to NPK fertilizer in term of plant height, biomass weight, number of pods, weight of 100 seeds, and yield.

Beside the limitation by 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 variety has higher conductance (2.28 mol H_2O m^{-2} s^{-1}) than Anjasmoro variety (2.09 mol H_2O m^{-2} s^{-1}) and it increases faster with the increase of PAR from 500 to 2,000 µmol (photon) m^{-2} s^{-1}. Along with this increase, internal CO_2 concentration in Dena 1 variety decreae at a rate slower than in Anjasmoro variety (Table 2). This indicates that stomata of Dena 1 variety is more resilient to keep the internal CO_2 concentration higher than Anjasmoro variety as a demand for CO_2 increase

It has been known widely that light affect stomatal opening, and so leaf conductance. The effect of light to the stomatal response occurs in two ways. The first one is through decrease in intercellular CO_2 concentration due to increase in photosynthesis, and the second is through direct activation of guard cells (Driesen et al., 2020). McAusland et al. (2016) also reported a significant variation in the rapidity of stomatal responses amongst species to light change. For soybean, Bunce (2016) found 15 cultivars differed significantly in stomatal conductance.

Unlike at normal condition, under *Actinomycetes spp*. treatment, the decrease in internal CO_2 concentration due to light increase in Dena 1 variety is faster than Anjasmoro. This is brought about by high response of Anjasmoro variety to *Actinomicetes spp.* than Dena 1 variety. As discussed earlier, Anjasmoro variety responses better to soil fertilization than Dena 1 variety.

CONCLUSIONS

Initial light use efficiency and maximum photosynthesis of Dena 1 variety is 0.068 µmol (CO2) $µmol^{-1}$ (photons) and 45.64 µmol (CO2) m^{-2} s^{-1} respectively. while Anjasmoro variety is 0.068 µmol (CO2) $µmol^{-1}$ (photons) and 34.81 µmol (CO2) m^{-2} s^{-1} respectively. High initial light use efficiency of Dena-1 could be one of the reasons that made Dena 1 variety tolerant to shading. Responses of stomatal conductance and internal CO_2 concentration to light is higher in Anjasmoro than in Dena 1 variety.

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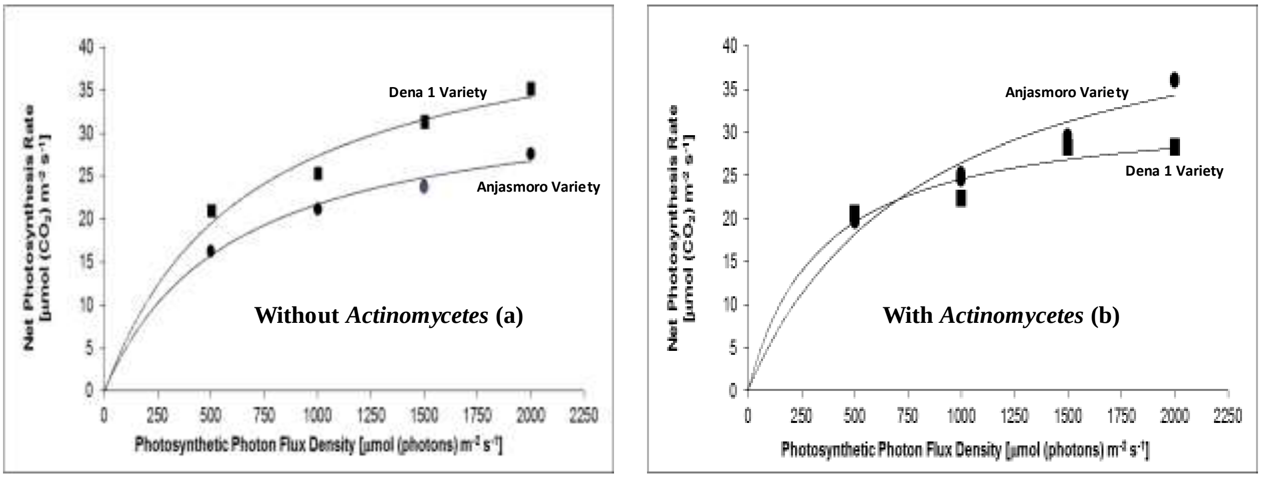

Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

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The following are the editable graph for Figure 1.

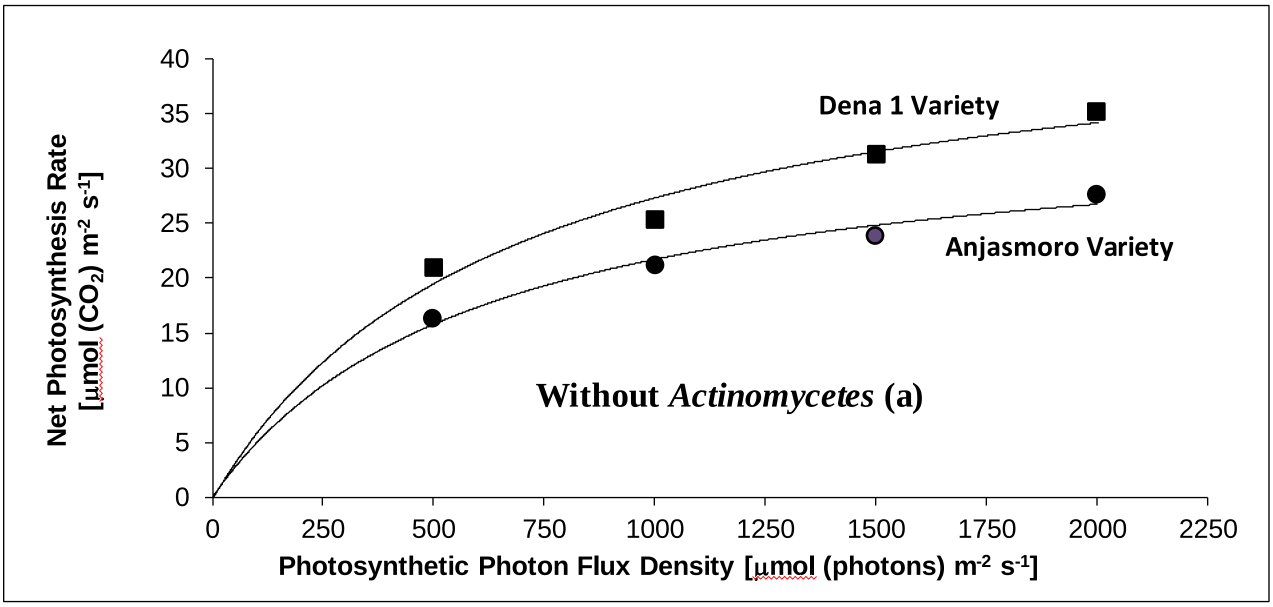

Figure 1.a. Without Actinomycetes

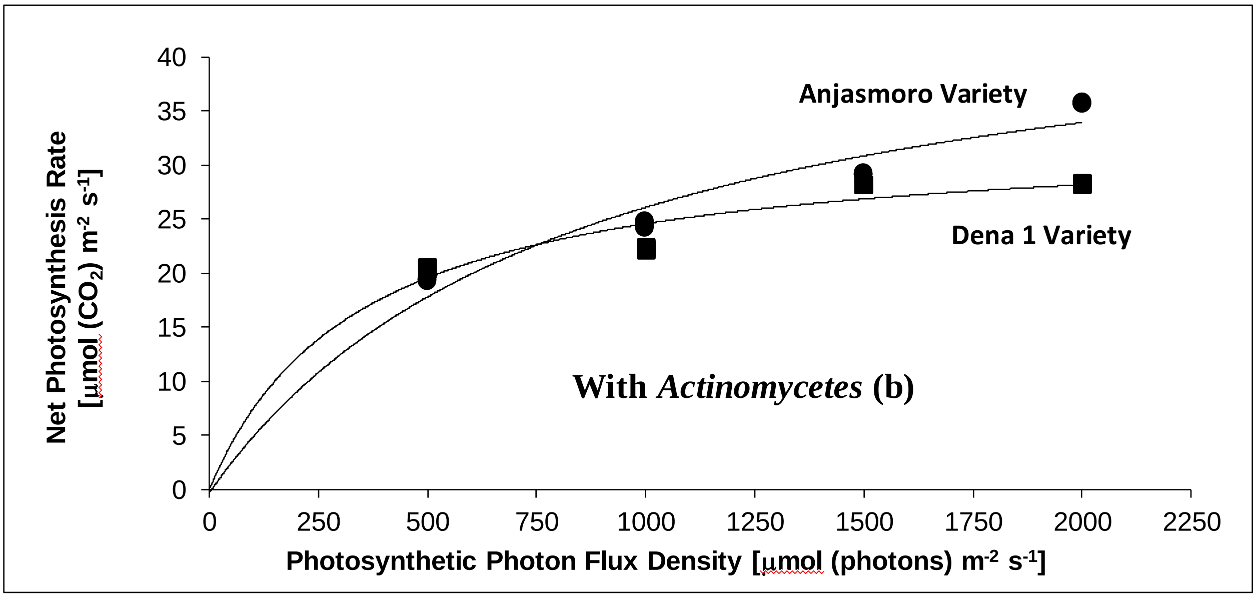

Figure 1.b . With Actinomycetes

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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) m^{-2} s^{-1})	(µmol (CO_2) µmol^{-1} (photons))	(µmol photons) m^{-2} s^{-1})	(µmol (photons) m^{-2} s^{-1})	(µmol (photons) m^{-2} s-1)	(µmol (photons) m^{-2} s^{-1})	(µmol (CO_2) m^{-2} s^{-1})	(µmol (CO_2) µmol^{-1} (photons))	(µmol (CO_2) µmol^{-1} (photons))
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 H2O and Intercellular CO2 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 $m^{-2}s^{-1}$				Intercellular CO_2 Concentration µmol CO_2 mol^{-1}			
	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

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[AGRIVITA] Editor Decision

AGRIVITA <agrivita@ub.ac.id> 1 Mei 2021 14.31
Balas Ke: "Moch. Dawam Maghfoer, Prof." <dmaghfoer@yahoo.com>
Kepada: "Rusnadi Padjung, Dr" <rusnadi2015@gmail.com>
Cc: Elkawakib Syam'un <elkawakibsyam@gmail.com>, Nurlina Kasim <nina_nurlina@yahoo.com>

Rusnadi Padjung, Dr :

We have reached a decision regarding your submission to AGRIVITA, Journal of Agricultural Science, "Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties".

Our decision is to: Revision required
- Revisions should be sent to Editor before May 8, 2021

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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

ABSTRACT

Each variety has its own photosynthetic parameters required to run crop growth model. The research is aimed at characterizing photosynthetic parameters particularly maximum photosynthesis and initial light use efficiency of two soybean varieties widely planted in Indonesia, *Dena-1* and *Anjasmoro* variety. Photosynthetic performances were measured in an experiment designed 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 µ mol (photon) m^{-2} s^{-1}. The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (Pgmax) of *Dena-1* is 45.64 µmol (CO_2) m^{-2} s^{-1}, while *Anjasmoro* variety is only 34.81 µmol (CO_2) m^{-2} s^{-1}. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 µmol (CO_2) $µmol^{-1}$ (photons) compare to Anjasmoro 0.058 µmol (CO_2) $µmol^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomycetes spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 µmol (photon) m^{-2} s^{-1} and higher at PAR above it.

KEYWORDS

Actinomycetes spp., crop model, light efficiency, light response curve, maximum photosynthesis.

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 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 (Strada and Unger, 2016; Gu et al., 2017). 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 (Johnson and Murchie, 2011; Labo, et. al., 2013; Herrmann et al., 2020). There are two important parameters in the photosynthetic light response curve, i.e.: maximum photosynthesis (Pmax), and initial light use efficiency, and in some cases is light compensation point. Pmax 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* variety is preferred by farmers because it is suitable for *tempe* and *tofu* industry as it has yellow grain color, relatively big bean size, and high protein content (Isnaini et al., 2020; Krisnawati and 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* variety also resistant to major disease in soybean such as leaf rust, and it is logging resistant (Mahdiannoor et al., 2017). Leaf rust of soybean, caused by *Phakopsora pachyrhizi* may cause yield loss of 40% to 80%.

Dena-1 variety was released in 2015 particularly as shaded tolerate 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 to shading up to 50% of shading (Pratiwi and Artari, 2018). Hence, it is suitable for intercropping with

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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 enough 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 28^1East 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. Therefore the experimental design was Factorial Design, in which soybean varieties as first factor that consist of Dena-1 variety (V1) and Anjasmoro vatiety (V2), and the second factor is density of *Actinomycetes spp* that consist of no *Actinomycetes spp* (A0), *Actinomycetes spp* with concentration of 1x10^3 CFU mL^{-1} (A1), and *Actinomycetes spp* with concentration of 1x10^6 CFU mL^{-1} (A2). Each treatment combination was repeated three times and therefore there were 18 experimental units or plots in total. The plot size is 3 m x 4 m, and the soybeans were sowed in August 20, 2017 in a row of 20 cm x 40 cm with 2 seeds per hole. However, the photosynthetic measurements were not following this experimental design, but were taken at two contrasting *Actinomycetes spp* treatments of two varieties, i.e. no *Actinomycetes* and 1x10^6 CFU mL^{-1} *Actinomycetes* at Anjasmoro and Dena-1 varieties (W1A0, W1A2, W2A0, and W2A2).

