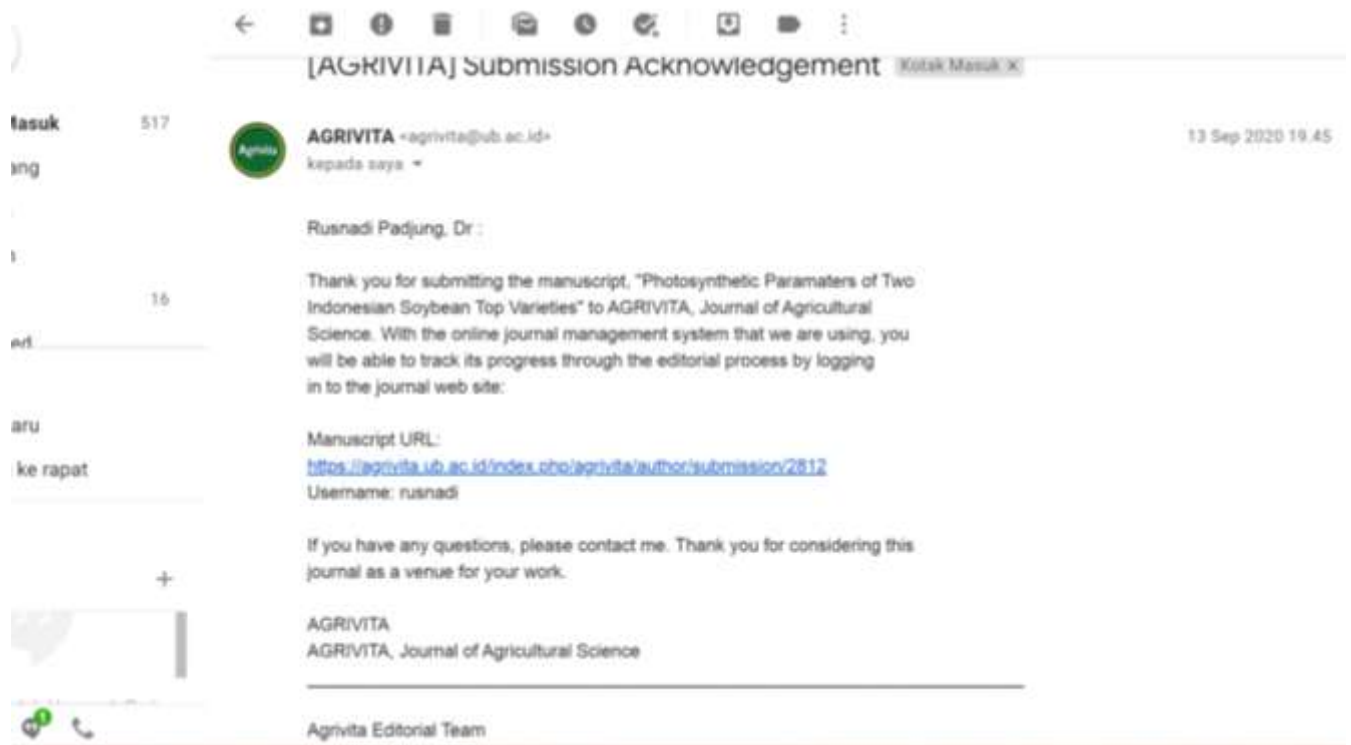
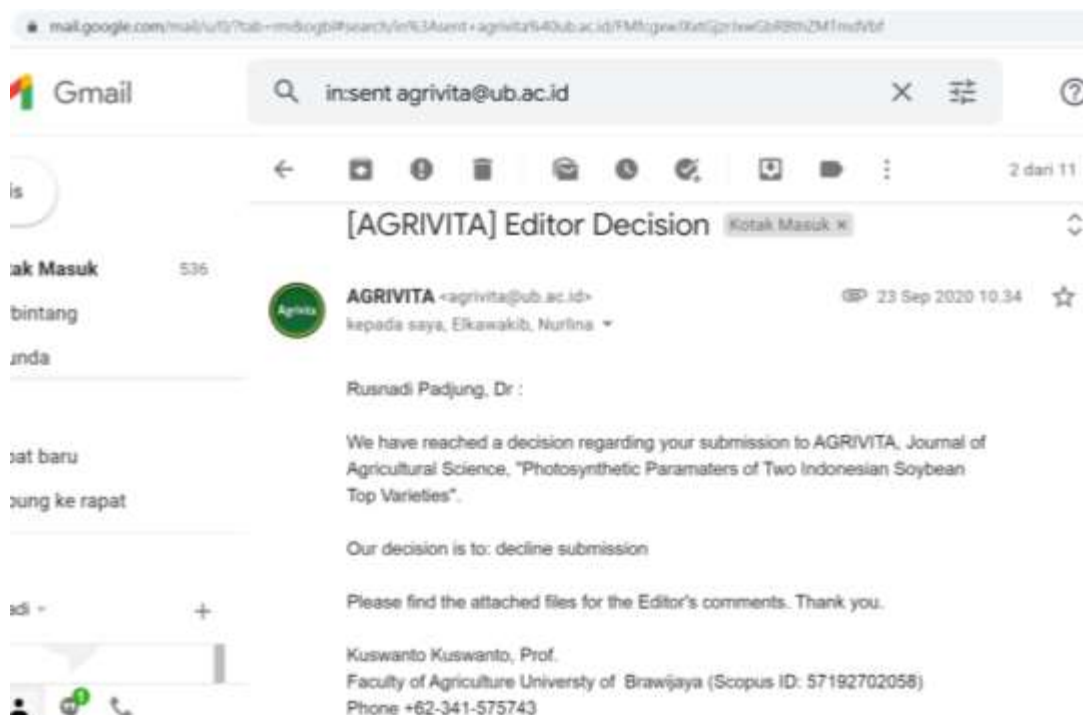


