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Photosynthetic Parameters of Two Indonesian Soybean Top Varieties

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I. Photosynthetic Parameters of Two Indonesian Soybean Top Varieties

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Photosynthetic Parameters 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 *Actinomyces 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 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$. 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 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$, while *Anjasmoro* variety is only 34.81 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons) compare to *Anjasmoro* 0.058 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomyces spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$ and higher at PAR above it.

KEYWORDS

Actinomyces 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 (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* 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 lodging 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

44 tolerant to shading up to 50% of shading (Pratiwi and Artari, 2018). Hence, it is suitable for intercropping with
45 young high estate crops, such as coconut, oil palm, and rubber. With large plantation area of those estate
46 crops Indonesia, expansion of soybean crop to plantation area is promising. *Dena-1* variety, along with *Dena*
47 2 variety as well, are considered as varieties suitable to be intercropped with young trees at community
48 forest (Abidin, 2015)

49 Characterizing photosynthetic parameters of *Dena-1* variety is also important to understand the
50 physiological trait underlying the capacity of the variety to tolerate shading. More importantly, it will give
51 physiological explanation up to which light condition this variety produce enough photosynthate for
52 reasonable yield.

53 MATERIALS AND METHODS

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

57 Photosynthetic performances were measured in an experiment designed to study the effect of
58 *Actinomyces spp* on growth and yield of soybean. Therefore the experimental design was Factorial Design,
59 in which soybean varieties as first factor that consist of *Dena-1* variety (V1) and Anjasmoro variety (V2), and
60 the second factor is density of *Actinomyces spp* that consist of no *Actinomyces spp* (A0), *Actinomyces*
61 *spp* with concentration of 1×10^3 CFU mL⁻¹ (A1), and *Actinomyces spp* with concentration of 1×10^6 CFU
62 mL⁻¹ (A2). Each treatment combination was repeated three times and therefore there were 18 experimental
63 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
64 of 20 cm x 40 cm with 2 seeds per hole. However, the photosynthetic measurements were not following this
65 experimental design, but were taken at two contrasting *Actinomyces spp* treatments of two varieties, i.e. no
66 *Actinomyces* and 1×10^6 CFU mL⁻¹ *Actinomyces* at Anjasmoro and *Dena-1* varieties (W1A0, W1A2,
67 W2A0, and W2A2).

68 The photosynthetic measurement was taken in October 15, 2017 using an open chamber portable
69 photosynthetic system (LI-6400, LI-COR, Inc., Logan, NE, USA). Mature leaf exposed to full sunlight was
70 flipped to the chamber. The size of the chamber used, or the area of leaf flipped in the chamber, is 2 cm x 3
71 cm, or 6m². To develop a light response curve, the photosynthesis was measured at variable
72 Photosynthetically Active Radiation (PAR), i.e. 500; 1,000; 1,500; and 2,000 μ mol (photon) m² s⁻¹.
73 Environment conditions during experiments were as follows: air temperature – 25-27 °C; block and leaf
74 temperature – 25-27 °C; air flow rate – 500 μ mol s⁻¹; CO₂ concentration in sample cell – 380–400 μ mol CO₂
75 mol⁻¹; and relative humidity in sample cell – 56-70 %. The measurements are repeated three times (once for
76 each experimental unit). In each replication the system run for 5 second, and the data were registered every
77 second, and therefore there are 15 data set available for each PAR level, or 60 data set for all replications
78 and PAR levels. The parameters used are photosynthetic rate (Pn) (μ mol CO₂ m⁻²s⁻¹), intercellular CO₂
79 concentration(Ci) (μ mol CO₂ mol air⁻¹), and conductance to H₂O (mol H₂O m⁻² s⁻¹)

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

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

88 Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$, while Anjasmoro
 89 variety is only $34.81 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Table 1). Along with high maximum photosynthesis, quantum yield
 90 at low light (initial light use efficiency) of Dena-1 variety is also higher which is $0.068 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$
 91 (photons) compare to Anjasmoro $0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Such a difference explains why Dena-
 92 1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-
 93 1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety both at light compensation point
 94 ($\phi(I_{comp})$) and at light between compensation point to 200 ($\phi(I_c-I_{200})$) is higher (0.07 and $0.05 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$
 95 (μmol^{-1} (photons)) than quantum yield of Anjasmoro variety (0.06 and $0.04 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons))
 96 (Table 1). In another word, photosynthesis at Dena-1 variety still occurs at acceptable rate even under low
 97 light or under shading.

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

106 The photosynthetic light response curves of these two varieties change under *Actinomyces*
 107 treatment. Under such condition the curve of Dena-1 variety is higher than that of Anjasmoro at the
 108 beginning or at low light but then as light increase, the quantum yield is decreasing at a rate faster in Dena-1
 109 than in Anjasmoro such that Dena-1 curve is surpassed by Anjasmoro curve at PAR $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$
 110 ($\mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$) (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than
 111 Anjasmoro at PAR below $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$, but it is the other way round at PAR above $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$.
 112 Initial light use efficiency of Dena-1 variety is higher ($0.096 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons))
 113 than Anjasmoro variety ($0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)). In contrast, the maximum photosynthesis
 114 (P_{gmax}) is lower in Dena-1 variety ($33.03 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$) then in Anjasmoro variety ($48.77 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$)
 115 (Table 1). This indicates that Anjasmoro variety responds better to *Actinomyces spp* variety than
 116 Dena-1 variety such that additional nutrient from *Actinomyces spp* can be converted well into increase in
 117 the capacity of photosynthetic apparatus. With an increase in capacity of photosynthetic apparatus,
 118 photosynthesis rate increases along with increase in light, and so increase in light saturation point, and
 119 maximum photosynthesis (Table 1). Hence, the rate of decrease in quantum yield from light compensation
 120 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
 121 17% (from 0.06 to 0.05).

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

133 Beside the limitation by energy transfer, photosynthesis at high light is apparently also limited by the
134 availability of CO₂ as can be indicated by conductance to H₂O and internal CO₂ concentration. Under normal
135 condition or no *Actinomycetes* treatment, Dena 1 variety has higher conductance (2.28 mol H₂O m⁻² s⁻¹) than
136 Anjasmoro variety (2.09 mol H₂O m⁻² s⁻¹) and it increases faster with the increase of PAR from 500 to 2,000
137 μmol (photon) m⁻² s⁻¹. Along with this increase, internal CO₂ concentration in Dena 1 variety decrease at a
138 rate slower than in Anjasmoro variety (Table 2). This indicates that stomata of Dena 1 variety is more
139 resilient to keep the internal CO₂ concentration higher than Anjasmoro variety as a demand for CO₂ increase

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

147 Unlike at normal condition, under *Actinomycetes spp.* treatment, the decrease in internal CO₂ concentration
148 due to light increase in Dena 1 variety is faster than Anjasmoro. This is brought about by high response of
149 Anjasmoro variety to *Actinomycetes spp.* than Dena 1 variety. As discussed earlier, Anjasmoro variety
150 responses better to soil fertilization than Dena 1 variety.

151

CONCLUSIONS

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

157

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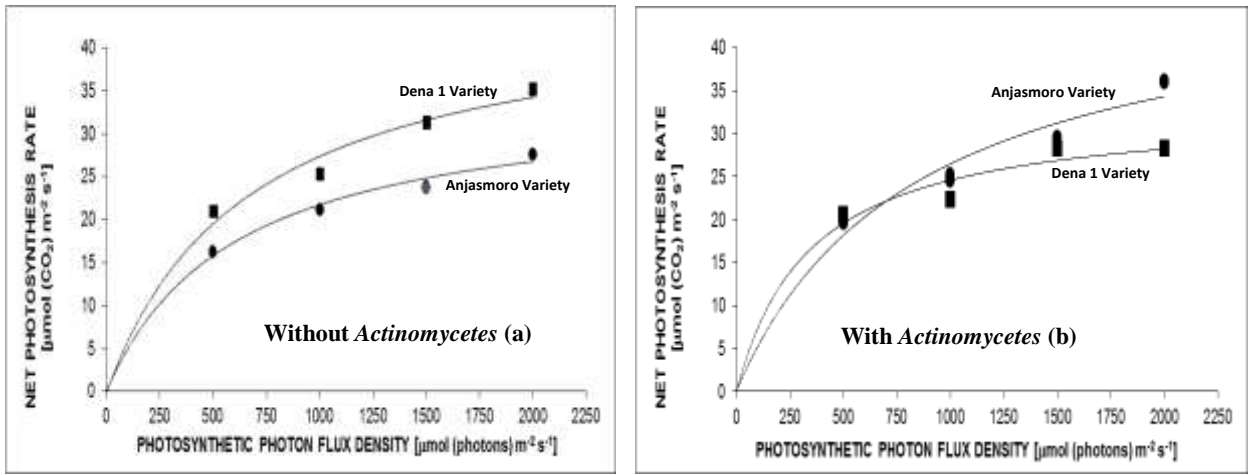
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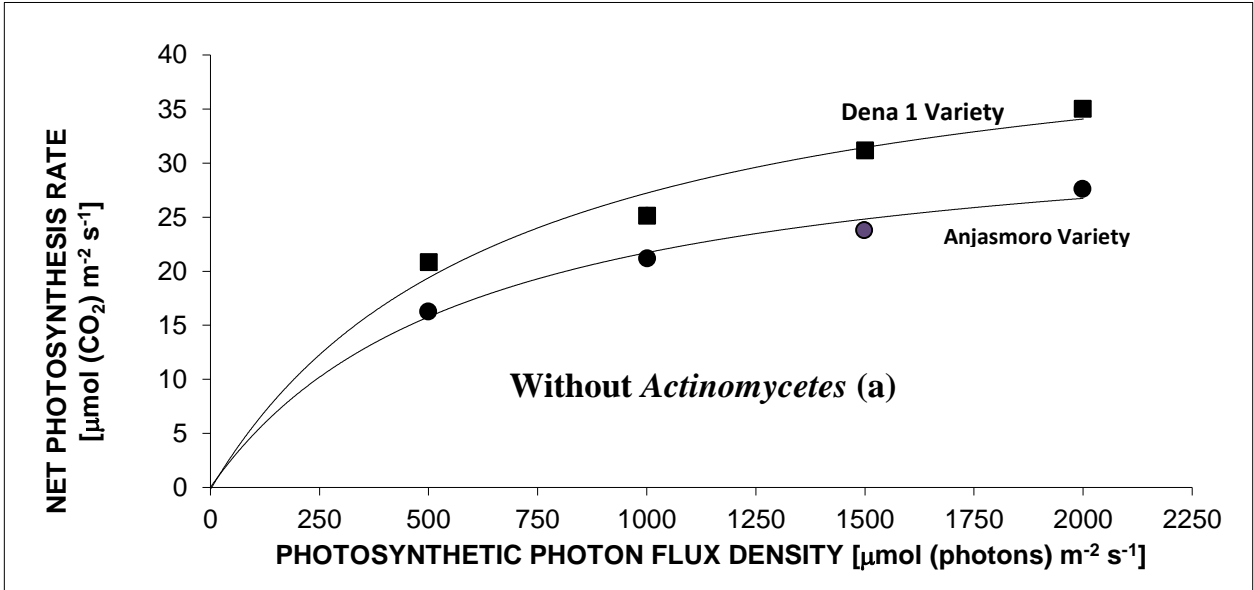
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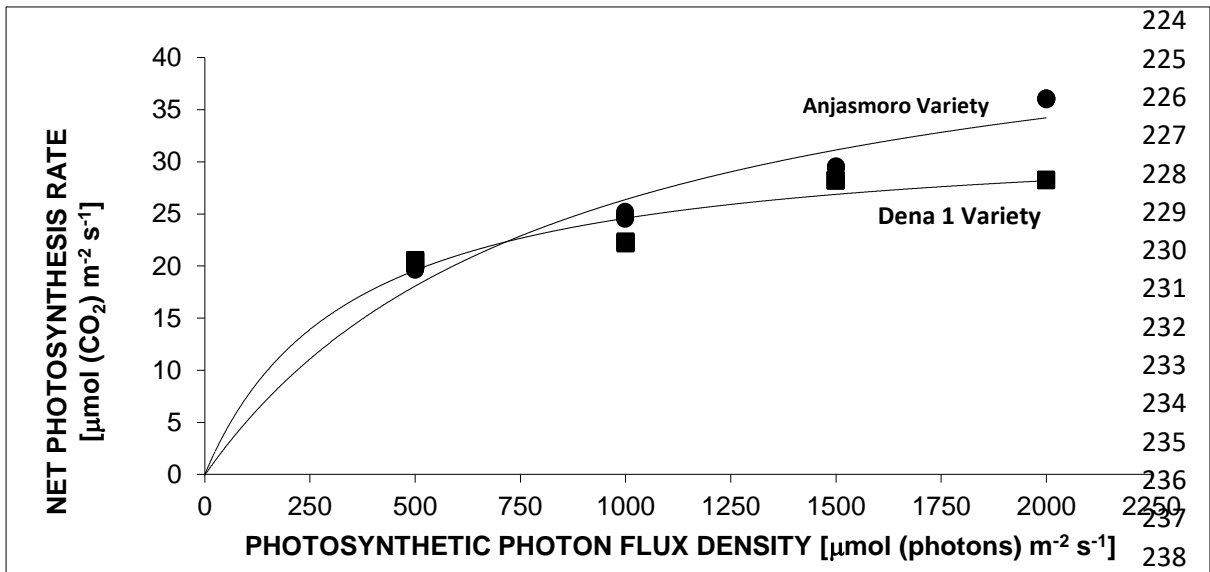
212 Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a),
 213 and under Actinomycetes treatment (b).

214

215 The following are the editable graph for Figure 1.
 216
 217 Figure 1.a. Without Actinomycetes
 218



219
 220
 221
 222 Figure 1.b . With Actinomycetes
 223



239
 240

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

244

Varieties and Actinomycetes Treatments	Standard Parameters		Light saturation point at				Light-saturated net CO ₂ uptake	Quantum yield at	
	Maximum Photosynthesis	quantum yield at I = 0	50 percentile	85 percentile	90 percentile	95 Percentile		light compensation point	LCP to I = 200
	P _{gmax} (μmol (CO ₂) m ⁻² s ⁻¹)	φ(I ₀) (μmol (CO ₂) μmol ⁻¹ (photons))	I _{sat(50)} (μmol photon s) m ⁻² s ⁻¹)	I _{sat(85)} (μmol (photons) m ⁻² s ⁻¹)	I _{sat(90)} (μmol (photons) m ⁻² s ⁻¹)	I _{sat(95)} (μmol (photons) m ⁻² s ⁻¹)	PN(I _{max}) (μmol (CO ₂) m ⁻² s ⁻¹)	φ(I _{comp}) (μmol (CO ₂) μmol ⁻¹ (photons))	φ(I _{c-1200}) (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

245

246

247

248 Table 2. Conductance to H₂O and Intercellular CO₂ concentration of Dena and Anjasmoro varieties with and
 249 without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjamoro – no Actinomycetes, Dena-1 –
 250 Actinomycetes, Anjasmoro – Actinomycetes at variable PAR

Varieties - Actinomycetes Treatments	Conductance to H ₂ O mol H ₂ O 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

251



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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".

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Photosynthetic Parameters 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 *Actinomyces 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 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$. The photosynthetic light response curve (PNI curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (P_{gmax}) of *Dena-1* is 45.64 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$, while *Anjasmoro* variety is only 34.81 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons) compare to *Anjasmoro* 0.058 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomyces spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$ and higher at PAR above it.

KEYWORDS

Actinomyces 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 (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* 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%.

43 *Dena-1* variety was released in 2015 particularly as shaded tolerate variety. In addition to some good
44 characters such as yellow color, big grain, high protein content, and resistant to leaf rust, *Dena-1* variety also
45 tolerant to shading up to 50% of shading (Pratiwi and Artari, 2018). Hence, it is suitable for intercropping with
46 young high estate crops, such as coconut, oil palm, and rubber. With large plantation area of those estate
47 crops Indonesia, expansion of soybean crop to plantation area is promising. *Dena-1* variety, along with *Dena*
48 2 variety as well, are considered as varieties suitable to be intercropped with young trees at community
49 forest (Abidin, 2015)

50 Characterizing photosynthetic parameters of *Dena-1* variety is also important to understand the
51 physiological trait underlying the capacity of the variety to tolerate shading. More importantly, it will give
52 physiological explanation up to which light condition this variety produce enough photosynthate for
53 reasonable yield.

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

56 MATERIALS AND METHODS

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

60 Photosynthetic performances were measured in an experiment designed to study the effect of
61 *Actinomyces spp* on growth and yield of soybean. Therefore the experimental design was Factorial Design,
62 in which soybean varieties as first factor that consist of *Dena-1* variety (V1) and Anjasmoro variety (V2), and
63 the second factor is density of *Actinomyces spp* that consist of no *Actinomyces spp* (A0), *Actinomyces*
64 *spp* with concentration of 1×10^3 CFU mL⁻¹ (A1), and *Actinomyces spp* with concentration of 1×10^6 CFU
65 mL⁻¹ (A2). Each treatment combination was repeated three times and therefore there were 18 experimental
66 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
67 of 20 cm x 40 cm with 2 seeds per hole. However, the photosynthetic measurements were not following this
68 experimental design, but were taken at two contrasting *Actinomyces spp* treatments of two varieties, i.e. no
69 *Actinomyces* and 1×10^6 CFU mL⁻¹ *Actinomyces* at Anjasmoro and *Dena-1* varieties (W1A0, W1A2,
70 W2A0, and W2A2).

71 The photosynthetic measurement was taken in October 15, 2017 using an open chamber portable
72 photosynthetic system (LI-6400, LI-COR, Inc., Logan, NE, USA). Mature leaf exposed to full sunlight was
73 flipped to the chamber. The size of the chamber used, or the area of leaf flipped in the chamber, is 2 cm x 3
74 cm, or 6m². To develop a light response curve, the photosynthesis was measured at variable
75 Photosynthetically Active Radiation (PAR), i.e. 500; 1,000; 1,500; and 2,000 μ mol (photon) m² s⁻¹.
76 Environment conditions during experiments were as follows: air temperature – 25-27 °C; block and leaf
77 temperature – 25-27 °C; air flow rate – 500 μ mol s⁻¹; CO₂ concentration in sample cell – 380–400 μ mol CO₂
78 mol⁻¹; and relative humidity in sample cell – 56-70 %. The measurements are repeated three times (once for
79 each experimental unit). In each replication the system run for 5 second, and the data were registered every
80 second, and therefore there are 15 data set available for each PAR level, or 60 data set for all replications
81 and PAR levels. The parameters used are photosynthetic rate (Pn) (μ mol CO₂ m⁻²s⁻¹), intercellular CO₂
82 concentration(Ci) (μ mol CO₂ mol air⁻¹), and conductance to H₂O (mol H₂O m⁻² s⁻¹)

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

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

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

91 Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$, while Anjasmoro
92 variety is only $34.81 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Table 1). Along with high maximum photosynthesis, quantum yield
93 at low light (initial light use efficiency) of Dena-1 variety is also higher which is $0.068 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$
94 (photons) compare to Anjasmoro $0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Such a difference explains why Dena-
95 1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-
96 1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety both at light compensation point
97 ($\phi(I_{comp})$) and at light between compensation point to 200 ($\phi(I_{c-200})$) is higher (0.07 and $0.05 \mu\text{mol (CO}_2\text{)}$
98 μmol^{-1} (photons)) than quantum yield of Anjasmoro variety (0.06 and $0.04 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons))
99 (Table 1). In another word, photosynthesis at Dena-1 variety still occurs at acceptable rate even under low
100 light or under shading.

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

109 The photosynthetic light response curves of these two varieties change under *Actinomyces*
110 treatment. Under such condition the curve of Dena-1 variety is higher than that of Anjasmoro at the
111 beginning or at low light but then as light increase, the quantum yield is decreasing at a rate faster in Dena-1
112 than in Anjasmoro such that Dena-1 curve is surpassed by Anjasmoro curve at PAR $706 \mu\text{mol (photon) m}^{-2}$
113 s^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than
114 Anjasmoro at PAR below $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$, but it is the other way round at PAR above $706 \mu\text{mol}$
115 $(\text{photon) m}^{-2} \text{ s}^{-1}$. Initial light use efficiency of Dena-1 variety is higher ($0.096 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons))
116 than Anjasmoro variety ($0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)). In contrast, the maximum photosynthesis
117 (P_{gmax}) is lower in Dena-1 variety ($33.03 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$) than in Anjasmoro variety ($48.77 \mu\text{mol (CO}_2\text{) m}^{-2}$
118 s^{-1}) (Table 1). This indicates that Anjasmoro variety responds better to *Actinomyces spp* variety than
119 Dena-1 variety such that additional nutrient from *Actinomyces spp* can be converted well into increase in
120 the capacity of photosynthetic apparatus. With an increase in capacity of photosynthetic apparatus,
121 photosynthesis rate increases along with increase in light, and so increase in light saturation point, and
122 maximum photosynthesis (Table 1). Hence, the rate of decrease in quantum yield from light compensation

123 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
124 17% (from 0.06 to 0.05).

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

136 Beside the limitation by energy transfer, photosynthesis at high light is apparently also limited by the
137 availability of CO₂ as can be indicated by conductance to H₂O and internal CO₂ concentration. Under normal
138 condition or no *Actinomyces* treatment, Dena 1 variety has higher conductance (2.28 mol H₂O m⁻² s⁻¹) than
139 Anjasmoro variety (2.09 mol H₂O m⁻² s⁻¹) and it increases faster with the increase of PAR from 500 to 2,000
140 μmol (photon) m⁻² s⁻¹. Along with this increase, internal CO₂ concentration in Dena 1 variety decrease at a
141 rate slower than in Anjasmoro variety (Table 2). This indicates that stomata of Dena 1 variety is more
142 resilient to keep the internal CO₂ concentration higher than Anjasmoro variety as a demand for CO₂ increase

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

150 Unlike at normal condition, under *Actinomyces spp.* treatment, the decrease in internal CO₂ concentration
151 due to light increase in Dena 1 variety is faster than Anjasmoro. This is brought about by high response of
152 Anjasmoro variety to *Actinomyces spp.* than Dena 1 variety. As discussed earlier, Anjasmoro variety
153 responses better to soil fertilization than Dena 1 variety.

154 CONCLUSIONS

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

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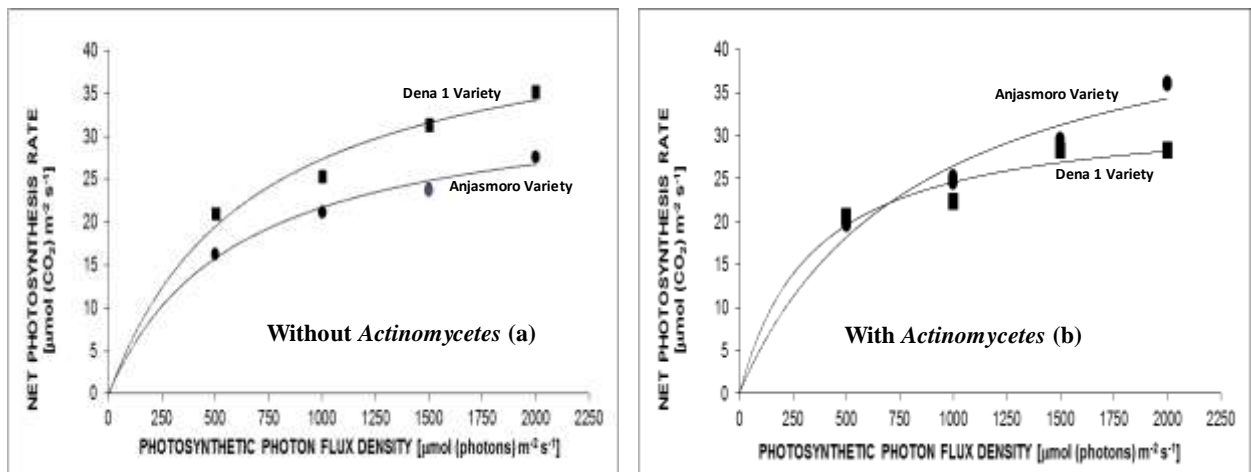
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213

214 lowercase, please for tell x axis and Y axis, for all figures



215

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

217 and under Actinomycetes treatment (b).

