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Cross-ecosystem utilizing primed seeds of upland rice varieties for enriching crop diversity at riparian wetland during dry season

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Abstract. *Ria RP, Lakitan B, Sulaiman F, Kartika K, Suwignyo RA. 2020. Cross-ecosystem utilizing primed seeds of upland rice varieties for enriching crop diversity at riparian wetland during dry season. Biodiversitas 21: 3008-3017.* Cultivation of rice during second growing season at riparian wetlands in Indonesia must deal with drought conditions at reproductive stage. Seed priming can speed up seed emergence and produces vigorous seedlings. Objective of this study was to screen upland rice varieties which were positively responded to seed priming and tolerant to drought during late vegetative and/or reproductive stage. Results of this study indicated that osmo-priming showed positive effects on seed emergence, percentage of germinated seed, and time to reach 50% germination. Effects of osmo-priming on seedling growth did not go beyond four weeks after seedlings had been transplanted. Among nine varieties screened, Inpago 10 exhibited better response to seed priming during late vegetative stage as it produced the highest number of tillers and total leaf area. However, at harvest, osmo-priming with 20% PEG lowered filled spikelet and weight of 100 grains but did not affect yield. Drought during late vegetative stage lessened number of tillers but after drought-treated plants recovered during reproductive stage, percentage of filled spikelet and grain size were comparable to those of control plants. Meanwhile, drought imposed during reproductive stage decreased percentage of filled spikelet and grain yield. Despite its better performance under drought conditions, leaf rolling score was higher during heading stage in Inpago 10. This phenomenon indicated that leaf rolling was not forced by drought, rather it was a quick response of Inpago 10 variety to limit water loss due to transpiration.

Keywords: Drought stress, rice diversity, riparian wetlands, seed priming, upland rice

Abbreviations: PEG: polyethylene glycol; TLA: total leaf area; WAT: weeks after transplanting

INTRODUCTION

Growing season at riparian wetlands is started after floodwater has subsided to at least 15 cm depth (Lakitan et al. 2018; Lakitan et al. 2019), marked with transplanting rice seedlings to paddy field, if prepared rice seedlings have reached height of 20 cm or taller. Rice seedling cannot survive under full submerged conditions (El-Hendawy et al. 2011). As main source of staple food, rice is always priority option for local farmers to cultivate during the first growing season (Irmawati et al. 2015). This option has been practiced for about a century at some locations in riparian wetlands.

The second growing season is commenced soon after the first rice crops have been harvested; concurrently with early dry season in tropical monsoon climatic zone, such as in Indonesia. Riparian wetlands landscape is not totally flat. Although differences in elevation seem to be small, only within 1-2 meter, yet the differences are matters for cultivation of rice or other annual food and horticultural crops. At shallowly flooded riparian wetland with maximum depth of floodwater during rainy season is less than 50 cm, the challenge in growing annual crops during the second season is drought condition at time the crops entering reproductive stage; in contrast, at deeper flooded riparian wetlands with depth of floodwater is more than 100 cm during rainy season, the challenge is to avoid early upcoming flooding occurrence before the crops are harvested (Lakitan et al. 2018).

Seed germination is the decisive stage in plant life cycle, and it can be enhanced with priming treatment (Dutta 2018). Farooq et al. (2006) reported that seed priming was not only enhanced seedling establishment, growth, and yield; but also improved quality of direct-seeded rice. Seed priming also improved tolerance of plant to biotic and abiotic stresses by accelerating seedling establishment under drought (Hussain et al. 2017) and submerged condition treatment (Sulaiman et al. 2016; Mulbah and Adjetey 2018).

This research was focused on second rice crop cultivated at shallowly flooded riparian wetlands with probable drought exposure during reproductive stage. Rice as most of other crops is very sensitive to drought stress during reproductive stage (Daryanto et al. 2017; Swamy et al. 2017). Drought stress caused stomatal closure, decreased photosynthetic, and other related physiological activities, and finally reduced rice yield (Singh et al. 2012). Severe drought stress during reproductive stage of rice accounted for economic losses of 48 to 94% (Kim et al. 2020). Furthermore, it also resulted in poor quality and aroma of rice grains (Arsa et al. 2017; Yang et al. 2019).

Use of drought-tolerant rice can be a viable alternative. Upland rice varieties can be reasonable candidates for the second rice-growing season in riparian wetlands. Kartina et al. (2019) had screened 14 doubled haploid lines and they used drought-tolerant varieties, i.e. Inpago 10, Limboto, and Salumpikit as benchmark. Meanwhile, we also included Inpago 10 of nine upland rice varieties pre-screened for their drought tolerant.

Cultivation of upland rice has not been intensively studied at riparian wetlands. Perhaps, due to unawareness of the fact that drought is the major constraint in rice cultivation during second growing season at riparian wetlands. In addition to screen for tolerant varieties, seed priming treatment was also studied for improving seed emergence and plant growth under drought stress conditions. Seed priming is pre-sowing treatments by soaking seed in water (hydro-priming) or in osmotic solutions (osmo-priming).

Objectives of this study were to evaluate effectiveness osmo-priming using PEG compared to commonly practiced hydro-priming on nine upland rice varieties and selecting tolerant varieties to drought stress imposed at late vegetative, booting, and heading stages.

MATERIALS AND METHODS

Procedures

Plant materials

Seeds of nine indica upland rice (new and established inbreeds) varieties with pre-tested germination of > 90% were used in this study. The new inbred rice varieties used were Inpago 4, Inpago 5, Inpago 8, Inpago 9, Inpago 10, and Inpago 12. The established varieties used were Batu Tegi, Rindang 1, and Rindang 2. All seeds were obtained from the Indonesian Center for Rice Research at Sukamandi, West Java, Indonesia. The initial moisture contents of seeds were 10.4%, 10.7%, 11.37%, 11.1%, 11.3%, 10.63%, 10.7%, 11.2%, and 11.03% for Inpago 4, Inpago 5, Inpago 8, Inpago 9, Inpago 10, Inpago 12, Batu Tegi, Rindang 1, and Rindang 2, respectively.