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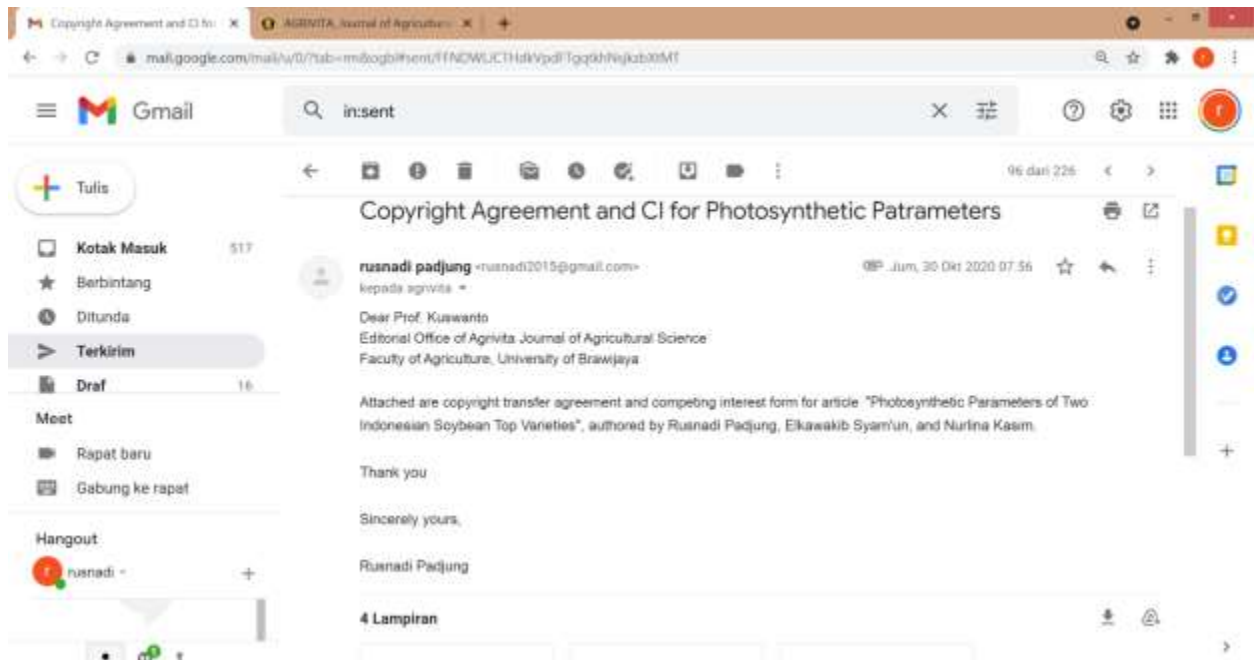
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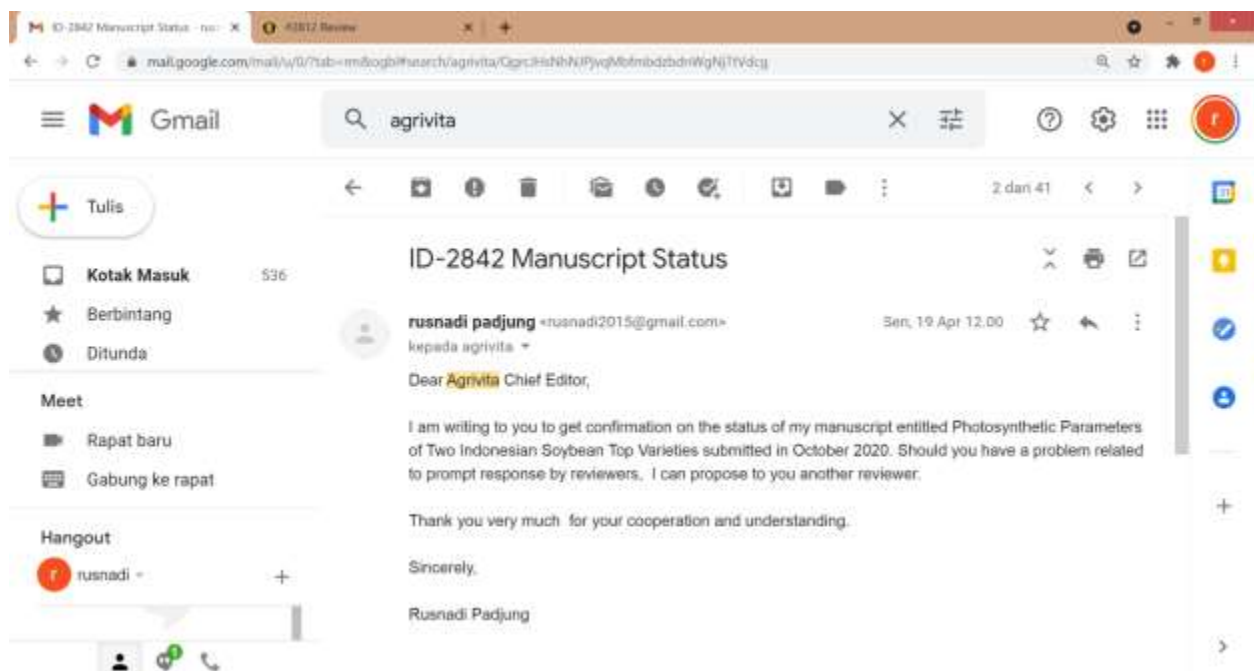
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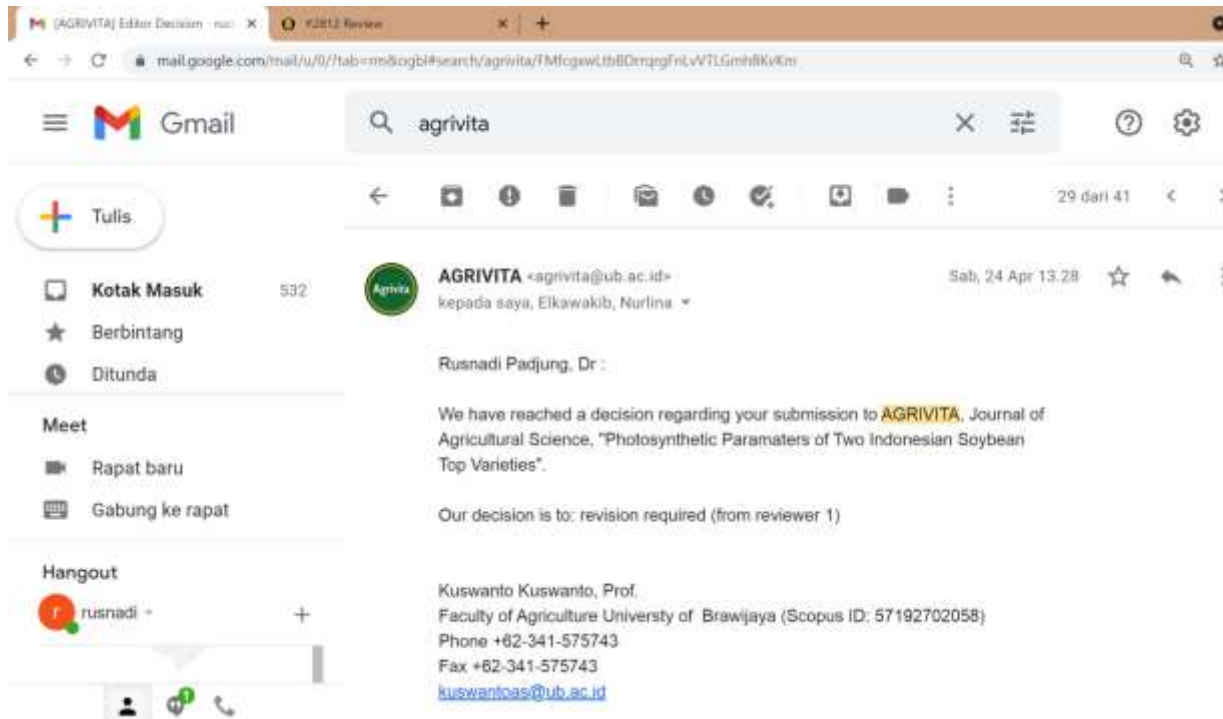