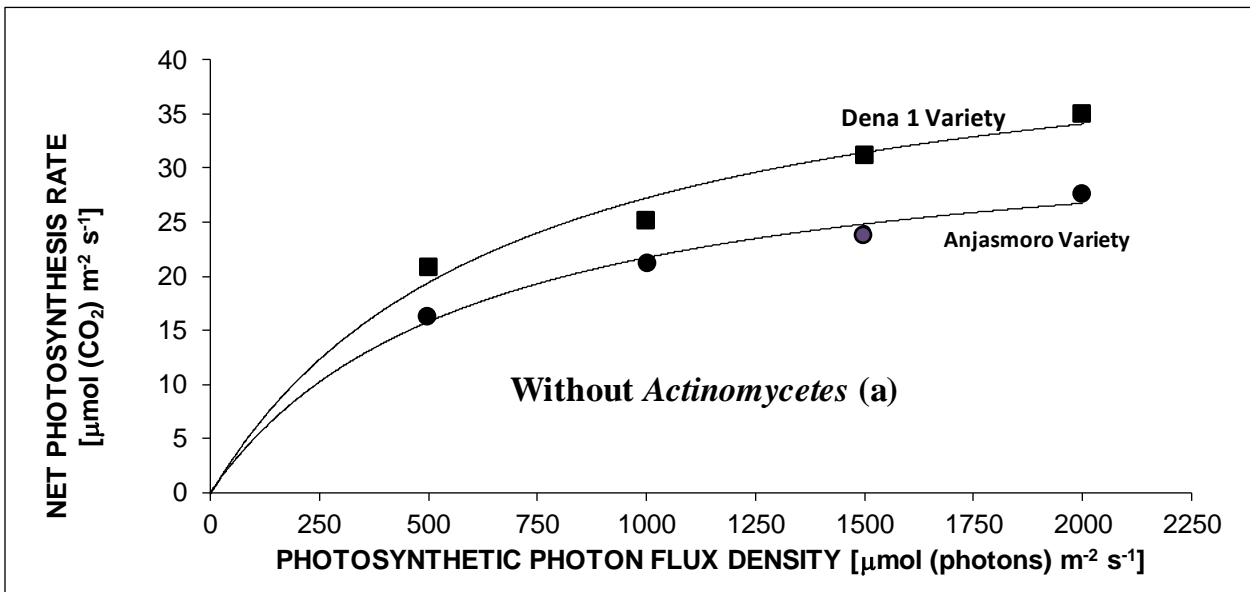
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219 The following are the editable graph for Figure 1.

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221 Figure 1.a. Without Actinomycetes

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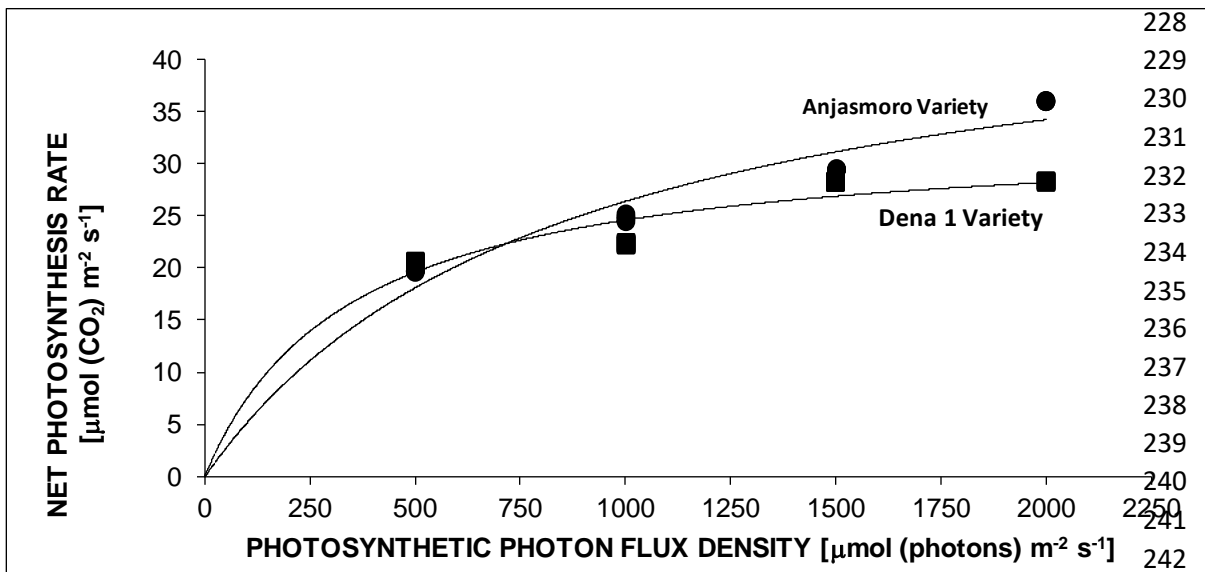
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226 Figure 1.b . With Actinomycetes

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

248

Varieties and Actinomycetes Treatments	Standard Parameters		Light saturation point at				Light-saturated net CO ₂ uptake	Quantum yield at light compensation point	
	Maximum Photosynthesis	quantum yield at I = 0	50 percentile	85 percentile	90 percentile	95 Percentile		LCP to I = 200	
	P _{gmax} (μmol (CO ₂) m ⁻² s ⁻¹)	φ(I ₀) (μmol (CO ₂) μmol ⁻¹ (photons))	I _{sat(50)} (μmol photons m ⁻² s ⁻¹)	I _{sat(85)} (μmol photons m ⁻² s ⁻¹)	I _{sat(90)} (μmol photons m ⁻² s ⁻¹)	I _{sat(95)} (μmol photons m ⁻² s ⁻¹)	PN(I _{max}) (μmol (CO ₂) m ⁻² s ⁻¹)	φ(I _{comp}) (μmol (CO ₂) μmol ⁻¹ (photons))	φ(I _{c-200}) (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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252 Table 2. Conductance to H₂O and Intercellular CO₂ concentration of Dena and Anjasmoro varieties with and
 253 without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjamoro – no Actinomycetes, Dena-1 –
 254 Actinomycetes, Anjasmoro – Actinomycetes at variable PAR

Varieties - Actinomycetes Treatments	Conductance to H ₂ O mol H ₂ O 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

255



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[AGRIVITA] Editor Decision

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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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[AGRIVITA] Editor Decision

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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 Parameters 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 *Actinomyces 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 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$. The photosynthetic light response curve (PNI curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (P_{gmax}) of *Dena-1* is 45.64 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$, while *Anjasmoro* variety is only 34.81 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons) compare to *Anjasmoro* 0.058 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomyces spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$ and higher at PAR above it.

KEYWORDS

Actinomyces 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 (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* 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

44 young high estate crops, such as coconut, oil palm, and rubber. With large plantation area of those estate
45 crops Indonesia, expansion of soybean crop to plantation area is promising. *Dena-1* variety, along with *Dena*
46 2 variety as well, are considered as varieties suitable to be intercropped with young trees at community
47 forest (Abidin, 2015)

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

53 MATERIALS AND METHODS

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

57 Photosynthetic performances were measured in an experiment designed to study the effect of
58 *Actinomyces spp* on growth and yield of soybean. Therefore the experimental design was Factorial Design,
59 in which soybean varieties as first factor that consist of *Dena-1* variety (V1) and Anjasmoro variety (V2), and
60 the second factor is density of *Actinomyces spp* that consist of no *Actinomyces spp* (A0), *Actinomyces*
61 *spp* with concentration of 1×10^3 CFU mL⁻¹ (A1), and *Actinomyces spp* with concentration of 1×10^6 CFU
62 mL⁻¹ (A2). Each treatment combination was repeated three times and therefore there were 18 experimental
63 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
64 of 20 cm x 40 cm with 2 seeds per hole. However, the photosynthetic measurements were not following this
65 experimental design, but were taken at two contrasting *Actinomyces spp* treatments of two varieties, i.e. no
66 *Actinomyces* and 1×10^6 CFU mL⁻¹ *Actinomyces* at Anjasmoro and *Dena-1* varieties (W1A0, W1A2,
67 W2A0, and W2A2).

68 The photosynthetic measurement was taken in October 15, 2017 using an open chamber portable
69 photosynthetic system (LI-6400, LI-COR, Inc., Logan, NE, USA). Mature leaf exposed to full sunlight was
70 flipped to the chamber. The size of the chamber used, or the area of leaf flipped in the chamber, is 2 cm x 3
71 cm, or 6m². To develop a light response curve, the photosynthesis was measured at variable
72 Photosynthetically Active Radiation (PAR), i.e. 500; 1,000; 1,500; and 2,000 μ mol (photon) m² s⁻¹.
73 Environment conditions during experiments were as follows: air temperature – 25-27 °C; block and leaf
74 temperature – 25-27 °C; air flow rate – 500 μ mol s⁻¹; CO₂ concentration in sample cell – 380–400 μ mol CO₂
75 mol⁻¹; and relative humidity in sample cell – 56-70 %. The measurements are repeated three times (once for
76 each experimental unit). In each replication the system run for 5 second, and the data were registered every
77 second, and therefore there are 15 data set available for each PAR level, or 60 data set for all replications
78 and PAR levels. The parameters used are photosynthetic rate (Pn) (μ mol CO₂ m⁻²s⁻¹), intercellular CO₂
79 concentration(Ci) (μ mol CO₂ mol air⁻¹), and conductance to H₂O (mol H₂O m⁻² s⁻¹)

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

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

88 Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$, while Anjasmoro
 89 variety is only $34.81 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Table 1). Along with high maximum photosynthesis, quantum yield
 90 at low light (initial light use efficiency) of Dena-1 variety is also higher which is $0.068 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$
 91 (photons) compare to Anjasmoro $0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Such a difference explains why Dena-
 92 1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-
 93 1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety both at light compensation point
 94 ($\phi(I_{comp})$) and at light between compensation point to 200 ($\phi(I_c-I_{200})$) is higher (0.07 and $0.05 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$
 95 μmol^{-1} (photons)) than quantum yield of Anjasmoro variety (0.06 and $0.04 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons))
 96 (Table 1). In another word, photosynthesis at Dena-1 variety still occurs at acceptable rate even under low
 97 light or under shading.

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

106 The photosynthetic light response curves of these two varieties change under *Actinomyces*
 107 treatment. Under such condition the curve of Dena-1 variety is higher than that of Anjasmoro at the
 108 beginning or at low light but then as light increase, the quantum yield is decreasing at a rate faster in Dena-1
 109 than in Anjasmoro such that Dena-1 curve is surpassed by Anjasmoro curve at PAR $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$
 110 s^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than
 111 Anjasmoro at PAR below $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$, but it is the other way round at PAR above $706 \mu\text{mol}$
 112 $\text{(photon) m}^{-2} \text{ s}^{-1}$. Initial light use efficiency of Dena-1 variety is higher ($0.096 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons))
 113 than Anjasmoro variety ($0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)). In contrast, the maximum photosynthesis
 114 (P_{gmax}) is lower in Dena-1 variety ($33.03 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$) then in Anjasmoro variety ($48.77 \mu\text{mol (CO}_2\text{) m}^{-2}$
 115 s^{-1}) (Table 1). This indicates that Anjasmoro variety responds better to *Actinomyces spp* variety than
 116 Dena-1 variety such that additional nutrient from *Actinomyces spp* can be converted well into increase in
 117 the capacity of photosynthetic apparatus. With an increase in capacity of photosynthetic apparatus,
 118 photosynthesis rate increases along with increase in light, and so increase in light saturation point, and
 119 maximum photosynthesis (Table 1). Hence, the rate of decrease in quantum yield from light compensation
 120 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
 121 17% (from 0.06 to 0.05).

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

133 Beside the limitation by energy transfer, photosynthesis at high light is apparently also limited by the
134 availability of CO₂ as can be indicated by conductance to H₂O and internal CO₂ concentration. Under normal
135 condition or no *Actinomyces* treatment, Dena 1 variety has higher conductance (2.28 mol H₂O m⁻² s⁻¹) than
136 *Anjasmoro* variety (2.09 mol H₂O m⁻² s⁻¹) and it increases faster with the increase of PAR from 500 to 2,000
137 μmol (photon) m⁻² s⁻¹. Along with this increase, internal CO₂ concentration in Dena 1 variety decrease at a
138 rate slower than in *Anjasmoro* variety (Table 2). This indicates that stomata of Dena 1 variety is more
139 resilient to keep the internal CO₂ concentration higher than *Anjasmoro* variety as a demand for CO₂ increase

140 It has been known widely that light affect stomatal opening, and so leaf conductance. The effect of
141 light to the stomatal response occurs in two ways. The first one is through decrease in intercellular CO₂
142 concentration due to increase in photosynthesis, and the second is through direct activation of guard cells
143 (Driesen et al., 2020). McAusland et al. (2016) also reported a significant variation in the rapidity of stomatal
144 responses amongst species to light change. For soybean, Bunce (2016) found 15 cultivars differed
145 significantly in stomatal conductance.

146 Unlike at normal condition, under *Actinomyces spp.* treatment, the decrease in internal CO₂ concentration
147 due to light increase in Dena 1 variety is faster than *Anjasmoro*. This is brought about by high response of
148 *Anjasmoro* variety to *Actinomyces spp.* than Dena 1 variety. As discussed earlier, *Anjasmoro* variety
149 responses better to soil fertilization than Dena 1 variety.

150 CONCLUSIONS

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

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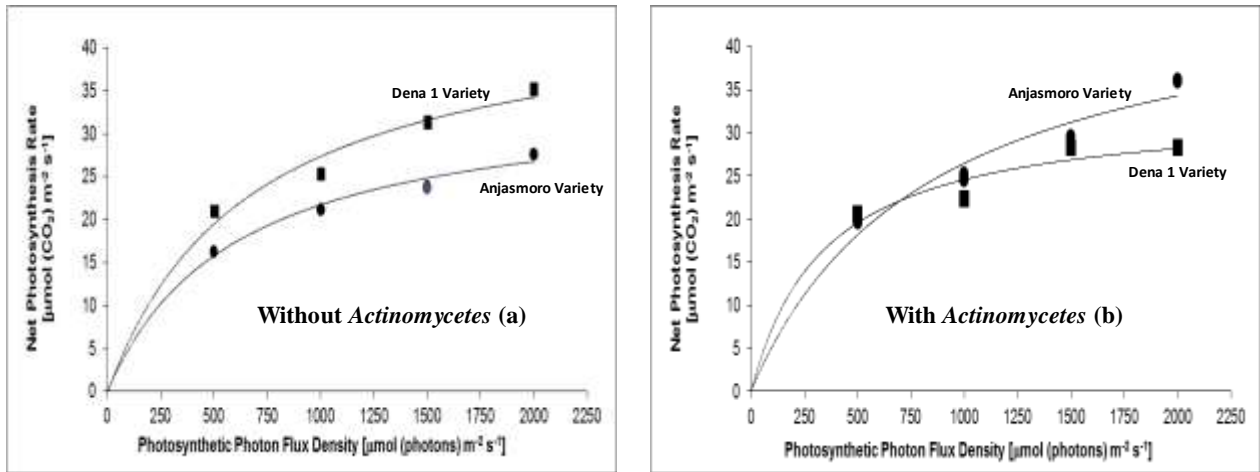


Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

226 The following are the editable graph for Figure 1.

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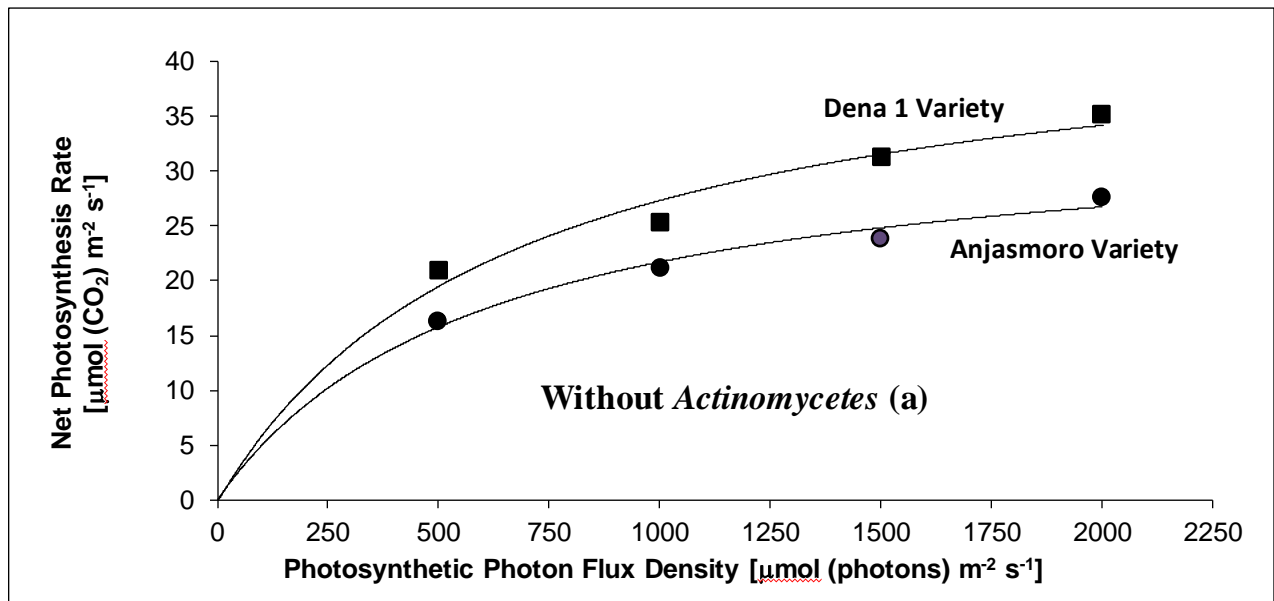
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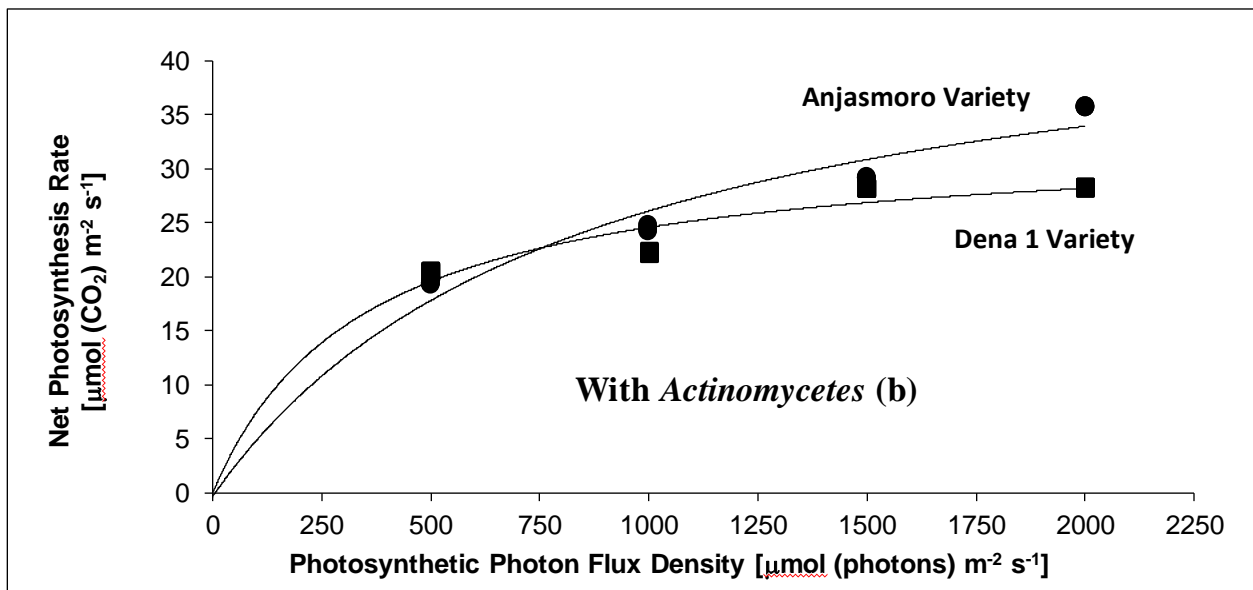


239 Figure 1.a. Without Actinomycetes

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244 Figure 1.b . With Actinomycetes

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

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Varieties and Actinomycetes Treatments	Standard Parameters		Light saturation point at				Light-saturated net CO ₂ uptake	Quantum yield at light compensation point	
	Maximum Photosynthesis	quantum yield at I = 0	50 percentile	85 percentile	90 percentile	95 Percentile		LCP to I = 200	
	P _{gmax} (μmol (CO ₂) m ⁻² s ⁻¹)	φ(I ₀) (μmol (CO ₂) μmol ⁻¹ (photons))	I _{sat(50)} (μmol photons m ⁻² s ⁻¹)	I _{sat(85)} (μmol photons m ⁻² s ⁻¹)	I _{sat(90)} (μmol photons m ⁻² s ⁻¹)	I _{sat(95)} (μmol photons m ⁻² s ⁻¹)	PN(I _{max}) (μmol (CO ₂) m ⁻² s ⁻¹)	φ(I _{comp}) (μmol (CO ₂) μmol ⁻¹ (photons))	φ(I _{c-200}) (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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255 Table 2. Conductance to H₂O and Intercellular CO₂ concentration of Dena and Anjasmoro varieties with and
 256 without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjamoro – no Actinomycetes, Dena-1 –
 257 Actinomycetes, Anjasmoro – Actinomycetes at variable PAR

Varieties - Actinomycetes Treatments	Conductance to H ₂ O mol H ₂ O 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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Kepada: Agrivita UB <agrivitaaperta@gmail.com>, "Moch. Dawam Maghfoer, Prof." <dmaghfoer@yahoo.com>

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 Parameters 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 *Actinomyces 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 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$. The photosynthetic light response curve (PNI curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (P_{gmax}) of *Dena-1* is 45.64 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$, while *Anjasmoro* variety is only 34.81 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons) compare to *Anjasmoro* 0.058 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomyces spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$ and higher at PAR above it.