Seed priming treatments

Priming treatments consisted of hydro-priming with 0% PEG, osmo-priming with 10%, 15%, and 20% PEG. The priming treatments were conducted in complete darkness at 28 ± 2˚C for 12 hours. The primed seeds were washed with distilled water for 3-4 times and air-dried at 28 ± 2˚C until the moisture content returned to pre-treatment level for each variety.

Germination and seedling growth

Twenty seeds for each replication in each treatment were germinated on two layers wet filter papers in 9-cm diameter Petri dishes. Filter papers were moistened by gently pouring 30 ml of water to each petri dish and covered with lid for minimizing evaporation. All Petri dishes were placed on steel racks within an incubator. Germinated seeds were counted every 4 hours until 32 hours after initiation. Germinated seeds were sown in seedling trays filled with soil for 14 days. The trays were labeled according to rice varieties, priming treatments, and replications. Data on seedling height, number of leaves, root length, shoot, and root fresh and dry weights were daily collected during the first 2-week period of seedling growth.

Pot experiment and drought stress treatment

Three upland rice varieties were chosen in pot experiment for representing categories of tolerant new inbred variety (Inpago 10), susceptible new inbred variety (Inpago 4), and susceptible established variety (Rindang 1). The selection of varieties used was based on percent of germination and seedling morphologic performance. Seedlings of selected varieties were transplanted into soil-filled pots and orderly arranged in an open field. The pot dimensions are 26 cm in height, 22 cm in diameter at base, and 30 cm at upper diameter of the pot. One seedling was planted in each pot.

Pots were laid out according to the factorial randomized block design with 3 replications. Plants were well-watered during early vegetative stage. Drought stresses were exposed to selected rice varieties at three different growth stages, i.e. late vegetative stage, booting stage, and heading stage. During drought stress treatment, plants were placed in a plastic house for avoiding rainfall. Assigned plants were without water supply for 14 consecutive days at late vegetative stage and 12 consecutive days at booting stage and heading stage. Soil moisture content was monitored daily during drought treatments. At termination of drought treatment, all drought-treated plants were returned to their original position at the open field area. Then, the plants were sufficiently re-watered until harvest.

Data collection

Percentage of seed emergence was counted every 4 hours starting from 12 to 32 hours after initiation of germination test. The time for obtaining 50% germination (T_{50}) was calculated according to Coolbear et al. (1984):

$$T_{50} = t_i + \frac{\left(\frac{N}{2} - n_i\right)(t_j - t_i)}{(n_j - n_i)}$$

Soil moisture was measured using soil moisture meter (Lutron PMS-714) at depth of 10 cm below soil surface on the last day of drought stress treatment during vegetative, booting, and heading stages. Leaf SPAD was measured using chlorophyll meter (Konica Minolta SPAD-502Plus). Leaf area was measured using digital image analyzer developed by Easlon and Bloom (2014). Leaf rolling was scored between noon to 1 p.m. during the last two days of drought stress by following the Standard Evaluation System for Rice (IRRI, 2002). Measurement of dry weight of plant materials was done after the materials were dried in oven at 70ºC for 48 hours. At harvest, data of some important traits were recorded, including day of physiological maturity, number of total panicles, panicle length, percentage of filled and sterile spikelets, weight of 100 grains, and grain yield.

Data analysis

All data on seed germination and seedling growth were organized and analyzed using the statistical analysis software (SAS 9.0 for Windows, SAS Institute Inc., Cary, North Carolina, US). Analysis of variance was used for evaluating significance of individual treatments and their interactions. Least significant difference test was carried out to access the significant difference among varieties and priming treatments in all sets of collected data. $P < 0.05$ was used to indicate statistical significance.

RESULTS AND DISCUSSION

Seed emergence and seedling growth

Results of this study indicated that seed emergence was enhanced in osmo-primed seeds at rate of 20% PEG. More than 50% of seeds germinated within less than 20 hours after initiation and reached 98.41% after 32 hours (Table 1). Osmo-priming at 20% PEG was also effective in enhancing seed emergence and was significantly better than hydro-priming, especially at early stage and final percentage of seed emergence. Top three in seed emergence test were Inpago 10, Inpago 12, and Inpago 5; while bottom three were Rindang1, Rindang 2, and Inpago 4. However, the highest total percentage of emergence (100%) after 32 hours was exhibited by Inpago 5. It was much better than Rindang 1 (< 90%). Overall, new inbred varieties performed better germination than established varieties, except for Batu Tegi variety.

Drought tolerance is complex quantitative trait with complicated phenotypes that affect different developmental stages in plants. Level of susceptibility or tolerance to various drought conditions in rice was coordinated by action of many drought-responsive genes, in relation to different stress sources (Oladosu et al. 2019). Two plant organs are directly associated with drought-tolerant, i.e. roots and total leaf area. Longer roots have been frequently mentioned as an advantage under drought condition, since the longer roots make it possible to cover larger volume of the rhizosphere in search of water and nutrients. Meanwhile, larger leaf areas can be disadvantage since more sunlight is captured; therefore, it increases leaf temperature. In order to maintain leaf temperature, excessive heat energy should be used for evaporating water in leaf; therefore, it increases transpiration rate.

In this study, there was significant effect of osmo-priming on root length. Osmo-priming at 15% PEG solution resulted the highest number of leaves in upland rice (Table 2). Therefore, seed priming using PEG might not be beneficial under drought conditions. Meanwhile, among nine evaluated varieties, Inpago10 variety showed the best performance during seedling stage.