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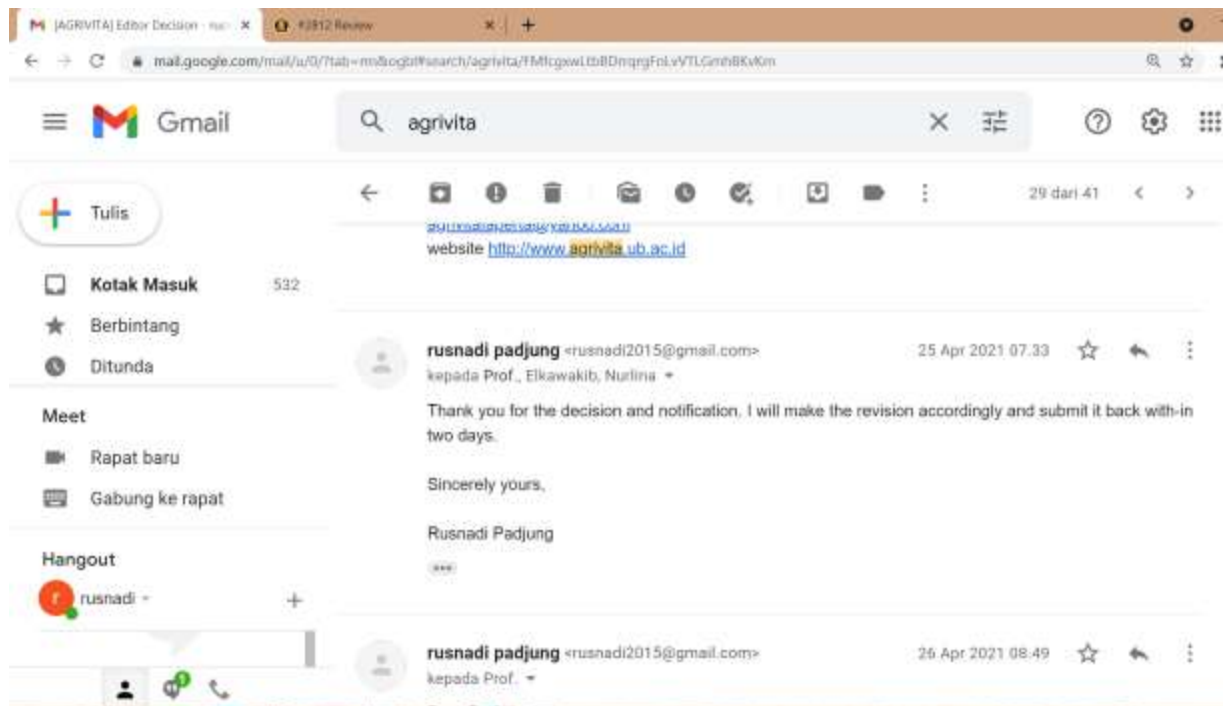
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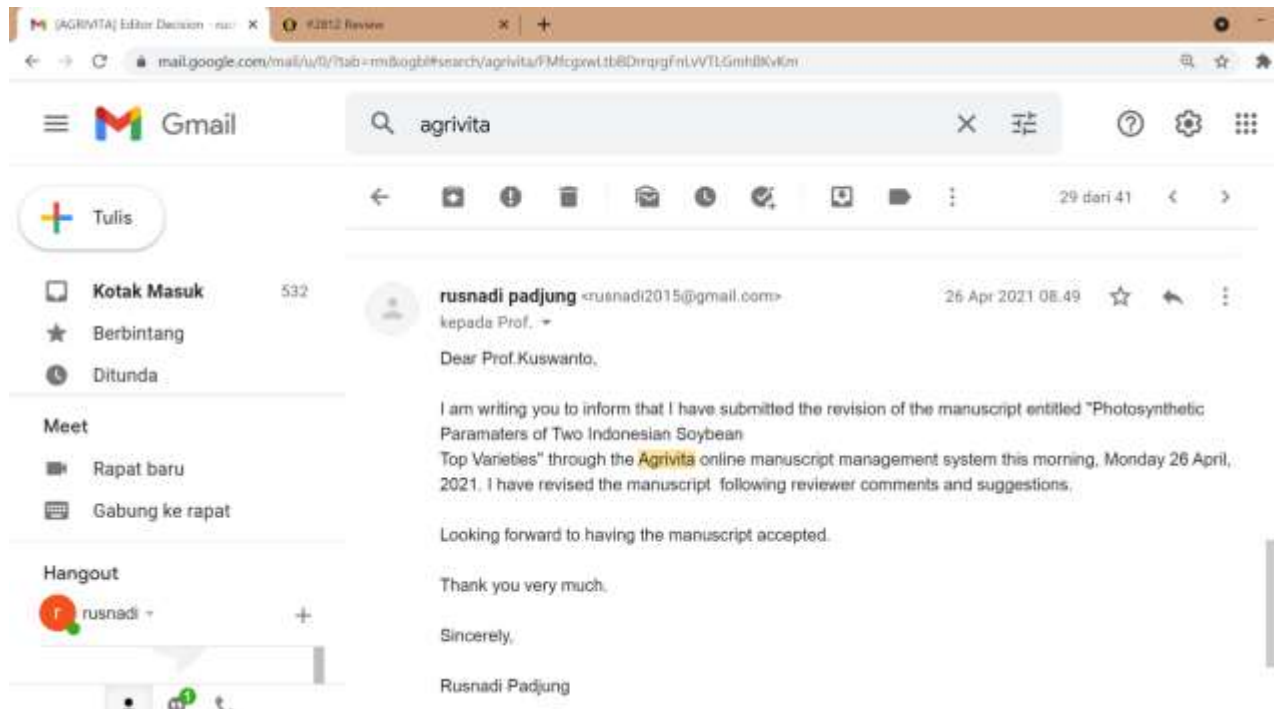
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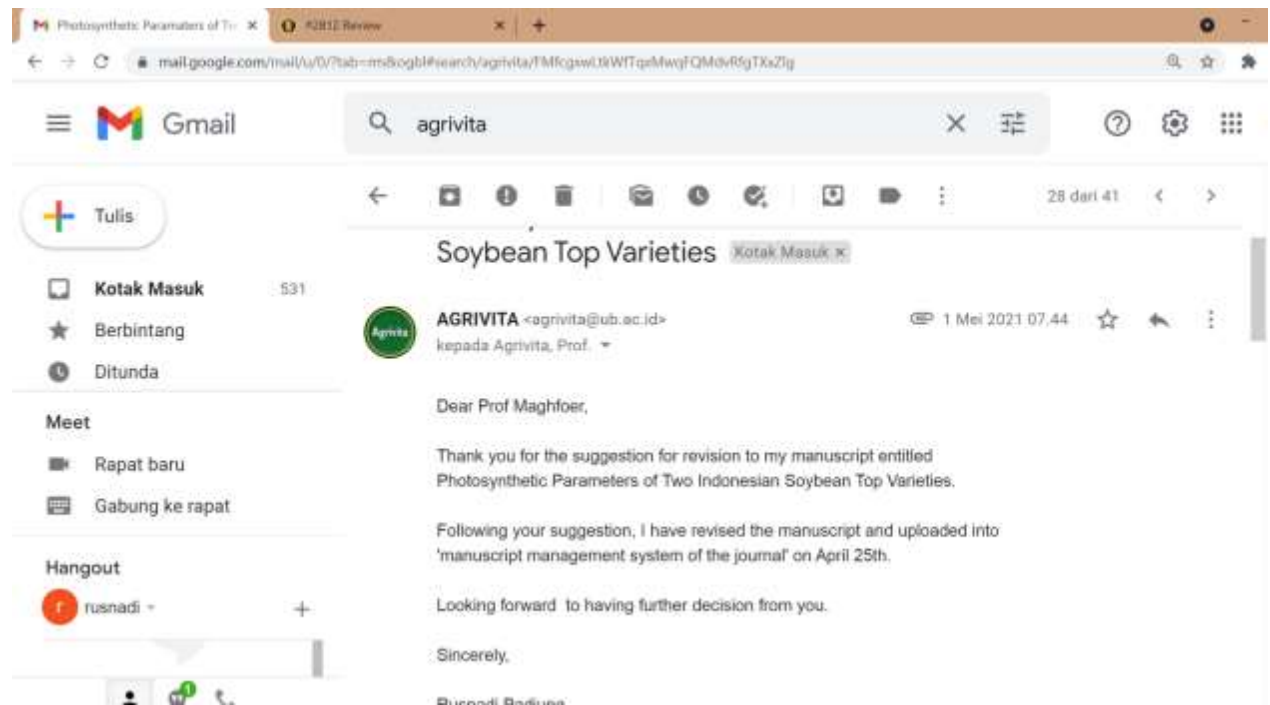