Commented [WU1]: This research explained only design with two factors, without the experimental design and statistical analysis. Its Okay!

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 cm x 3 cm, or 6m^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 µ mol (photon) m^2 s^{-1}. Environment conditions during experiments were as follows: air temperature – 25-27 °C; block and leaf temperature – 25-27 °C; air flow rate – 500 µmol s^{-1}; CO_2 concentration in sample cell – 380–400 µmol CO_2 mol^{-1}; 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 (Pn) (µmol CO2 m^{-2}s^{-1}), intercellular CO_2 concentration(Ci) (µmol CO_2 mol air^{-1}), and conductance to H2O (mol H2O m^{-2} s^{-1})

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

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RESULTS AND DISCUSSION

Commented [WU2]: The results and discussion only explained without and with Actynomycetes treatments, whereas there were three treatments for Actinomycetes population (without (0), population $1x10^3$ and population $1x10^6$ CFU mL^{-1}). Why not described all three? See Table 1 and 2, also Figure 1 and 2.

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

Maximum gross photosynthesis (Pgmax) of Dena-1 is 45.64 µmol (CO2) m^{-2} s^{-1}, while Anjasmoro variety is only 34.81 µmol (CO2) m^{-2} s^{-1} (Table 1). Along with high maximum photosynthesis, quantum yield at low light (initial light use efficiency) of Dena-1 variety is also higher which is 0.068 µmol (CO_2) µmol-1 (photons) compare to Anjasmoro 0.058 µmol (CO_2) µmol-1 (photons). Such a difference explains why Dena-1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety 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 (CO2) µmol-1 (photons)) than quantum yield of Anjasmoro variety (0.06 and 0.04 µmol (CO2) µmol-1 (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 variety is consistently higher at percentile 50 % all the way up to 95% than that of Anjasmoro variety. Light saturation point at 50% percentile of Dena-1 variety is 667 µmol (photons) m^{-2} s^{-1}, while Anjasmoro is 603 µmol (photons) m^{-2} s^{-1}. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 µmol (photons) m^{-2} s^{-1}, while Anjasmoro variety is 5,429 µmol (photons) m^{-2} s^{-1} (Table 2). High light saturation point indicates that Dena-1 varieties 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 variety 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 variety is higher than that of Anjasmoro at the beginning or at low light but then 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^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than Anjasmoro at PAR below 706 µmol (photon) m^{-2} s^{-1}, but it is the other way round at PAR above 706 µmol (photon) m^{-2} s^{-1}. Intial light use efficiency of Dena-1 variety is higher (0.096 µmol (CO_2) $µmol^{-1}$ (photons)) than Anjasmoro variety (0.058 µmol (CO_2) $µmol^{-1}$ (photons)). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 variety (33.03 µmol (CO_2) m^{-2} s^{-1}) then in Anjasmoro variety (48.77 µmol (CO_2) m^{-2} s^{-1}) (Table 1). This indicates that Anjasmoro variety responses better to *Actinomycetes spp* variety than Dena-1 variety such that additional nutrient from *Actinomycetes spp* can be converted well into increase in 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 variety than in Anjasmoro variety, 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 et al., 2017), solubilize inorganic phosphates (Ghorbani-Nasrabadi et al., 2013), hydrolyze phytate, a dominant form of organic P in

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soils (Ghorbani-Nasrabadi et al., 2012), and so improve the availability of nutrients (Hozzein et al., 2019) particularly phosphorus. Phosphorus (P) is required in many compounds in cells and organelles that are closely associated with energy transfer (Carstensen et al., 2018). Anjasmoro variety seems response better than Dena-1 variety to *Actinomycetes spp* treatment such that more phosphorus is available for energy transfer in the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to accommodate light (PAR) increase. Mahdiannoor et al. (2017) reported that growth and yield responses of *Anjasmoro* variety are much higher than local soybean variety to bio-fertilizer application. Similar result was also found by Timotiwu et al. (2020) that *Anjasmoro* variety responded better than *Dena-1* variety to NPK fertilizer in term of plant height, biomass weight, number of pods, weight of 100 seeds, and yield.

Beside the limitation by 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 variety has higher conductance (2.28 mol H_2O m^{-2} s^{-1}) than Anjasmoro variety (2.09 mol H_2O m^{-2} s^{-1}) and it increases faster with the increase of PAR from 500 to 2,000 µmol (photon) m^{-2} s^{-1}. Along with this increase, internal CO_2 concentration in Dena 1 variety decreae at a rate slower than in Anjasmoro variety (Table 2). This indicates that stomata of Dena 1 variety is more resilient to keep the internal CO_2 concentration higher than Anjasmoro variety as a demand for CO_2 increase

It has been known widely that light affect stomatal opening, and so leaf conductance. The effect of light to the stomatal response occurs in two ways. The first one is through decrease in intercellular CO_2 concentration due to increase in photosynthesis, and the second is through direct activation of guard cells (Driesen et al., 2020). McAusland et al. (2016) also reported a significant variation in the rapidity of stomatal responses amongst species to light change. For soybean, Bunce (2016) found 15 cultivars differed significantly in stomatal conductance.

Unlike at normal condition, under *Actinomycetes spp*. treatment, the decrease in internal CO_2 concentration due to light increase in Dena 1 variety is faster than Anjasmoro. This is brought about by high response of Anjasmoro variety to *Actinomicetes spp.* than Dena 1 variety. As discussed earlier, Anjasmoro variety responses better to soil fertilization than Dena 1 variety.

CONCLUSIONS

Initial light use efficiency and maximum photosynthesis of Dena 1 variety is 0.068 µmol (CO2) μmol^{-1} (photons) and 45.64 µmol (CO2) m^{-2} s^{-1} respectively. while Anjasmoro variety is 0.068 µmol (CO2) μmol^{-1} (photons) and 34.81 µmol (CO2) m^{-2} s^{-1} respectively. High initial light use efficiency of Dena-1 could be one of the reasons that made Dena 1 variety tolerant to shading. Responses of stomatal conductance and internal CO_2 concentration to light is higher in Anjasmoro than in Dena 1 variety.

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Commented [WU3]: We recommend that the number of references should be added

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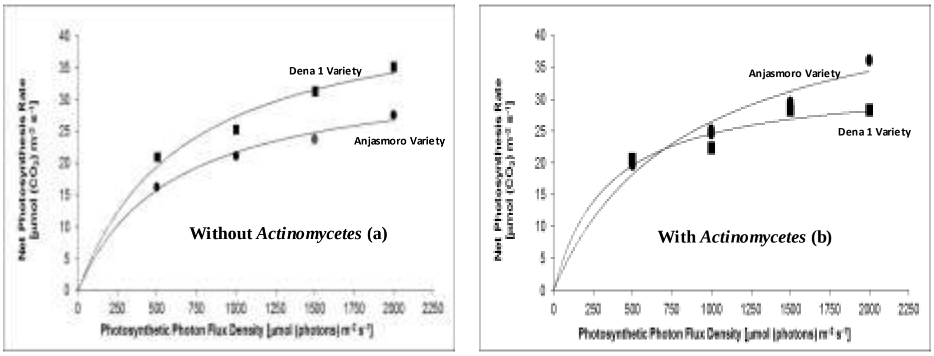

Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

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The following are the editable graph for Figure 1.

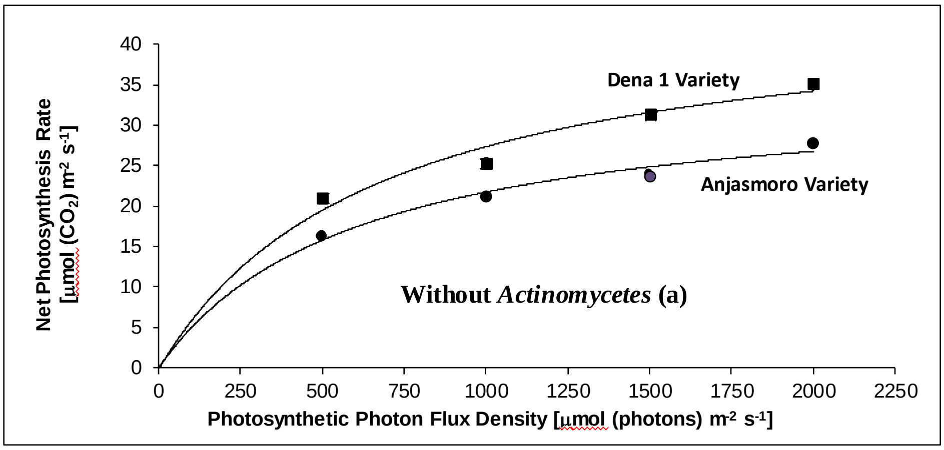

Figure 1.a. Without Actinomycetes

With *Actinomycetes* (b)

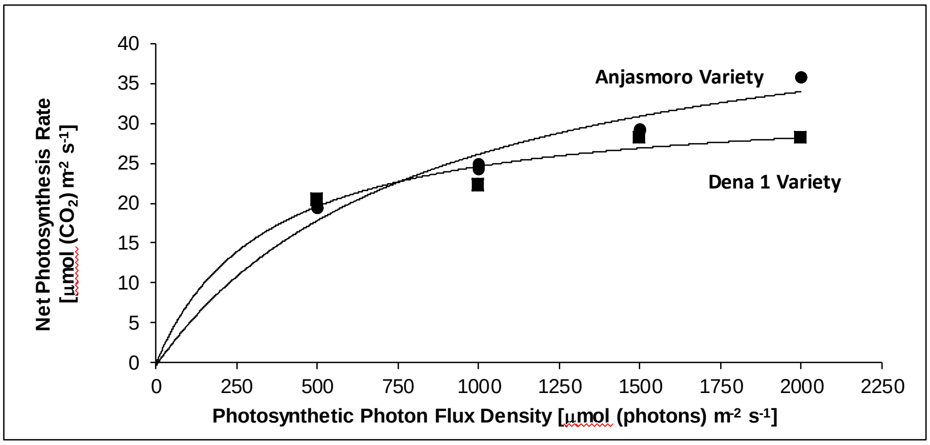

Figure 1.b . With Actinomycetes

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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) m^{-2} s^{-1})	(µmol (CO_2) $µmol^{-1}$ (photons))	(µmol photons) m^{-2} s^{-1})	(µmol (photons) m^{-2} s^{-1})	(µmol (photons) m^{-2} s-1)	(µmol (photons) m^{-2} s^{-1})	(µmol (CO_2) m^{-2} s^{-1})	(µmol (CO_2) $µmol^{-1}$ (photons))	(µmol (CO_2) $µmol^{-1}$ (photons))
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 H2O and Intercellular CO2 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 $m^{-2}s^{-1}$				Intercellular CO_2 Concentration µmol CO_2 mol^{-1}			
	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

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[AGRIVITA] Editor Decision

rusnadi padjung <rusnadi2015@gmail.com> 6 Mei 2021 07.26
Kepada: "Moch. Dawam Maghfoer, Prof." <dmaghfoer@yahoo.com>

Dear Prof. Maghfoer,

Thank you very much for your comments and suggestion to my manuscript entitled "Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties".

Following your comments and suggestion, I have made correction as follow:

1. I have corrected the materials and methods section such that it aligns with Results and Conclusion as well as with tables and figures.

2. I have added 12 references such that the number of references now are 31.

3. Along with addition of references, I am also inserting some sentences to keep a good flow of and coherent sentences.

The revised version of the manuscript is attached.

Should you want me to make some more corrections, please let me know and I will be more than happy to do so.

Looking forward to having your decision.

Thank you very much.

Sincerely,

Rusnadi Padjung

[Kutipan teks disembunyikan]

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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

ABSTRACT

Each variety has its own photosynthetic parameters required to run crop growth model. The research is aimed at characterizing photosynthetic parameters particularly maximum photosynthesis and initial light use efficiency of two soybean varieties widely planted in Indonesia, *Dena-1* and *Anjasmoro* variety. Photosynthetic performances were measured in an experiment designed 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 µ mol (photon) m^{-2} s^{-1}. The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (Pgmax) of *Dena-1* is 45.64 µmol (CO_2) m^{-2} s^{-1}, while *Anjasmoro* variety is only 34.81 µmol (CO_2) m^{-2} s^{-1}. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 µmol (CO_2) $µmol^{-1}$ (photons) compare to Anjasmoro 0.058 µmol (CO_2) $µmol^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomycetes spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 µmol (photon) m^{-2} s^{-1} and higher at PAR above it.

KEYWORDS

Actinomycetes spp., crop model, light efficiency, light response curve, maximum photosynthesis.