Many studies had reported that priming improved seed emergence (Khaliq et al. 2015; Zheng et al. 2016; Hussain et al. 2017). Besides improving time of seed emergence, seed priming also increased percentage of germinating seeds and enhancing seedling growth. Hussain et al. (2016) suggested that better performance and greater tolerance of primed rice seedlings were associated with enhanced starch metabolism, high respiration rate, lower lipid peroxidation, and strong antioxidative defense system under abiotic stress. Furthermore, Khaliq et al. (2015) found that improved starch metabolism, greater membrane stability, and increased activity of antioxidants were considered as possible mechanisms responsible for such improvements in emergence and seedling vigor in rice.

Table 1. Seed emergence (%) counted every 4 hours starting from 12 to 32 hours after initiation of germination test and calculated time to achieve 50% germination (T_{50})

	Time after initiation (hour)						
	12	**16**	**20**	**24**	**28**	**32**	T_{50}
				Priming treatment			
PEG 0%	5.18 b	20.00 cd	47.77 b	66.29 b	80.00 c	86.29 b	22.67 bc
PEG 10%	3.17 b	14.28 cd	44.97 b	73.01 b	91.00 b	95.23 a	26.74 a
PEG 15%	12.17 a	41.80 b	52.38 b	65.60 b	83.59 c	98.41 a	23.40 ab
PEG 20%	13.22 a	32.80 a	68.78 a	89.41 a	97.35 a	98.41 a	19.55 c
$LSD_{.05}$	3.57	8.32	10.70	9.29	6.30	3.92	3.61
				Upland rice variety			
Inpago 4	2.02 de	12.02 de	52.02 cd	76.66 bc	95.47 a	98.33 a	22.33 abc
Inpago 5	0.83 de	30.12 bc	67.97 bc	86.66 ab	100.00 a	100.00 a	19.66 c
Inpago 8	5.59 cd	27.50 bc	51.66 d	70.83 cd	85.71 b	89.76 bc	21.66 abc
Inpago 9	4.76 cde	37.50 b	62.97 bcd	85.95 ab	95.47 a	97.97 a	20.66 bc
Inpago 10	40.00 a	72.02 a	87.26 a	94.16 a	96.67 a	96.66 a	25.83 ab
Inpago 12	13.21 b	34.64 b	76.78 ab	87.14 ab	96.78 a	99.16 a	20.33 c
Rindang 1	1.19 de	5.23 e	25.00 e	42.61 e	65.00 d	88.57 bc	27.00 a
Rindang 2	0.00 e	6.42 e	23.33 e	57.02 d	75.95 c	94.28 ab	26.33 a
BatuTegi	8.33 bc	19.52 cd	34.28 e	61.19 d	80.83 bc	86.54 c	24.00 abc
$LSD_{.05}$	5.36	12.49	16.06	13.94	9.45	5.88	5.42

Means followed by the different letters within each column of priming treatments and upland rice varieties are significantly different based on the LSD at $P \leq 0.05$

Table 2. Shoot and root lengths, leaf area and number of leaves at seedling stage as affected by seed priming in upland rice varieties

	Shoot length (cm)	Root length (cm)	Leaf area (cm^2)	Number of leaves
		Priming treatment		
PEG 0 %	20.12 a	13.99 a	5.08 a	2.96 b
PEG 10 %	20.28 a	14.83 a	5.84 a	3.00 ab
PEG 15 %	19.85 a	13.91 a	5.70 a	3.11 a
PEG 20 %	19.93 a	14.04 a	5.35 a	2.96 b
$LSD_{.05}$	1.37	1.72	0.85	0.11
		Upland rice variety		
Inpago 4	20.1 ab	14.73 a	5.39 ab	3.00 ab
Inpago 5	20.22 ab	14.28 a	5.65 ab	2.83 b
Inpago 8	20.65 ab	14.85 a	4.86 b	3.00 ab
Inpago 9	21.45 a	13.23 a	5.89 ab	3.00 ab
Inpago 10	23.26 a	13.39 a	6.54 a	3.00 ab
Inpago 12	19.92 ab	12.71 a	6.00 ab	3.00 ab
Rindang 1	19.08 b	15.25 a	5.34 ab	3.08 a
Rindang 2	18.65 b	14.71 a	5.07 b	3.08 a
BatuTegi	19.09 b	13.60 a	4.79 b	3.08 a
$LSD_{.05}$	2.06	2.58	1.28	0.17

Note: Means followed by the different letters within each column of priming treatments and upland rice varieties are significantly different based on the LSD at $P \leq 0.05$

Seed emergence is commonly used as an early indicator of drought-tolerant varieties. Screening based on percentage of seed emergence has been practiced in search of tolerant plants or cultivars, including in rice. Under drought conditions, germination processes are restrained due to limited available water for imbibition. Drought condition inhibited percentage of germination by complete inhibition of enzyme activity in germination process or delaying seeds germination but did not prevent germination.

Seed priming basically a pre-conditioning for triggering starch metabolism processes by infiltrating water into seed. Osmo-priming using PEG was more effective than hydro-priming in enhancing seed emergence and showed further advantage during early seedling growth, i.e. the first two weeks. Application of 10% PEG solution produced higher fresh and dry weight of stem and roots in studied rice seedlings. However, there were no significant differences in shoot and root length, leaf area, leaf weight (Table 2 and Table 3). Du et al. (2019) also reported that seedlings primed with low selenite concentration were superior to those primed with water, as indicated by higher fresh weight, dry weight, soluble carbohydrate, and protein content in selenite-primed seedlings

Carry-over effect of seed priming on vegetative growth in rice

Based on performance in seed emergence and seedling growth during the first two weeks, three upland varieties were selected, i.e. Inpago 10 represents tolerant variety; plus Inpago 4 and Rindang 1 represent susceptible new inbreed and established varieties to drought stress. There were inconsistent differences among osmo-priming treatments on plant height. However, there was clear evidence that height of Rindang 1 variety significantly taller than the other two cultivars (Table 4).