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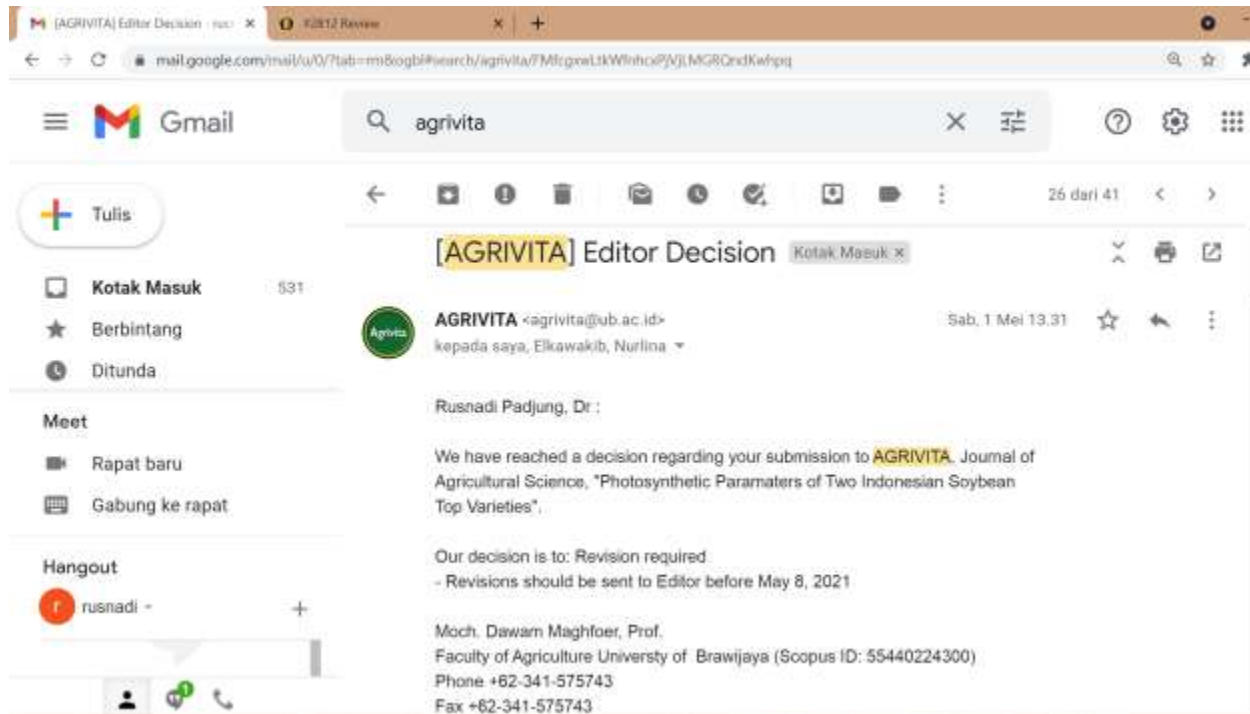
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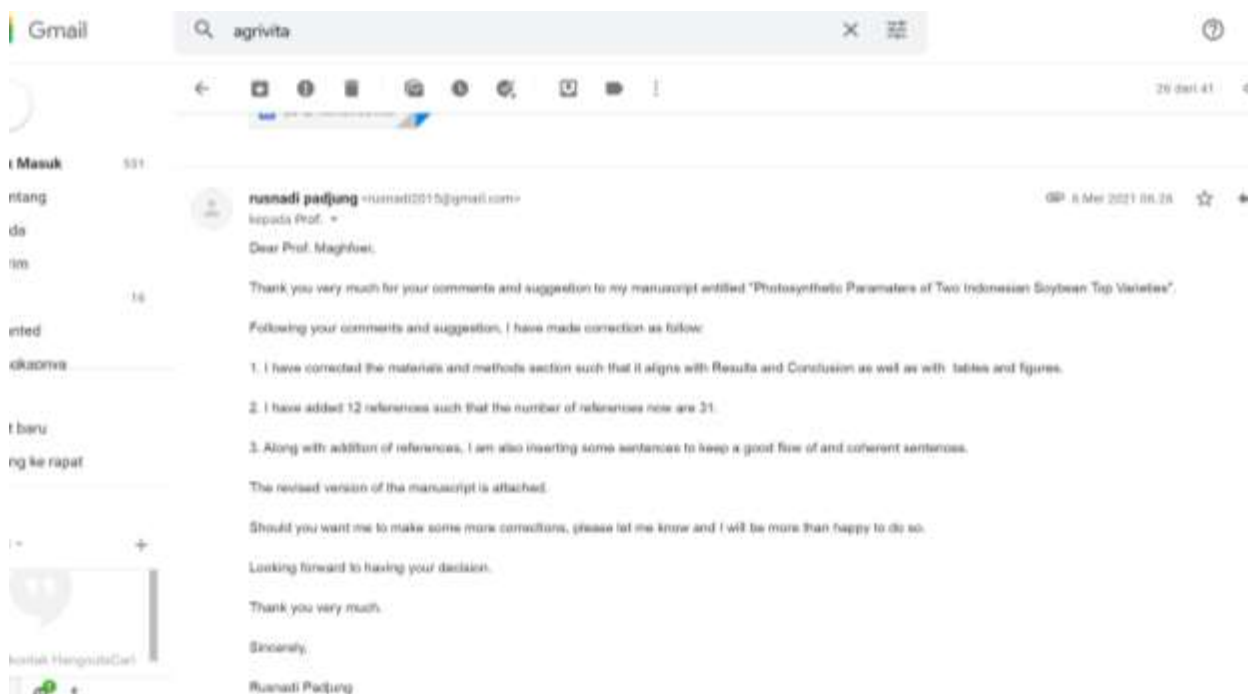
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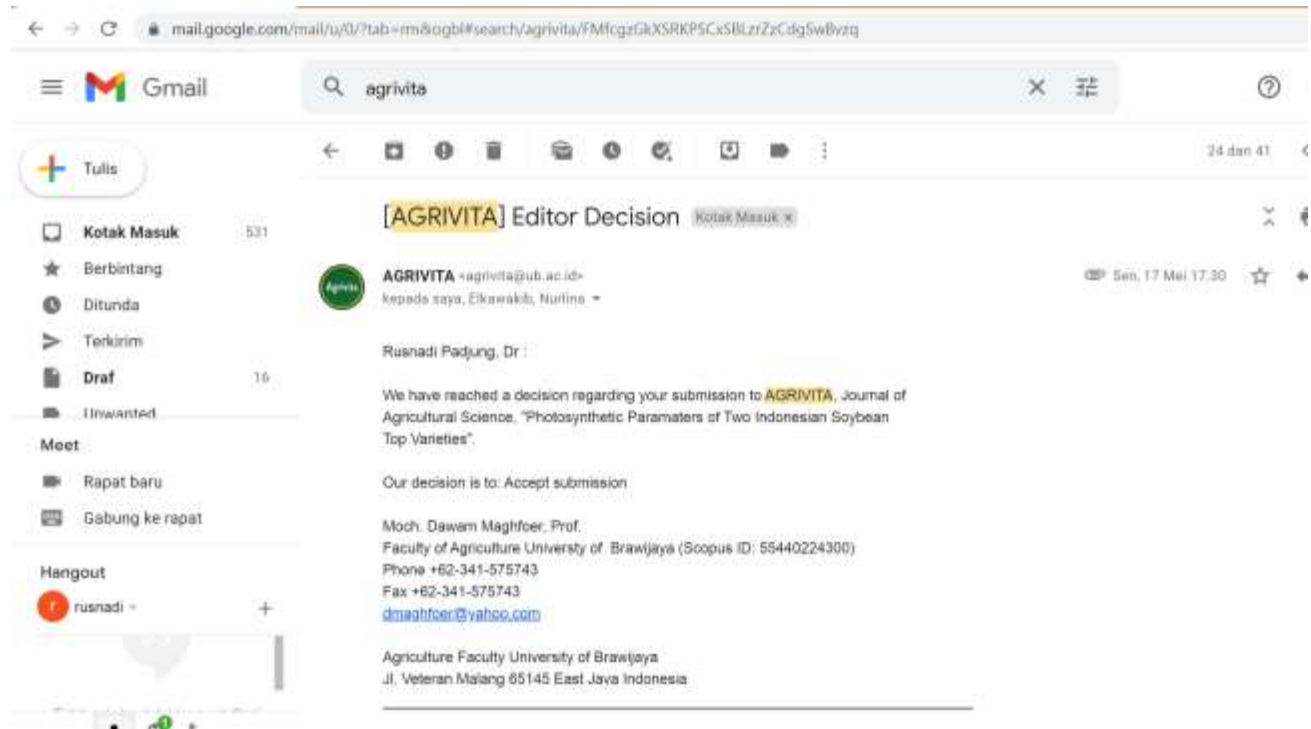