KEYWORDS

Actinomyces 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 (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* 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

44 young high estate crops, such as coconut, oil palm, and rubber. With large plantation area of those estate
45 crops Indonesia, expansion of soybean crop to plantation area is promising. *Dena-1* variety, along with *Dena*
46 2 variety as well, are considered as varieties suitable to be intercropped with young trees at community
47 forest (Abidin, 2015)

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

53 MATERIALS AND METHODS

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

57 Photosynthetic performances were measured in an experiment designed to study the effect of
58 *Actinomyces spp* on growth and yield of soybean. Therefore the experimental design was Factorial Design,
59 in which soybean varieties as first factor that consist of *Dena-1* variety (V1) and Anjasmoro variety (V2), and
60 the second factor is density of *Actinomyces spp* that consist of no *Actinomyces spp* (A0), *Actinomyces*
61 *spp* with concentration of 1×10^3 CFU mL⁻¹ (A1), and *Actinomyces spp* with concentration of 1×10^6 CFU
62 mL⁻¹ (A2). Each treatment combination was repeated three times and therefore there were 18 experimental
63 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
64 of 20 cm x 40 cm with 2 seeds per hole. However, the photosynthetic measurements were not following this
65 experimental design, but were taken at two contrasting *Actinomyces spp* treatments of two varieties, i.e. no
66 *Actinomyces* and 1×10^6 CFU mL⁻¹ *Actinomyces* at Anjasmoro and *Dena-1* varieties (W1A0, W1A2,
67 W2A0, and W2A2).

68 The photosynthetic measurement was taken in October 15, 2017 using an open chamber portable
69 photosynthetic system (LI-6400, LI-COR, Inc., Logan, NE, USA). Mature leaf exposed to full sunlight was
70 flipped to the chamber. The size of the chamber used, or the area of leaf flipped in the chamber, is 2 cm x 3
71 cm, or 6m². To develop a light response curve, the photosynthesis was measured at variable
72 Photosynthetically Active Radiation (PAR), i.e. 500; 1,000; 1,500; and 2,000 μ mol (photon) m² s⁻¹.
73 Environment conditions during experiments were as follows: air temperature – 25-27 °C; block and leaf
74 temperature – 25-27 °C; air flow rate – 500 μ mol s⁻¹; CO₂ concentration in sample cell – 380–400 μ mol CO₂
75 mol⁻¹; and relative humidity in sample cell – 56-70 %. The measurements are repeated three times (once for
76 each experimental unit). In each replication the system run for 5 second, and the data were registered every
77 second, and therefore there are 15 data set available for each PAR level, or 60 data set for all replications
78 and PAR levels. The parameters used are photosynthetic rate (Pn) (μ mol CO₂ m⁻²s⁻¹), intercellular CO₂
79 concentration(Ci) (μ mol CO₂ mol air⁻¹), and conductance to H₂O (mol H₂O m⁻² s⁻¹)

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

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

88 Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$, while Anjasmoro
 89 variety is only $34.81 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Table 1). Along with high maximum photosynthesis, quantum yield
 90 at low light (initial light use efficiency) of Dena-1 variety is also higher which is $0.068 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$
 91 (photons) compare to Anjasmoro $0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Such a difference explains why Dena-
 92 1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-
 93 1 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety both at light compensation point
 94 ($\phi(I_{comp})$) and at light between compensation point to 200 ($\phi(I_c-I_{200})$) is higher (0.07 and $0.05 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$
 95 (μmol^{-1} (photons)) than quantum yield of Anjasmoro variety (0.06 and $0.04 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons))
 96 (Table 1). In another word, photosynthesis at Dena-1 variety still occurs at acceptable rate even under low
 97 light or under shading.

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

106 The photosynthetic light response curves of these two varieties change under *Actinomyces*
 107 treatment. Under such condition the curve of Dena-1 variety is higher than that of Anjasmoro at the
 108 beginning or at low light but then as light increase, the quantum yield is decreasing at a rate faster in Dena-1
 109 than in Anjasmoro such that Dena-1 curve is surpassed by Anjasmoro curve at PAR $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$
 110 (μmol^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than
 111 Anjasmoro at PAR below $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$, but it is the other way round at PAR above $706 \mu\text{mol}$
 112 (μmol^{-1} (photon) $\text{m}^{-2} \text{ s}^{-1}$). Initial light use efficiency of Dena-1 variety is higher ($0.096 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons))
 113 than Anjasmoro variety ($0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)). In contrast, the maximum photosynthesis
 114 (P_{gmax}) is lower in Dena-1 variety ($33.03 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$) then in Anjasmoro variety ($48.77 \mu\text{mol (CO}_2\text{) m}^{-2}$
 115 s^{-1}) (Table 1). This indicates that Anjasmoro variety responds better to *Actinomyces spp* variety than
 116 Dena-1 variety such that additional nutrient from *Actinomyces spp* can be converted well into increase in
 117 the capacity of photosynthetic apparatus. With an increase in capacity of photosynthetic apparatus,
 118 photosynthesis rate increases along with increase in light, and so increase in light saturation point, and
 119 maximum photosynthesis (Table 1). Hence, the rate of decrease in quantum yield from light compensation
 120 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
 121 17% (from 0.06 to 0.05).

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

133 Beside the limitation by energy transfer, photosynthesis at high light is apparently also limited by the
134 availability of CO₂ as can be indicated by conductance to H₂O and internal CO₂ concentration. Under normal
135 condition or no *Actinomyces* treatment, Dena 1 variety has higher conductance (2.28 mol H₂O m⁻² s⁻¹) than
136 *Anjasmoro* variety (2.09 mol H₂O m⁻² s⁻¹) and it increases faster with the increase of PAR from 500 to 2,000
137 μmol (photon) m⁻² s⁻¹. Along with this increase, internal CO₂ concentration in Dena 1 variety decrease at a
138 rate slower than in *Anjasmoro* variety (Table 2). This indicates that stomata of Dena 1 variety is more
139 resilient to keep the internal CO₂ concentration higher than *Anjasmoro* variety as a demand for CO₂ increase

140 It has been known widely that light affect stomatal opening, and so leaf conductance. The effect of
141 light to the stomatal response occurs in two ways. The first one is through decrease in intercellular CO₂
142 concentration due to increase in photosynthesis, and the second is through direct activation of guard cells
143 (Driesen et al., 2020). McAusland et al. (2016) also reported a significant variation in the rapidity of stomatal
144 responses amongst species to light change. For soybean, Bunce (2016) found 15 cultivars differed
145 significantly in stomatal conductance.

146 Unlike at normal condition, under *Actinomyces spp.* treatment, the decrease in internal CO₂ concentration
147 due to light increase in Dena 1 variety is faster than *Anjasmoro*. This is brought about by high response of
148 *Anjasmoro* variety to *Actinomyces spp.* than Dena 1 variety. As discussed earlier, *Anjasmoro* variety
149 responses better to soil fertilization than Dena 1 variety.

150 CONCLUSIONS

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

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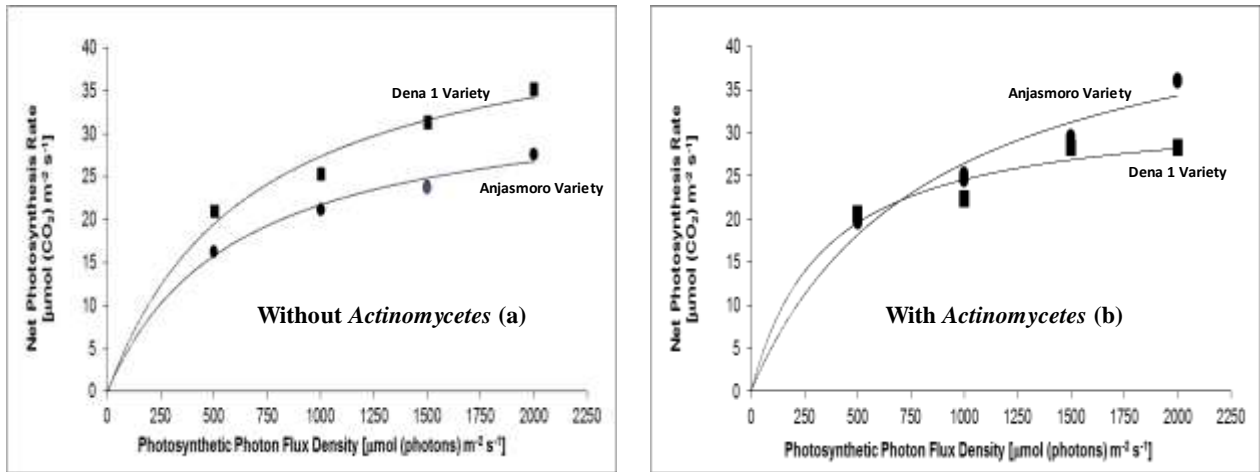


Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

226 The following are the editable graph for Figure 1.

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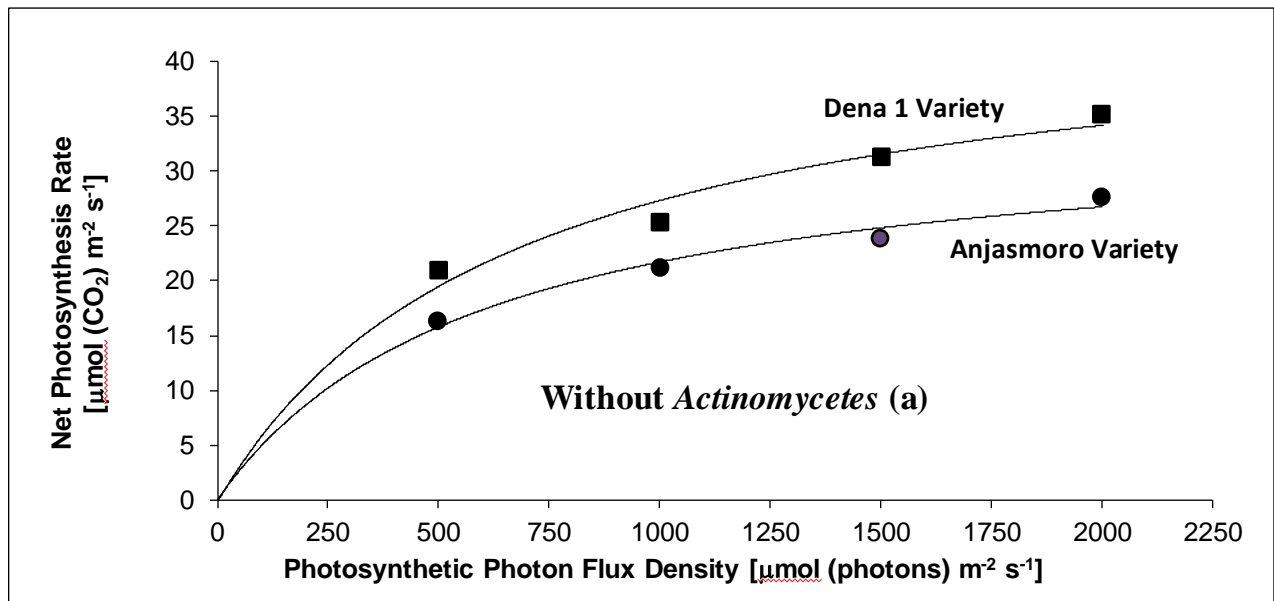
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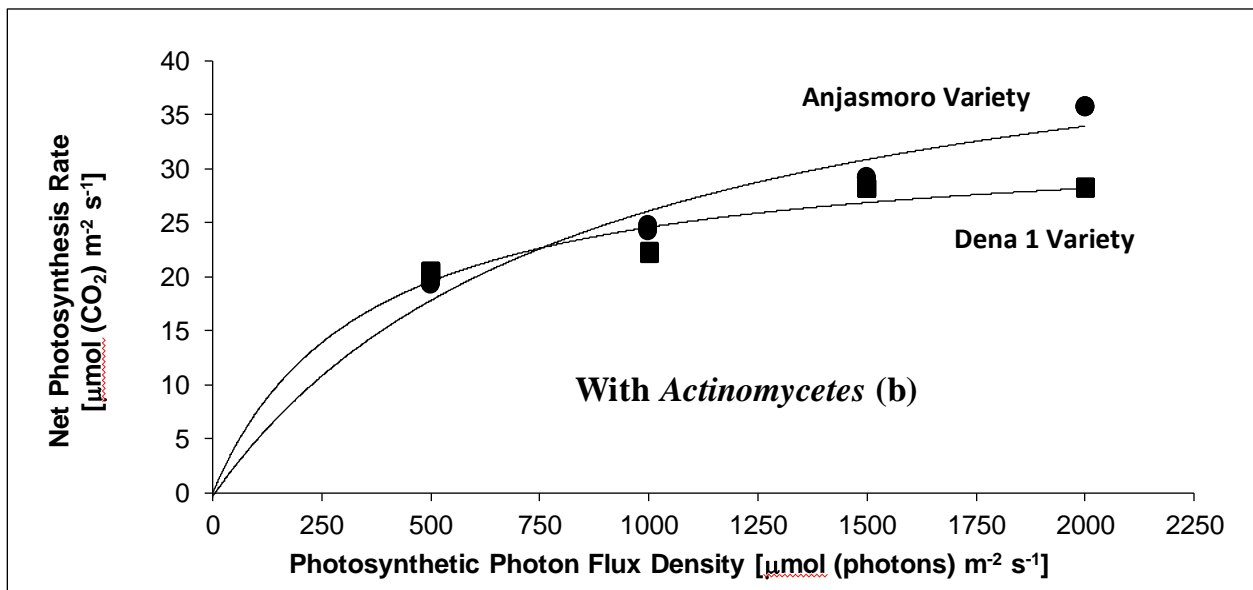


239 Figure 1.a. Without Actinomycetes

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244 Figure 1.b . With Actinomycetes

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

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Varieties and Actinomycetes Treatments	Standard Parameters		Light saturation point at				Light-saturated net CO ₂ uptake	Quantum yield at light compensation point	
	Maximum Photosynthesis	quantum yield at I = 0	50 percentile	85 percentile	90 percentile	95 Percentile		compensation point	LCP to I = 200
	P _{gmax} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	$\phi(I_0)$ ($\mu\text{mol CO}_2 \text{ mol}^{-1}$ (photons))	I _{sat(50)} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	I _{sat(85)} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	I _{sat(90)} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	I _{sat(95)} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	PN(I _{max}) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	$\phi(I_{comp})$ ($\mu\text{mol CO}_2 \text{ mol}^{-1}$ (photons))	$\phi(I_{200})$ ($\mu\text{mol CO}_2 \text{ mol}^{-1}$ (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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254

255 Table 2. Conductance to H₂O and Intercellular CO₂ concentration of Dena and Anjasmoro varieties with and
 256 without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjamoro – no Actinomycetes, Dena-1 –
 257 Actinomycetes, Anjasmoro – Actinomycetes at variable PAR

Varieties - Actinomycetes Treatments	Conductance to H ₂ O $\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$				Intercellular CO ₂ Concentration $\mu\text{mol CO}_2 \text{ mol}^{-1}$			
	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

258



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[AGRIVITA] Editor Decision

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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

- Revisions should be sent to Editor before May 8, 2021

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Photosynthetic Parameters 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 *Actinomyces 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 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$. The photosynthetic light response curve (PNII curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (Pgmax) of *Dena-1* is 45.64 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$, while *Anjasmoro* variety is only 34.81 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons) compare to *Anjasmoro* 0.058 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomyces spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$ and higher at PAR above it.

KEYWORDS

Actinomyces 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 lodging 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

44 young high estate crops, such as coconut, oil palm, and rubber. With large plantation area of those estate
45 crops Indonesia, expansion of soybean crop to plantation area is promising. *Dena-1* variety, along with *Dena*
46 2 variety as well, are considered as varieties suitable to be intercropped with young trees at community forest
47 (Abidin, 2015)

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

53 MATERIALS AND METHODS

54 The experiment was conducted in Tarowang farm, owned by a smallholder farmer in Tarowang village, district
55 of Takalar, South Sulawesi province, Indonesia from August to November 2017. Tarowang is located at 119°
56 28' East and 5° 39' South with altitude of 15 m above sea level.

57 Photosynthetic performances were measured in an experiment designed to study the effect of
58 *Actinomyces spp* on growth and yield of soybean. Therefore the experimental design was Factorial Design,
59 in which soybean varieties as first factor that consist of *Dena-1 variety (V1) and Anjasmoro variety (V2), and*
60 *the second factor is density of Actinomyces spp that consist of no Actinomyces spp (A0), Actinomyces*
61 *spp with concentration of 1x10³ CFU mL⁻¹ (A1), and Actinomyces spp with concentration of 1x10⁶ CFU mL⁻¹*
62 *(A2). Each treatment combination was repeated three times and therefore there were 18 experimental units*
63 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
64 cm x 40 cm with 2 seeds per hole. However, the photosynthetic measurements were not following this
65 experimental design, but were taken at two contrasting *Actinomyces spp* treatments of two varieties, i.e. no
66 *Actinomyces* and 1x10⁶ CFU mL⁻¹ *Actinomyces* at *Anjasmoro* and *Dena-1* varieties (W1A0, W1A2, W2A0,
67 and W2A2).

68 The photosynthetic measurement was taken in October 15, 2017 using an open chamber portable
69 photosynthetic system (LI-6400, LI-COR, Inc., Logan, NE, USA). Mature leaf exposed to full sunlight was
70 flipped to the chamber. The size of the chamber used, or the area of leaf flipped in the chamber, is 2 cm x 3
71 cm, or 6m². To develop a light response curve, the photosynthesis was measured at variable
72 Photosynthetically Active Radiation (PAR), i.e. 500; 1,000; 1,500; and 2,000 μ mol (photon) m² s⁻¹.
73 Environment conditions during experiments were as follows: air temperature – 25-27 °C; block and leaf
74 temperature – 25-27 °C; air flow rate – 500 μmol s⁻¹; CO₂ concentration in sample cell – 380–400 μmol CO₂
75 mol⁻¹; and relative humidity in sample cell – 56-70 %. The measurements are repeated three times (once for
76 each experimental unit). In each replication the system run for 5 second, and the data were registered every
77 second, and therefore there are 15 data set available for each PAR level, or 60 data set for all replications and
78 PAR levels. The parameters used are photosynthetic rate (Pn) (μmol CO₂ m⁻²s⁻¹), intercellular CO₂
79 concentration(Ci) (μmol CO₂ mol air⁻¹), and conductance to H₂O (mol H₂O m⁻² s⁻¹)

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

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

RESULTS AND DISCUSSION

83

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

88 Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$, while Anjasmoro
89 variety is only $34.81 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Table 1). Along with high maximum photosynthesis, quantum yield
90 at low light (initial light use efficiency) of Dena-1 variety is also higher which is $0.068 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$
91 (photons) compare to Anjasmoro $0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Such a difference explains why Dena-
92 1 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-1
93 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety both at light compensation point
94 ($\phi(l_{comp})$) and at light between compensation point to 200 ($\phi(l_{c-}l_{200})$) is higher (0.07 and 0.05 $\mu\text{mol (CO}_2\text{)}$
95 μmol^{-1} (photons)) than quantum yield of Anjasmoro variety (0.06 and 0.04 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons))
96 (Table 1). In another word, photosynthesis at Dena-1 variety still occurs at acceptable rate even under low
97 light or under shading.

98 Along with high maximum gross photosynthesis, initial light use efficiency, and quantum yield, the light
99 saturation point of Dena-1 variety is consistently higher at percentile 50 % all the way up to 95% than that of
100 Anjasmoro variety. Light saturation point at 50% percentile of Dena-1 variety is $667 \mu\text{mol (photons) m}^{-2} \text{ s}^{-1}$,
101 while Anjasmoro is $603 \mu\text{mol (photons) m}^{-2} \text{ s}^{-1}$. At 95 percentile, the light saturation point of Dena-1 variety is
102 $6,004 \mu\text{mol (photons) m}^{-2} \text{ s}^{-1}$, while Anjasmoro variety is $5,429 \mu\text{mol (photons) m}^{-2} \text{ s}^{-1}$ (Table 2). High light
103 saturation point indicates that Dena-1 varieties is not only tolerant to shading but also tolerant to high light. In
104 another word, increase in light intensity can be accommodated by Dena-1 variety due to high capacity of its
105 photosynthetic apparatus.

106 The photosynthetic light response curves of these two varieties change under *Actinomyces*
107 treatment. Under such condition the curve of Dena-1 variety is higher than that of Anjasmoro at the beginning
108 or at low light but then as light increase, the quantum yield is decreasing at a rate faster in Dena-1 than in
109 Anjasmoro such that Dena-1 curve is surpassed by Anjasmoro curve at PAR $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$ (Figure
110 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than Anjasmoro at
111 PAR below $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$, but it is the other way round at PAR above $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$.
112 Initial light use efficiency of Dena-1 variety is higher ($0.096 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)) than Anjasmoro variety
113 ($0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1
114 variety ($33.03 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$) than in Anjasmoro variety ($48.77 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$) (Table 1). This indicates
115 that Anjasmoro variety responds better to *Actinomyces spp* variety than Dena-1 variety such that additional
116 nutrient from *Actinomyces spp* can be converted well into increase in the capacity of photosynthetic
117 apparatus. With an increase in capacity of photosynthetic apparatus, photosynthesis rate increases along with
118 increase in light, and so increase in light saturation point, and maximum photosynthesis (Table 1). Hence, the
119 rate of decrease in quantum yield from light compensation point (l_c) to l_{200} is much higher in Dena-1 variety
120 than in Anjasmoro variety, i.e. 40 % (from 0.10 to 0.04) vs 17% (from 0.06 to 0.05).

121 *Actinomyces spp.* play an important role in soil nutrient cycling (Bhatti et al., 2017), solubilize
122 inorganic phosphates (Ghorbani-Nasrabadi et al., 2013), hydrolyze phytate, a dominant form of organic P in

Commented [WU2]: The results and discussion only explained without and with *Actinomyces* treatments, whereas there were three treatments for *Actinomyces* population (without (0), population 1×10^3 and population 1×10^6 CFU mL^{-1}). Why not described all three? See Table 1 and 2, also Figure 1 and 2.

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

132 Beside the limitation by energy transfer, photosynthesis at high light is apparently also limited by the
133 availability of CO₂ as can be indicated by conductance to H₂O and internal CO₂ concentration. Under normal
134 condition or no *Actinomyces* treatment, Dena 1 variety has higher conductance (2.28 mol H₂O m⁻² s⁻¹) than
135 Anjasmoro variety (2.09 mol H₂O m⁻² s⁻¹) and it increases faster with the increase of PAR from 500 to 2,000
136 μmol (photon) m⁻² s⁻¹. Along with this increase, internal CO₂ concentration in Dena 1 variety decrease at a rate
137 slower than in Anjasmoro variety (Table 2). This indicates that stomata of Dena 1 variety is more resilient to
138 keep the internal CO₂ concentration higher than Anjasmoro variety as a demand for CO₂ increase

139 It has been known widely that light affect stomatal opening, and so leaf conductance. The effect of
140 light to the stomatal response occurs in two ways. The first one is through decrease in intercellular CO₂
141 concentration due to increase in photosynthesis, and the second is through direct activation of guard cells
142 (Driesen et al., 2020). McAusland et al. (2016) also reported a significant variation in the rapidity of stomatal
143 responses amongst species to light change. For soybean, Bunce (2016) found 15 cultivars differed significantly
144 in stomatal conductance.