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 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 (Strada and Unger, 2016; Gu et al., 2017). 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 (Johnson and Murchie, 2011; Labo, et. al., 2013; Herrmann et al., 2020). There are two important parameters in the photosynthetic light response curve, i.e.: maximum photosynthesis (Pmax), and initial light use efficiency, and in some cases is light compensation point. Pmax 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* variety is preferred by farmers because it is suitable for *tempe* and *tofu* industry as it has yellow grain color, relatively big bean size, and high protein content (Isnaini et al., 2020; Krisnawati and 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* variety also resistant to major disease in soybean such as leaf rust, and it is logging resistant (Mahdiannoor et al., 2017). Leaf rust of soybean, caused by *Phakopsora pachyrhizi* may cause yield loss of 40% to 80%.

Dena-1 variety was released in 2015 particularly as shaded tolerate 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 to shading up to 50% of shading (Pratiwi and 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 enough 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 28^1East 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 variety (V1) and Anjasmoro vatiety (V2), and the second factor is *Actinomycetes spp* application that consist of no *Actinomycetes spp* (A0), and *Actinomycetes spp* with concentration of $1x10^6$ CFU mL^{-1} (A1). Each treatment combination was repeated three times and therefore there were 12 experimental units or plots in total. The plot size is 3 m x 4 m, and the soybeans were sowed in August 20, 2017 in a row of 20 cm x 40 cm with 2 seeds per hole.

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 cm x 3 cm, or $6m^2$. 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 µ mol (photon) m^2 s^{-1}. Environment conditions during experiments were as follows: air temperature – 25-27 ^oC; block and leaf temperature – 25-27 °C; air flow rate – 500 µmol $s^{–1}$; CO_2 concentration in sample cell – 380–400 µmol CO_2 $mol^{–1}$; 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 (Pn) (µmol CO2 $m^{–2}s^{–1}$), intercellular CO_2 concentration(Ci) (µmol CO_2 mol $air^{–1}$), and conductance to H2O (mol H2O m^{-2} s^{-1})

The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel to fit it to the model suggested by Labo, 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 Figure 1. Under normal condition or no *Actinomycetes* the curve of Dena-1 variety is higher than that of Anjasmoro (Figure

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1.a.). This indicates that Dena-1 variety responses better than Anjasmoro variety to light, as it has higher initial light use efficiency as well as higher maximum photosynthesis.

Maximum gross photosynthesis (Pgmax) of Dena-1 is 45.64 µmol (CO2) m^{-2} s^{-1}, while Anjasmoro variety is only 34.81 µmol (CO2) m^{-2} s^{-1} (Table 1). Reported maximum net photosynthesis (Pnmax) of other soybean varieties are 28.8 µmol (CO2) m^{-2} s^{-1} (Yao et al., 2017), 29.9 µmol (CO2) m^{-2} s^{-1} (Zhang et al., 2011), and 34.8 µmol (CO2) m^{-2} s^{-1} (Sakoda et al., 2016). Net photosynthesis (Pn) is gross photosynthesis (Pg) minus dark respiration (Rd). The values of dark respiration are 3.19 µmol (CO2) m^{-2} s^{-1} (Yao et al., 2017), and 6.72 µmol (CO2) m^{-2} s^{-1} (Zhang et al., 2011). Along with high maximum photosynthesis, quantum yield at low light (initial light use efficiency) of Dena-1 variety is also higher which is 0.068 µmol (CO_2) µmol^{-1} (photons) compare to Anjasmoro 0.058 µmol (CO_2) µmol^{-1} (photons). Both Yao et al. (2017), and Zhang et al. (2011) reported a similar quantum yield of soybean at µmol (CO_2) µmol^{-1} (photons). Such a difference in Pgmax and quantum yield between Dena-1 variety and Anjasmoro variety explains why Dena-1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety 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 (CO2) µmol^{-1} (photons)) than quantum yield of Anjasmoro variety (0.06 and 0.04 µmol (CO2) µmol^{-1} (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 variety is consistently higher at percentile 50 % all the way up to 95% than that of Anjasmoro variety. Light saturation point at 50% percentile of Dena-1 variety is 667 µmol (photons) m^{-2} s^{-1}, while Anjasmoro is 603 µmol (photons) m^{-2} s^{-1}. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 µmol (photons) m^{-2} s^{-1}, while Anjasmoro variety is 5,429 µmol (photons) m^{-2} s^{-1} (Table 2). High light saturation point indicates that Dena-1 varieties 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 variety 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 variety is higher than that of Anjasmoro at the beginning or at low light but then 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^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than Anjasmoro at PAR below 706 µmol (photon) m^{-2} s^{-1}, but it is the other way round at PAR above 706 µmol (photon) m^{-2} s^{-1}. Intial light use efficiency of Dena-1 variety is higher (0.096 µmol (CO_2) µmol^{-1} (photons)) than Anjasmoro variety (0.058 µmol (CO_2) µmol^{-1} (photons)). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 variety (33.03 µmol (CO_2) m^{-2} s^{-1}) then in Anjasmoro variety (48.77 µmol (CO_2) m^{-2} s^{-1}) (Table 1). This indicates that Anjasmoro variety responses better to *Actinomycetes spp* variety than Dena-1 variety such that additional nutrient from *Actinomycetes spp* can be converted well into increase in 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

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point (I_c) to I_{200} is much higher in Dena-1 variety than in Anjasmoro variety, 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 et al., 2017), solubilize inorganic phosphates (Pragya et al., 2012; Ghorbani-Nasrabadi et al., 2013; Saif et al., 2014), hydrolyze phytate, a dominant form of organic P in soils (Ghorbani-Nasrabadi et al., 2012; Schneider et al., 2016), and so improve the availability of nutrients (Hozzein et al., 2019; AbdElgawad et al., 2020) particularly phosphorus. *Actinomycetes spp.* is not only increasing the availability of phosphorus, but also nitrogen (AbdElgawad et al., 2020).

Increase the availability of phosphorus and nitrogen in the soil may lead to increase in crop growth and yield (Amule et al., 2018; Soe et al., 2012; Sahur et al, 2018) . Crop response to available nutrient, however, differs among species. Mahdiannoor et al. (2017) reported that growth and yield responses of *Anjasmoro* variety are much higher than local soybean variety to bio-fertilizer application. Similar result was also found by Timotiwu et al. (2020) that *Anjasmoro* variety responded better than *Dena-1* variety 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).). Anjasmoro variety seems response better than Dena-1 variety to Actinomycetes spp treatment such that more chlorophylls are available and energy transfers are more efficient in the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to accommodate light (PAR) increase.

Beside the limitation by availability of chlorophyll 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 variety has higher conductance (2.28 mol H_2O m^{-2} s^{-1}) than Anjasmoro variety (2.09 mol H_2O m^{-2} s^{-1}) and it increases faster with the increase of PAR from 500 to 2,000 μmol (photon) m^{-2} s^{-1}. Along with this increase, internal CO_2 concentration in Dena 1 variety decrease at a rate slower than in Anjasmoro variety (Table 2). This indicates that stomata of Dena 1 variety is more resilient to keep the internal CO_2 concentration higher than Anjasmoro variety as a 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 one is through decrease in intercellular CO_2 concentration due to increase in photosynthesis, and the second is through direct activation of guard cells (Elhaddad et al., 2014; Driesen et al., 2020; 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 variety is faster than Anjasmoro. Limitation in availability of internal CO2 at high light can be overcome by *Actinomycetes spp.* in Anjasmoro variety. A significant variation in the rapidity of stomatal responses amongst species to light change exist (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.*

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CONCLUSIONS

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

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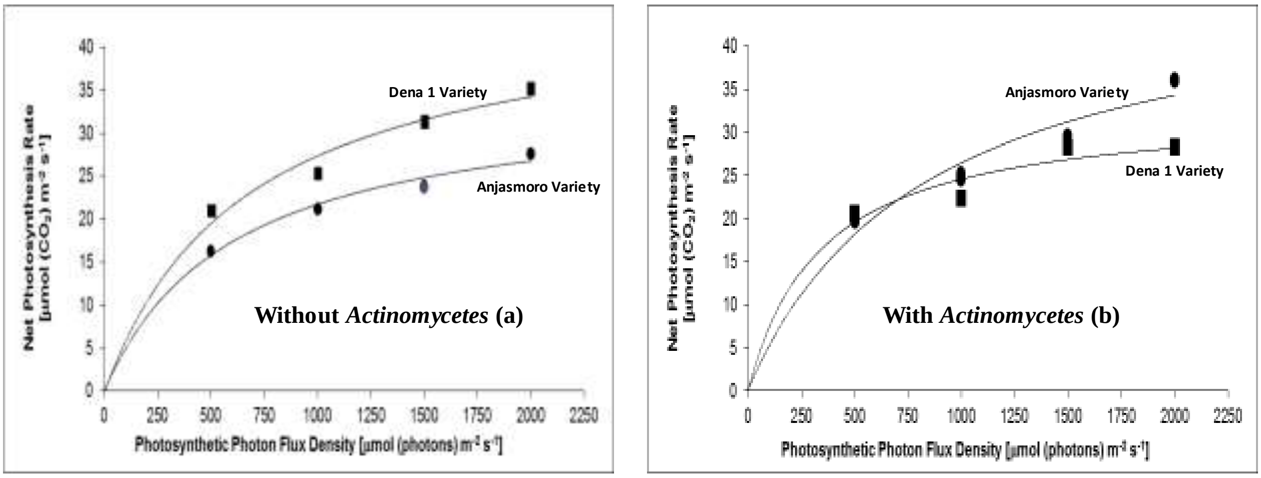

Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

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The following are the editable graph for Figure 1.