In most cases, yield in rice is strongly correlated with number of productive tillers per hill (Yeh et al. 2015; Lakitan et al. 2018). In this study, osmo-priming did not show significantly different effects on number of tillers (Table 5). Meanwhile, among upland rice varieties used, Inpago 10 produced significantly higher number of tillers than the other two varieties (Table 5). There were specific genes functioned as a positive regulator in response to drought stress and controlled tiller development (Jung et al. 2015; Kang et al. 2017).

Table 3. Fresh and dry weights of leaf, stem, and roots of seedlings in nine upland rice varieties treated with osmo-priming

	Leaf fresh weight (g)	Leaf dry weight (g)	Stem fresh weight (g)	Stem dry weight (g)	Root fresh weight (g)	Root dry weight (g)
			Priming treatment			
PEG 0 %	0.049 a	0.011 a	0.060 b	0.009 b	0.060 b	0.020 a
PEG 10 %	0.048 a	0.011 a	0.075 a	0.012 a	0.075 a	0.021 a
PEG 15 %	0.047 a	0.010 a	0.060 b	0.009 b	0.060 b	0.018 a
PEG 20 %	0.051 a	0.011 a	0.060 b	0.009 b	0.060 b	0.019 a
$LSD_{.05}$	0.006	0.001	0.009	0.001	0.009	0.003
			Upland rice variety			
Inpago 4	0.048 b	0.010 ab	0.064 ab	0.010 ab	0.064 ab	0.017 b
Inpago 5	0.048 b	0.010 ab	0.07 a	0.011 a	0.070 a	0.023 a
Inpago 8	0.045 b	0.011 a	0.064 ab	0.010 ab	0.064 ab	0.019 ab
Inpago 9	0.052 ab	0.012 a	0.07 a	0.010 ab	0.070 a	0.022 a
Inpago 10	0.058 a	0.012 a	0.07 a	0.011 ab	0.070 a	0.018 ab
Inpago 12	0.050 ab	0.012 a	0.062 ab	0.009 ab	0.062 ab	0.018 ab
Rindang 1	0.045 b	0.011 a	0.055 b	0.009 ab	0.055 b	0.017 b
Rindang 2	0.044 b	0.009 b	0.06 ab	0.008 b	0.060 ab	0.018 ab
BatuTegi	0.047 b	0.010 ab	0.059 ab	0.010 ab	0.059 ab	0.019 ab
$LSD_{.05}$	0.009	0.002	0.013	0.002	0.013	0.005

Note: Means followed by the different letters within each column of priming treatments and upland rice varieties are significantly different based on the LSD at $P \leq 0.05$

Table 4. Plant height during early vegetative growth stage from 2 to 7 WAT as affected by seed priming at varied PEG concentrations in Inpago 4, Inpago 10 and Rindang 1 varieties

	Plant height (cm)					
	2 WAT	3 WAT	4 WAT	5 WAT	6 WAT	7 WAT
Priming treatment						
PEG 0 %	38.55 b	52.28 bc	68.40 b	78.61 a	81.52 a	84.74 a
PEG 10 %	39.31 b	54.47 ab	68.09 b	77.13 a	81.42 a	85.01 a
PEG 15 %	39.06 b	50.37 c	66.25 b	71.71 b	77.60 b	84.84 a
PEG 20 %	42.98 a	56.35 a	74.00 a	78.30 a	82.61 a	84.04 a
$LSD_{.05}$	2.43	3.83	3.35	2.24	3.28	4.08
Upland rice variety						
Inpago 4	38.85 b	51.72 b	66.34 b	73.63 b	76.57 b	84.47 b
Inpago 10	38.11 b	50.29 b	65.48 b	73.20 b	78.79 b	81.64 b
Rindang 1	42.96 a	58.10 a	75.74 a	82.48 a	87.00 a	90.86 a
$LSD_{.05}$	2.11	3.32	2.90	1.94	2.84	3.54

Note: Means followed by the different letters within each column of priming treatments and upland rice varieties are significantly different based on the LSD at P ≤ 0.05

Table 5. Number of tillers during early vegetative growth stage from 2 to 7 WAT as affected by seed priming at varied PEG concentrations in Inpago 4, Inpago 10 and Rindang 1 varieties

	Number of tillers					
	2 WAT	3 WAT	4 WAT	5 WAT	6 WAT	7 WAT
Priming treatment						
PEG 0%	3.51 a	4.08 a	9.07 b	15.74 a	17.55 a	17.81 a
PEG 10 %	3.40 ab	4.17 a	9.37 b	16.29 a	17.85 a	18.77 a
PEG 15 %	2.77 b	4.15 a	11.74 a	16.99 a	19.15 a	19.59 a
PEG 20 %	2.85 ab	5.18 a	12.11 a	17.85 a	19.11 a	19.92 a
$LSD_{.05}$	0.69	1.21	2.16	2.83	3.12	3.23
Upland rice variety						
Inpago 4	3.44 a	5.19 a	11.77 a	18.13 a	19.39 a	18.94 ab
Inpago 10	3.02 a	4.29 ab	11.16 a	17.75 a	19.75 a	20.66 a
Rindang 1	2.94 a	3.72 b	8.70 b	14.27 b	16.11 b	17.47 b
$LSD_{.05}$	0.60	1.05	1.87	2.45	2.70	2.80

Note: Means followed by the different letters within each column of priming treatments and upland rice varieties are significantly different based on the LSD at P ≤ 0.05

SPAD measurements were conducted at 4 WAT for representing carry-over effect of seed priming on leaf chlorophyll during early vegetative growth in rice. Both leaf SPAD value and total leaf area (TLA) per plant were not significantly affected by osmo-priming treatments. There was no significant difference in leaf SPAD value amongst three rice varieties examined. Significant difference amongst varieties was only observed in TLA whereas Inpago 10 exhibited significantly higher TLA than Inpago 4 (Table 6). Plant with larger TLA could inherit potential disadvantage, since larger TLA is associated with more light energy captured and higher transpiration rate per individual plant. However, if soil moisture was kept high, i.e. prior to application of drought stress treatment, high transpiration rate was compensated with equivalent water uptake by roots. This might be the case of Inpago 10. Beneficial effects of seed priming on leaf SPAD value and TLA did not go far beyond vegetative stage.