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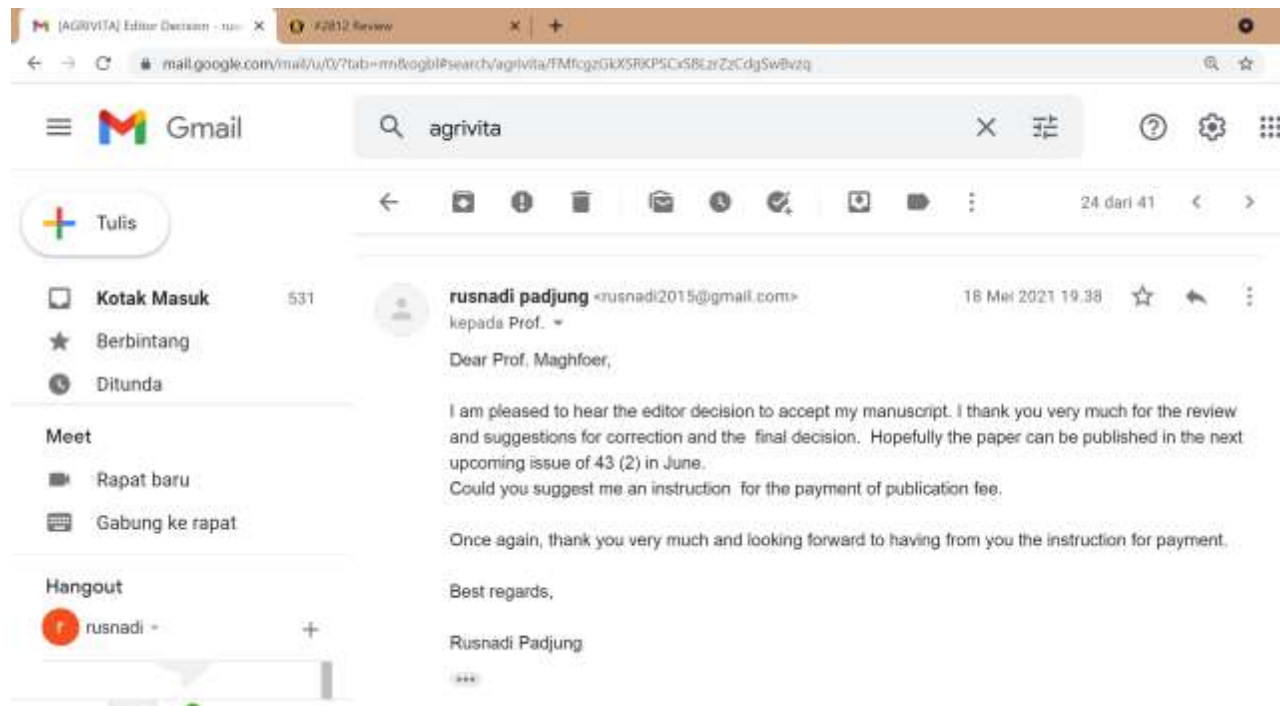
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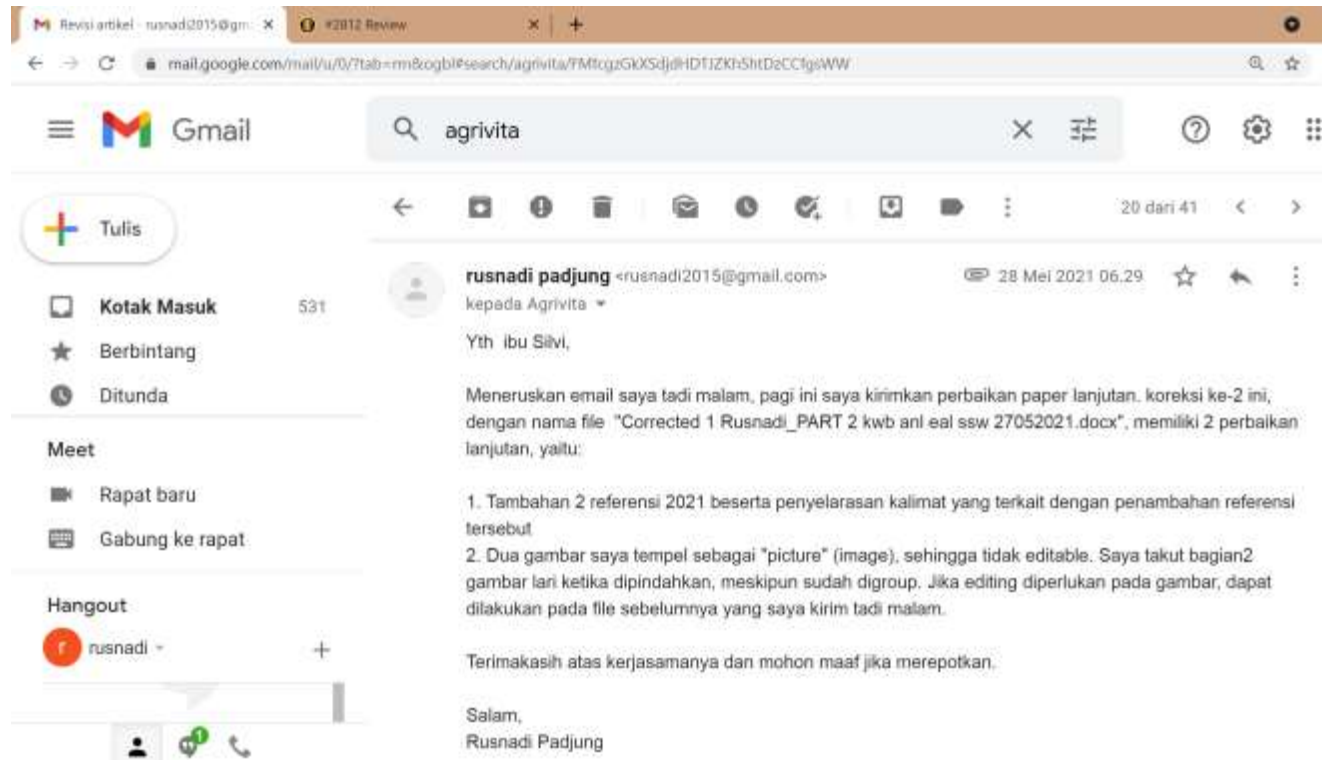
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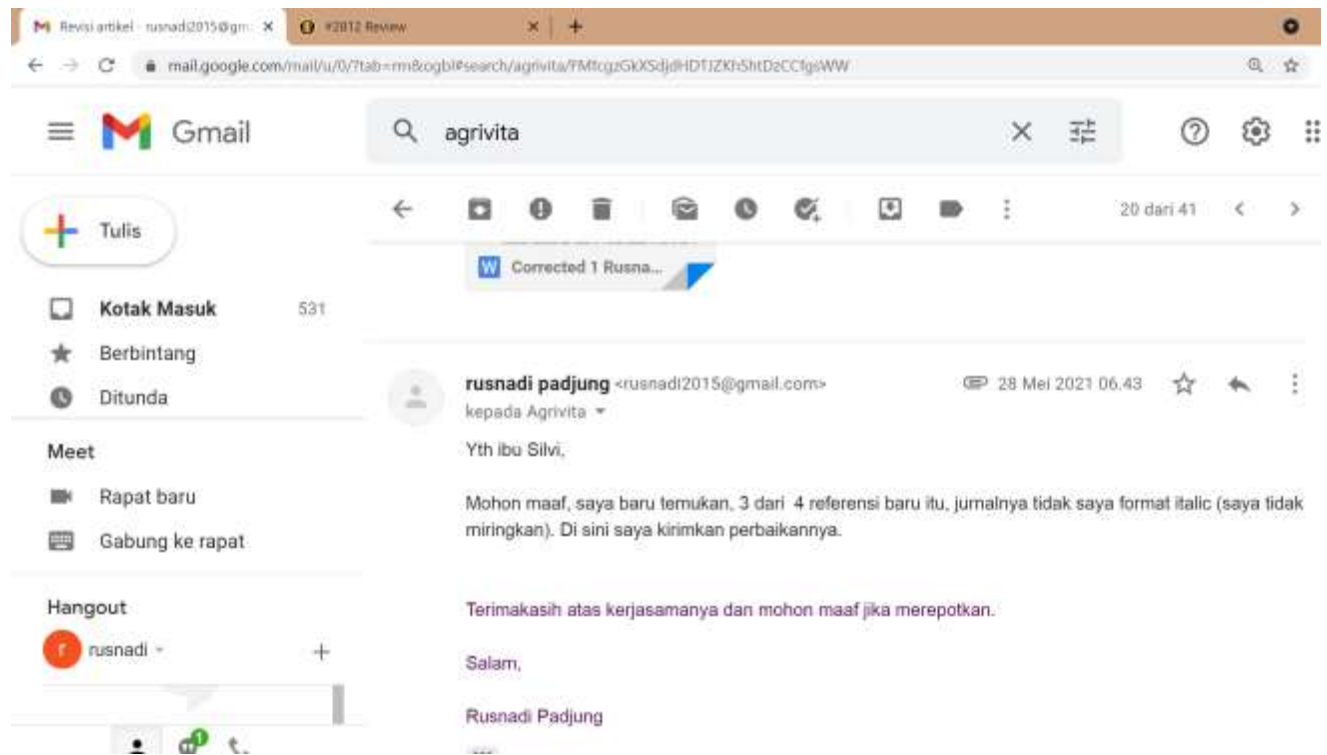