145 Unlike at normal condition, under *Actinomyces spp.* treatment, the decrease in internal CO₂ concentration
146 due to light increase in Dena 1 variety is faster than Anjasmoro. This is brought about by high response of
147 Anjasmoro variety to *Actinomyces spp.* than Dena 1 variety. As discussed earlier, Anjasmoro variety
148 responses better to soil fertilization than Dena 1 variety.

149 CONCLUSIONS

150 Initial light use efficiency and maximum photosynthesis of Dena 1 variety is 0.068 μmol (CO₂) μmol⁻¹ (photons)
151 and 45.64 μmol (CO₂) m⁻² s⁻¹ respectively. while Anjasmoro variety is 0.068 μmol (CO₂) μmol⁻¹ (photons) and
152 34.81 μmol (CO₂) m⁻² s⁻¹ respectively. High initial light use efficiency of Dena-1 could be one of the reasons
153 that made Dena 1 variety tolerant to shading. Responses of stomatal conductance and internal CO₂
154 concentration to light is higher in Anjasmoro than in Dena 1 variety.

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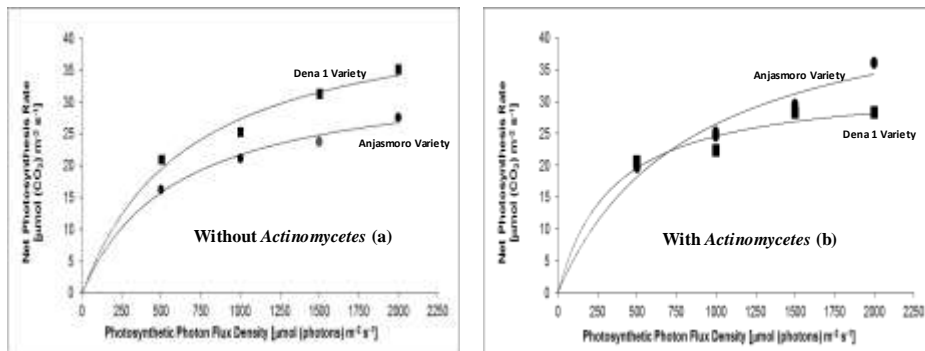


Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

225 The following are the editable graph for Figure 1.

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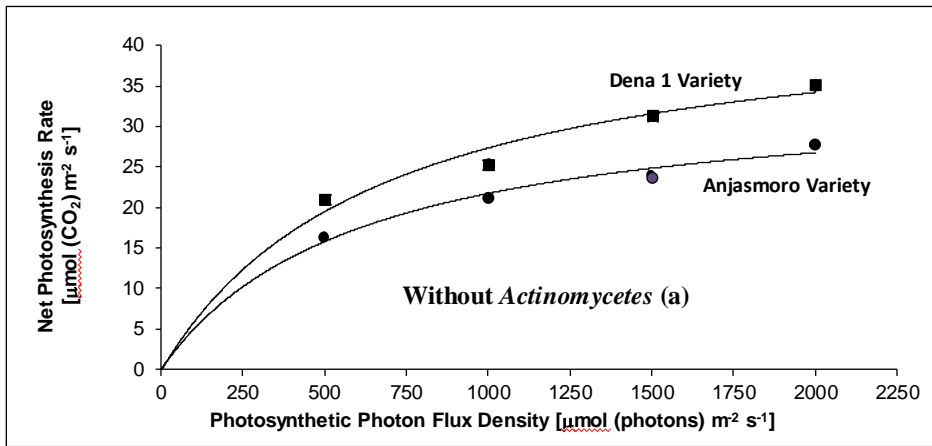
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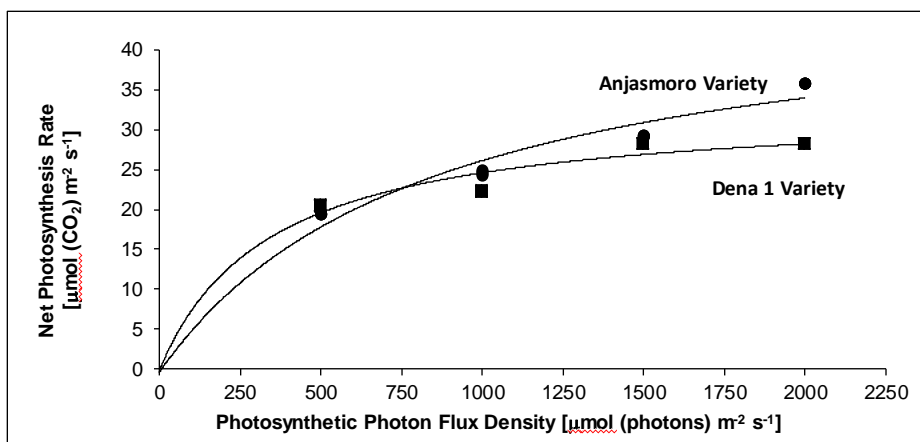
238 Figure 1.a. Without Actinomycetes

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238 **With Actinomycetes (b)**



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243 Figure 1.b . With Actinomycetes

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

250

Varieties and Actinomycetes Treatments	Standard Parameters		Light saturation point at				Light-saturated net CO ₂ uptake	Quantum yield at	
	Maximum Photosynthesis	quantum yield at I = 0	50 percentile	85 percentile	90 percentile	95 Percentile		light compensation point	LCP to I = 200
	P _{gmax} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	$\phi(I_0)$ ($\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ photons}$)	I _{sat(50)} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	I _{sat(85)} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	I _{sat(90)} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	I _{sat(95)} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	PN(I _{max}) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	$\phi(I_{comp})$ ($\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ photons}$)	$\phi(I_{200})$ ($\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ photons}$)
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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253

254 Table 2. Conductance to H₂O and Intercellular CO₂ concentration of Dena and Anjasmoro varieties with and
 255 without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjasmoro – no Actinomycetes, Dena-1 –
 256 Actinomycetes, Anjasmoro – Actinomycetes at variable PAR

Varieties - Actinomycetes Treatments	Conductance to H ₂ O $\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$				Intercellular CO ₂ Concentration $\mu\text{mol CO}_2 \text{ mol}^{-1}$				
	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	

257



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[AGRIVITA] Editor Decision

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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

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[Kutipan teks disembunyikan]

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Photosynthetic Parameters 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 *Actinomyces 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 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$. The photosynthetic light response curve (PNI curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (P_{gmax}) of *Dena-1* is 45.64 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$, while *Anjasmoro* variety is only 34.81 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons) compare to *Anjasmoro* 0.058 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomyces spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$ and higher at PAR above it.

KEYWORDS

Actinomyces 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 (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* 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

44 young high estate crops, such as coconut, oil palm, and rubber. With large plantation area of those estate
45 crops Indonesia, expansion of soybean crop to plantation area is promising. *Dena-1* variety, along with *Dena*
46 2 variety as well, are considered as varieties suitable to be intercropped with young trees at community
47 forest (Abidin, 2015)

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

53 MATERIALS AND METHODS

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

57 Photosynthetic performances were measured in an experiment designed to study the effect of
58 *Actinomyces spp* on growth and yield of soybean. The experimental design was Factorial Design, in which
59 soybean varieties as first factor that consist of *Dena-1* variety (V1) and Anjasmoro variety (V2), and the
60 second factor is *Actinomyces spp* application that consist of no *Actinomyces spp* (A0), and
61 *Actinomyces spp* with concentration of 1×10^6 CFU mL⁻¹ (A1). Each treatment combination was repeated
62 three times and therefore there were 12 experimental units or plots in total. The plot size is 3 m x 4 m, and
63 the soybeans were sowed in August 20, 2017 in a row of 20 cm x 40 cm with 2 seeds per hole.

64 The photosynthetic measurement was taken in October 15, 2017 using an open chamber portable
65 photosynthetic system (LI-6400, LI-COR, Inc., Logan, NE, USA). Mature leaf exposed to full sunlight was
66 flipped to the chamber. The size of the chamber used, or the area of leaf flipped in the chamber, is 2 cm x 3
67 cm, or 6m². To develop a light response curve, the photosynthesis was measured at variable
68 Photosynthetically Active Radiation (PAR), i.e. 500; 1,000; 1,500; and 2,000 μ mol (photon) m² s⁻¹.
69 Environment conditions during experiments were as follows: air temperature – 25-27 °C; block and leaf
70 temperature – 25-27 °C; air flow rate – 500 μ mol s⁻¹; CO₂ concentration in sample cell – 380–400 μ mol CO₂
71 mol⁻¹; and relative humidity in sample cell – 56-70 %. The measurements are repeated three times (once for
72 each experimental unit). In each replication the system run for 5 second, and the data were registered every
73 second, and therefore there are 15 data set available for each PAR level, or 60 data set for all replications
74 and PAR levels. The parameters used are photosynthetic rate (Pn) (μ mol CO₂ m⁻²s⁻¹), intercellular CO₂
75 concentration(Ci) (μ mol CO₂ mol air⁻¹), and conductance to H₂O (mol H₂O m⁻² s⁻¹)

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

79 RESULTS AND DISCUSSION

80 Photosynthetic light response curves of Anjasmoro and *Dena-1* varieties are shown in Figure 1. Under
81 normal condition or no *Actinomyces* the curve of *Dena-1* variety is higher than that of Anjasmoro (Figure

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

84 Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$, while Anjasmoro
85 variety is only $34.81 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Table 1). Reported maximum net photosynthesis (P_{nmax}) of other
86 soybean varieties are $28.8 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Yao et al., 2017), $29.9 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Zhang et al.,
87 2011), and $34.8 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Sakoda et al., 2016). Net photosynthesis (P_n) is gross photosynthesis
88 (P_g) minus dark respiration (R_d). The values of dark respiration are $3.19 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Yao et al.,
89 2017), and $6.72 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Zhang et al., 2011). Along with high maximum photosynthesis, quantum
90 yield at low light (initial light use efficiency) of Dena-1 variety is also higher which is $0.068 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$
91 (photons) compare to Anjasmoro $0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Both Yao et al. (2017), and Zhang et
92 al. (2011) reported a similar quantum yield of soybean at $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Such a difference in
93 P_{gmax} and quantum yield between Dena-1 variety and Anjasmoro variety explains why Dena-1 variety is
94 more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-1 variety is
95 tolerant shading up to 50%. Quantum yield of Dena-1 variety both at light compensation point ($\phi(I_{comp})$) and
96 at light between compensation point to 200 ($\phi(I_{c-200})$) is higher (0.07 and $0.05 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$
97 (photons)) than quantum yield of Anjasmoro variety (0.06 and $0.04 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)) (Table 1).
98 In another word, photosynthesis at Dena-1 variety still occurs at acceptable rate even under low light or
99 under shading.

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

108 The photosynthetic light response curves of these two varieties change under *Actinomyces*
109 treatment. Under such condition the curve of Dena-1 variety is higher than that of Anjasmoro at the
110 beginning or at low light but then as light increase, the quantum yield is decreasing at a rate faster in Dena-1
111 than in Anjasmoro such that Dena-1 curve is surpassed by Anjasmoro curve at PAR $706 \mu\text{mol (photon) m}^{-2}$
112 s^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than
113 Anjasmoro at PAR below $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$, but it is the other way round at PAR above $706 \mu\text{mol}$
114 (photon) $\text{m}^{-2} \text{ s}^{-1}$. Initial light use efficiency of Dena-1 variety is higher ($0.096 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons))
115 than Anjasmoro variety ($0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)). In contrast, the maximum photosynthesis
116 (P_{gmax}) is lower in Dena-1 variety ($33.03 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$) then in Anjasmoro variety ($48.77 \mu\text{mol (CO}_2\text{) m}^{-2}$
117 s^{-1}) (Table 1). This indicates that Anjasmoro variety responses better to *Actinomyces spp* variety than
118 Dena-1 variety such that additional nutrient from *Actinomyces spp* can be converted well into increase in
119 the capacity of photosynthetic apparatus. With an increase in capacity of photosynthetic apparatus,
120 photosynthesis rate increases along with increase in light, and so increase in light saturation point, and
121 maximum photosynthesis (Table 1). Hence, the rate of decrease in quantum yield from light compensation

122 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
123 17% (from 0.06 to 0.05).

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

130 Increase the availability of phosphorus and nitrogen in the soil may lead to increase in crop growth
131 and yield (Amule et al., 2018; Soe et al., 2012; Sahur et al, 2018) . Crop response to available nutrient,
132 however, differs among species. Mahdiannoor et al. (2017) reported that growth and yield responses of
133 *Anjasmoro* variety are much higher than local soybean variety to bio-fertilizer application. Similar result was
134 also found by Timotiwu et al. (2020) that *Anjasmoro* variety responded better than *Dena-1* variety to NPK
135 fertilizer in term of plant height, biomass weight, number of pods, weight of 100 seeds, and yield. Research
136 by AbdElgawad et al. (2020) may explain such a different in responses. They found that all tested legumes
137 (soybean, kidney bean, chickpea, lentil, and pea crops) increase in its chlorophyll a and b content after
138 enrichment with biologically active *actinomyces spp.* isolates. They further found that different plants
139 responded differently to the same isolate. In relation to photosynthesis, Phosphorus play an important role in
140 energy transfer (Carstensen et al., 2018).). *Anjasmoro* variety seems response better than *Dena-1* variety to
141 *Actinomyces spp* treatment such that more chlorophylls are available and energy transfers are more
142 efficient in the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to
143 accommodate light (PAR) increase.

144 Beside the limitation by availability of chlorophyll and energy transfer, photosynthesis at high light is
145 apparently also limited by the availability of CO₂ as can be indicated by conductance to H₂O and internal CO₂
146 concentration. Under normal condition or no *Actinomyces* treatment, *Dena 1* variety has higher
147 conductance (2.28 mol H₂O m⁻² s⁻¹) than *Anjasmoro* variety (2.09 mol H₂O m⁻² s⁻¹) and it increases faster
148 with the increase of PAR from 500 to 2,000 μmol (photon) m⁻² s⁻¹. Along with this increase, internal CO₂
149 concentration in *Dena 1* variety decrease at a rate slower than in *Anjasmoro* variety (Table 2). This indicates
150 that stomata of *Dena 1* variety is more resilient to keep the internal CO₂ concentration higher than *Anjasmoro*
151 variety as a demand for CO₂ increase.

152 It has been known widely that light affect stomatal opening, and so leaf conductance. The effect of
153 light intensity to the stomatal response occurs in two ways. The first one is through decrease in intercellular
154 CO₂ concentration due to increase in photosynthesis, and the second is through direct activation of guard
155 cells (Elhaddad et al., 2014; Driesen et al., 2020; Ye et al., 2020). Unlike at normal condition, under
156 *Actinomyces spp.* treatment, the decrease in internal CO₂ concentration due to light increase in *Dena 1*
157 variety is faster than *Anjasmoro*. Limitation in availability of internal CO₂ at high light can be overcome by
158 *Actinomyces spp.* in *Anjasmoro* variety. A significant variation in the rapidity of stomatal responses
159 amongst species to light change exist (McAusland et al., 2016). For soybean, Bunce (2016) found 15
160 cultivars differed significantly in stomatal conductance. Variation in rapidity of stomatal responses to light
161 could be altered by application of *Actinomyces spp.*

162

CONCLUSIONS

163 Initial light use efficiency and maximum photosynthesis of Dena 1 variety is 0.068 $\mu\text{mol}(\text{CO}_2) \mu\text{mol}^{-1}$
 164 (photons) and 45.64 $\mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$ respectively. while Anjasmoro variety is 0.068 $\mu\text{mol}(\text{CO}_2) \mu\text{mol}^{-1}$
 165 (photons) and 34.81 $\mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$ respectively. High initial light use efficiency of Dena-1 could be one
 166 of the reasons that made Dena 1 variety tolerant to shading. Application of *Actinomyces spp.* alters light
 167 response curve such that photosynthesis rate of Anjasmoro variety is higher than Dena-1 variety at PAR
 168 above 706 $\mu\text{mol}(\text{photon}) \text{m}^{-2} \text{s}^{-1}$ and consequently maximum photosynthesis (P_{max}) of Anjasmoro is also
 169 higher than Dena-1 variety, i.e. 48.77 and 33.03 $\mu\text{mol}(\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$ respectively. Such alteration could be
 170 brought about by higher increase in the capacity of photosynthetic apparatus of Anjasmoro than in Dena 1
 171 variety under *Actinomyces spp.* treatment.

172

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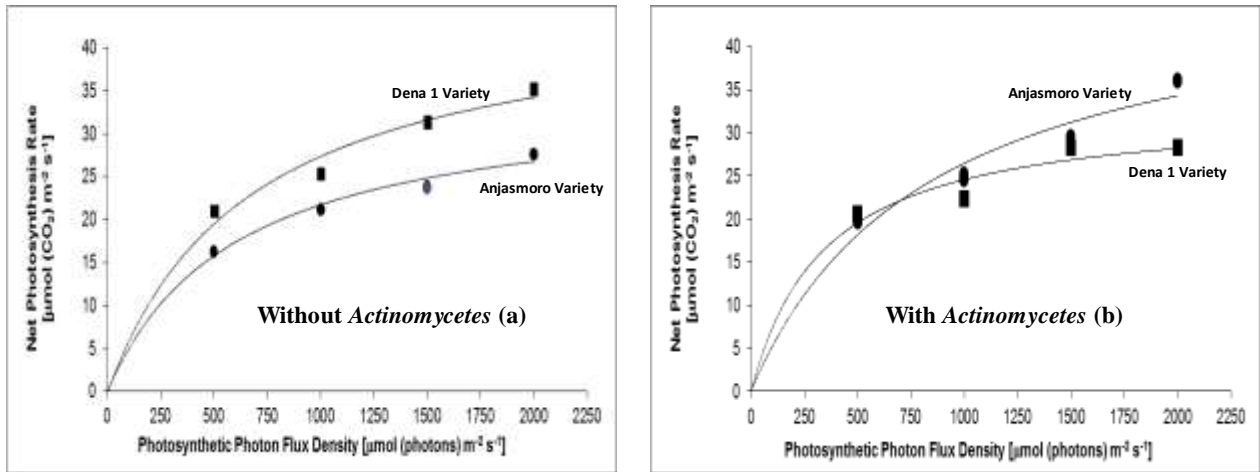
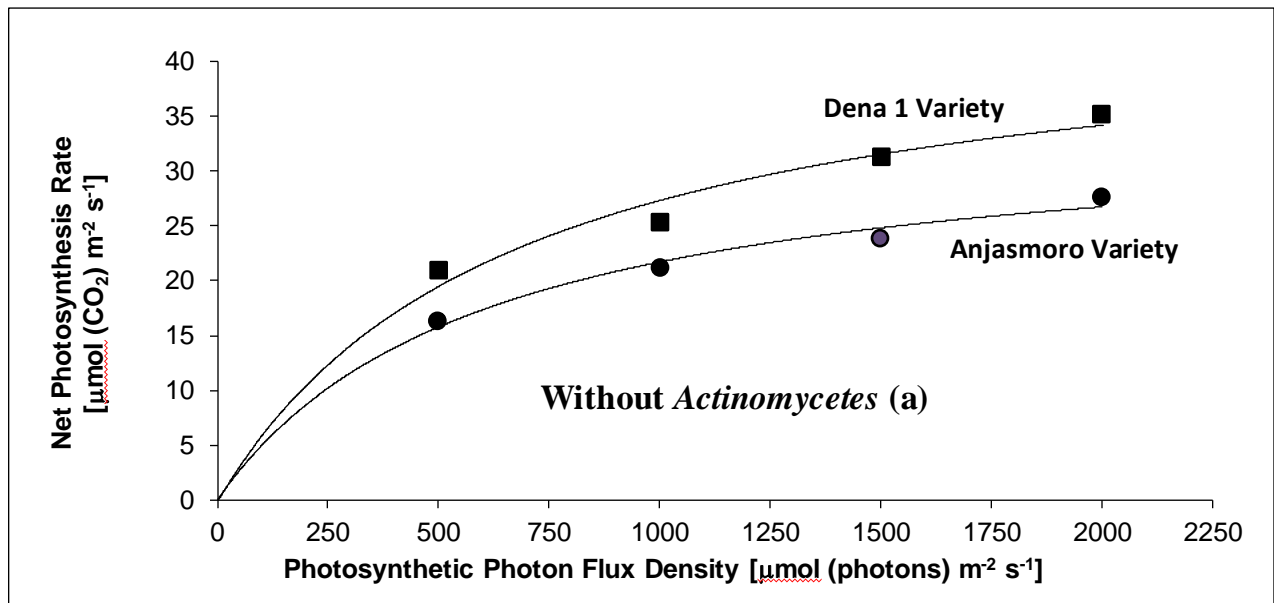


Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

282 The following are the editable graph for Figure 1.

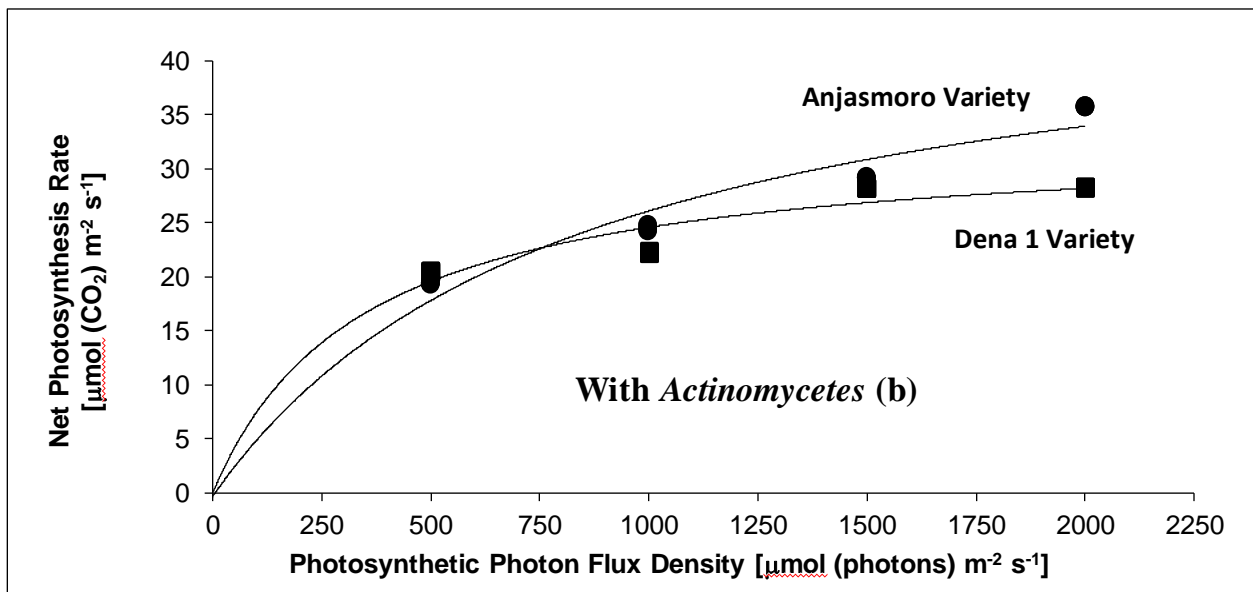
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295 Figure 1.a. Without Actinomycetes

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300 Figure 1.b . With Actinomycetes

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

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Varieties and Actinomycetes Treatments	Standard Parameters		Light saturation point at				Light-saturated net CO ₂ uptake	Quantum yield at light compensation point	
	Maximum Photosynthesis	quantum yield at I = 0	50 percentile	85 percentile	90 percentile	95 Percentile		light compensation point	LCP to I = 200
	P _{gmax} ($\mu\text{mol CO}_2$ m ⁻² s ⁻¹)	$\phi(I_0)$ ($\mu\text{mol CO}_2$ μmol^{-1} (photons))	I _{sat(50)} ($\mu\text{mol photons m}^{-2}$ s ⁻¹)	I _{sat(85)} ($\mu\text{mol photons m}^{-2}$ s ⁻¹)	I _{sat(90)} ($\mu\text{mol photons m}^{-2}$ s ⁻¹)	I _{sat(95)} ($\mu\text{mol photons m}^{-2}$ s ⁻¹)	PN(I _{max}) ($\mu\text{mol CO}_2$ m ⁻² s ⁻¹)	$\phi(I_{comp})$ ($\mu\text{mol CO}_2$ μmol^{-1} (photons))	$\phi(I_{200})$ ($\mu\text{mol CO}_2$ 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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311 Table 2. Conductance to H₂O and Intercellular CO₂ concentration of Dena and Anjasmoro varieties with and
 312 without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjamoro – no Actinomycetes, Dena-1 –
 313 Actinomycetes, Anjasmoro – Actinomycetes at variable PAR

Varieties - Actinomycetes Treatments	Conductance to H ₂ O mol H ₂ O m ⁻² s ⁻¹				Intercellular CO ₂ Concentration $\mu\text{mol CO}_2$ 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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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

Virus-free. www.avg.com

[Kutipan teks disembunyikan]

**2842- Author Revision 3 Photosynthetic May 6.docx**
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Photosynthetic Parameters 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 *Actinomyces 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 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$. The photosynthetic light response curve (PNI curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (P_{gmax}) of *Dena-1* is 45.64 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$, while *Anjasmoro* variety is only 34.81 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons) compare to *Anjasmoro* 0.058 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomyces spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$ and higher at PAR above it.