Table 6. SPAD value at 4 WAT and total leaf area at 7 WAT during vegetative growth as affected by seed priming at varied PEG concentrations in Inpago 4, Inpago 10 and Rindang 1 varieties

	SPAD	TLA (dm^2)
Priming treatment		
PEG 0%	42.08 a	16.32 a
PEG 10 %	44.55 a	14.18 a
PEG 15 %	41.61 a	14.85 a
PEG 20 %	40.87 a	15.61 a
$LSD_{.05}$	5.28	3.07
Upland rice variety		
Inpago 4	40.33 a	13.06 b
Inpago 10	43.12 a	16.99 a
Rindang 1	43.39 a	15.67 ab
$LSD_{.05}$	4.57	2.66

Note: WAT: week after transplanting. Means followed by the different letters within each column of priming treatments and upland rice varieties are significantly different based on the LSD at P ≤ 0.05

Table 7. Soil moisture monitored at the last day of drought stress at vegetative, booting, and heading stages as associated with seed priming at varied PEG concentrations in Inpago 4, Inpago 10 and Rindang 1 varieties

	Soil moisture (%)		
	Vegetative	Booting	Heading
Priming treatment			
PEG 0%	10.24 a	8.78 a	9.38 ab
PEG 10 %	11.34 a	8.71 a	10.80 a
PEG 15 %	10.36 a	7.95 a	10.00 ab
PEG 20 %	8.60 a	8.12 a	8.31 b
$LSD_{.05}$	3.16	2.77	2.05
Upland rice variety			
Inpago 4	8.10 b	8.80 a	9.01 a
Inpago 10	11.08 a	8.10 a	9.41 a
Rindang 1	11.23 a	8.27 a	10.44 a
$LSD_{.05}$	2.74	2.39	1.77

Note: Means followed by the different letters within each column of priming treatments and upland rice varieties are significantly different based on the LSD at P ≤ 0.05

At end of two-week period without watering, overall soil moisture on average was varied from 8.12% to 11.34% (Table 7). but high air humidity during the treatment period kept evaporation low; therefore, slowing soil drying process. Significantly lower soil moisture was observed during heading stage in plants pre-treated with seed priming at 20% PEG concentration. This lower soil moisture was associated with more water uptake by plant roots since plants were fully avoided from rain during drought treatment and all plants were exposed to the same microclimate within a plastic house. Therefore, lower soil moisture indicated that the plants pre-treated with osmo-priming at 20% PEG had higher capacity in absorbing water due to larger root biomass and longer roots (Table 8).

Kim et al. (2020) confirmed that there were some adaptive mechanisms in rice roots under drought stress, i.e. osmotic adjustment, increase density, deeper penetration, and increase root-to-shoot ratio. Under low soil moisture conditions, allocation of assimilates was directed toward roots to enhance growth and enlarged surface area. Kartika et al. (2020) reported that growth and development of fine roots were increased during drought stress conditions in rice. Fine roots branched from coarse root contributed to increase of root volume and surface area for escalating water uptake (Comas et al. 2013).

Application of 20% PEG did not only significantly increase root length and root biomass, but also consistently generated the highest fresh and dry weights of stem. Inpago 10 variety exhibited higher fresh and dry weights of both below (roots) and above ground organs but shorted roots (Table 8). Higher biomass but shorter roots indicated that root branching was more intensive in Inpago 10 variety. This phenomenon gave an advantage to Inpago 10 variety in utilizing fertilizer applied mostly at upper layer of rhizosphere. Intensive branching of shorter roots also explained the lower soil moisture measured at 10 cm below soil surface in rhizosphere grown with Inpago 10 variety (Table 7).

It was interesting to note that weights of roots and stem, and length of roots, were decreased from booting to heading stage (Table 8). The decrease occurred due to some older leaves had dried out and were not included in measurements. It appeared that soil drought conditions accelerated the drying process of older leaves and part of fine roots. Nonetheless, quantitative measurements on this issue had not been conducted in our present study.

During reproductive stage, from flowering to physiological maturity stage, dry matter of vegetative organ in rice was reduced by 35% as transport of assimilates to panicles increased (Fageria 2007). Assimilate relocation is vital for grain development. Carbohydrate stored in stem was used as an alternative source under stress condition (Pandey et al. 2016). Competition amongst organs could decrease partitioning of assimilates directed to rice spikelets during grain filling stage, causing increase of sterile spikelets.

Leaf rolling is a mechanism in rice plants to prevent water loss via transpiration during drought stress (Singh et al. 2012) and leaf rolling score (LRS) has been used widely in research on drought stress in rice plants. After 12 to 14 days imposed to gradual soil drying process during late vegetative, booting, and heading stages, all rice plants had visually performed leaf rolling movement to form O-shaped cross-section view, one side of leaf edge had curved and touched the leaf edge at the other side or had reached LRS $\geq$ 7.0. However, there was no significant difference in LRS amongst rice plants pre-treated with hydro-priming and osmo-priming at different PEG concentrations up to 20% if drought treatment was imposed during late vegetative stage (Table 9).

LRS scores were significantly higher in plants pre-treated with osmo-priming of 20% PEG solution than those pre-treated with 10% PEG if drought stress was imposed for 12days during booting stage or heading stages. In both cases, results implied that it took almost 2 weeks to see differences in effect of seed priming on LRS in rice plants. Leaf rolling as response to drought during heading stage did not reach the maximum score (LRS = 9.0) until 14 days. Leaf rolling correlated with leaf water status, in turn, depended on water availability in soil.

Differences in LRS were observed among varieties. Rindang 1 variety consistently exhibited lower LRS but both Inpago 10 and Inpago 4 varieties showed higher value of LRS (Table 9). This result confirmed that drought tolerance variety characterized by the early leaf rolling ability to prevent water loss with faster recovery after the stress was terminated. Leaf rolling enabled partial stomatal closure and allowed plants to alter the microclimate surrounding the leaf (Kartika et al. 2020). Leaf rolling caused the plant to adjust transpiration rate and maintained leaf water potential during water deficiency conditions (Saglam et al. 2014).