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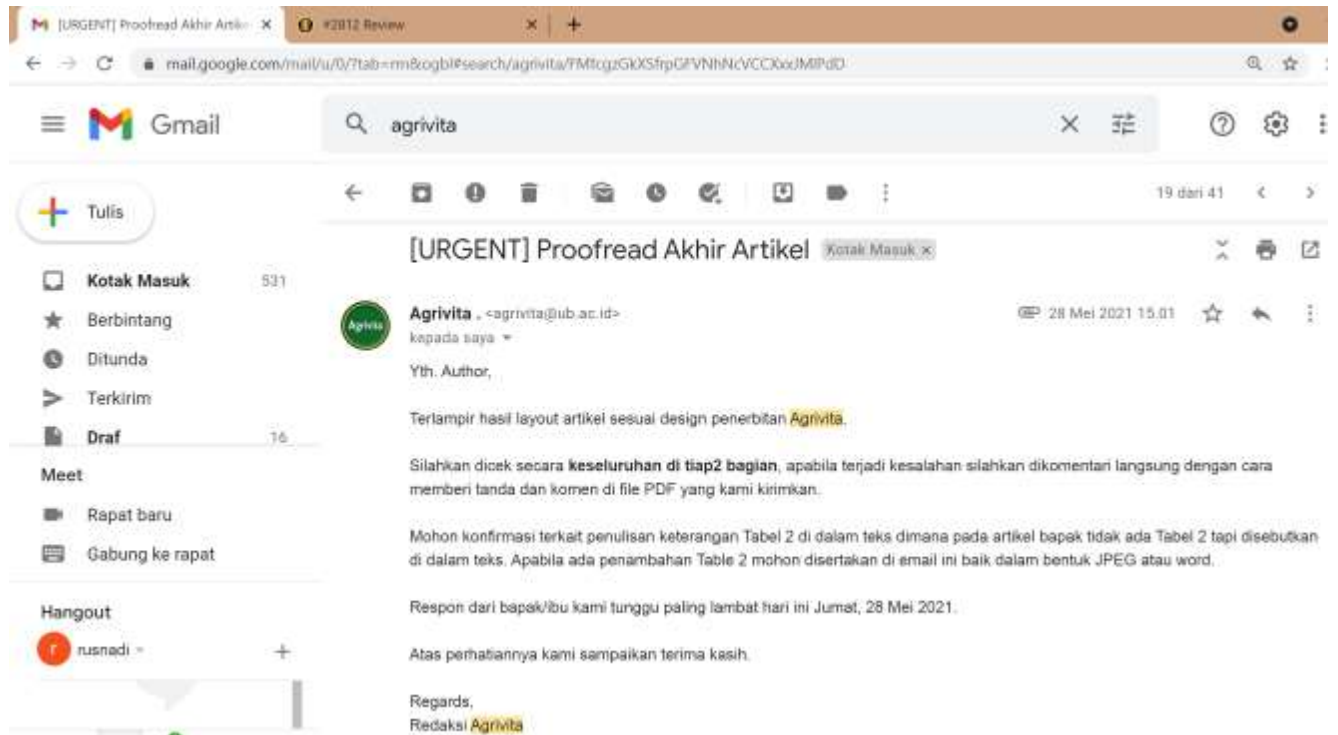
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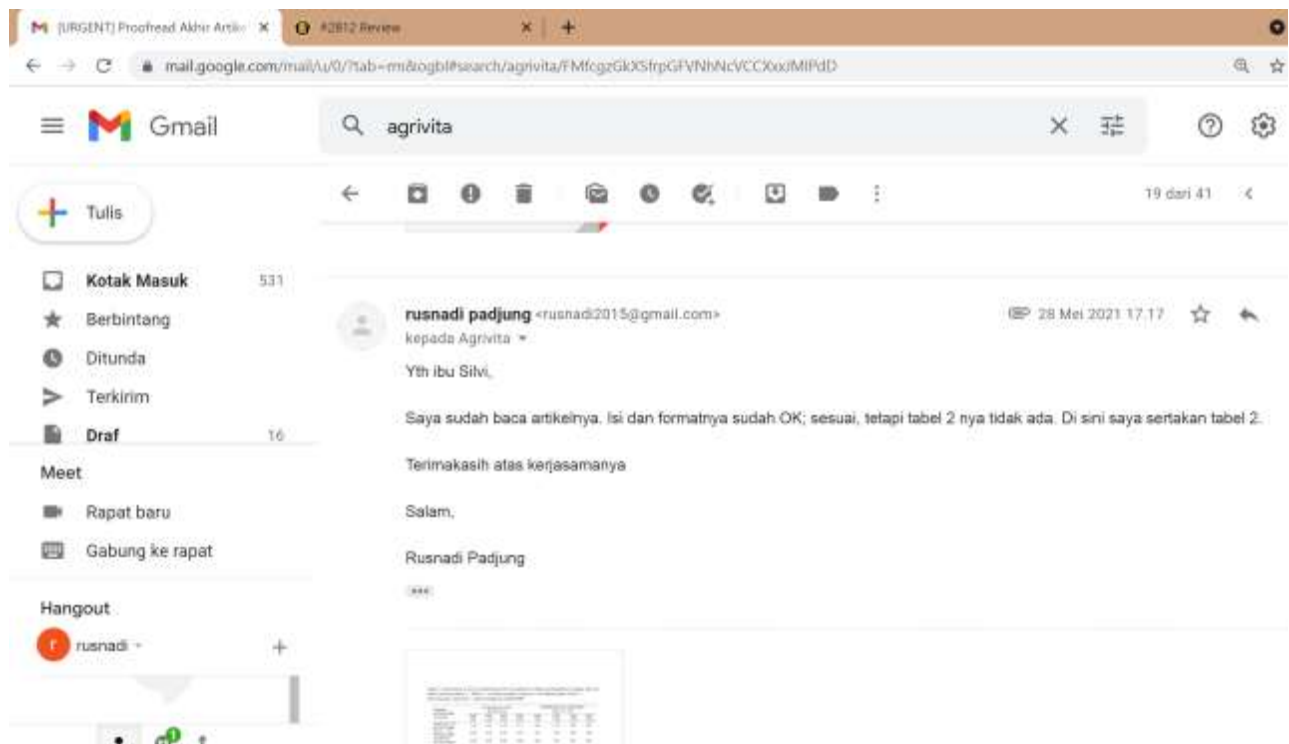
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I. Photosynthetic Parameters of Two Indonesian Soybean Top Varieties