KEYWORDS

Actinomyces 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 (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* 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

44 young high estate crops, such as coconut, oil palm, and rubber. With large plantation area of those estate
45 crops Indonesia, expansion of soybean crop to plantation area is promising. *Dena-1* variety, along with *Dena*
46 2 variety as well, are considered as varieties suitable to be intercropped with young trees at community
47 forest (Abidin, 2015)

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

53 MATERIALS AND METHODS

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

57 Photosynthetic performances were measured in an experiment designed to study the effect of
58 *Actinomyces spp* on growth and yield of soybean. The experimental design was Factorial Design, in which
59 soybean varieties as first factor that consist of *Dena-1* variety (V1) and Anjasmoro variety (V2), and the
60 second factor is *Actinomyces spp* application that consist of no *Actinomyces spp* (A0), and
61 *Actinomyces spp* with concentration of 1×10^6 CFU mL⁻¹ (A1). Each treatment combination was repeated
62 three times and therefore there were 12 experimental units or plots in total. The plot size is 3 m x 4 m, and
63 the soybeans were sowed in August 20, 2017 in a row of 20 cm x 40 cm with 2 seeds per hole.

64 The photosynthetic measurement was taken in October 15, 2017 using an open chamber portable
65 photosynthetic system (LI-6400, LI-COR, Inc., Logan, NE, USA). Mature leaf exposed to full sunlight was
66 flipped to the chamber. The size of the chamber used, or the area of leaf flipped in the chamber, is 2 cm x 3
67 cm, or 6m². To develop a light response curve, the photosynthesis was measured at variable
68 Photosynthetically Active Radiation (PAR), i.e. 500; 1,000; 1,500; and 2,000 μ mol (photon) m² s⁻¹.
69 Environment conditions during experiments were as follows: air temperature – 25-27 °C; block and leaf
70 temperature – 25-27 °C; air flow rate – 500 μ mol s⁻¹; CO₂ concentration in sample cell – 380–400 μ mol CO₂
71 mol⁻¹; and relative humidity in sample cell – 56-70 %. The measurements are repeated three times (once for
72 each experimental unit). In each replication the system run for 5 second, and the data were registered every
73 second, and therefore there are 15 data set available for each PAR level, or 60 data set for all replications
74 and PAR levels. The parameters used are photosynthetic rate (Pn) (μ mol CO₂ m⁻²s⁻¹), intercellular CO₂
75 concentration(Ci) (μ mol CO₂ mol air⁻¹), and conductance to H₂O (mol H₂O m⁻² s⁻¹)

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

79 RESULTS AND DISCUSSION

80 Photosynthetic light response curves of Anjasmoro and *Dena-1* varieties are shown in Figure 1. Under
81 normal condition or no *Actinomyces* the curve of *Dena-1* variety is higher than that of Anjasmoro (Figure

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

84 Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$, while Anjasmoro
85 variety is only $34.81 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Table 1). Reported maximum net photosynthesis (P_{nmax}) of other
86 soybean varieties are $28.8 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Yao et al., 2017), $29.9 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Zhang et al.,
87 2011), and $34.8 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Sakoda et al., 2016). Net photosynthesis (P_n) is gross photosynthesis
88 (P_g) minus dark respiration (R_d). The values of dark respiration are $3.19 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Yao et al.,
89 2017), and $6.72 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Zhang et al., 2011). Along with high maximum photosynthesis, quantum
90 yield at low light (initial light use efficiency) of Dena-1 variety is also higher which is $0.068 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$
91 (photons) compare to Anjasmoro $0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Both Yao et al. (2017), and Zhang et
92 al. (2011) reported a similar quantum yield of soybean at $0.053 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Such a
93 difference in P_{gmax} and quantum yield between Dena-1 variety and Anjasmoro variety explains why Dena-1
94 variety is more tolerant to shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-1
95 variety is tolerant shading up to 50%. Quantum yield of Dena-1 variety both at light compensation point
96 ($\phi(I_{comp})$) and at light between compensation point to 200 ($\phi(I_{c-200})$) is higher (0.07 and $0.05 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$
97 μmol^{-1} (photons)) than quantum yield of Anjasmoro variety (0.06 and $0.04 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons))
98 (Table 1). In another word, photosynthesis at Dena-1 variety still occurs at acceptable rate even under low
99 light or under shading.

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

108 The photosynthetic light response curves of these two varieties change under *Actinomyces*
109 treatment. Under such condition the curve of Dena-1 variety is higher than that of Anjasmoro at the
110 beginning or at low light but then as light increase, the quantum yield is decreasing at a rate faster in Dena-1
111 than in Anjasmoro such that Dena-1 curve is surpassed by Anjasmoro curve at PAR $706 \mu\text{mol (photon) m}^{-2}$
112 s^{-1} (Figure 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than
113 Anjasmoro at PAR below $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$, but it is the other way round at PAR above $706 \mu\text{mol}$
114 $\text{(photon) m}^{-2} \text{ s}^{-1}$. Initial light use efficiency of Dena-1 variety is higher ($0.096 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons))
115 than Anjasmoro variety ($0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)). In contrast, the maximum photosynthesis
116 (P_{gmax}) is lower in Dena-1 variety ($33.03 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$) then in Anjasmoro variety ($48.77 \mu\text{mol (CO}_2\text{) m}^{-2}$
117 s^{-1}) (Table 1). This indicates that Anjasmoro variety responses better to *Actinomyces spp* variety than
118 Dena-1 variety such that additional nutrient from *Actinomyces spp* can be converted well into increase in
119 the capacity of photosynthetic apparatus. With an increase in capacity of photosynthetic apparatus,
120 photosynthesis rate increases along with increase in light, and so increase in light saturation point, and
121 maximum photosynthesis (Table 1). Hence, the rate of decrease in quantum yield from light compensation

122 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
123 17% (from 0.06 to 0.05).

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

130 Increase the availability of phosphorus and nitrogen in the soil may lead to increase in crop growth
131 and yield (Amule et al., 2018; Soe et al., 2012; Sahur et al, 2018) . Crop response to available nutrient,
132 however, differs among species. Mahdiannoor et al. (2017) reported that growth and yield responses of
133 *Anjasmoro* variety are much higher than local soybean variety to bio-fertilizer application. Similar result was
134 also found by Timotiwu et al. (2020) that *Anjasmoro* variety responded better than *Dena-1* variety to NPK
135 fertilizer in term of plant height, biomass weight, number of pods, weight of 100 seeds, and yield. Research
136 by AbdElgawad et al. (2020) may explain such a different in responses. They found that all tested legumes
137 (soybean, kidney bean, chickpea, lentil, and pea crops) increase in its chlorophyll a and b content after
138 enrichment with biologically active *actinomyces spp.* isolates. They further found that different plants
139 responded differently to the same isolate. In relation to photosynthesis, Phosphorus play an important role in
140 energy transfer (Carstensen et al., 2018).). *Anjasmoro* variety seems response better than *Dena-1* variety to
141 *Actinomyces spp* treatment such that more chlorophylls are available and energy transfers are more
142 efficient in the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to
143 accommodate light (PAR) increase.

144 Beside the limitation by availability of chlorophyll and energy transfer, photosynthesis at high light is
145 apparently also limited by the availability of CO₂ as can be indicated by conductance to H₂O and internal CO₂
146 concentration. Under normal condition or no *Actinomyces* treatment, *Dena 1* variety has higher
147 conductance (2.28 mol H₂O m⁻² s⁻¹) than *Anjasmoro* variety (2.09 mol H₂O m⁻² s⁻¹) and it increases faster
148 with the increase of PAR from 500 to 2,000 μmol (photon) m⁻² s⁻¹. Along with this increase, internal CO₂
149 concentration in *Dena 1* variety decrease at a rate slower than in *Anjasmoro* variety (Table 2). This indicates
150 that stomata of *Dena 1* variety is more resilient to keep the internal CO₂ concentration higher than *Anjasmoro*
151 variety as a demand for CO₂ increase.

152 It has been known widely that light affect stomatal opening, and so leaf conductance. The effect of
153 light intensity to the stomatal response occurs in two ways. The first one is through decrease in intercellular
154 CO₂ concentration due to increase in photosynthesis, and the second is through direct activation of guard
155 cells (Elhaddad et al., 2014; Driesen et al., 2020; Ye et al., 2020). Unlike at normal condition, under
156 *Actinomyces spp.* treatment, the decrease in internal CO₂ concentration due to light increase in *Dena 1*
157 variety is faster than *Anjasmoro*. Limitation in availability of internal CO₂ at high light can be overcome by
158 *Actinomyces spp.* in *Anjasmoro* variety. A significant variation in the rapidity of stomatal responses
159 amongst species to light change exist (McAusland et al., 2016). For soybean, Bunce (2016) found 15
160 cultivars differed significantly in stomatal conductance. Variation in rapidity of stomatal responses to light
161 could be altered by application of *Actinomyces spp.*

162

CONCLUSIONS

163 Initial light use efficiency and maximum photosynthesis of Dena 1 variety is 0.068 $\mu\text{mol}(\text{CO}_2)\mu\text{mol}^{-1}$
 164 (photons) and 45.64 $\mu\text{mol}(\text{CO}_2)\text{m}^{-2}\text{s}^{-1}$ respectively. while Anjasmoro variety is 0.068 $\mu\text{mol}(\text{CO}_2)\mu\text{mol}^{-1}$
 165 (photons) and 34.81 $\mu\text{mol}(\text{CO}_2)\text{m}^{-2}\text{s}^{-1}$ respectively. High initial light use efficiency of Dena-1 could be one
 166 of the reasons that made Dena 1 variety tolerant to shading. Application of *Actinomyces spp.* alters light
 167 response curve such that photosynthesis rate of Anjasmoro variety is higher than Dena-1 variety at PAR
 168 above 706 $\mu\text{mol}(\text{photon})\text{m}^{-2}\text{s}^{-1}$ and consequently maximum photosynthesis (P_{max}) of Anjasmoro is also
 169 higher than Dena-1 variety, i.e. 48.77 and 33.03 $\mu\text{mol}(\text{CO}_2)\text{m}^{-2}\text{s}^{-1}$ respectively. Such alteration could be
 170 brought about by higher increase in the capacity of photosynthetic apparatus of Anjasmoro than in Dena 1
 171 variety under *Actinomyces spp.* treatment.

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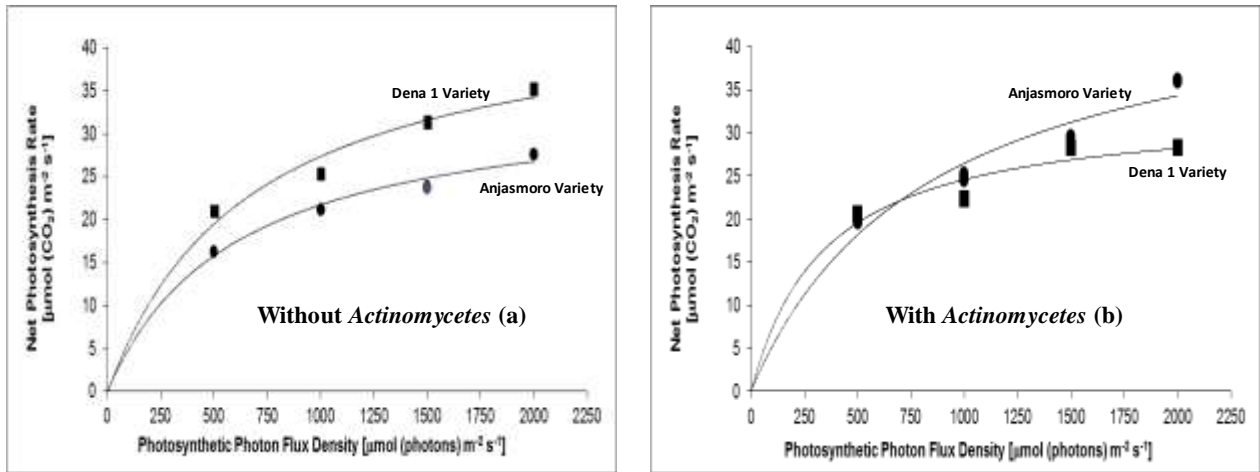
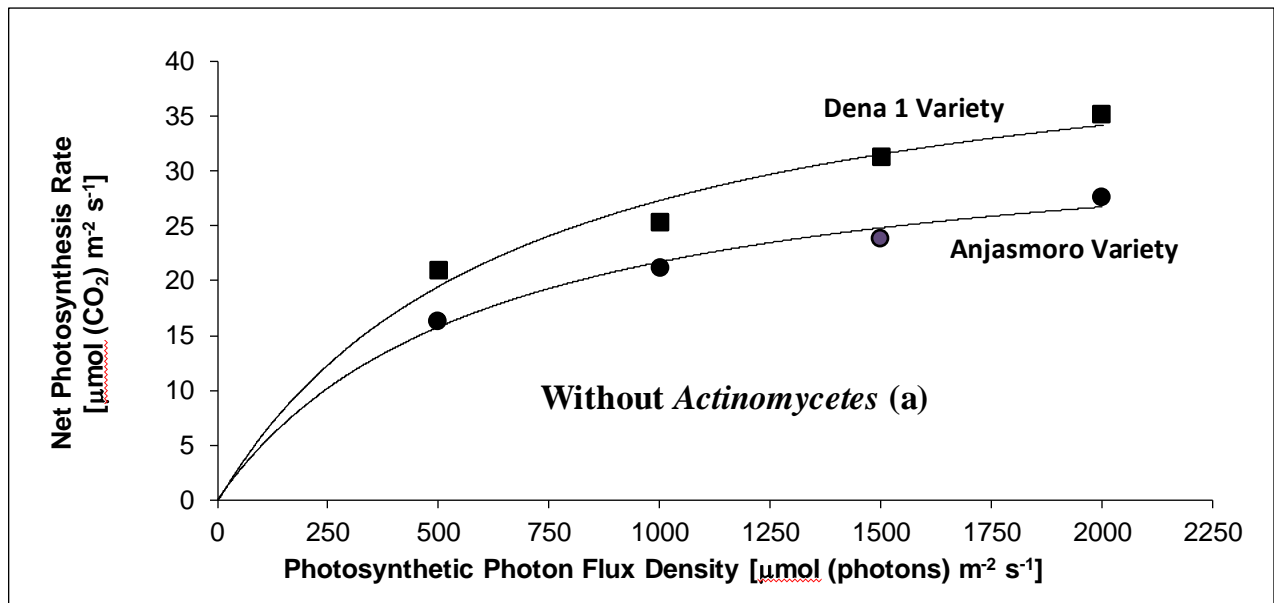


Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b).

282 The following are the editable graph for Figure 1.

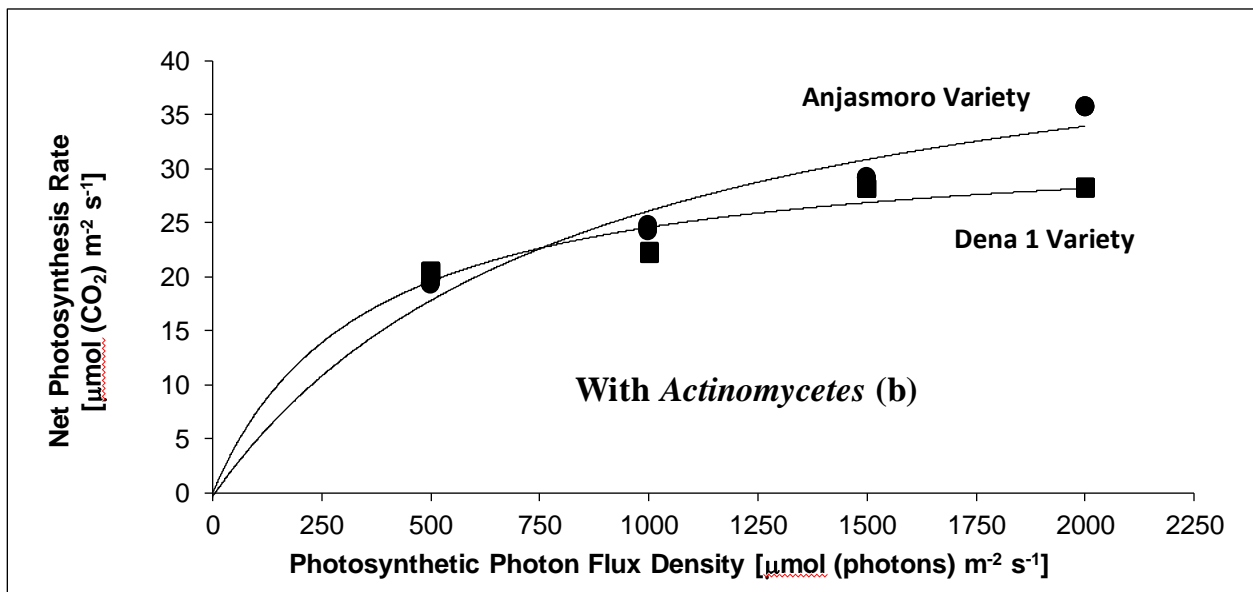
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295 Figure 1.a. Without Actinomycetes

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300 Figure 1.b . With Actinomycetes

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

307

Varieties and Actinomycetes Treatments	Standard Parameters		Light saturation point at				Light-saturated net CO ₂ uptake	Quantum yield at	
	Maximum Photosynthesis	quantum yield at I = 0	50 percent	85 percent	90 percent	95 Percent		light compensation point	LCP to I = 200
	P _{gmax} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	$\phi(I_0)$ ($\mu\text{mol CO}_2 \text{ mol}^{-1}$ (photons))	I _{sat(50)} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	I _{sat(85)} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	I _{sat(90)} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	I _{sat(95)} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	PN(I _{max}) ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	$\phi(I_{comp})$ ($\mu\text{mol CO}_2 \text{ mol}^{-1}$ (photons))	$\phi(I_{200})$ ($\mu\text{mol CO}_2 \text{ mol}^{-1}$ (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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311 Table 2. Conductance to H₂O and Intercellular CO₂ concentration of Dena and Anjasmoro varieties with and
 312 without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjamoro – no Actinomycetes, Dena-1 –
 313 Actinomycetes, Anjasmoro – Actinomycetes at variable PAR

Varieties - Actinomycetes Treatments	Conductance to H ₂ O $\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$				Intercellular CO ₂ Concentration $\mu\text{mol CO}_2 \text{ mol}^{-1}$			
	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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Kepada: "Rusnadi Padjung, Dr" <rusnadi2015@gmail.com>

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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: Accept submission

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Photosynthetic Parameters 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 *Actinomyces 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 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$. The photosynthetic light response curve (PNII curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (P_{gmax}) of *Dena-1* is 45.64 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$, while *Anjasmoro* variety is only 34.81 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{s}^{-1}$. Quantum yield at low light (initial light use efficiency) of *Dena-1* variety is also higher which is 0.068 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons) compare to *Anjasmoro* 0.058 $\mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Hence light response curve of *Dena-1* variety is consistently higher than *Anjasmoro*. Under *Actinomyces spp* treatment the light response curve is higher in *Dena-1* than in *Anjasmoro* at PAR lower than 706 $\mu\text{mol (photon) m}^{-2} \text{s}^{-1}$ and higher at PAR above it.

KEYWORDS

Actinomyces 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 (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* 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 lodging 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

44 young high estate crops, such as coconut, oil palm, and rubber. With large plantation area of those estate
45 crops Indonesia, expansion of soybean crop to plantation area is promising. *Dena-1* variety, along with *Dena*
46 2 variety as well, are considered as varieties suitable to be intercropped with young trees at community forest
47 (Abidin, 2015)

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

53 MATERIALS AND METHODS

54 The experiment was conducted in Tarowang farm, owned by a smallholder farmer in Tarowang village, district
55 of Takalar, South Sulawesi province, Indonesia from August to November 2017. Tarowang is located at 119°
56 28' East and 5° 39' South with altitude of 15 m above sea level.

57 Photosynthetic performances were measured in an experiment designed to study the effect of
58 *Actinomyces spp* on growth and yield of soybean. The experimental design was Factorial Design, in which
59 soybean varieties as first factor that consist of *Dena-1* variety (V1) and *Anjasmoro* variety (V2), and the second
60 factor is *Actinomyces spp* application that consist of no *Actinomyces spp* (A0), and *Actinomyces spp*
61 with concentration of 1×10^6 CFU mL⁻¹ (A1). Each treatment combination was repeated three times and
62 therefore there were 12 experimental units or plots in total. The plot size is 3 m x 4 m, and the soybeans were
63 sowed in August 20, 2017 in a row of 20 cm x 40 cm with 2 seeds per hole.