Table 8. Fresh and dry weights of roots, root length, and fresh and dry weights of stems at harvest in Inpago 4, Inpago 10 and Rindang 1 treated with seed priming and exposed to drought stress

	Root fresh weight (g)	Root dry weight (g)	Root length (cm)	Stem fresh weight (g)	Stem dry weight (g)
Priming treatment					
PEG 0%	101.51 b	23.13 b	47.34 a	109.70 b	23.41 b
PEG 10%	115.29 a	23.65 b	46.28 ab	124.25 b	26.60 b
PEG 15%	116.88 a	27.29 ab	44.34 b	119.92 b	26.43 b
PEG 20%	126.03 a	28.96 a	47.50 a	142.88 a	32.64 a
$LSD_{.05}$	11.94	4.38	2.79	17.08	4.95
Upland rice variety					
Inpago 4	109.08 b	24.32 b	47.76 a	127.75 a	28.80 a
Inpago 10	129.88 a	31.04 a	44.88 b	134.69 a	29.18 a
Rindang 1	105.82 b	21.91 b	46.46 ab	110.13 b	23.83 b
$LSD_{.05}$	10.34	3.79	2.42	14.79	4.28
Timing of drought stress					
Vegetative	111.333 a	24.537 a	45.51 b	120.88 ab	27.20 ab
Booting	121.028 a	28.094 a	48.06 a	135.55 a	29.97 a
Heading	112.444 a	24.655 a	45.53 b	116.13 b	24.64 b
$LSD_{.05}$	10.344	3.793	2.42	14.79	4.28

Note: Means followed by the different letters within each column of priming treatments, upland rice varieties, and timing of drought exposure are significantly different based on the LSD at $P \leq 0.05$

Table 9. Leaf rolling score monitored at 2 last days of drought stress treatments during vegetative, booting, or heading stage

	Leaf rolling score					
	Vegetative		Booting		Heading	
	Day 13	Day 14	Day 11	Day 12	Day 11	Day 12
Priming treatment						
PEG 0%	7.11 a	7.77 a	7.44 ab	8.66 a	6.33 a	9.00 a
PEG 10 %	7.33 a	7.66 a	6.88 b	8.40 a	5.88 a	8.33 b
PEG 15 %	6.66 a	7.11 a	8.00 ab	8.40 a	6.33 a	8.33 b
PEG 20 %	7.11 a	7.22 a	8.22 a	8.77 a	7.00 a	9.00 a
LSD.05	1.2	1.3	1.19	0.84	1.21	0.45
Upland rice variety						
Inpago 4	7.83 a	8.33 a	8.08 a	8.75 a	6.33 a	8.83 a
Inpago 10	6.75 b	6.91 b	8.00 a	8.58 a	6.33 a	9.00 a
Rindang 1	6.58 b	7.08 b	6.83 b	8.08 a	6.50 a	8.16 b
LSD.05	1.04	1.12	1.03	0.73	1.04	0.38

Note: Means followed by the different letters within each column of priming treatments and upland rice varieties are significantly different based on the LSD at $P \leq 0.05$

Table 10. Fresh and dry weights of leaf at harvest in Inpago 4, Inpago 10 and Rindang 1 treated with osmo-priming and exposed to drought stress

	Leaf fresh weight (g)	Leaf dry weight (g)
Priming treatment		
PEG 0%	26.58 a	4.96 a
PEG 10 %	27.49 a	5.37 a
PEG 15 %	15.54 a	4.87 a
PEG 20 %	16.28 a	4.73 a
$LSD_{.05}$	2.89	0.97
Upland rice variety		
Inpago 4	15.40 b	4.63 b
Inpago 10	18.03 a	5.81 a
Rindang 1	15.98 ab	4.50 b
$LSD_{.05}$	2.50	0.84
Timing of drought stress		
Vegetative	15.62 b	4.92 ab
Booting	18.73 a	5.65 a
Heading	15.06 b	4.37 b
$LSD_{.05}$	2.50	0.84

Note: Means followed by the different letters within each column of priming treatment, upland rice variety, and timing of drought stress treatment are significantly different based on the LSD at P ≤ 0.05

Table 11. Inflorescence and yield traits of Inpago 4, Inpago 10 and Rindang 1 pre-treated with priming dan imposed to drought at different growth stages

	Day of physiological maturity	panicle length (cm)	Weight 100 grains (g)	Yield (ton/ha)
Priming treatment				
PEG 0%	115.11 a	25.16 a	2.35 a	2.78 a
PEG 10%	114.66 a	25.07 a	2.37 a	3.10 a
PEG 15%	118.77 a	24.91 a	2.23 ab	2.55 a
PEG 20%	116.77 a	25.33 a	2.16 b	2.56 a
$LSD_{.05}$	7.87	0.77	0.15	0.98
Upland rice variety				
Inpago 4	112.75 a	24.90 b	2.29 ab	2.45 a
Inpago 10	119.41 a	26.19 a	2.17 b	2.89 a
Rindang 1	116.83 a	24.26 b	2.38 a	2.87 a
$LSD_{.05}$	6.82	0.67	0.13	0.85
Drought stress				
Vegetative	108.91 b	25.51 a	2.48 a	2.66 a
Booting	127.75 a	24.16 b	2.27 b	3.01 a
Heading	112.33 b	25.68 a	2.08 c	2.55 a
$LSD_{.05}$	6.82	0.67	0.13	0.85

Note: Means followed by the different letters within each column of priming treatment, upland rice variety, and timing of drought stress treatment are significantly different based on the LSD at P ≤ 0.05

Drought effects at vegetative and reproductive stage

Effects of drought treatments in rice pre-treated with osmo-priming at different concentrations were not evident on leaf fresh and dry weights at harvest. However, there were differences among varieties examined. Leaf fresh and dry weights were significantly higher in Inpago 10 than in Inpago 4 and Rindang 1. Leaf fresh and dry weights were significantly higher if drought treatment was imposed during booting stage than either during vegetative or heading stage (Table 10).