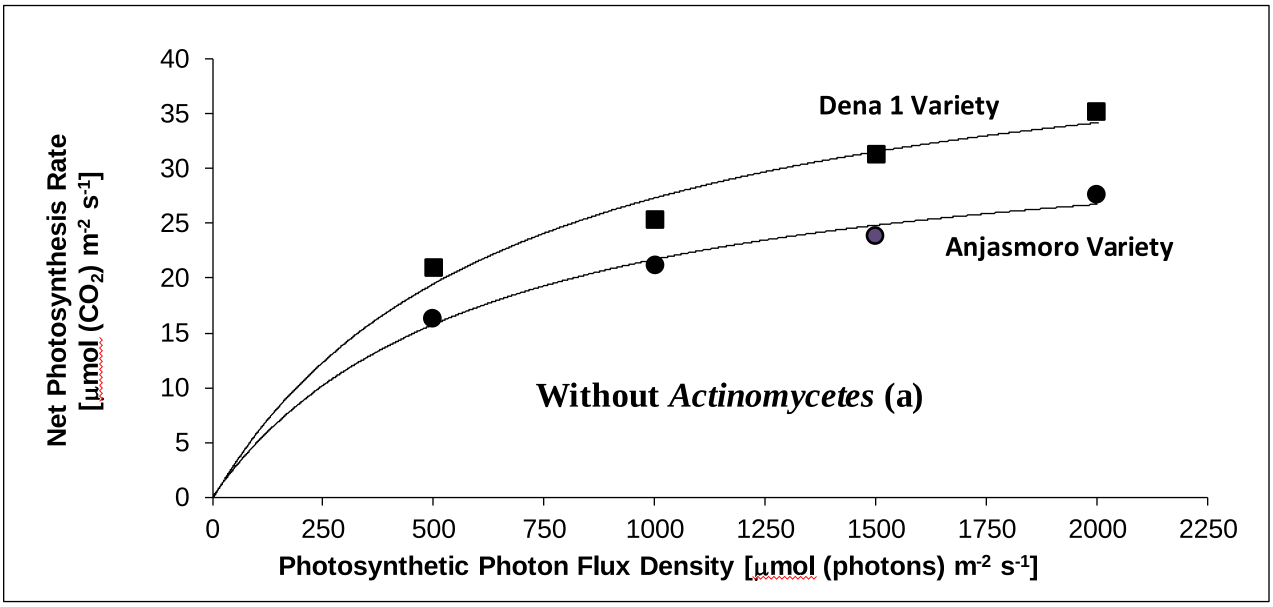

Figure 1.a. Without Actinomycetes

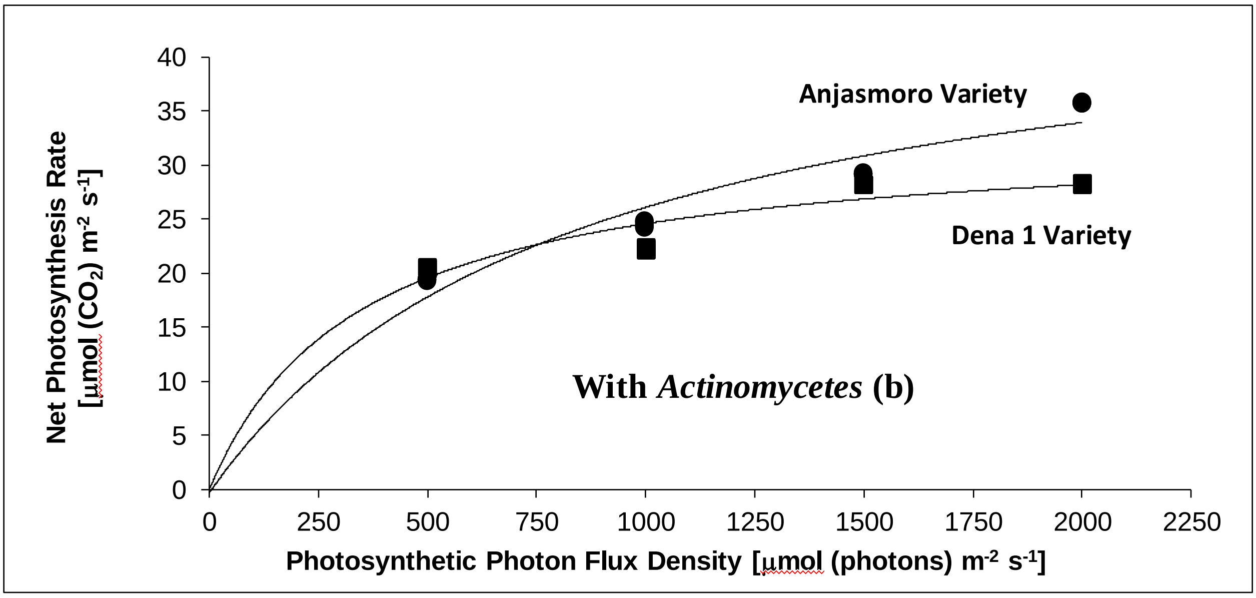

Figure 1.b . With Actinomycetes

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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) m^{-2} s^{-1})	(µmol (CO_2) $µmol^{-1}$ (photons))	(µmol photons) m^{-2} s^{-1})	(µmol (photons) m^{-2} s^{-1})	(µmol (photons) m^{-2} s-1)	(µmol (photons) m^{-2} s^{-1})	(µmol (CO_2) m^{-2} s^{-1})	(µmol (CO_2) $µmol^{-1}$ (photons))	(µmol (CO_2) $µmol^{-1}$ (photons))
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 H2O and Intercellular CO2 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 $m^{-2}s^{-1}$				Intercellular CO_2 Concentration µmol CO_2 mol^{-1}			
	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

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[AGRIVITA] Editor Decision

rusnadi padjung <rusnadi2015@gmail.com> 6 Mei 2021 14.14
Kepada: "Moch. Dawam Maghfoer, Prof." <dmaghfoer@yahoo.com>

Dear Prof. Maghfoer,

Following my previous email a while on above subject matter, I just found a missing figure (value) in line no 92.

In the previous revision it is written : " *. . . .soybean at μmol . . . ."*

It should be written as : *" . . . .. .soybean at **0,053** μmol . . . . ."*

The correction has been incorporated into the attached file of the revised version.

I am so sorry for any inconvenience it may cause.

Thank you

Rusnadi Padjung

[Kutipan teks disembunyikan]

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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

ABSTRACT

Each variety has its own photosynthetic parameters required to run crop growth model. The research is aimed at characterizing photosynthetic parameters particularly maximum photosynthesis and initial light use efficiency of two soybean varieties widely planted in Indonesia, *Dena-1* and *Anjasmoro* variety. Photosynthetic performances were measured in an experiment designed 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 µ mol (photon) m^{-2} s^{-1}. The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (Pgmax) of *Dena-1* is 45.64 µmol (CO_2) m^{-2} s^{-1}, while *Anjasmoro* variety is only 34.81 µmol (CO_2) m^{-2} s^{-1}. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 µmol (CO_2) $µmol^{-1}$ (photons) compare to Anjasmoro 0.058 µmol (CO_2) $µmol^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomycetes spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 µmol (photon) m^{-2} s^{-1} and higher at PAR above it.

KEYWORDS

Actinomycetes spp., crop model, light efficiency, light response curve, maximum photosynthesis.

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 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 (Strada and Unger, 2016; Gu et al., 2017). 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 (Johnson and Murchie, 2011; Labo, et. al., 2013; Herrmann et al., 2020). There are two important parameters in the photosynthetic light response curve, i.e.: maximum photosynthesis (Pmax), and initial light use efficiency, and in some cases is light compensation point. Pmax 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* variety is preferred by farmers because it is suitable for *tempe* and *tofu* industry as it has yellow grain color, relatively big bean size, and high protein content (Isnaini et al., 2020; Krisnawati and 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* variety also resistant to major disease in soybean such as leaf rust, and it is logging resistant (Mahdiannoor et al., 2017). Leaf rust of soybean, caused by *Phakopsora pachyrhizi* may cause yield loss of 40% to 80%.

Dena-1 variety was released in 2015 particularly as shaded tolerate 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 to shading up to 50% of shading (Pratiwi and Artari, 2018). Hence, it is suitable for intercropping with

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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 enough 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 28^1East 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 variety (V1) and Anjasmoro vatiety (V2), and the second factor is *Actinomycetes spp* application that consist of no *Actinomycetes spp* (A0), and *Actinomycetes spp* with concentration of $1x10^6$ CFU mL^{-1} (A1). Each treatment combination was repeated three times and therefore there were 12 experimental units or plots in total. The plot size is 3 m x 4 m, and the soybeans were sowed in August 20, 2017 in a row of 20 cm x 40 cm with 2 seeds per hole.

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 cm x 3 cm, or $6m^2$. 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 µ mol (photon) m^2 s^{-1}. Environment conditions during experiments were as follows: air temperature – 25-27 ^oC; block and leaf temperature – 25-27 °C; air flow rate – 500 µmol $s^{–1}$; CO_2 concentration in sample cell – 380–400 µmol CO_2 $mol^{–1}$; 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 (Pn) (µmol CO2 $m^{–2}s^{–1}$), intercellular CO_2 concentration(Ci) (µmol CO_2 mol $air^{–1}$), and conductance to H2O (mol H2O m^{-2} s^{-1})

The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel to fit it to the model suggested by Labo, 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 Figure 1. Under normal condition or no *Actinomycetes* the curve of Dena-1 variety is higher than that of Anjasmoro (Figure

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1.a.). This indicates that Dena-1 variety responses better than Anjasmoro variety to light, as it has higher initial light use efficiency as well as higher maximum photosynthesis.

Maximum gross photosynthesis (Pgmax) of Dena-1 is 45.64 μmol (CO2) m^{-2} s^{-1}, while Anjasmoro variety is only 34.81 μmol (CO2) m^{-2} s^{-1} (Table 1). Reported maximum net photosynthesis (Pnmax) of other soybean varieties are 28.8 μmol (CO2) m^{-2} s^{-1} (Yao et al., 2017), 29.9 μmol (CO2) m^{-2} s^{-1} (Zhang et al., 2011), and 34.8 μmol (CO2) m^{-2} s^{-1} (Sakoda et al., 2016). Net photosynthesis (Pn) is gross photosynthesis (Pg) minus dark respiration (Rd). The values of dark respiration are 3.19 μmol (CO2) m^{-2} s^{-1} (Yao et al., 2017), and 6.72 μmol (CO2) m^{-2} s^{-1} (Zhang et al., 2011). Along with high maximum photosynthesis, quantum yield at low light (initial light use efficiency) of Dena-1 variety is also higher which is 0.068 μmol (CO_2) $μmol^{-1}$ (photons) compare to Anjasmoro 0.058 μmol (CO_2) $μmol^{-1}$ (photons). Both Yao et al. (2017), and Zhang et al. (2011) reported a similar quantum yield of soybean at 0.053 μmol (CO_2) $μmol^{-1}$ (photons). Such a difference in Pgmax and quantum yield between Dena-1 variety and Anjasmoro variety explains why Dena-1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety 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 (CO2) $μmol^{-1}$ (photons)) than quantum yield of Anjasmoro variety (0.06 and 0.04 μmol (CO2) $μmol^{-1}$ (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 variety is consistently higher at percentile 50 % all the way up to 95% than that of Anjasmoro variety. Light saturation point at 50% percentile of Dena-1 variety is 667 μmol (photons) m^{-2} s^{-1}, while Anjasmoro is 603 μmol (photons) m^{-2} s^{-1}. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 μmol (photons) m^{-2} s^{-1}, while Anjasmoro variety is 5,429 μmol (photons) m^{-2} s^{-1} (Table 2). High light saturation point indicates that Dena-1 varieties 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 variety 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 variety is higher than that of Anjasmoro at the beginning or at low light but then 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^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than Anjasmoro at PAR below 706 μmol (photon) m^{-2} s^{-1}, but it is the other way round at PAR above 706 μmol (photon) m^{-2} s^{-1}. Intial light use efficiency of Dena-1 variety is higher (0.096 μmol (CO_2) $μmol^{-1}$ (photons)) than Anjasmoro variety (0.058 μmol (CO_2) $μmol^{-1}$ (photons)). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 variety (33.03 μmol (CO_2) m^{-2} s^{-1}) then in Anjasmoro variety (48.77 μmol (CO_2) m^{-2} s^{-1}) (Table 1). This indicates that Anjasmoro variety responses better to *Actinomycetes spp* variety than Dena-1 variety such that additional nutrient from *Actinomycetes spp* can be converted well into increase in 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

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point (I_c) to I_{200} is much higher in Dena-1 variety than in Anjasmoro variety, 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 et al., 2017), solubilize inorganic phosphates (Pragya et al., 2012; Ghorbani-Nasrabadi et al., 2013; Saif et al., 2014), hydrolyze phytate, a dominant form of organic P in soils (Ghorbani-Nasrabadi et al., 2012; Schneider et al., 2016), and so improve the availability of nutrients (Hozzein et al., 2019; AbdElgawad et al., 2020) particularly phosphorus. *Actinomycetes spp.* is not only increasing the availability of phosphorus, but also nitrogen (AbdElgawad et al., 2020).

Increase the availability of phosphorus and nitrogen in the soil may lead to increase in crop growth and yield (Amule et al., 2018; Soe et al., 2012; Sahur et al, 2018) . Crop response to available nutrient, however, differs among species. Mahdiannoor et al. (2017) reported that growth and yield responses of *Anjasmoro* variety are much higher than local soybean variety to bio-fertilizer application. Similar result was also found by Timotiwu et al. (2020) that *Anjasmoro* variety responded better than *Dena-1* variety 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).). Anjasmoro variety seems response better than Dena-1 variety to Actinomycetes spp treatment such that more chlorophylls are available and energy transfers are more efficient in the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to accommodate light (PAR) increase.

Beside the limitation by availability of chlorophyll 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 variety has higher conductance (2.28 mol H_2O m^{-2} s^{-1}) than Anjasmoro variety (2.09 mol H_2O m^{-2} s^{-1}) and it increases faster with the increase of PAR from 500 to 2,000 µmol (photon) m^{-2} s^{-1}. Along with this increase, internal CO_2 concentration in Dena 1 variety decrease at a rate slower than in Anjasmoro variety (Table 2). This indicates that stomata of Dena 1 variety is more resilient to keep the internal CO_2 concentration higher than Anjasmoro variety as a 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 one is through decrease in intercellular CO_2 concentration due to increase in photosynthesis, and the second is through direct activation of guard cells (Elhaddad et al., 2014; Driesen et al., 2020; 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 variety is faster than Anjasmoro. Limitation in availability of internal CO2 at high light can be overcome by *Actinomycetes spp.* in Anjasmoro variety. A significant variation in the rapidity of stomatal responses amongst species to light change exist (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.*

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CONCLUSIONS

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

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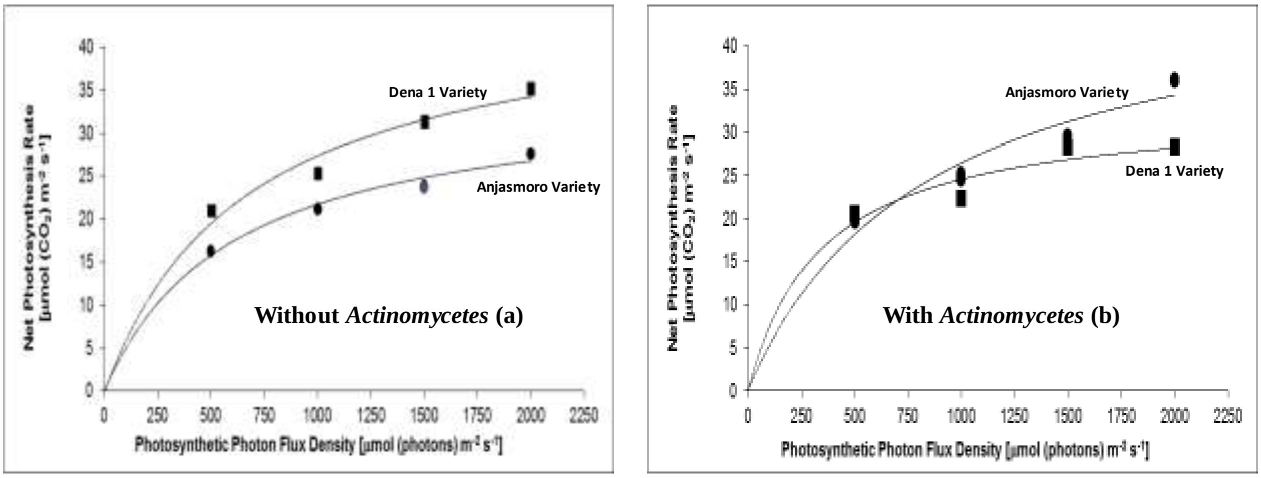

Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

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The following are the editable graph for Figure 1.