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V. Acknowledgement

The research was funded by Ministry of Research Technology and Higher Education of Republic of Indonesia through University Focus Research grant scheme; Contract No. 717/UN4.21/LK.23 /2017

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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 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.

52 MATERIALS AND METHODS

53 The experiment was conducted in Tarowang farm, owned by a smallholder farmer in Tarowang village, district
54 of Takalar, South Sulawesi province, Indonesia from August to November 2017. Tarowang is located at 119°
55 28¹East and 5° 39¹ South with altitude of 15 m above sea level.

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

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

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

82 RESULTS AND DISCUSSION

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

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

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

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

120 *Actinomyces spp.* play an important role in soil nutrient cycling (Elliot and Lynch, 1995), solubilize
121 inorganic phosphates (Ghorbani-Nasrabadi et al., 2013), hydrolyze phytate, a dominant form of organic P in
122 soils (Ghorbani-Nasrabadi et al., 2012), and so improve the availability of nutrients (Bhatti et al., 2017)
123 particularly phosphorus. Phosphorus (P) is required in many compounds in cells and organelles that are closely

124 associated with energy transfer (Rychter and Rao, 2005). Anjasmoro variety seems response better than
125 Dena-1 variety to *Actinomyces spp* treatment such that more phosphorus is available for energy transfer in
126 the photosynthetic system that in turn increase the capacity of photosynthetic metabolism to accommodate
127 light (PAR) increase. Mahdiannoor et al. (2017) reported that growth and yield responses of *Anjasmoro* variety
128 are much higher than local soybean variety to bio-fertilizer application. Similar result was also found by
129 Maysaroh (2018) that *Anjasmoro* variety responded better than *Dena-1* variety to NPK fertilizer in term of plant
130 height, biomass weight, number of pods, weight of 100 seeds, and yield.