Drought condition occurred during vegetative stage could inhibit tiller initiation and its further development in rice plant. Limited tiller initiation and growth during reproductive stage were due to water shortage (Singh et al. 2018) and after entering reproductive stage were due to more photosynthates were allocated for supporting development of reproductive organs (Hidayati et al. 2016). Significantly lower leaf fresh and dry weights in rice plants exposed to drought during heading stage were more likely due to early drying of the older leaves. Dead leaves were not included in measurement of fresh weight and dry weight.

Higher concentration of PEG (20%) negatively affected weight of 100 grains. Better results were achieved if osmo-priming was applied at lower (10%) or without addition of PEG. Inpago 10 variety exhibited significantly longer panicle but smaller grain size, indicated by lower weight of 100 grains. Suppression on growth and development during late vegetative stage due to drought conditions did not affect inflorescence and yield traits, except on number of total panicles. Less panicle produced in plants imposed on drought during vegetative stage was compensated with higher weight of filled spikelet and larger seed size, indicated by heavier weight of 100 grains (Table 11).

Number of panicles is equivalent to number of productive tillers, but not all tillers develop panicles. Therefore, by default, number of panicles never exceed total number of tillers. Most tillers in rice are developed during late vegetative stage. Drought occurred during late vegetative stage limited number and/or retarded growth of tillers. Lower number of panicles observed during late vegetative stage in this study was associated with negative effect of drought treatment (Figure 1).

Plants imposed on drought during reproductive stage had opportunity to develop more tillers during their vegetative stage. Thus, their number of tillers and in this case also number of panicles were higher than the plants exposed to drought during late vegetative stage (Figure 1). Furthermore, drought imposed during booting phase had already developed panicle organ but still shielded within layers of leaf sheaths and mostly survived during drought exposure period and emerged unharmed. Meanwhile, drought imposed during heading phase disclosed the newly emerged panicle to dry air. This dry condition interrupted panicle development and dehydrated pollens if panicle developed further. In this case, number of panicles was reduced (Figure 1) and percentage of sterile spikelets increased (Figure 2).

Spikelet filling period lasted about 25-35 days to achieve physiological maturity under tropical environment (Fageria 2007); hence, 12 consecutive days of drought period should affect spikelet filling process. Barnabás et al. (2008) reported that grain sterility was caused by poor anther dehiscence and low pollen production. Raveendran et al. (2011) emphasized that drought at heading stage prevented peduncle (uppermost internode) elongation which trapping spikelet lower down the panicle and increased percentage of sterile spikelet.

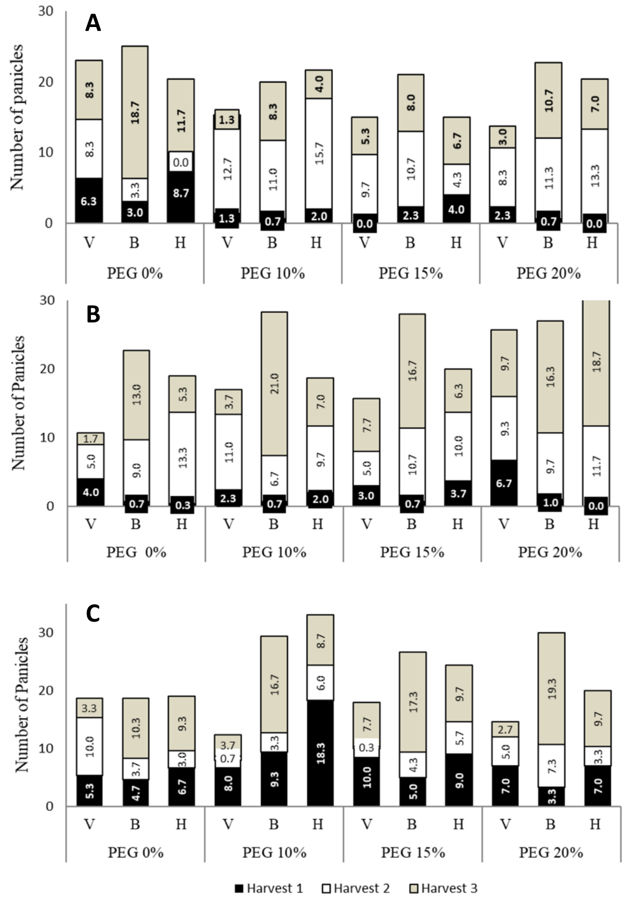

Figure 1. Number of panicles in Inpago 4 (A), Inpago 10 (B), and Rindang 1 (C) varieties pre-treated with seed priming and imposed to drought condition during vegetative (V), booting (B), or heading stages (H). Bars were stacked based on three-time of harvests