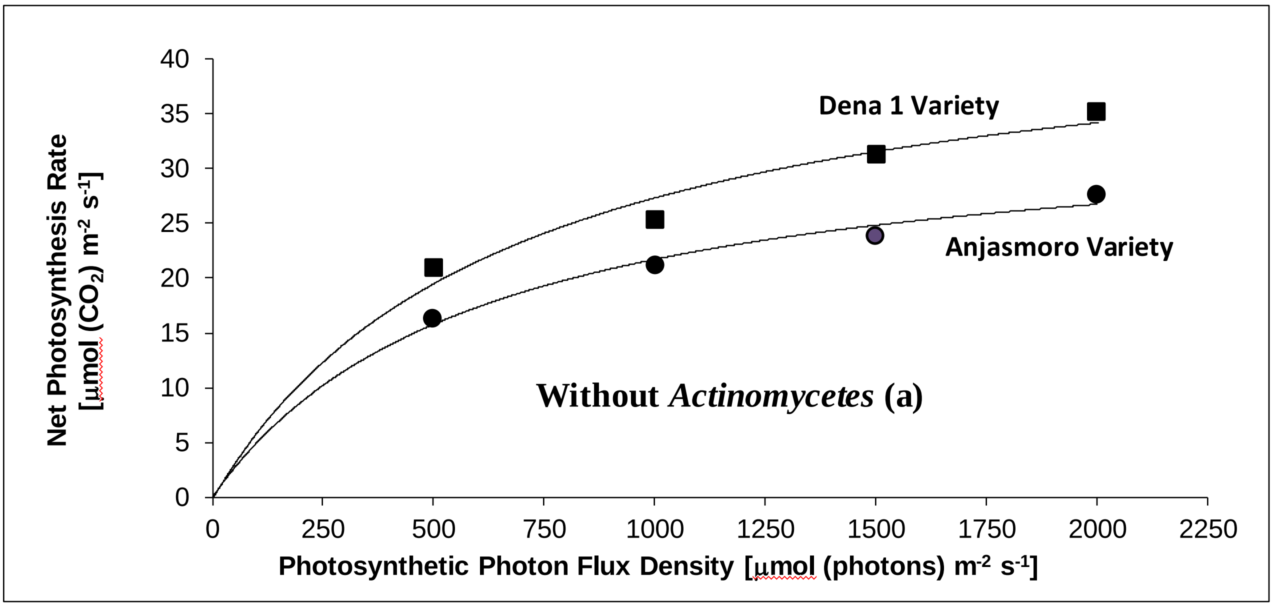

Figure 1.a. Without Actinomycetes

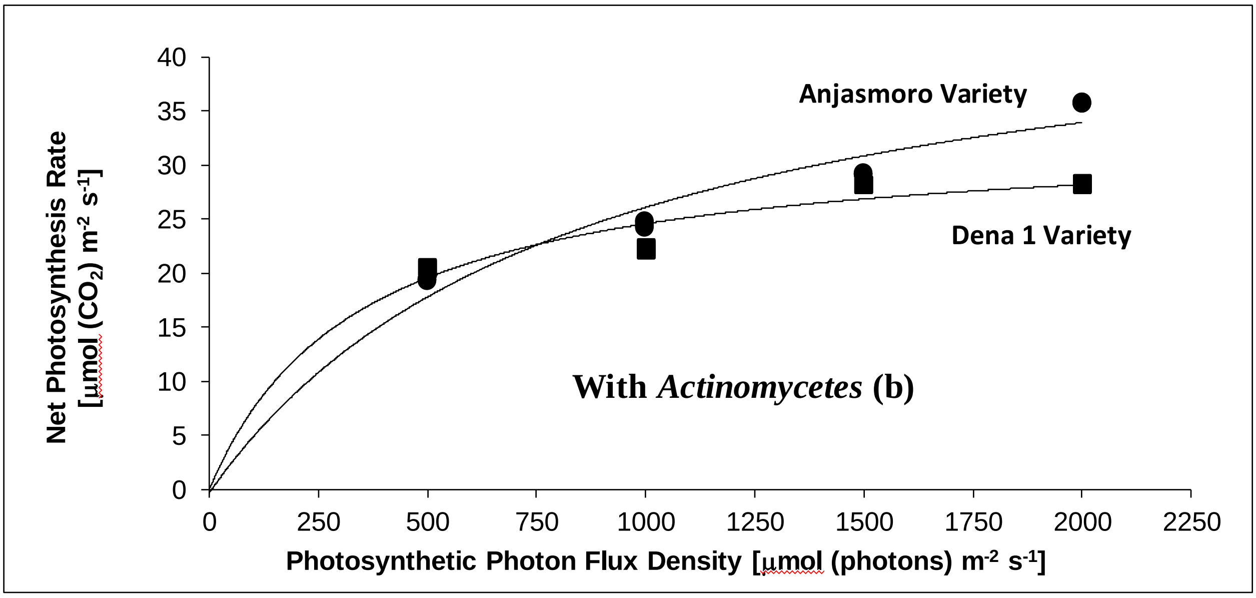

Figure 1.b . With Actinomycetes

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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) m^{-2} s^{-1})	(µmol (CO_2) $µmol^{-1}$ (photons))	(µmol photons) m^{-2} s^{-1})	(µmol (photons) m^{-2} s^{-1})	(µmol (photons) m^{-2} s-1)	(µmol (photons) m^{-2} s^{-1})	(µmol (CO_2) m^{-2} s^{-1})	(µmol (CO_2) $µmol^{-1}$ (photons))	(µmol (CO_2) $µmol^{-1}$ (photons))
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 H2O and Intercellular CO2 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 $m^{-2}s^{-1}$				Intercellular CO_2 Concentration µmol CO_2 mol^{-1}			
	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

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[AGRIVITA] Editor Decision

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Balas Ke: "Moch. Dawam Maghfoer, Prof." <dmaghfoer@yahoo.com>
Kepada: "Rusnadi Padjung, Dr" <rusnadi2015@gmail.com>
Cc: Elkawakib Syam'un <elkawakibsyam@gmail.com>, Nurlina Kasim <nina_nurlina@yahoo.com>

Rusnadi Padjung, Dr :

We have reached a decision regarding your submission to AGRIVITA, Journal of Agricultural Science, "Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties".

Our decision is to: Accept submission

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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

ABSTRACT

Each variety has its own photosynthetic parameters required to run crop growth model. The research is aimed at characterizing photosynthetic parameters particularly maximum photosynthesis and initial light use efficiency of two soybean varieties widely planted in Indonesia, *Dena-1* and *Anjasmoro* variety. Photosynthetic performances were measured in an experiment designed 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 µ mol (photon) m^{-2} s^{-1}. The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (Pgmax) of *Dena-1* is 45.64 µmol (CO_2) m^{-2} s^{-1}, while *Anjasmoro* variety is only 34.81 µmol (CO_2) m^{-2} s^{-1}. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 µmol (CO_2) $µmol^{-1}$ (photons) compare to Anjasmoro 0.058 µmol (CO_2) $µmol^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomycetes spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 µmol (photon) m^{-2} s^{-1} and higher at PAR above it.

KEYWORDS

Actinomycetes spp., crop model, light efficiency, light response curve, maximum photosynthesis.

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 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 (Strada and Unger, 2016; Gu et al., 2017). 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 (Johnson and Murchie, 2011; Labo, et. al., 2013; Herrmann et al., 2020). There are two important parameters in the photosynthetic light response curve, i.e.: maximum photosynthesis (Pmax), and initial light use efficiency, and in some cases is light compensation point. Pmax 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* variety is preferred by farmers because it is suitable for *tempe* and *tofu* industry as it has yellow grain color, relatively big bean size, and high protein content (Isnaini et al., 2020; Krisnawati and 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* variety also resistant to major disease in soybean such as leaf rust, and it is logging resistant (Mahdiannoor et al., 2017). Leaf rust of soybean, caused by *Phakopsora pachyrhizi* may cause yield loss of 40% to 80%.

Dena-1 variety was released in 2015 particularly as shaded tolerate 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 to shading up to 50% of shading (Pratiwi and 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 enough 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 28^1East 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 variety (V1) and Anjasmoro vatiety (V2), and the second factor is *Actinomycetes spp* application that consist of no *Actinomycetes spp* (A0), and *Actinomycetes spp* with concentration of $1x10^6$ CFU mL^{-1} (A1). Each treatment combination was repeated three times and therefore there were 12 experimental units or plots in total. The plot size is 3 m x 4 m, and the soybeans were sowed in August 20, 2017 in a row of 20 cm x 40 cm with 2 seeds per hole.

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 cm x 3 cm, or $6m^2$. 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 µ mol (photon) m^2 s^{-1}. Environment conditions during experiments were as follows: air temperature – 25-27 ºC; block and leaf temperature – 25-27 °C; air flow rate – 500 µmol $s^{–1}$; CO_2 concentration in sample cell – 380–400 µmol CO_2 $mol^{–1}$; 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 (Pn) (µmol CO2 $m^{–2}s^{–1}$), intercellular CO_2 concentration(Ci) (µmol CO_2 mol $air^{–1}$), and conductance to H2O (mol H2O m^{-2} s^{-1})

The photosynthetic light response curve (PN/I curve) was developed using Solver function of Microsoft Excel to fit it to the model suggested by Labo, 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 Figure 1. Under normal condition or no *Actinomycetes* the curve of Dena-1 variety is higher than that of Anjasmoro (Figure 1.a.). This

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indicates that Dena-1 variety responses better than Anjasmoro variety to light, as it has higher initial light use efficiency as well as higher maximum photosynthesis.

Maximum gross photosynthesis (Pgmax) of Dena-1 is 45.64 μmol (CO2) m^{-2} s^{-1}, while Anjasmoro variety is only 34.81 μmol (CO2) m^{-2} s^{-1} (Table 1). Reported maximum net photosynthesis (Pnmax) of other soybean varieties are 28.8 μmol (CO2) m^{-2} s^{-1} (Yao et al., 2017), 29.9 μmol (CO2) m^{-2} s^{-1} (Zhang et al., 2011), and 34.8 μmol (CO2) m^{-2} s^{-1} (Sakoda et al., 2016). Net photosynthesis (Pn) is gross photosynthesis (Pg) minus dark respiration (Rd). The values of dark respiration are 3.19 μmol (CO2) m^{-2} s^{-1} (Yao et al., 2017), and 6.72 μmol (CO2) m^{-2} s^{-1} (Zhang et al., 2011). Along with high maximum photosynthesis, quantum yield at low light (initial light use efficiency) of Dena-1 variety is also higher which is 0.068 μmol (CO_2) $μmol^{-1}$ (photons) compare to Anjasmoro 0.058 μmol (CO_2) $μmol^{-1}$ (photons). Both Yao et al. (2017), and Zhang et al. (2011) reported a similar quantum yield of soybean at 0.053 μmol (CO_2) $μmol^{-1}$ (photons). Such a difference in Pgmax and quantum yield between Dena-1 variety and Anjasmoro variety explains why Dena-1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety 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 (CO2) $μmol^{-1}$ (photons)) than quantum yield of Anjasmoro variety (0.06 and 0.04 μmol (CO2) $μmol^{-1}$ (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 variety is consistently higher at percentile 50 % all the way up to 95% than that of Anjasmoro variety. Light saturation point at 50% percentile of Dena-1 variety is 667 μmol (photons) m^{-2} s^{-1}, while Anjasmoro is 603 μmol (photons) m^{-2} s^{-1}. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 μmol (photons) m^{-2} s^{-1}, while Anjasmoro variety is 5,429 μmol (photons) m^{-2} s^{-1} (Table 2). High light saturation point indicates that Dena-1 varieties 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 variety 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 variety is higher than that of Anjasmoro at the beginning or at low light but then 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^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than Anjasmoro at PAR below 706 μmol (photon) m^{-2} s^{-1}, but it is the other way round at PAR above 706 μmol (photon) m^{-2} s^{-1}. Intial light use efficiency of Dena-1 variety is higher (0.096 μmol (CO_2) $μmol^{-1}$ (photons)) than Anjasmoro variety (0.058 μmol (CO_2) $μmol^{-1}$ (photons)). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 variety (33.03 μmol (CO_2) m^{-2} s^{-1}) then in Anjasmoro variety (48.77 μmol (CO_2) m^{-2} s^{-1}) (Table 1). This indicates that Anjasmoro variety responses better to *Actinomycetes spp* variety than Dena-1 variety such that additional nutrient from *Actinomycetes spp* can be converted well into increase in 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 variety than in Anjasmoro variety, i.e. 40 % (from 0.10 to 0.04) vs 17% (from 0.06 to 0.05).