64 The photosynthetic measurement was taken in October 15, 2017 using an open chamber portable
65 photosynthetic system (LI-6400, LI-COR, Inc., Logan, NE, USA). Mature leaf exposed to full sunlight was
66 flipped to the chamber. The size of the chamber used, or the area of leaf flipped in the chamber, is 2 cm x 3
67 cm, or 6m². To develop a light response curve, the photosynthesis was measured at variable
68 Photosynthetically Active Radiation (PAR), i.e. 500; 1,000; 1,500; and 2,000 μ mol (photon) m² s⁻¹.
69 Environment conditions during experiments were as follows: air temperature – 25-27 °C; block and leaf
70 temperature – 25-27 °C; air flow rate – 500 μ mol s⁻¹; CO₂ concentration in sample cell – 380–400 μ mol CO₂
71 mol⁻¹; and relative humidity in sample cell – 56-70 %. The measurements are repeated three times (once for
72 each experimental unit). In each replication the system run for 5 second, and the data were registered every
73 second, and therefore there are 15 data set available for each PAR level, or 60 data set for all replications and
74 PAR levels. The parameters used are photosynthetic rate (Pn) (μ mol CO₂ m⁻²s⁻¹), intercellular CO₂
75 concentration(Ci) (μ mol CO₂ mol air⁻¹), and conductance to H₂O (mol H₂O m⁻² s⁻¹)

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

79 RESULTS AND DISCUSSION

80 Photosynthetic light response curves of *Anjasmoro* and *Dena-1* varieties are shown in Figure 1. Under normal
81 condition or no *Actinomyces* the curve of *Dena-1* variety is higher than that of *Anjasmoro* (Figure 1.a.). This

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

84 Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$, while Anjasmoro
85 variety is only $34.81 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Table 1). Reported maximum net photosynthesis (P_{nmax}) of other
86 soybean varieties are $28.8 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Yao et al., 2017), $29.9 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Zhang et al., 2011),
87 and $34.8 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Sakoda et al., 2016). Net photosynthesis (P_n) is gross photosynthesis (P_g) minus
88 dark respiration (R_d). The values of dark respiration are $3.19 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Yao et al., 2017), and 6.72
89 $\mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$ (Zhang et al., 2011). Along with high maximum photosynthesis, quantum yield at low light
90 (initial light use efficiency) of Dena-1 variety is also higher which is $0.068 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons) compare
91 to Anjasmoro $0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Both Yao et al. (2017), and Zhang et al. (2011) reported a
92 similar quantum yield of soybean at $0.053 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons). Such a difference in P_{gmax} and
93 quantum yield between Dena-1 variety and Anjasmoro variety explains why Dena-1 variety is more tolerant to
94 shading than Anjasmoro variety. As reported by Pratiwi and Artari (2018). Dena-1 variety is tolerant shading
95 up to 50%. Quantum yield of Dena-1 variety both at light compensation point ($\phi(I_{comp})$) and at light between
96 compensation point to 200 ($\phi(I_c-I_{200})$) is higher (0.07 and $0.05 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)) than quantum
97 yield of Anjasmoro variety (0.06 and $0.04 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)) (Table 1). In another word,
98 photosynthesis at Dena-1 variety still occurs at acceptable rate even under low light or under shading.

99 Along with high maximum gross photosynthesis, initial light use efficiency, and quantum yield, the light
100 saturation point of Dena-1 variety is consistently higher at percentile 50 % all the way up to 95% than that of
101 Anjasmoro variety. Light saturation point at 50% percentile of Dena-1 variety is $667 \mu\text{mol (photons) m}^{-2} \text{ s}^{-1}$,
102 while Anjasmoro is $603 \mu\text{mol (photons) m}^{-2} \text{ s}^{-1}$. At 95 percentile, the light saturation point of Dena-1 variety is
103 $6,004 \mu\text{mol (photons) m}^{-2} \text{ s}^{-1}$, while Anjasmoro variety is $5,429 \mu\text{mol (photons) m}^{-2} \text{ s}^{-1}$ (Table 2). High light
104 saturation point indicates that Dena-1 varieties is not only tolerant to shading but also tolerant to high light. In
105 another word, increase in light intensity can be accommodated by Dena-1 variety due to high capacity of its
106 photosynthetic apparatus.

107 The photosynthetic light response curves of these two varieties change under *Actinomyces*
108 treatment. Under such condition the curve of Dena-1 variety is higher than that of Anjasmoro at the beginning
109 or at low light but then as light increase, the quantum yield is decreasing at a rate faster in Dena-1 than in
110 Anjasmoro such that Dena-1 curve is surpassed by Anjasmoro curve at PAR $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$ (Figure
111 1.b.). In another word, the photosynthetic light-response curve of Dena-1 variety is higher than Anjasmoro at
112 PAR below $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$, but it is the other way round at PAR above $706 \mu\text{mol (photon) m}^{-2} \text{ s}^{-1}$.
113 Initial light use efficiency of Dena-1 variety is higher ($0.096 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)) than Anjasmoro variety
114 ($0.058 \mu\text{mol (CO}_2\text{) } \mu\text{mol}^{-1}$ (photons)). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1
115 variety ($33.03 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$) then in Anjasmoro variety ($48.77 \mu\text{mol (CO}_2\text{) m}^{-2} \text{ s}^{-1}$) (Table 1). This indicates
116 that Anjasmoro variety responses better to *Actinomyces spp* variety than Dena-1 variety such that additional
117 nutrient from *Actinomyces spp* can be converted well into increase in the capacity of photosynthetic
118 apparatus. With an increase in capacity of photosynthetic apparatus, photosynthesis rate increases along with
119 increase in light, and so increase in light saturation point, and maximum photosynthesis (Table 1). Hence, the
120 rate of decrease in quantum yield from light compensation point (I_c) to I_{200} is much higher in Dena-1 variety
121 than in Anjasmoro variety, i.e. 40 % (from 0.10 to 0.04) vs 17% (from 0.06 to 0.05).

122 *Actinomycetes spp.* play an important role in soil nutrient cycling (Bhatti et al., 2017), solubilize
123 inorganic phosphates (Pragya et al., 2012; Ghorbani-Nasrabadi et al., 2013; Saif et al., 2014), hydrolyze
124 phytate, a dominant form of organic P in soils (Ghorbani-Nasrabadi et al., 2012; Schneider et al., 2016), and
125 so improve the availability of nutrients (Hozzein et al., 2019; AbdElgawad et al., 2020) particularly phosphorus.
126 *Actinomycetes spp.* is not only increasing the availability of phosphorus, but also nitrogen (AbdElgawad et al.,
127 2020).

128 Increase the availability of phosphorus and nitrogen in the soil may lead to increase in crop growth
129 and yield (Amule et al., 2018; Soe et al., 2012; Sahur et al, 2018) . Crop response to available nutrient,
130 however, differs among species. Mahdiannoor et al. (2017) reported that growth and yield responses of
131 *Anjasmoro* variety are much higher than local soybean variety to bio-fertilizer application. Similar result was
132 also found by Timotiwu et al. (2020) that *Anjasmoro* variety responded better than *Dena-1* variety to NPK
133 fertilizer in term of plant height, biomass weight, number of pods, weight of 100 seeds, and yield. Research by
134 AbdElgawad et al. (2020) may explain such a different in responses. They found that all tested legumes
135 (soybean, kidney bean, chickpea, lentil, and pea crops) increase in its chlorophyll a and b content after
136 enrichment with biologically active *actinomycetes spp.* isolates. They further found that different plants
137 responded differently to the same isolate. In relation to photosynthesis, Phosphorus play an important role in
138 energy transfer (Carstensen et al., 2018).). *Anjasmoro* variety seems response better than *Dena-1* variety to
139 *Actinomycetes spp* treatment such that more chlorophylls are available and energy transfers are more efficient
140 in the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to accommodate
141 light (PAR) increase.

142 Beside the limitation by availability of chlorophyll and energy transfer, photosynthesis at high light is
143 apparently also limited by the availability of CO₂ as can be indicated by conductance to H₂O and internal CO₂
144 concentration. Under normal condition or no *Actinomycetes* treatment, *Dena 1* variety has higher conductance
145 (2.28 mol H₂O m⁻² s⁻¹) than *Anjasmoro* variety (2.09 mol H₂O m⁻² s⁻¹) and it increases faster with the increase
146 of PAR from 500 to 2,000 μmol (photon) m⁻² s⁻¹. Along with this increase, internal CO₂ concentration in *Dena*
147 *1* variety decrease at a rate slower than in *Anjasmoro* variety (Table 2). This indicates that stomata of *Dena 1*
148 variety is more resilient to keep the internal CO₂ concentration higher than *Anjasmoro* variety as a demand for
149 CO₂ increase.

150 It has been known widely that light affect stomatal opening, and so leaf conductance. The effect of
151 light intensity to the stomatal response occurs in two ways. The first one is through decrease in intercellular
152 CO₂ concentration due to increase in photosynthesis, and the second is through direct activation of guard cells
153 (Elhaddad et al., 2014; Driesen et al., 2020; Ye et al., 2020). Unlike at normal condition, under *Actinomycetes*
154 *spp.* treatment, the decrease in internal CO₂ concentration due to light increase in *Dena 1* variety is faster than
155 *Anjasmoro*. Limitation in availability of internal CO₂ at high light can be overcome by *Actinomycetes spp.* in
156 *Anjasmoro* variety. A significant variation in the rapidity of stomatal responses amongst species to light change
157 exist (McAusland et al., 2016). For soybean, Bunce (2016) found 15 cultivars differed significantly in stomatal
158 conductance. Variation in rapidity of stomatal responses to light could be altered by application of
159 *Actinomycetes spp.*

160

CONCLUSIONS

161 Initial light use efficiency and maximum photosynthesis of Dena 1 variety is $0.068 \mu\text{mol} (\text{CO}_2) \mu\text{mol}^{-1}$ (photons)
162 and $45.64 \mu\text{mol} (\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$ respectively. while Anjasmoro variety is $0.068 \mu\text{mol} (\text{CO}_2) \mu\text{mol}^{-1}$ (photons) and
163 $34.81 \mu\text{mol} (\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$ respectively. High initial light use efficiency of Dena-1 could be one of the reasons
164 that made Dena 1 variety tolerant to shading. Application of *Actinomyces spp.* alters light response curve
165 such that photosynthesis rate of Anjasmoro variety is higher than Dena-1 variety at PAR above $706 \mu\text{mol}$
166 (photon) $\text{m}^{-2} \text{s}^{-1}$ and consequently maximum photosynthesis (Pmax) of Anjasmoro is also higher than Dena-1
167 variety, i.e. 48.77 and $33.03 \mu\text{mol} (\text{CO}_2) \text{m}^{-2} \text{s}^{-1}$ respectively. Such alteration could be brought about by higher
168 increase in the capacity of photosynthetic apparatus of Anjasmoro than in Dena 1 variety under *Actinomyces*
169 *spp.* treatment.

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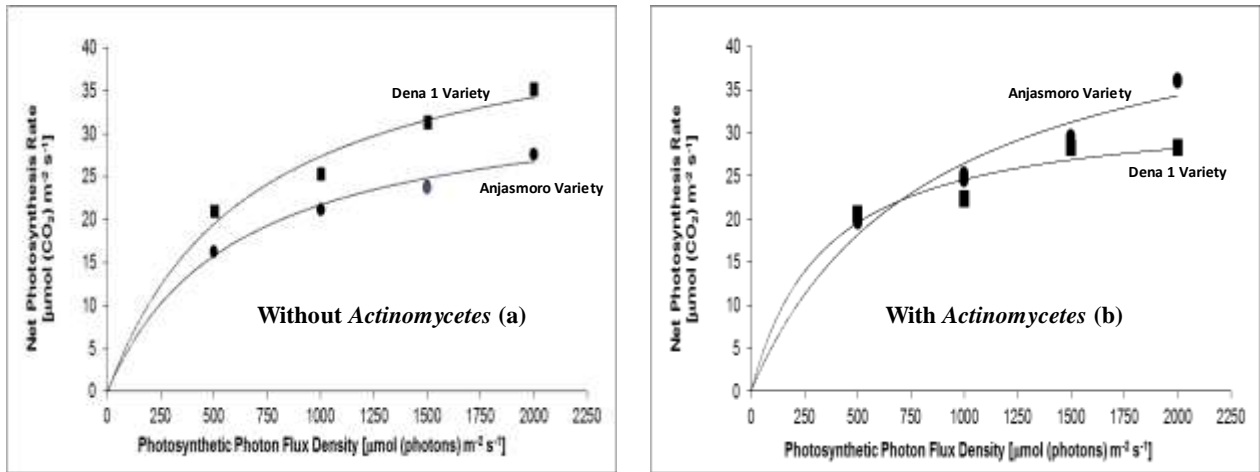
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274 Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a),
275 and under Actinomycetes treatment (b).
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277 The following are the editable graph for Figure 1.

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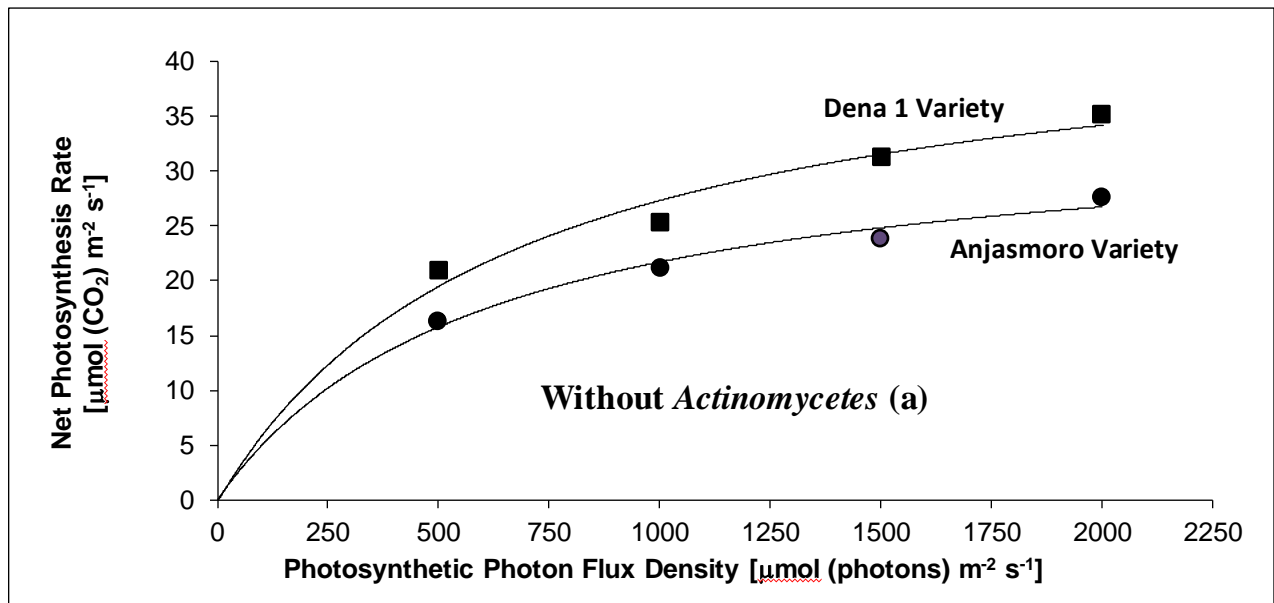
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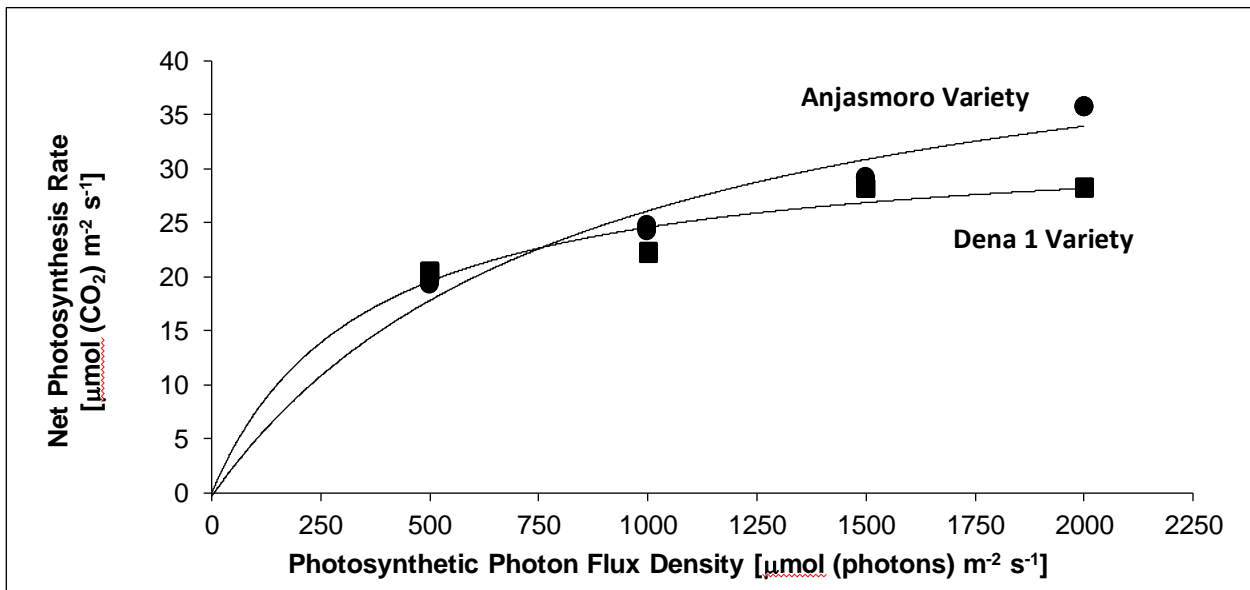
290 Figure 1.a. Without Actinomycetes

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With Actinomycetes (b)



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295 Figure 1.b . With Actinomycetes

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

302

Varieties and Actinomycetes Treatments	Standard Parameters		Light saturation point at				Light-saturated net CO ₂ uptake	Quantum yield at	
	Maximum Photosynthesis	quantum yield at I = 0	50 percent-ile	85 percent-ile	90 percent-ile	95 Percent-ile		light compensation point	LCP to I = 200
	P _{gmax} ($\mu\text{mol CO}_2$ $\text{m}^{-2} \text{s}^{-1}$)	$\phi(I_0)$ ($\mu\text{mol CO}_2$ μmol^{-1} (photons))	I _{sat(50)} ($\mu\text{mol photon s}$) m^{-2} s^{-1})	I _{sat(85)} ($\mu\text{mol photons}$) m^{-2} s^{-1})	I _{sat(90)} ($\mu\text{mol photons}$) m^{-2} s^{-1})	I _{sat(95)} ($\mu\text{mol photons}$) m^{-2} s^{-1})	PN(I _{max}) ($\mu\text{mol CO}_2$ $\text{m}^{-2} \text{s}^{-1}$)	$\phi(I_{\text{comp}})$ ($\mu\text{mol CO}_2$ μmol^{-1} (photons))	$\phi(I_{\text{c-200}})$ ($\mu\text{mol CO}_2$ 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

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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>
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27 Mei 2021 13.11

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.

 **Rusnadi_PART 2 kwb anl eal ssw 27052021.docx**
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Photosynthetic Parameters 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 *Actinomyces* 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 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$. The photosynthetic light response curve (PNI curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis (P_{gmax}) of Dena-1 is 45.64 $\mu\text{mol (CO}_2)/\text{m}^2/\text{s}$, while Anjasmoro variety is only 34.81 $\mu\text{mol (CO}_2)/\text{m}^2/\text{s}$. Quantum yield at low light (initial light use efficiency) of Dena-1 is also higher with the value of 0.068 $\mu\text{mol (CO}_2)/\mu\text{mol(photon)}$ compared to Anjasmoro that have 0.058 $\mu\text{mol (CO}_2)/\mu\text{mol (photons)}$. Hence light response curve of Dena-1 variety is consistently higher than Anjasmoro. Under *Actinomyces* spp. treatment the light response curve of Dena-1 is higher than Anjasmoro at PAR lower than 706 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$ and higher at PAR above it.

Keywords: *Actinomyces* 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 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° 28' East and 5° 39' South with altitude of 15 m above sea level.

Photosynthetic performances were measured in an experiment designed to study the effect of *Actinomyces* 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 *Actinomyces* spp. application that consist of no *Actinomyces* spp. (A0), and *Actinomyces* spp. with concentration of 1×10^6 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 m² (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)/m²/s. 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; CO₂ concentration in sample cell – 380–400 μmol CO₂ /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 CO₂/m²/s), intercellular CO₂ concentration (Ci) (μmol CO₂/mol air), and conductance to H₂O (mol H₂O/m²/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 *Actinomyces* the curve of Dena-1 variety is higher than that of Anjasmoro (Fig. 1a). This indicates that Dena-1 responses better than Anjasmoro to light, as it has higher initial light use efficiency as well as higher maximum photosynthesis.

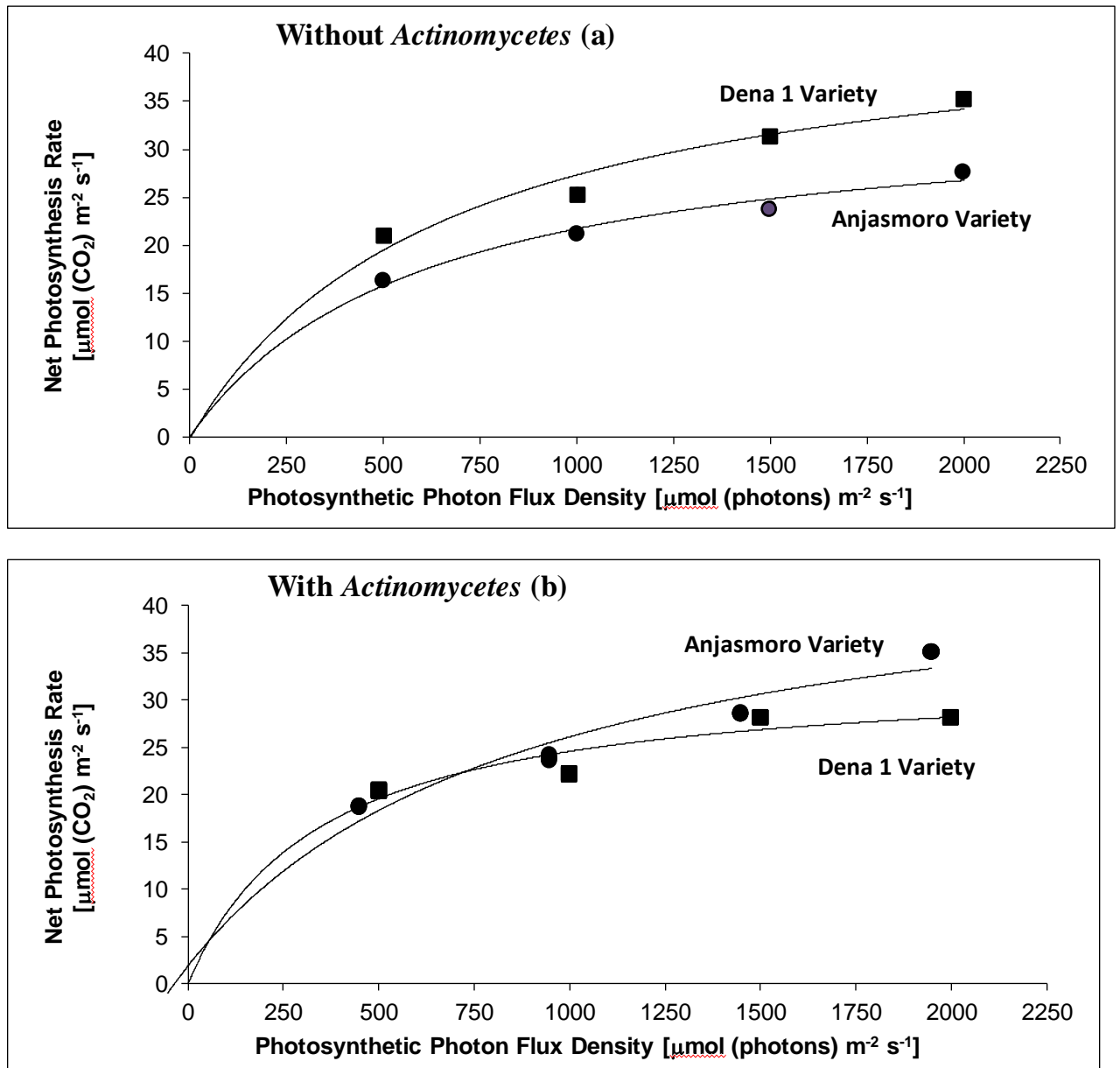


Fig. 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under Actinomycetes treatment (b). (please group the picture, mohon sesuaikan satuan yang ada di gambar dengan satuan di teks)

Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$, while Anjasmoro variety is only $34.81 \mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$ (Table 1). Reported maximum net photosynthesis (P_{nmax}) of other soybean varieties are $28.8 \mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$ (Yao et al., 2017), $29.9 \mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$ (Zhang, Hu, Luo, Chow, & Zhang, 2011), and $34.8 \mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$ (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 $\mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$ (Yao et al., 2017), and 6.72 $\mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$ (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 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$ compared to Anjasmoro 0.058 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$. Both Yao et al. (2017) and Zhang, Hu, Luo, Chow, & Zhang (2011) reported a similar quantum yield of soybean at 0.053 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$. 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 ($\phi(I_{comp})$) and at light between compensation point to 200 ($\phi(I_{c-1200})$) is higher (0.07 and 0.05 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$) than quantum yield of Anjasmoro (0.06 and 0.04 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$) (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 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$, while Anjasmoro is 603 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$, while Anjasmoro is 5,429 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$ (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 *Actinomyces* 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 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$ (Figure 1b). In another word, the photosynthetic light-response curve of Dena-1 is higher than Anjasmoro at PAR below 706 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$, but it is the other way round at PAR above 706 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$. Initial light use efficiency of Dena-1 is higher (0.096 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$) than Anjasmoro (0.058 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$). 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 $\mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$) than in Anjasmoro (48.77 $\mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$) (Table 1). This indicates that Anjasmoro responses better to *Actinomyces* spp. than Dena-1. The better response includes the conversion of additional nutrient from *Actinomyces* 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).