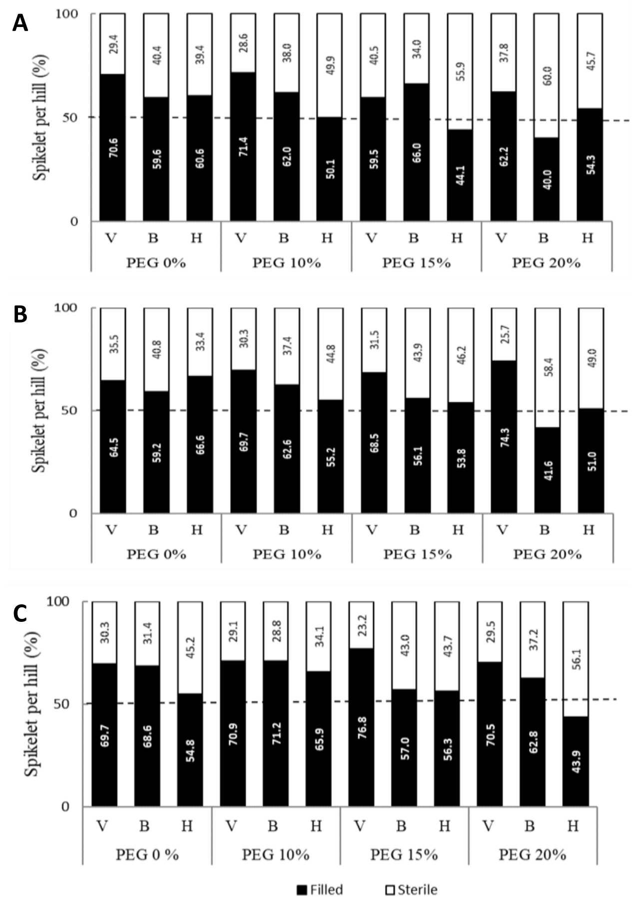

Figure 2. Comparison of filled and sterile spikelet in Inpago 4 (A), Inpago 10 (B) and Rindang 1 (C) varieties pre-treated with seed priming and imposed to drought condition during vegetative (V), booting (B), or heading stages (H)

There were recognizable patterns on percentage of sterile spikelets in rice varieties studied. Percentages of sterile spikelets in response to timing of drought exposure were comparable amongst Inpago 4, Inpago 10, and Rindang 1 varieties. The lowest percentages of sterile spikelets in drought exposed rice were observed during vegetative stage for all three varieties. The percentages were 29.4% in Inpago 4 pre-treated with PEG 0%, 25.7% in Inpago 10 pre-treated with PEG 20%, and 23.2% in Rindang 1 pre-treated with PEG 15%, respectively. Meanwhile, the highest sterile spikelet was observed in plants pre-treated with 20% PEG, in Inpago 4 was 60.0%at booting stage, in Inpago10 was 58.4%also at booting stage, and in Rindang 1was56.1%at heading stage (Figure 2).

Different seed priming treatments did not show different effects on rice yield under drought stress conditions. However, drought stress reduced rice yield of 33% to 37% as compared to average yield of Inpago 4, Inpago 10, and Rindang 1 of about 4 tons ha^{-1} . At present study, drought stress occurrence at vegetative, booting, or heading stage reduce similar amount of yield. Yield reduction when drought stress occurred during vegetative stage, was attributed mostly due to reduction in number of productive tillers per hill (Sarvestani et al. 2008). The reduction could reach up to 30% (Hossain et al. 2016). Rice yield could significantly decrease if drought occurred during panicle development (Pantuwan et al. 2002) or flowering (Zhang et al. 2018). The most critical component which determines viability of rice reproductive organs is associated with supply of assimilates. Yield reduction in plants exposed to drought stress was due to limited supply of assimilating produced via photosynthesis (Moonmoon and Islam 2017). Photosynthetic activity declined during several days of drought stress, while assimilates were continuously demanded respiration. This imbalance in carbohydrate metabolism could severely halt development of reproductive organs that might lead to abortion (Barnabás et al. 2008). Furthermore, Singh et al. (2012) reported that drought stress during flowering reduced pollination success, increased flower abortion, reduced grain size, and increased percentage of sterile grains. In addition, drought stress affected capacity of reproductive organ to utilize the supplied assimilates that caused flower abortion (Farooq et al. 2009).

During rice seed germination and seedling growth test, priming with 20% PEG solution fastened germination, i.e. T50 was achieved within 19.55 h. However, seedling growth was not affected by PEG priming up to 20%. Positive effects of higher (20%) PEG concentration on seedling growth seemed to be short, only up to 4 WAT and at 7 WAT the effect was diminished. Measurement during vegetative stage at 7 WAT revealed that osmo-priming at 15-20% PEG only induced early tiller development but produced non-significantly different number of tillers, leaf SPAD value, and total leaf area.

After 32 h, all Inpago varieties performed better (>95%), except for Inpago 8 and other varieties which germinated at <95%. Amongst nine varieties evaluated, the highest leaf, stem, and roots weights were revealed in seedling of Inpago 10, During vegetative stage, Inpago 10 variety also produced the highest number of tillers and total leaf area. Variety of Rindang 1 consistently smaller than all other varieties.

At harvest, root and stem fresh and dry weighs were favored in rice plant pre-treated with osmo-priming at 20% PEG, least negatively affected by drought exposure during booting compared to late vegetative or heading period, and highest in Inpago 10 compared to other varieties. However, priming with 20% PEG lowered filled spikelet and grain weight. Drought during late vegetative stage lessened number of tillers but after recovery during reproductive stage, percentage of filled spikelet and grain size was not affected. Meanwhile, drought during reproductive stage decreased percentage of filled spikelets. Despite its better performance under drought conditions, leaf rolling score was higher during heading stage in Inpago 10 or plants pre-treated with osmo-priming with 20% PEG. These phenomena indicated that leaf rolling was not a post effect of drought, rather it was a quick response of Inpago 10 variety to limit water loss due to transpiration.

In conclusion, osmo-priming using PEG solution showed better effect on rice growth than hydro-priming. However, the positive effect of osmo-priming was more pronounce during germination, seedling growth, and early vegetative growth in rice varieties studied. Carryover effect of osmo-priming into reproductive stage was not very clear, perhaps the effect was superimposed by drought treatments. Less negative impact of drought exposure was observed during late vegetative stage; although number of tillers was reduced, grain filling was not affected due to ability of rice plants to recover after drought treatment was terminated. Leaf rolling was a strategy for limiting water loss, not a passive response to drought as indicated by better yield performance of Inpago 10 variety which exhibited fully rolled leaves (LRS = 9). Amongst nine varieties evaluated, Inpago 10 exhibited better response to priming treatments as indicated by seed emergence and early seedling growth performance and was the least negatively affected by drought exposure.

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