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Actinomycetes spp. play an important role in soil nutrient cycling (Bhatti et al., 2017), solubilize inorganic phosphates (Pragya et al., 2012; Ghorbani-Nasrabadi et al., 2013; Saif et al., 2014), hydrolyze phytate, a dominant form of organic P in soils (Ghorbani-Nasrabadi et al., 2012; Schneider et al., 2016), and so improve the availability of nutrients (Hozzein et al., 2019; AbdElgawad et al., 2020) particularly phosphorus. *Actinomycetes spp.* is not only increasing the availability of phosphorus, but also nitrogen (AbdElgawad et al., 2020).

Increase the availability of phosphorus and nitrogen in the soil may lead to increase in crop growth and yield (Amule et al., 2018; Soe et al., 2012; Sahur et al, 2018) . Crop response to available nutrient, however, differs among species. Mahdiannoor et al. (2017) reported that growth and yield responses of *Anjasmoro* variety are much higher than local soybean variety to bio-fertilizer application. Similar result was also found by Timotiwu et al. (2020) that *Anjasmoro* variety responded better than *Dena-1* variety 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).). Anjasmoro variety seems response better than Dena-1 variety to Actinomycetes spp treatment such that more chlorophylls are available and energy transfers are more efficient in the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to accommodate light (PAR) increase.

Beside the limitation by availability of chlorophyll 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 variety has higher conductance (2.28 mol H_2O m^{-2} s^{-1}) than Anjasmoro variety (2.09 mol H_2O m^{-2} s^{-1}) and it increases faster with the increase of PAR from 500 to 2,000 μmol (photon) m^{-2} s^{-1}. Along with this increase, internal CO_2 concentration in Dena 1 variety decrease at a rate slower than in Anjasmoro variety (Table 2). This indicates that stomata of Dena 1 variety is more resilient to keep the internal CO_2 concentration higher than Anjasmoro variety as a 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 one is through decrease in intercellular CO_2 concentration due to increase in photosynthesis, and the second is through direct activation of guard cells (Elhaddad et al., 2014; Driesen et al., 2020; 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 variety is faster than Anjasmoro. Limitation in availability of internal CO2 at high light can be overcome by *Actinomycetes spp.* in Anjasmoro variety. A significant variation in the rapidity of stomatal responses amongst species to light change exist (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.*

CONCLUSIONS

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

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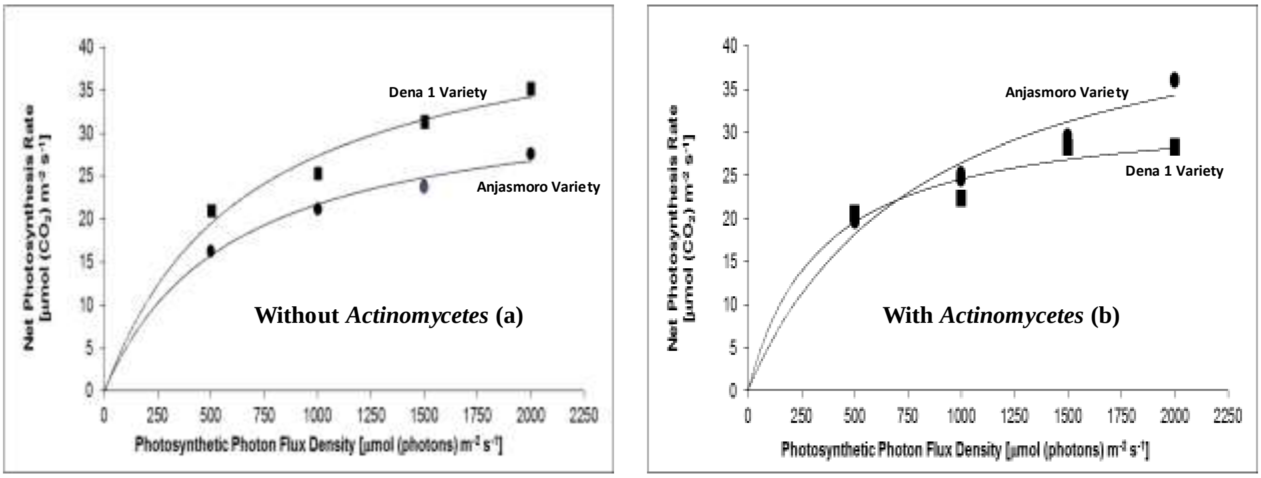

Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

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The following are the editable graph for Figure 1.

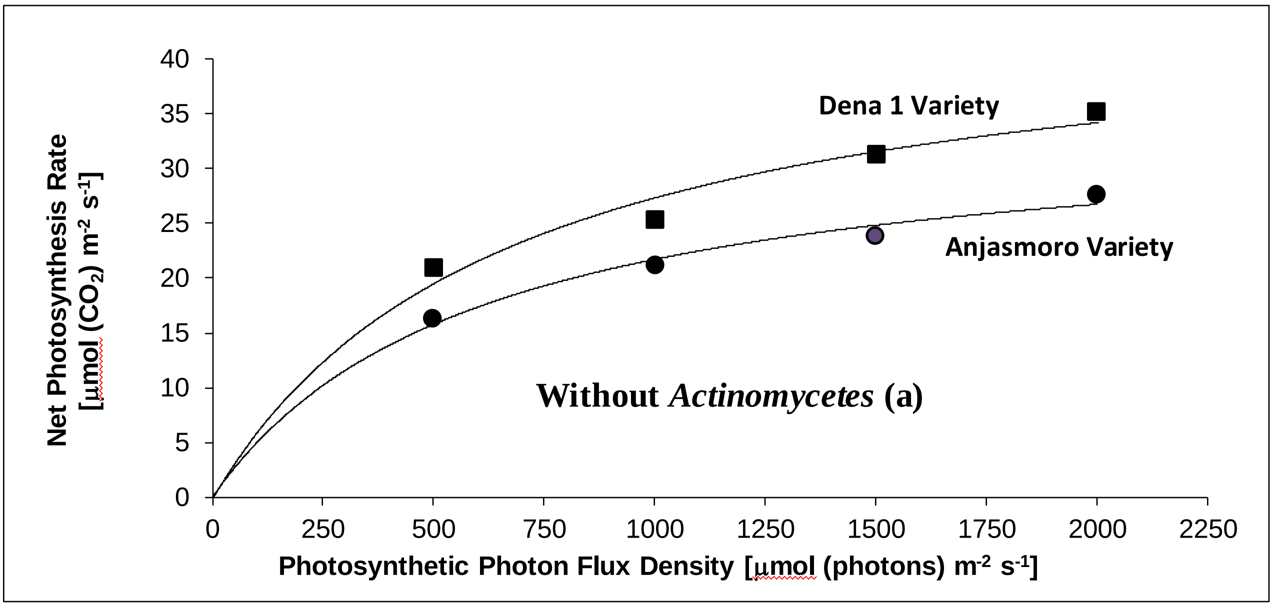

Figure 1.a. Without Actinomycetes

With *Actinomycetes* (b)

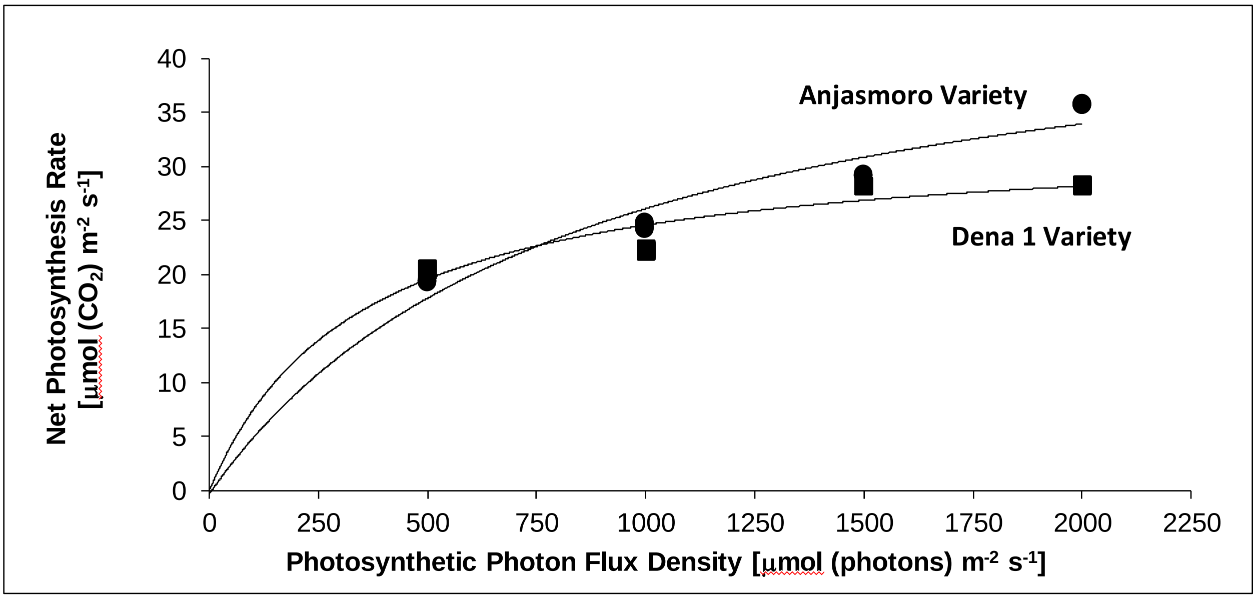

Figure 1.b . With Actinomycetes

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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) m^{-2} s^{-1})	(μmol (CO_2) $μmol^{-1}$ (photons))	(μmol photons) m^{-2} s^{-1})	(μmol (photons) m^{-2} s^{-1})	(μmol (photons) m^{-2} s-1)	(μmol (photons) m^{-2} s^{-1})	(μmol (CO_2) m^{-2} s^{-1})	(μmol (CO_2) $μmol^{-1}$ (photons))	(μmol (CO_2) $μmol^{-1}$ (photons))
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

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[AGRIVITA] Editor Decision

rusnadi padjung <rusnadi2015@gmail.com> 18 Mei 2021 20.38
Kepada: "Moch. Dawam Maghfoer, Prof." <dmaghfoer@yahoo.com>

Dear Prof. Maghfoer,

I am pleased to hear the editor decision to accept my manuscript. I thank you very much for the review and suggestions for correction and the final decision. Hopefully the paper can be published in the next upcoming issue of 43 (2) in June.
Could you suggest me an instruction for the payment of publication fee.

Once again, thank you very much and looking forward to having from you the instruction for payment.

Best regards,

Rusnadi Padjung
[Kutipan teks disembunyikan]

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Revisi artikel

Agrivita . <agrivita@ub.ac.id> 27 Mei 2021 13.11
Kepada: rusnadi2015@gmail.com

Bersama ini kami kirimkan dnegan hormat artikel Bapak yang akan kami proses ke penerbitan selanjutnya.

Perbaikan kami tunggu besok hari Jumat 28 Mei 2021 tidak lebih dari pukul 11.00 WIB di email kami ini.

Terima kasih.

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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties
(Running title: consist of 3-5 words or phrases and should be arranged as a sentence).
Check the editors comment in the text.

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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 (Pgmax) 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.

Keywords: *Actinomycetes* spp.; Crop model; Light efficiency; Light response curve; Maximum photosynthesis

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 (Pmax), and initial light use efficiency, and in some cases is light compensation point. Pmax 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 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

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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 m^2 **(please check again)**. 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% **(please check again the unit, and if they're not negative number, do not use dash before the number)**. 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 (Pn) (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.