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

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

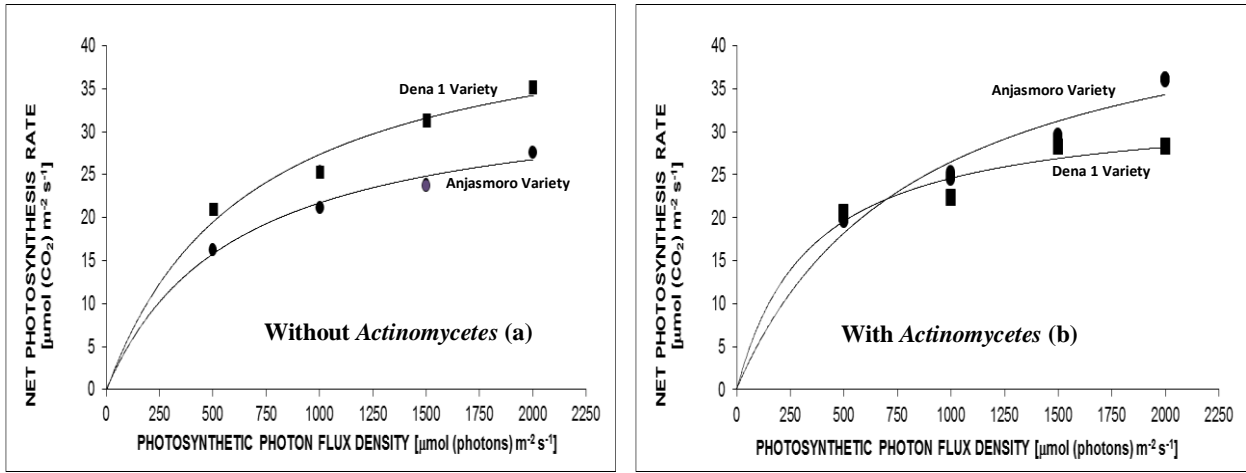
150 Initial light use efficiency and maximum photosynthesis of Dena 1 variety is 0.068 μmol (CO₂) μmol⁻¹ (photons)
151 and 45.64 μmol (CO₂) m⁻² s⁻¹ respectively. while *Anjasmoro* variety is 0.068 μmol (CO₂) μmol⁻¹ (photons) and
152 34.81 μmol (CO₂) m⁻² s⁻¹ respectively. High initial light use efficiency 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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210 Figure 1. Photosynthetic light response curve of Dena-1 and Anjasmoro variety under normal condition (a),
 211 and under Actinomycetes treatment (b).
 212

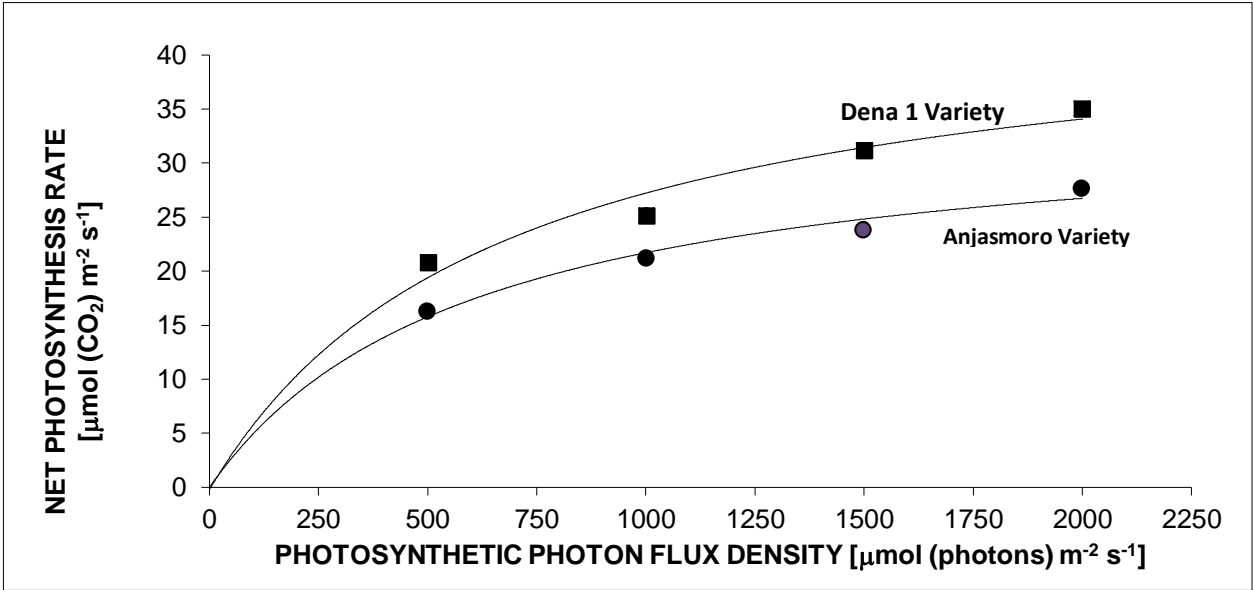
Without Actinomyces (a)

213 The following are the editable graph for Figure 1.

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215 Figure 1.a. Without Actinomyces

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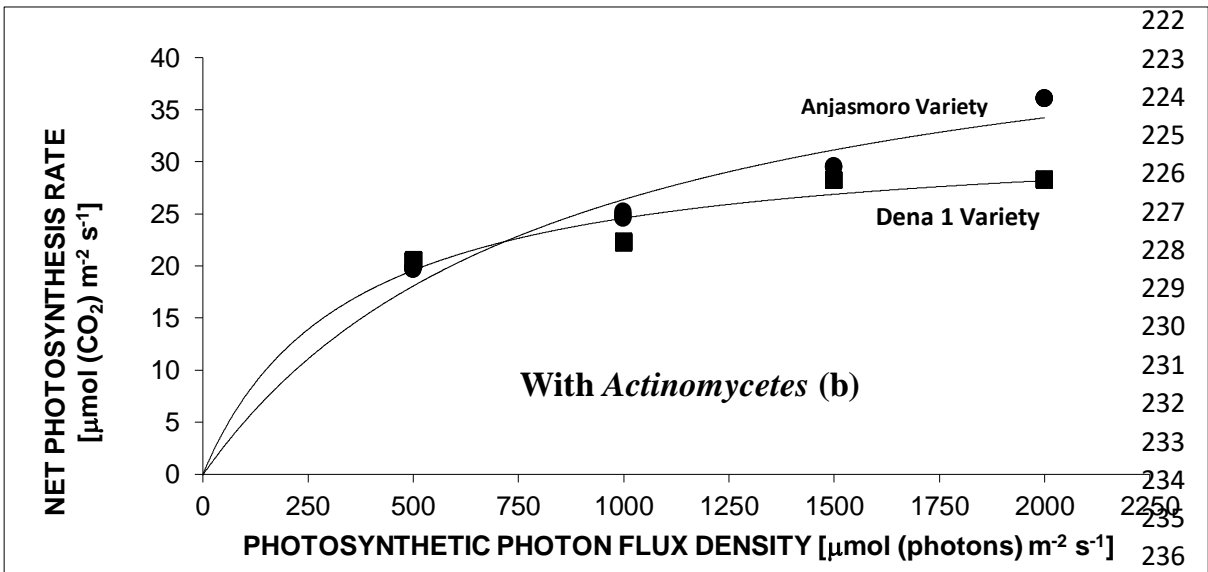
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220 Figure 1.b . With Actinomyces

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

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

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246 Table 2. Conductance to H₂O and Intercellular CO₂ concentration of Dena and Anjasmoro varieties with and
 247 without Actinomycetes, i.e. Dena-1 – no Actinomycetes, Anjamoro – no Actinomycetes, Dena-1 –
 248 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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