Actinomyces spp. play an important role in soil nutrient cycling (Bhatti, Haq, & Bhat, 2017), inorganic phosphates solubilizing (Ghorbani-Nasrabadi, Greiner, Alikhani, Hamed, & Yakhchali, 2013; Pragma, Yasmin, & Anshula, 2012; Saif, Khan, Zaidi, & Ahmad, 2014), phytate hydrolyzing, a dominant form of organic P in soils (Ghorbani-Nasrabadi, Greiner, Alikhani, & Hamed, 2012; Schneider, Cade-Menun, Lynch, & Voroney, 2016), and so improvement of nutrients availability (AbdElgawad et al., 2020; Hozzein et al., 2019) particularly phosphorus. *Actinomyces* 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 *Actinomyces* 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

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

Varieties and Actinomycetes Treatments	Standard Parameters		Light saturation point at				Light-saturated net CO ₂ uptake	Quantum yield at	
	Maximum Photosynthesis	Quantum yield at I = 0	50 percentile	85 percentile	90 percentile	95 Percent-tile		Light compensation point	LCP to I = 200
	P _{gmax}	φ(I ₀)	I _{sat(50)}	I _{sat(85)}	I _{sat(90)}	I _{sat(95)}	PN (I _{max})	φ(I _{comp})	φ(I _{c-200})
	(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 CO₂ as can be indicated by conductance to H₂O and internal CO₂ concentration. Under normal condition or no Actinomycetes treatment, Dena 1 has higher conductance (2.28 mol H₂O/m²/s) than Anjasmoro (2.09 mol H₂O/m²/s) and it increases faster with the increase of PAR from 500 to 2,000 μmol (photon)/m²/s. Along with this increase, internal CO₂ 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 CO₂ concentration higher than Anjasmoro when the demand for CO₂ 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 CO₂ 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 CO₂ concentration due to light increase in Dena 1 is faster than Anjasmoro. Limitation in availability of internal CO₂ 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 (CO₂)/μmol (photons) and 45.64 μmol (CO₂)/m²/s, respectively. While, Anjasmoro is 0.068 μmol (CO₂)/μmol (photons) and 34.81 μmol (CO₂)/m²/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)/m²/s and consequently, maximum photosynthesis (P_{max}) of Anjasmoro is also higher than Dena-1, i.e. 48.77 and 33.03 μmol (CO₂)/m²/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 Parameters of Two Indonesian Soybean Top Varieties

Running title: *Actinomyces* 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 *Actinomyces* 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 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$. The photosynthetic light response curve (PNI curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis ($P_{g\text{max}}$) of Dena-1 is 45.64 $\mu\text{mol (CO}_2)/\text{m}^2/\text{s}$, while Anjasmoro variety is only 34.81 $\mu\text{mol (CO}_2)/\text{m}^2/\text{s}$. Quantum yield at low light (initial light use efficiency) of Dena-1 is also higher with the value of 0.068 $\mu\text{mol (CO}_2)/\mu\text{mol (photons)}$ compared to Anjasmoro that have 0.058 $\mu\text{mol (CO}_2)/\mu\text{mol (photons)}$. Hence light response curve of Dena-1 variety is consistently higher than Anjasmoro. Under *Actinomyces* spp. treatment the light response curve of Dena-1 is higher than Anjasmoro at PAR lower than 706 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$ and higher at PAR above it.

Keywords: *Actinomyces* 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 lodging 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° 28' East and 5° 39' South with altitude of 15 m above sea level.

Photosynthetic performances were measured in an experiment designed to study the effect of *Actinomyces* 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 *Actinomyces* spp. application that consist of no *Actinomyces* spp. (A0), and *Actinomyces* spp. with concentration of 1×10^6 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 cm². 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 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$. Environment conditions during experiments were as follows: air temperature 25-27°C; block and leaf temperature 25-27°C; air flow rate 500 $\mu\text{mol}/\text{s}$; CO₂ concentration in sample cell 380–400 $\mu\text{mol CO}_2/\text{mol}$; 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) ($\mu\text{mol CO}_2/\text{m}^2/\text{s}$), intercellular CO₂ concentration (C_i) ($\mu\text{mol CO}_2/\text{mol air}$), and conductance to H₂O ($\text{mol H}_2\text{O}/\text{m}^2/\text{s}$)

The photosynthetic light response curve (PNI 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 *Actinomyces* the curve of Dena-1 variety is higher than that of Anjasmoro (Fig. 1a). This indicates that Dena-1 responses better than Anjasmoro to light, as it has higher initial light use efficiency as well as higher maximum photosynthesis.

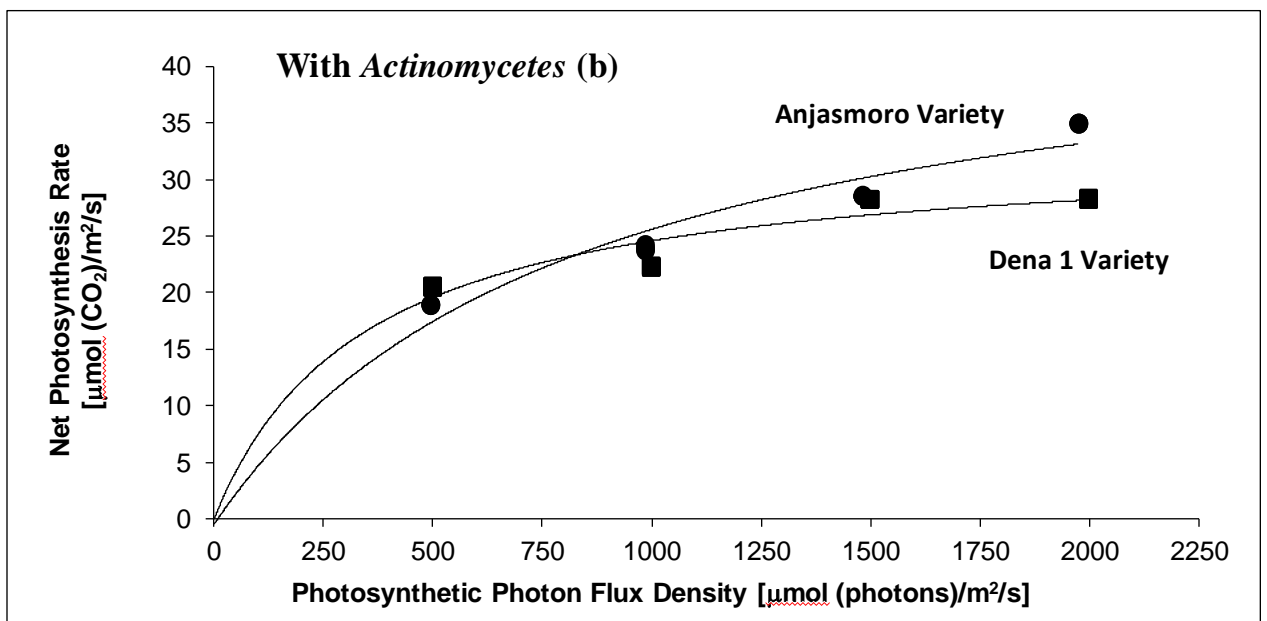
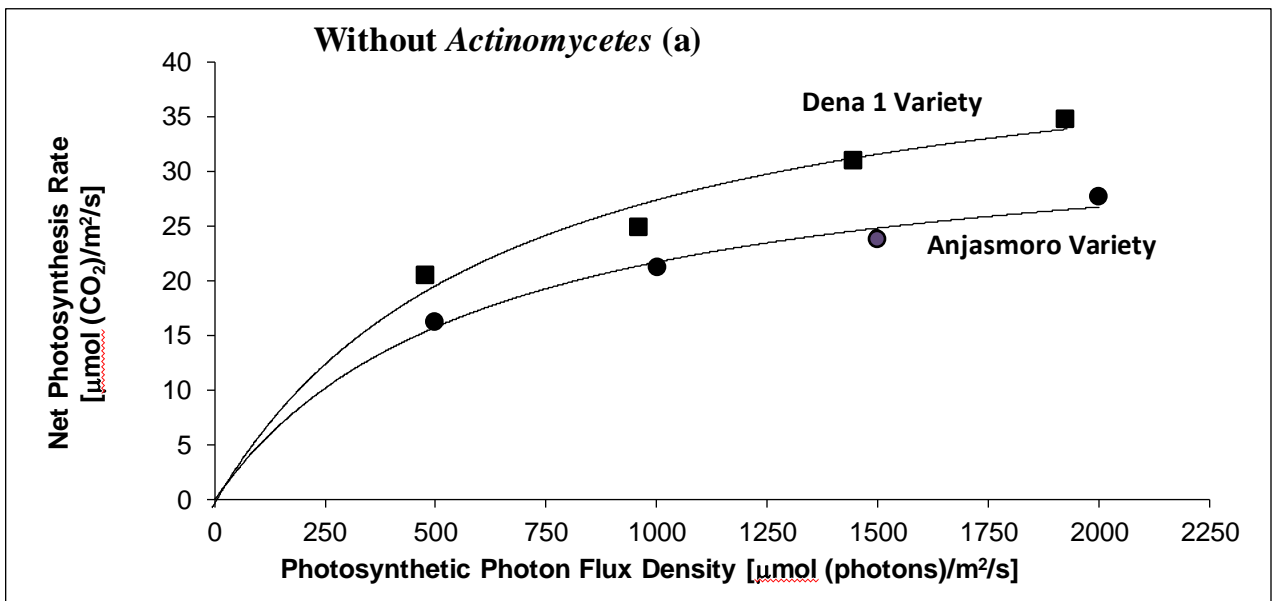


Fig. 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under *Actinomycetes* spp. treatment (b).

Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$, while Anjasmoro variety is only $34.81 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (Table 1). Reported maximum net photosynthesis (P_{nmax}) of other soybean varieties are $28.8 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (Yao et al., 2017), $29.9 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (Zhang, Hu, Luo, Chow, & Zhang, 2011), and $34.8 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (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 $3.19 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (Yao et al., 2017), and $6.72 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (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 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$ compared to Anjasmoro 0.058 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$. Both Yao et al. (2017) and Zhang, Hu, Luo, Chow, & Zhang (2011) reported a similar quantum yield of soybean at 0.053 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$. 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 ($\phi(I_{comp})$) and at light between compensation point to 200 ($\phi(I_{c-1200})$) is higher (0.07 and 0.05 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$) than quantum yield of Anjasmoro (0.06 and 0.04 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$) (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 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$, while Anjasmoro is 603 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$, while Anjasmoro is 5,429 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$ (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 *Actinomyces* 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 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$ (Figure 1b). In another word, the photosynthetic light-response curve of Dena-1 is higher than Anjasmoro at PAR below 706 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$, but it is the other way round at PAR above 706 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$. Initial light use efficiency of Dena-1 is higher (0.096 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$) than Anjasmoro (0.058 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 (33.03 $\mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$) then in Anjasmoro (48.77 $\mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$) (Table 1). This indicates that Anjasmoro responses better to *Actinomyces* spp. than Dena-1. The better response includes the conversion of additional nutrient from *Actinomyces* 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).

Actinomyces spp. play an important role in soil nutrient cycling (Bhatti, Haq, & Bhat, 2017), inorganic phosphates solubilizing (Ghorbani-Nasrabadi, Greiner, Alikhani, Hamedi, & Yakhchali, 2013; Pragma, 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. *Actinomyces* 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 *Actinomyces* 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 *Actinomyces* 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 *Actinomyces* 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 Treatments	Standard Parameters		Light saturation point at				Light-saturated net CO ₂ uptake	Quantum yield at	
	Maximum Photosynthesis	Quantum yield at I = 0	50 percentile	85 percentile	90 percentile	95 Percent-tile		Light compensation point	LCP to I = 200
	P _{gmax}	φ(I ₀)	I _{sat(50)}	I _{sat(85)}	I _{sat(90)}	I _{sat(95)}	PN (I _{max})	φ(I _{comp})	φ(I _c -I ₂₀₀)
	(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 CO₂ as can be indicated by conductance to H₂O and internal CO₂ concentration. Under normal condition or no Actinomycetes treatment, Dena 1 has higher conductance (2.28 mol H₂O/m²/s) than Anjasmoro (2.09 mol H₂O/m²/s) and it increases faster with the increase of PAR from 500 to 2,000 μmol (photon)/m²/s. Along with this increase, internal CO₂ 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 CO₂ concentration higher than Anjasmoro when the demand for CO₂ 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 CO₂ 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 CO₂ concentration due to light increase in Dena 1 is faster than Anjasmoro. Limitation in availability of internal CO₂ 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 (CO₂)/μmol (photons) and 45.64 μmol (CO₂)/m²/s, respectively. While, Anjasmoro is 0.068 μmol (CO₂)/μmol (photons) and 34.81 μmol (CO₂)/m²/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)/m²/s and consequently, maximum photosynthesis (P_{max}) of Anjasmoro is also higher than Dena-1, i.e. 48.77 and 33.03 μmol (CO₂)/m²/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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Kepada: "Agrivita ." <agrivita@ub.ac.id>

Yth ibu Silvi,

Meneruskan email saya tadi malam, pagi ini saya kirimkan perbaikan paper lanjutan. koreksi ke-2 ini, dengan nama file "Corrected 1 Rusnadi_PART 2 kwb anl eal ssw 27052021.docx", memiliki 2 perbaikan lanjutan, yaitu:

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Terimakasih atas kerjasamanya dan mohon maaf jika merepotkan.

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Photosynthetic Parameters of Two Indonesian Soybean Top Varieties

Running title: *Actinomyces* 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 *Actinomyces* 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 (PNI curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis ($P_{g\text{max}}$) 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 *Actinomyces* 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: *Actinomyces* 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 lodging 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° 28' East and 5° 39' South with altitude of 15 m above sea level.

Photosynthetic performances were measured in an experiment designed to study the effect of *Actinomyces* 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 *Actinomyces* spp. application that consist of no *Actinomyces* spp. (A0), and *Actinomyces* spp. with concentration of 1×10^6 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 cm². 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 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$. Environment conditions during experiments were as follows: air temperature 25-27°C; block and leaf temperature 25-27°C; air flow rate 500 $\mu\text{mol}/\text{s}$; CO₂ concentration in sample cell 380–400 $\mu\text{mol CO}_2/\text{mol}$; 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) ($\mu\text{mol CO}_2/\text{m}^2/\text{s}$), intercellular CO₂ concentration (C_i) ($\mu\text{mol CO}_2/\text{mol air}$), and conductance to H₂O ($\text{mol H}_2\text{O}/\text{m}^2/\text{s}$)

The photosynthetic light response curve (PNI 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 *Actinomyces* the curve of Dena-1 variety is higher than that of Anjasmoro (Fig. 1a). This indicates that Dena-1 responses better than Anjasmoro to light, as it has higher initial light use efficiency as well as higher maximum photosynthesis.

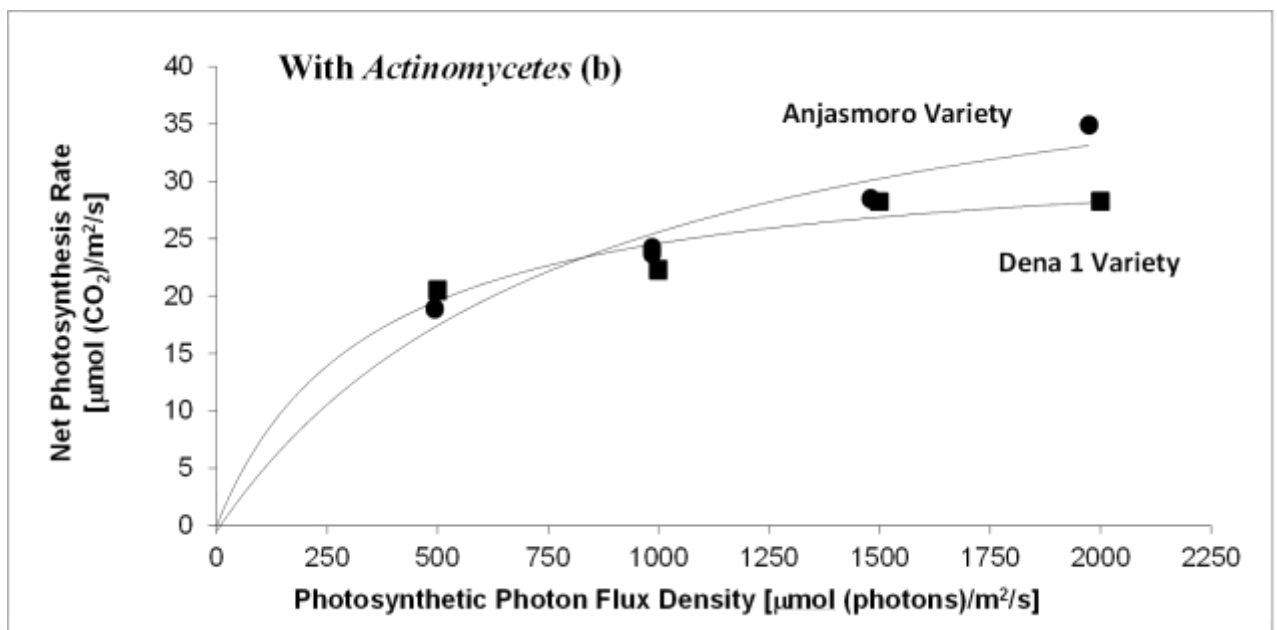
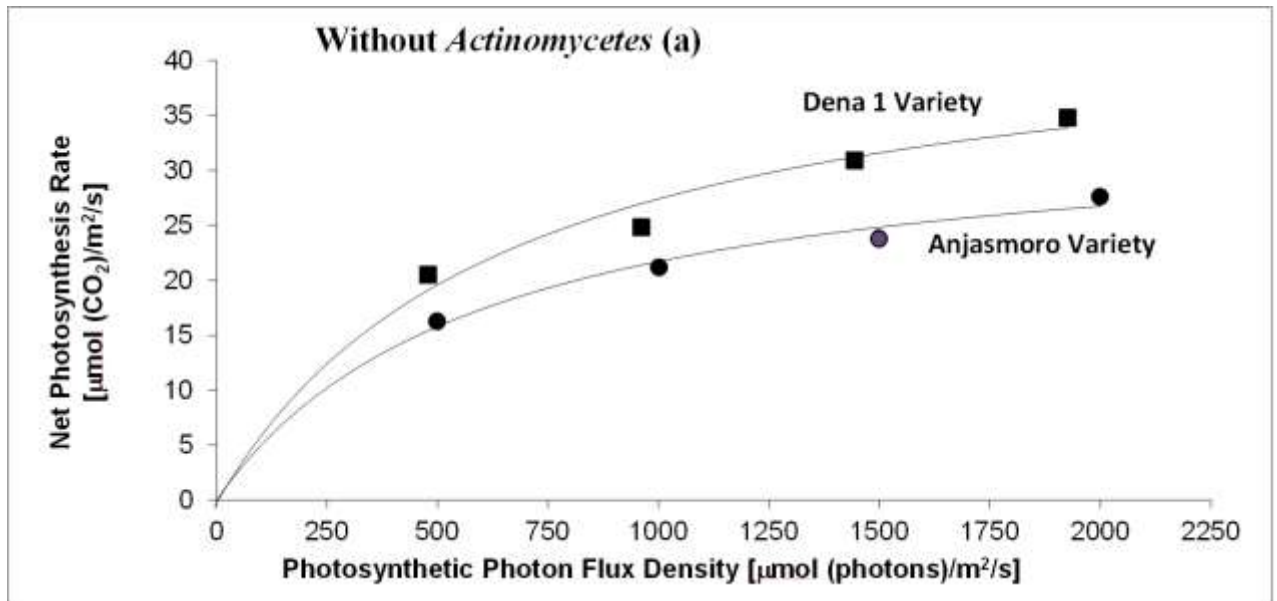


Fig. 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under *Actinomycetes* spp. treatment (b).

Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$, while Anjasmoro variety is only $34.81 \mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$ (Table 1). Reported maximum net photosynthesis (P_{nmax}) of other soybean varieties are $28.8 \mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$ (Yao et al., 2017), $29.9 \mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$ (Zhang, Hu, Luo, Chow, & Zhang, 2011), and $34.8 \mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$ (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 $3.19 \mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$ (Yao et al., 2017), and $6.72 \mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$ (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 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$ compared to Anjasmoro 0.058 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$. Both Yao et al. (2017) and Zhang, Hu, Luo, Chow, & Zhang (2011) reported a similar quantum yield of soybean at 0.053 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$. 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 ($\phi(I_{comp})$) and at light between compensation point to 200 ($\phi(I_{c-1200})$) is higher (0.07 and 0.05 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$) than quantum yield of Anjasmoro (0.06 and 0.04 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$) (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 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$, while Anjasmoro is 603 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$, while Anjasmoro is 5,429 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$ (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 *Actinomyces* 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 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$ (Figure 1b). In another word, the photosynthetic light-response curve of Dena-1 is higher than Anjasmoro at PAR below 706 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$, but it is the other way round at PAR above 706 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$. Initial light use efficiency of Dena-1 is higher (0.096 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$) than Anjasmoro (0.058 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 (33.03 $\mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$) then in Anjasmoro (48.77 $\mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$) (Table 1). This indicates that Anjasmoro responses better to *Actinomyces* spp. than Dena-1. The better response includes the conversion of additional nutrient from *Actinomyces* 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).