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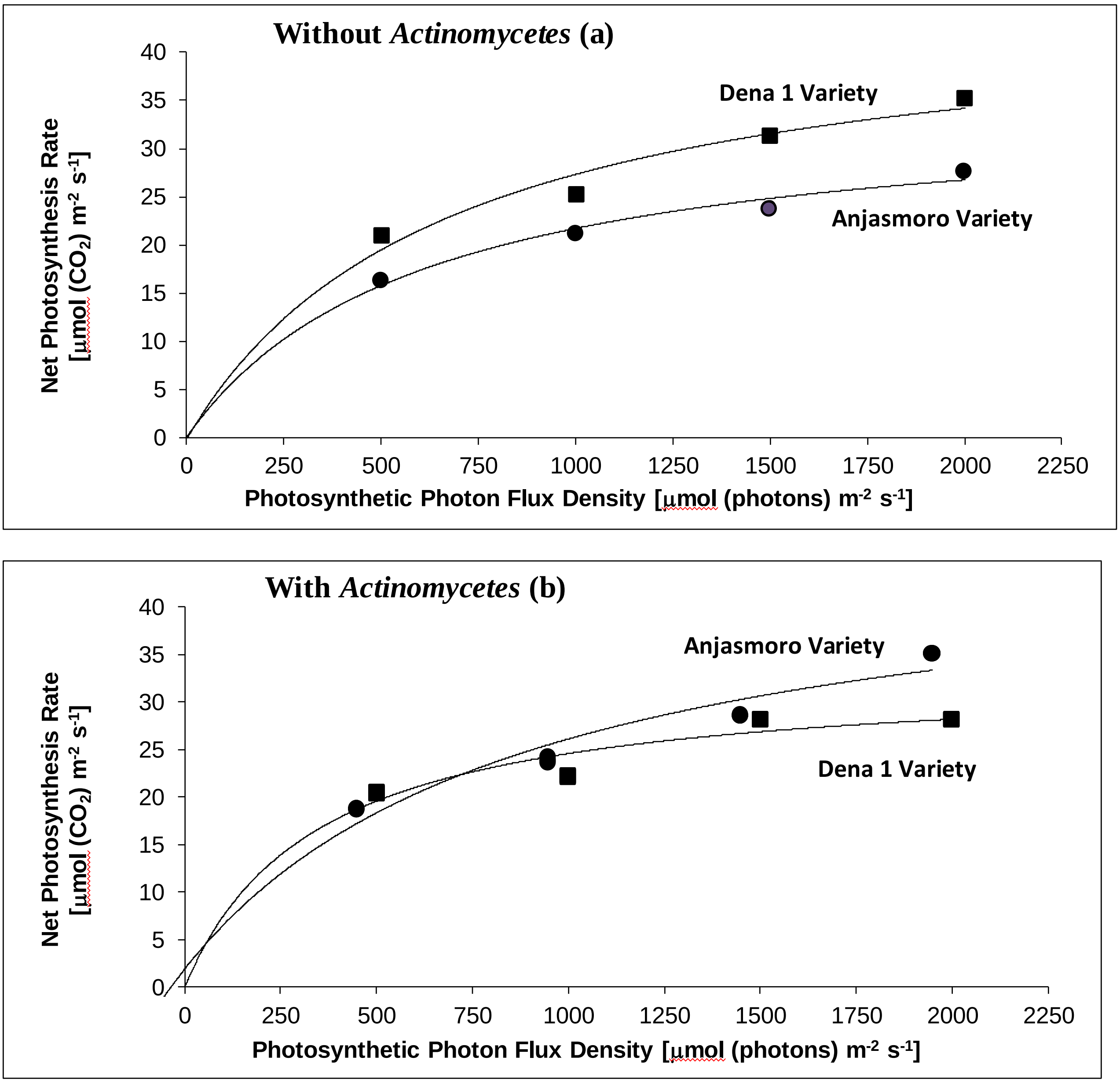

Fig. 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b). **(please group the picture, mohon sesuaikan satuan yang ada di gambar dengan satuan di teks)**

Maximum gross photosynthesis (Pgmax) 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 (Pnmax) 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 (Pn) is gross photosynthesis (Pg) minus dark respiration (Rd). 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 Pgmax 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}) **(mohon untuk dapat konsisten dengan format penulisan yang seperti ini, please check the whole text)** 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).

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). Anjasmoro seems to response better than Dena-1 to

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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.

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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. **(mohon diperiksa satuan unit dan keseluruhan table)**

Varieties and Actinomycetes Tratments	Standard Parameters		Light saturation point at					Quantum yield at	
	Maximum Photosynthesis	**Quantum yield at I = 0**	**50 percen-tile**	**85 percen-tile**	**90 percen-tile**	**95 Percent-tile**	**Light-saturated net CO_2 uptake**	**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)/m^2/s)	(μmol (CO_2) /μmol (photons))	(μmol photons)/ m^2/s)	(μmol (photons)/ m^2/s)	(μmol (photons)/ m^2/s)	(μmol (photons)/ m^2/s)	(μmol (CO_2) /m^2/s)	(μmol (CO_2)/μmol (photons))	(μmol (CO_2)/ μmol (photons))
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

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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, 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 (Pmax) 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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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

Running title: *Actinomycetess* spp. alters photosynthetic parameters of soybean.

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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.

Keywords: *Actinomycetes* spp.; Crop model; Light efficiency; Light response curve; Maximum photosynthesis

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 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

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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.

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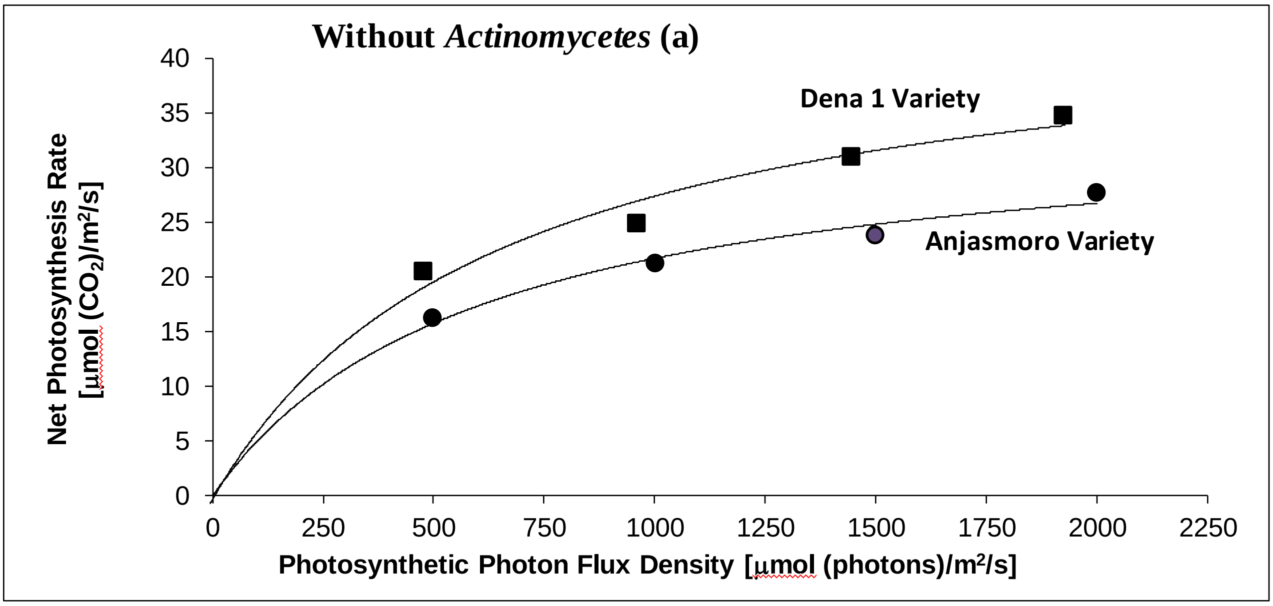

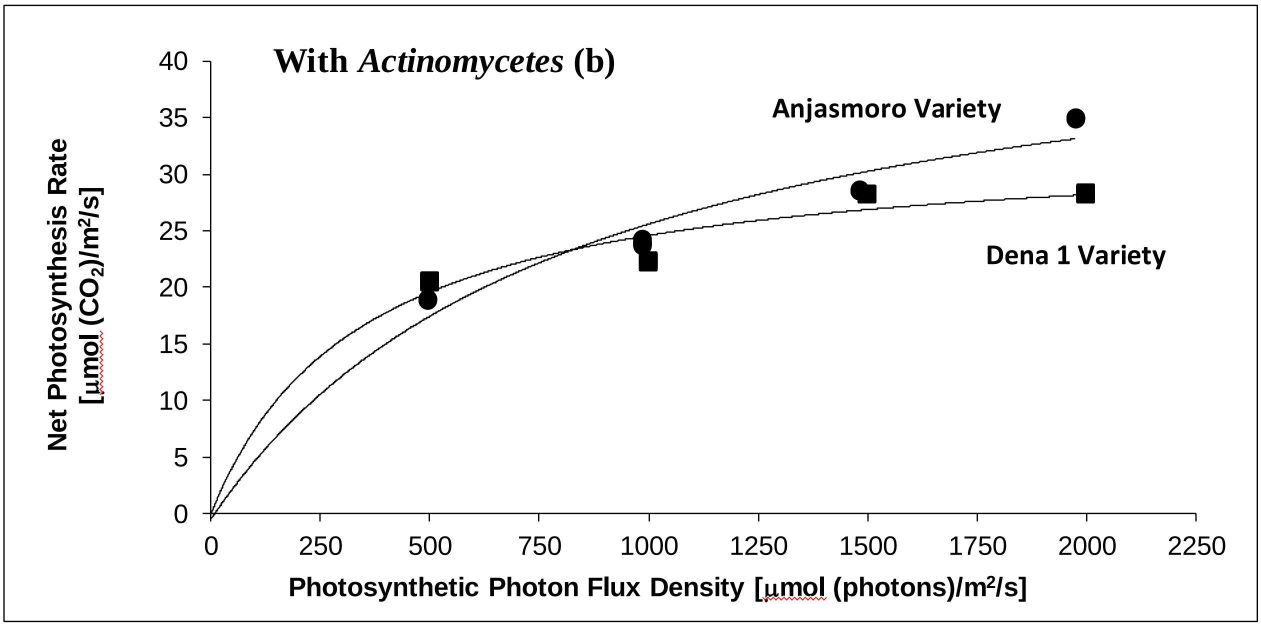

Fig. 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under *Actinomycetes* spp. treatment (b).

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

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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 Pgmax 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

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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). 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.

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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)/m^2/s)	(µmol (CO_2) /µmol (photons))	(µmol photons)/m^2/s)	(µmol (photons)/m^2/s)	(µmol (photons)/m^2/s)	(µmol (photons)/m^2/s)	(µmol (CO_2) /m^2/s)	(µmol (CO_2)/µmol (photons))	(µmol (CO_2)/ µmol (photons))
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

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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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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

Running title: *Actinomycetess* spp. alters photosynthetic parameters of soybean.

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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.

Keywords: *Actinomycetes* spp.; Crop model; Light efficiency; Light response curve; Maximum photosynthesis

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 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

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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.

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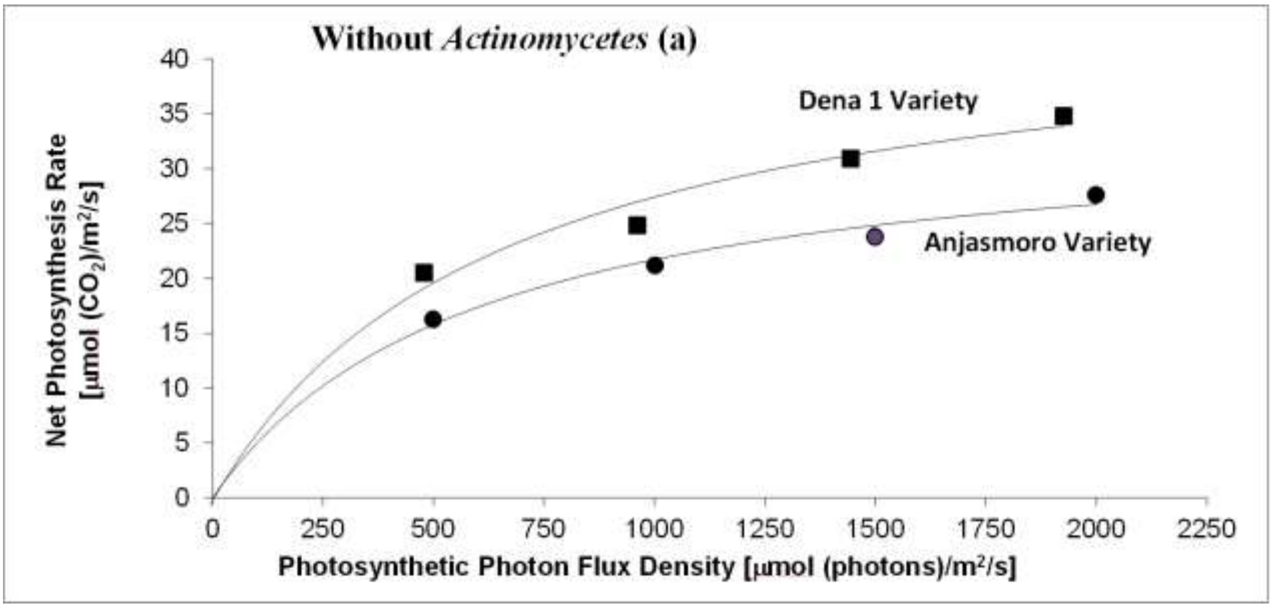