Actinomyces spp. play an important role in soil nutrient cycling (Bhatti, Haq, & Bhat, 2017), inorganic phosphates solubilizing (Ghorbani-Nasrabadi, Greiner, Alikhani, Hamedi, & Yakhchali, 2013; Pragma, 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. *Actinomyces* 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 *Actinomyces* 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 *Actinomyces* 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 *Actinomyces* 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 Treatments	Standard Parameters		Light saturation point at				Light-saturated net CO ₂ uptake	Quantum yield at	
	Maximum Photosynthesis	Quantum yield at I = 0	50 percentile	85 percentile	90 percentile	95 Percent-tile		Light compensation point	LCP to I = 200
	P _{gmax}	φ(I ₀)	I _{sat(50)}	I _{sat(85)}	I _{sat(90)}	I _{sat(95)}	PN (I _{max})	φ(I _{comp})	φ(I _c -I ₂₀₀)
	(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 CO₂ as can be indicated by conductance to H₂O and internal CO₂ concentration. Under normal condition or no Actinomycetes treatment, Dena 1 has higher conductance (2.28 mol H₂O/m²/s) than Anjasmoro (2.09 mol H₂O/m²/s) and it increases faster with the increase of PAR from 500 to 2,000 μmol (photon)/m²/s. Along with this increase, internal CO₂ 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 CO₂ concentration higher than Anjasmoro when the demand for CO₂ 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 CO₂ 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 CO₂ concentration due to light increase in Dena 1 is faster than Anjasmoro. Limitation in availability of internal CO₂ 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 (CO₂)/μmol (photons) and 45.64 μmol (CO₂)/m²/s, respectively. While, Anjasmoro is 0.068 μmol (CO₂)/μmol (photons) and 34.81 μmol (CO₂)/m²/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)/m²/s and consequently, maximum photosynthesis (P_{max}) of Anjasmoro is also higher than Dena-1, i.e. 48.77 and 33.03 μmol (CO₂)/m²/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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Mohon maaf, saya baru temukan, 3 dari 4 referensi baru itu, jurnalnya tidak saya format italic (saya tidak miringkan).
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Photosynthetic Parameters of Two Indonesian Soybean Top Varieties

Running title: *Actinomyces* 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 *Actinomyces* 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 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$. The photosynthetic light response curve (PNI curve) was developed using Solver function of Microsoft Excel. Maximum gross photosynthesis ($P_{g\text{max}}$) of Dena-1 is 45.64 $\mu\text{mol (CO}_2)/\text{m}^2/\text{s}$, while Anjasmoro variety is only 34.81 $\mu\text{mol (CO}_2)/\text{m}^2/\text{s}$. Quantum yield at low light (initial light use efficiency) of Dena-1 is also higher with the value of 0.068 $\mu\text{mol (CO}_2)/\mu\text{mol (photons)}$ compared to Anjasmoro that have 0.058 $\mu\text{mol (CO}_2)/\mu\text{mol (photons)}$. Hence light response curve of Dena-1 variety is consistently higher than Anjasmoro. Under *Actinomyces* spp. treatment the light response curve of Dena-1 is higher than Anjasmoro at PAR lower than 706 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$ and higher at PAR above it.

Keywords: *Actinomyces* 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 lodging 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° 28' East and 5° 39' South with altitude of 15 m above sea level.

Photosynthetic performances were measured in an experiment designed to study the effect of *Actinomyces* 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 *Actinomyces* spp. application that consist of no *Actinomyces* spp. (A0), and *Actinomyces* spp. with concentration of 1×10^6 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 cm². 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 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$. Environment conditions during experiments were as follows: air temperature 25-27°C; block and leaf temperature 25-27°C; air flow rate 500 $\mu\text{mol}/\text{s}$; CO₂ concentration in sample cell 380–400 $\mu\text{mol CO}_2/\text{mol}$; 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) ($\mu\text{mol CO}_2/\text{m}^2/\text{s}$), intercellular CO₂ concentration (C_i) ($\mu\text{mol CO}_2/\text{mol air}$), and conductance to H₂O ($\text{mol H}_2\text{O}/\text{m}^2/\text{s}$)

The photosynthetic light response curve (PNI 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 *Actinomyces* the curve of Dena-1 variety is higher than that of Anjasmoro (Fig. 1a). This indicates that Dena-1 responses better than Anjasmoro to light, as it has higher initial light use efficiency as well as higher maximum photosynthesis.

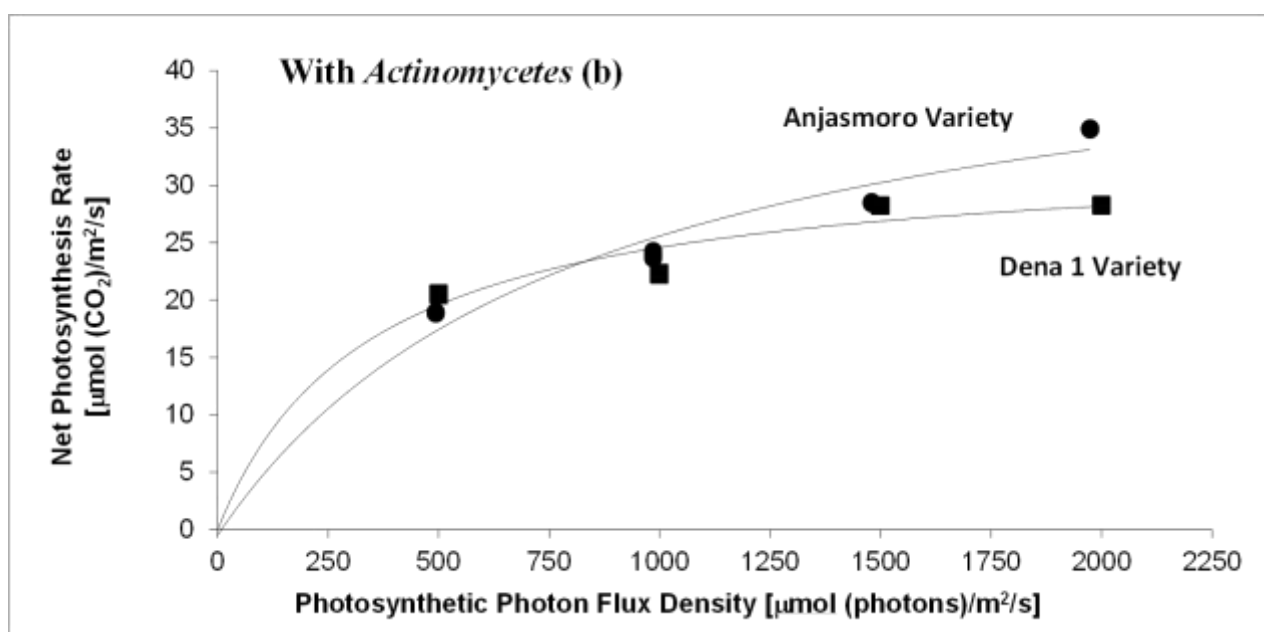
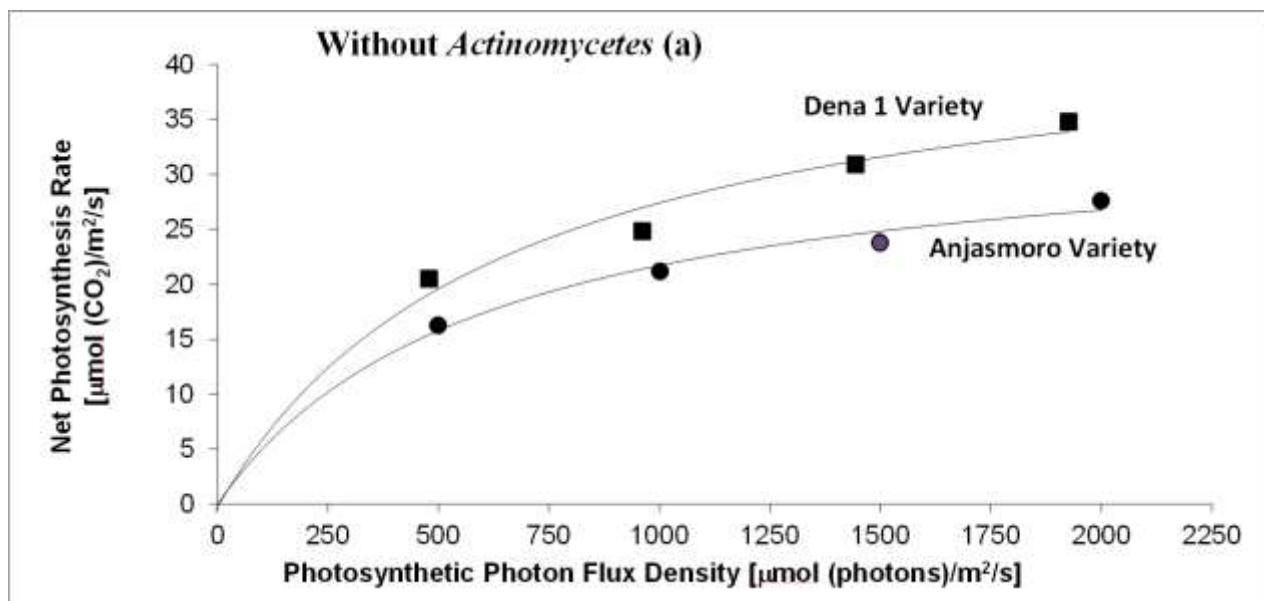


Fig. 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under *Actinomycetes* spp. treatment (b).

Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$, while Anjasmoro variety is only $34.81 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (Table 1). Reported maximum net photosynthesis (P_{nmax}) of other soybean varieties are $28.8 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (Yao et al., 2017), $29.9 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (Zhang, Hu, Luo, Chow, & Zhang, 2011), and $34.8 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (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 $3.19 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (Yao et al., 2017), and $6.72 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (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 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$ compared to Anjasmoro 0.058 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$. Both Yao et al. (2017) and Zhang, Hu, Luo, Chow, & Zhang (2011) reported a similar quantum yield of soybean at 0.053 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$. 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 ($\phi(I_{comp})$) and at light between compensation point to 200 ($\phi(I_{c-1200})$) is higher (0.07 and 0.05 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$) than quantum yield of Anjasmoro (0.06 and 0.04 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$) (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 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$, while Anjasmoro is 603 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$. At 95 percentile, the light saturation point of Dena-1 variety is 6,004 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$, while Anjasmoro is 5,429 $\mu\text{mol (photons)}/\text{m}^2/\text{s}$ (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 *Actinomyces* 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 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$ (Figure 1b). In another word, the photosynthetic light-response curve of Dena-1 is higher than Anjasmoro at PAR below 706 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$, but it is the other way round at PAR above 706 $\mu\text{mol (photon)}/\text{m}^2/\text{s}$. Initial light use efficiency of Dena-1 is higher (0.096 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$) than Anjasmoro (0.058 $\mu\text{mol (CO}_2\text{)}/\mu\text{mol (photons)}$). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 (33.03 $\mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$) then in Anjasmoro (48.77 $\mu\text{mol (CO}_2\text{)}/\text{m}^2/\text{s}$) (Table 1). This indicates that Anjasmoro responses better to *Actinomyces* spp. than Dena-1. The better response includes the conversion of additional nutrient from *Actinomyces* 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).

Actinomyces spp. play an important role in soil nutrient cycling (Bhatti, Haq, & Bhat, 2017), inorganic phosphates solubilizing (Ghorbani-Nasrabadi, Greiner, Alikhani, Hamedi, & Yakhchali, 2013; Pragma, 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. *Actinomyces* 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 *Actinomyces* 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 *Actinomyces* 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, 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 *Actinomyces* 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, Anjasmoro – no Actinomycetes, Dena-1 – Actinomycetes, Anjasmoro - Actinomycetes.

Varieties and Actinomycetes Treatments	Standard Parameters		Light saturation point at				Light-saturated net CO ₂ uptake	Quantum yield at	
	Maximum Photosynthesis	Quantum yield at I = 0	50 percentile	85 percentile	90 percentile	95 Percent-tile		Light compensation point	LCP to I = 200
	P _{gmax}	φ(I ₀)	I _{sat(50)}	I _{sat(85)}	I _{sat(90)}	I _{sat(95)}	PN (I _{max})	φ(I _{comp})	φ(I _c -I ₂₀₀)
	(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 CO₂ as can be indicated by conductance to H₂O and internal CO₂ concentration. Under normal condition or no Actinomycetes treatment, Dena 1 has higher conductance (2.28 mol H₂O/m²/s) than Anjasmoro (2.09 mol H₂O/m²/s) and it increases faster with the increase of PAR from 500 to 2,000 μmol (photon)/m²/s. Along with this increase, internal CO₂ 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 CO₂ concentration higher than Anjasmoro when the demand for CO₂ 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 CO₂ 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 CO₂ concentration due to light increase in Dena 1 is faster than Anjasmoro. Limitation in availability of internal CO₂ 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 (CO₂)/μmol (photons) and 45.64 μmol (CO₂)/m²/s, respectively. While, Anjasmoro is 0.068 μmol (CO₂)/μmol (photons) and 34.81 μmol (CO₂)/m²/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)/m²/s and consequently, maximum photosynthesis (P_{max}) of Anjasmoro is also higher than Dena-1, i.e. 48.77 and 33.03 μmol (CO₂)/m²/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 *Actinomyces* 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 ($P_{g\text{max}}$) 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 *Actinomyces* 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° 28' East and 5° 39' South with altitude of 15 m above sea level.

Photosynthetic performances were measured in an experiment designed to study the effect of *Actinomyces* 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 *Actinomyces* spp. application that consist of no *Actinomyces* spp. (A0), and *Actinomyces* spp. with concentration of 1×10^6 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 cm². 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)/m²/s. Environment conditions during experiments were as follows: air temperature 25-27°C; block and leaf temperature 25-27°C; air flow rate 500 $\mu\text{mol/s}$; CO₂ concentration in sample cell 380–400 $\mu\text{mol CO}_2$ / 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) ($\mu\text{mol CO}_2$ /m²/s), intercellular CO₂ concentration (C_i) ($\mu\text{mol CO}_2$ /mol air), and conductance to H₂O (mol H₂O/m²/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 *Actinomyces* the curve of Dena-1 variety is higher than that of Anjasmoro (Fig. 1a). This indicates that Dena-1 responses better than Anjasmoro to light, as it has higher initial light use efficiency as well as higher maximum photosynthesis.

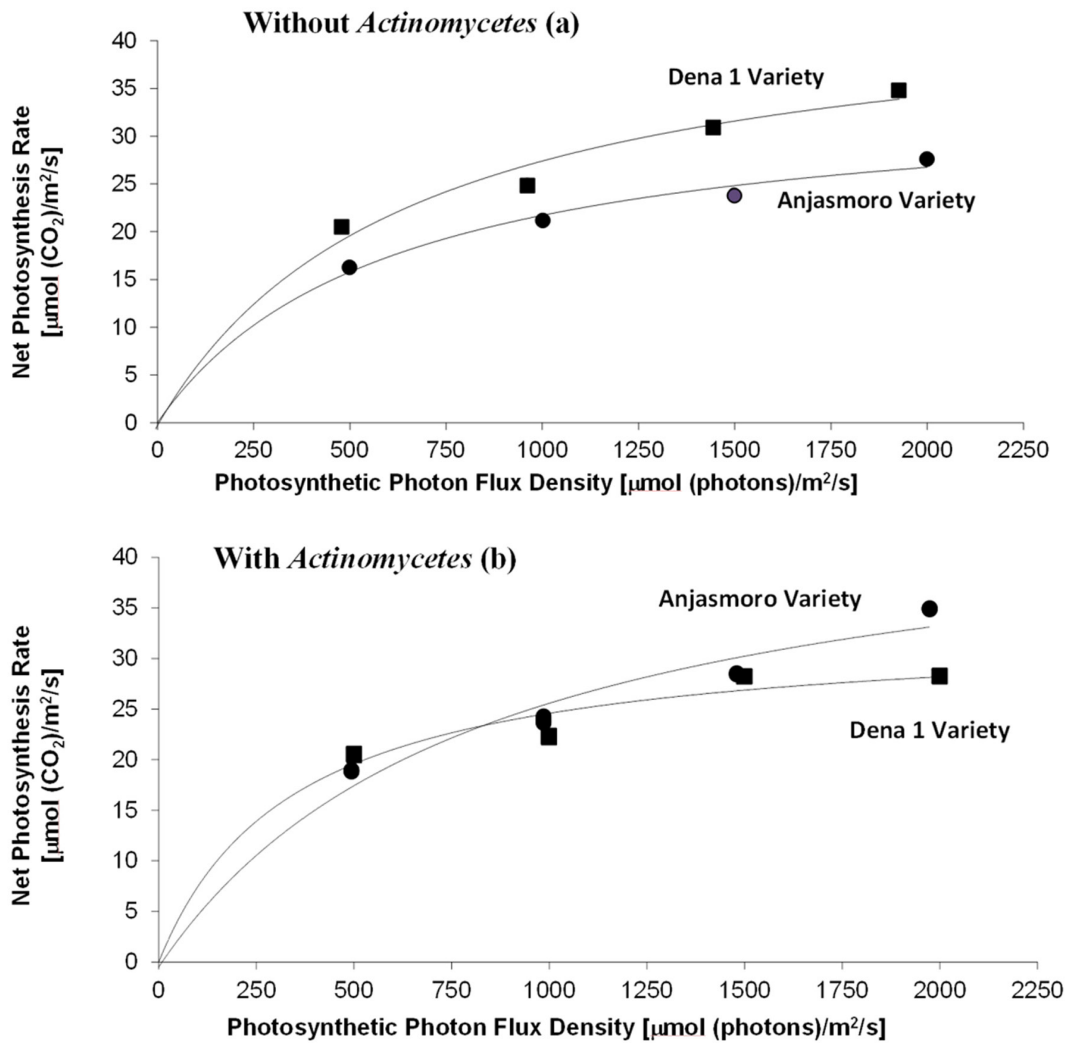


Fig. 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a), and under *Actinomycetes* spp. treatment (b)

Maximum gross photosynthesis (P_{gmax}) of Dena-1 is $45.64 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$, while Anjasmoro variety is only $34.81 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (Table 1). Reported maximum net photosynthesis (P_{nmax}) of other soybean varieties are $28.8 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (Yao et al., 2017), $29.9 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (Zhang, Hu, Luo, Chow, & Zhang, 2011), and $34.8 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (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 $3.19 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (Yao et al., 2017), and $6.72 \mu\text{mol (CO}_2)/\text{m}^2/\text{s}$ (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 $0.068 \mu\text{mol (CO}_2)/\mu\text{mol (photons)}$ compared to Anjasmoro $0.058 \mu\text{mol (CO}_2)/\mu\text{mol (photons)}$. Both Yao et al. (2017) and Zhang, Hu, Luo, Chow, & Zhang (2011) reported a similar quantum yield of soybean at $0.053 \mu\text{mol (CO}_2)/\mu\text{mol (photons)}$. 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 ($\phi(lcomp)$) and at light between compensation point to 200 ($\phi(lc-200)$) is higher (0.07 and $0.05 \mu\text{mol (CO}_2)/\mu\text{mol (photons)}$) than quantum

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yield of Anjasmoro (0.06 and 0.04 $\mu\text{mol}(\text{CO}_2)/\mu\text{mol}$ (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 *Actinomyces* 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 $\mu\text{mol}(\text{CO}_2)/\mu\text{mol}$ (photons)) than Anjasmoro (0.058 $\mu\text{mol}(\text{CO}_2)/\mu\text{mol}$ (photons)). In contrast, the maximum photosynthesis (P_{gmax}) is lower in Dena-1 (33.03 $\mu\text{mol}(\text{CO}_2)/\text{m}^2/\text{s}$) than in Anjasmoro (48.77 $\mu\text{mol}(\text{CO}_2)/\text{m}^2/\text{s}$) (Table 1). This indicates that Anjasmoro responds better to *Actinomyces* spp. than Dena-1. The better response includes the conversion of additional nutrient from *Actinomyces* 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).

Actinomyces spp. play an important role in soil nutrient cycling (Bhatti, Haq, & Bhat, 2017), inorganic phosphates solubilizing (Ghorbani-Nasrabadi, Greiner, Alikhani, Hamed, & 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, & Hamed, 2012; Schneider, Cade-Menun, Lynch, & Voroney, 2016), and so improvement of nutrients availability (AbdElgawad et al., 2020; Hozzein et al., 2019) particularly phosphorus. *Actinomyces* 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 *Actinomyces* 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 *Actinomyces* 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 respond better than Dena-1 to *Actinomyces* 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 Treatments	Standard Parameters					Light saturation point at				Light- saturated net CO ₂ uptake		Quantum yield at	
	Maximum Photosynthesis	Quantum yield at I = 0	50 percent-tile	85 percent-tile	90 percent-tile	95 Percent-tile	PN (I _{max})	Light compensation point	LCP to I = 200	PN (I _{max})	φ(I _{c-1200})	φ(I _{comp})	φ(I _{c-1200})
	P _{gmax}	φ(I ₀)	I _{sat(50)}	I _{sat(85)}	I _{sat(90)}	I _{sat(95)}	(μmol (CO ₂)/m ² /s)	(μmol (CO ₂)/μmol (photons))	(μmol (CO ₂)/m ² /s)				
Anjasmoro – No Actinomycetes	34.81	0.058	603.26	3,418.47	5,429.33	11,461.92	26.59	0.06	0.04	26.59	0.06	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	34.01	0.07	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	34.04	0.06	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	28.09	0.10	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 CO₂ as can be indicated by conductance to H₂O and internal CO₂ concentration. Under normal condition or no *Actinomycetes* treatment, Dena 1 has higher conductance (2.28 mol H₂O/m²/s) than Anjasmoro (2.09 mol H₂O/m²/s) and it increases faster with the increase of PAR from 500 to 2,000 μmol (photon)/m²/s. Along with this increase, internal CO₂ 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 CO₂ concentration higher than Anjasmoro when the demand for CO₂ 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 CO₂ 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 CO₂ concentration due to light increase in Dena 1 is faster than Anjasmoro. Limitation in availability of internal CO₂ 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 (CO₂)/μmol (photons) and 45.64 μmol (CO₂)/m²/s, respectively. While, Anjasmoro is 0.068 μmol (CO₂)/μmol (photons) and 34.81 μmol (CO₂)/m²/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)/m²/s and consequently,

maximum photosynthesis (P_{max}) of Anjasmoro is also higher than Dena-1, i.e. 48.77 and 33.03 μmol (CO₂)/m²/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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Yth ibu Silvi,


Saya sudah baca artikelnya. Isi dan formatnya sudah OK; sesuai, tetapi tabel 2 nya tidak ada. Di sini saya sertakan tabel 2.

Terimakasih atas kerjasamanya

Salam,

Rusnadi Padjung

[Kutipan teks disembunyikan]

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3 Table 2. Conductance to H₂O and Intercellular CO₂ concentration of Dena and Anjasmoro varieties with and
 4 without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjamoro – no Actinomycetes, Dena-1 –
 5 Actinomycetes, Anjasmoro – Actinomycetes at variable PAR

Varieties - Actinomycetes Treatments	Conductance to H ₂ O mol H ₂ O 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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