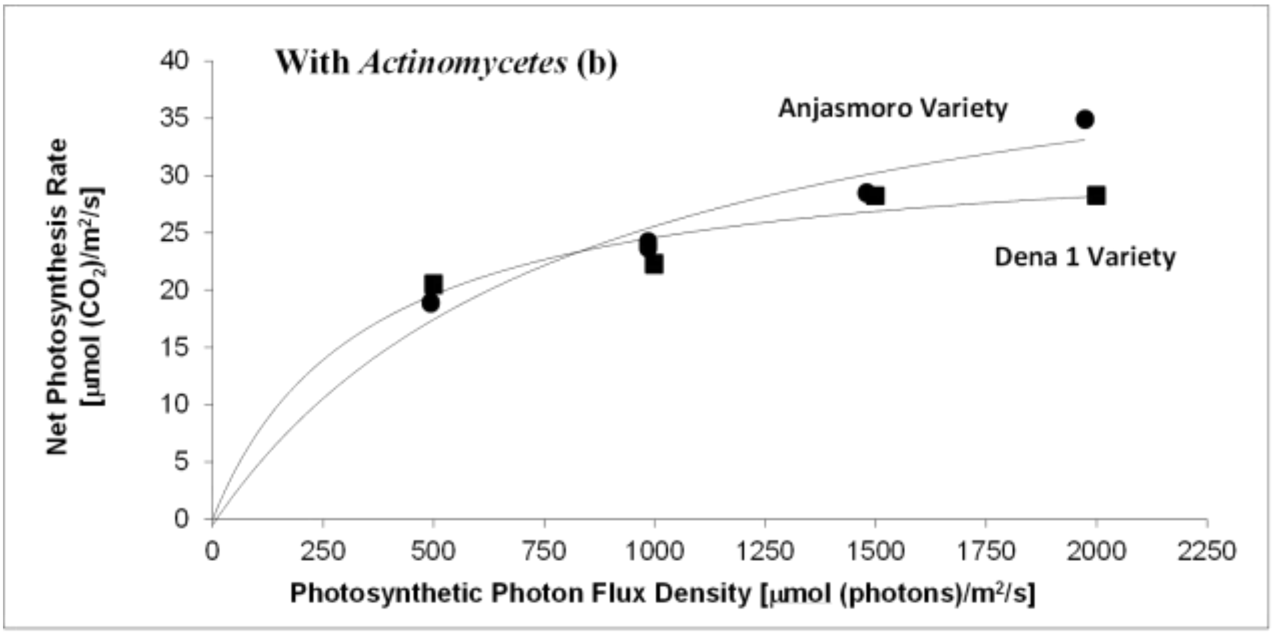

Fig. 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under *Actinomycetes* spp. treatment (b).

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

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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 Pgmax 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 too leaves (Muhammad, 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.

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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)/m^2/s)	(µmol (CO_2) /µmol (photons))	(µmol photons)/m^2/s)	(µmol (photons)/m^2/s)	(µmol (photons)/m^2/s)	(µmol (photons)/m^2/s)	(µmol (CO_2) /m^2/s)	(µmol (CO_2)/µmol (photons))	(µmol (CO_2)/ µmol (photons))
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

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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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Di sini saya kirimkan perbaikannya.

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Salam,

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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

Running title: *Actinomycetess* spp. alters photosynthetic parameters of soybean.

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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.

Keywords: *Actinomycetes* spp.; Crop model; Light efficiency; Light response curve; Maximum photosynthesis

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 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

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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.

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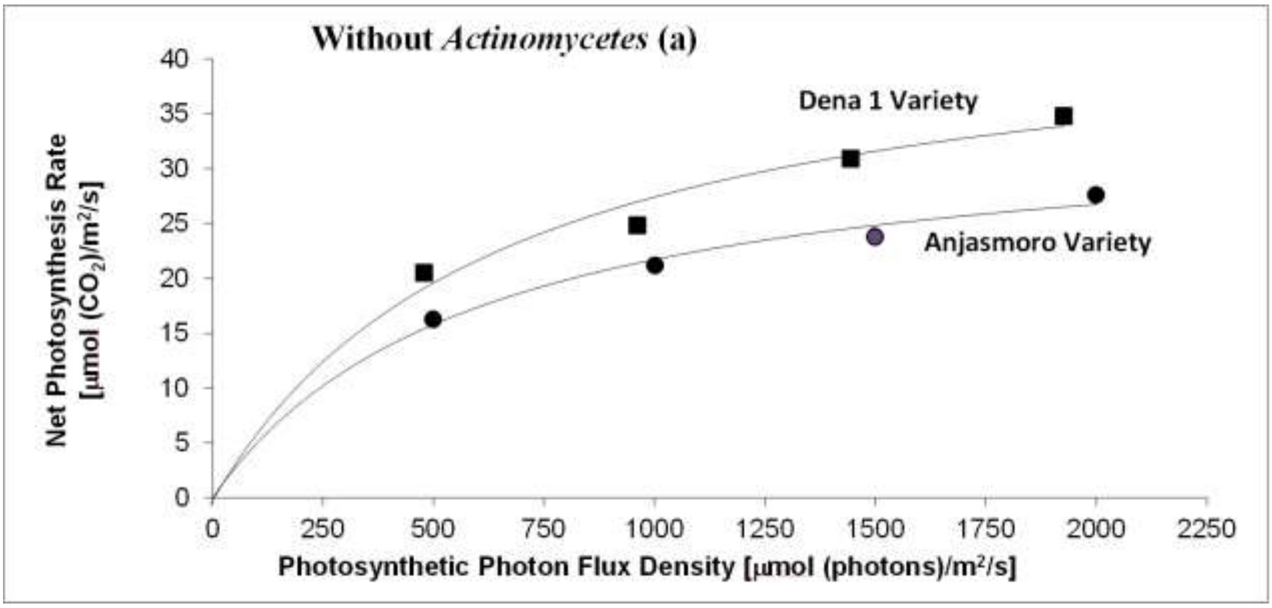

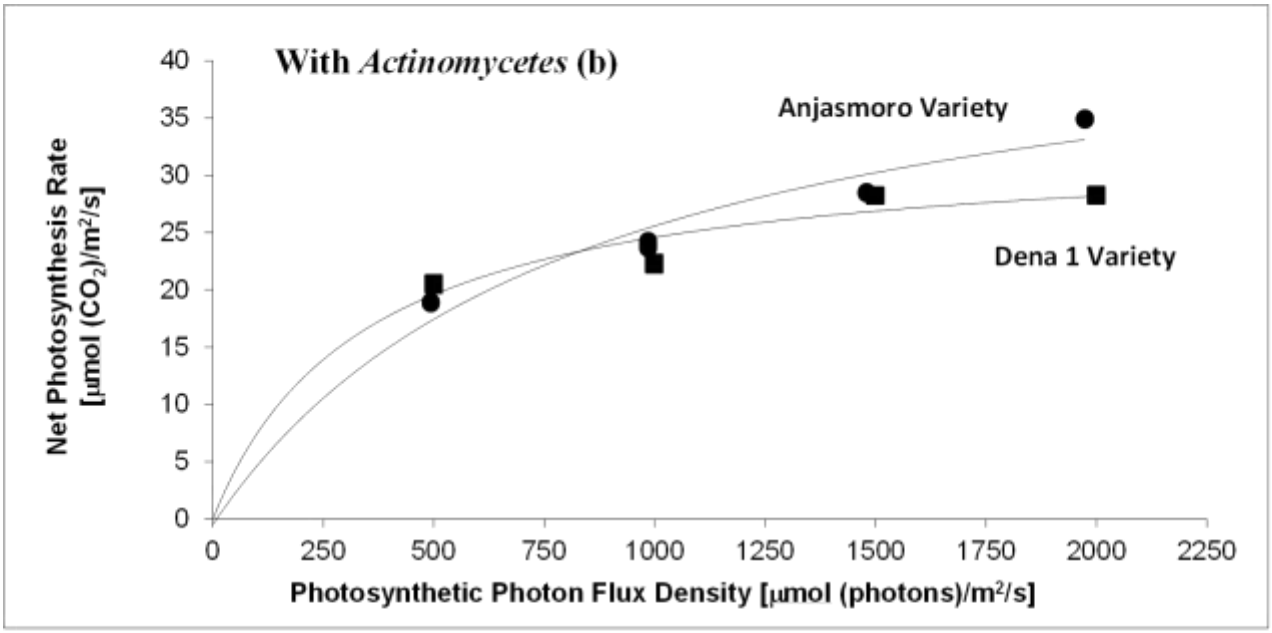

Fig. 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under *Actinomycetes* spp. treatment (b).

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

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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 Pgmax 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

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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, 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)/m^2/s)	(μmol (CO_2) /μmol (photons))	(μmol photons)/m^2/s)	(μmol (photons)/m^2/s)	(μmol (photons)/m^2/s)	(μmol (photons)/m^2/s)	(μmol (CO_2) /m^2/s)	(μmol (CO_2)/μmol (photons))	(μmol (CO_2)/ μmol (photons))
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

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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Photosynthetic Paramaters of Two Indonesian Soybean Top Varieties

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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.

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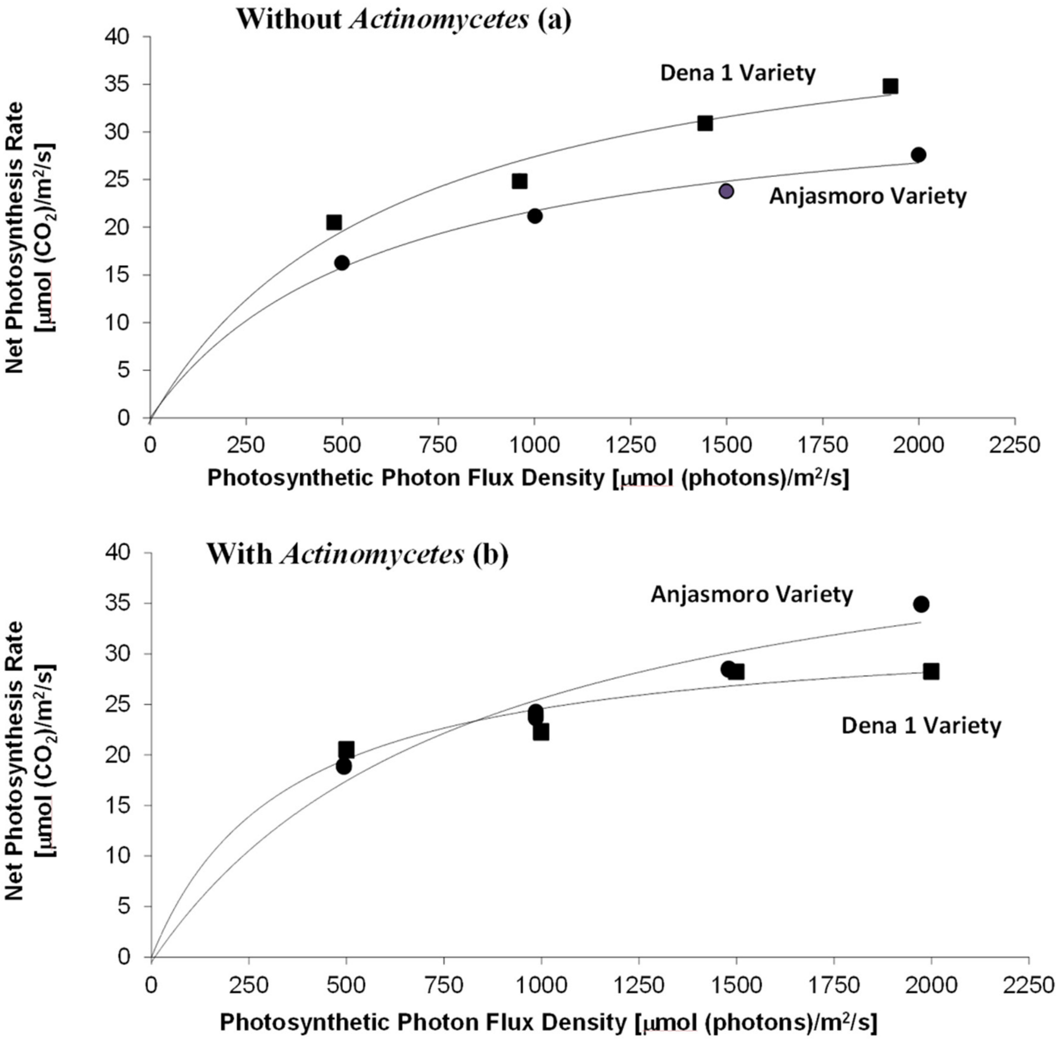

Fig. 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under *Actinomycetes* spp. treatment (b)

Maximum gross photosynthesis (P_{gmax}) of Dena-1 is 45.64 *µmol* (CO_2)/m²/s, while Anjasmoro variety is only 34.81 *µmol* (CO_2)/m²/s (Table 1). Reported maximum net photosynthesis (P_{nmax}) of other soybean varieties are 28.8 *µmol* (CO_2) /m²/s (Yao et al., 2017), 29.9 *µmol* (CO_2)/m²/s (Zhang, Hu, Luo, Chow, & Zhang, 2011), and 34.8 *µmol* (CO_2)/m²/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)/m²/s (Yao et al., 2017), and 6.72 *µmol* (CO_2)/m²/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

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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

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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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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

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