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Provenance variation in seed storability of jabon (*Neolamarckia cadamba*) and their response to seed invigoration by priming and gamma irradiation treatments

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Abstract. *Sudrajat DJ, Rustam E, Widyani N. 2022. Provenance variation in seed storability of jabon (*Neolamarckia cadamba*) and their response to seed invigoration by priming and gamma irradiation treatments. Biodiversitas 23: 5074-5084.* Jabon (*Neolamarckia cadamba* (Roxb.) Bosser) is a tree species native to Indonesia with a wide growth distribution and high economic potential, but the cultivation of this species is often hampered by low seed viability and vigor, especially for seeds that have undergone storage. This study aims to examine the provenance variation in seed germination and storability of *N. cadamba* and the effectiveness of invigoration treatments on the stored seed for 5 years. Hydro-priming, osmo-priming, hormone-priming, and gamma irradiation were tested to improve seed germination and seedling growth. The results showed that intra-population variation in seed germination and storability is quite high, ranging from 53.5%-82.8% for germination capacity and rate of germination decline ranging from 0.7%-61.6% after 5 years of storage. Pomalaa provenance had the best seed germination and storability compared to other provenances. The invigoration treatment significantly affected germination and seedling growth of all provenances. Hydro-priming with aquades for 48 hours gave the best germination capacity for Pomalla and Batuhijau provenances. For low initial germination, such as seed from Kapuas, Alas Purwo, and Kampar, the GA_3 500 ppm for 48 hours and PEG -1.2 MPa for 24 hours treatments could improve seed viability and vigor. GA3 and gamma irradiation gave the best seedling growth, although other treatments, such as PEG -0.8 MPa for 24 hours, also could increase seedling height and biomass of Kampar provenance. In general, the effectiveness of the invigoration treatment depends on the initial physiological conditions, the invigoration method, and its concentration.

Keywords: Invigoration, *Neolamarckia cadamba*, seed storage, viability

INTRODUCTION

Jabon [*Neolamarckia cadamba* (Roxb.) Bosser, synonym *Anthocephallus cadamba* (Roxb.) Miq] is a fast-growing native Indonesian tree species that are potential to be developed as a plantation crop and community forest (Sudrajat et al. 2015). The *N. cadamba* is categorized as multiple uses tree species that can be used for plywood, light construction, pulp, and particle board (Sudrajat 2015), and several parts of the plant (fruit, leaf, and bark) also are the potential for medicines (Fatima et al. 2016; Rubi et al. 2018; Khandelwal and Choudhary 2020). At present, the species have been cultivated in large areas and small-scale plantations, especially in Indonesia (Java and Sumatra) (Sudrajat 2016).

High interest in *N. cadamba* cultivation is not balanced with adequate knowledge and skill in silviculture practices, especially seed and seedling procurement techniques (Irawan and Purwanto 2014). Furthermore, the seed storability of *N. cadamba* is not yet precisely identified. According to Mansur (2012), *N. cadamba* seed is not recommended for long-term storage because the seed germination will be significantly decreased after 2-3 months of storage. On the other hand, Yulianti and Nurhasybi (2015) stated that the *N. cadamba* seed is categorized as an orthodox seed that can be stored in the long term in low temperatures and low seed moisture content (4-8%). Seed storability is influenced by many factors, such as seed structure, biochemical composition, dormancy (Lin et al. 2021), seed processing (Khatun et al. 2009), ecology of mother plant (Sudrajat 2016), storage period and condition (Suszka et al. 2014) and genetic (Arif et al. 2012; Hay et al. 2019). Seed storage is aimed at maintaining the seed quality (viability) at the highest level possible for preserving planting stocks from one season to the next or maintenance of germplasm over time for an improved plant breeding program (Chala and Bekana 2017).

Seed deterioration would occur as long as storage is caused by physical, physiological, and biochemical changes such as loss of membrane integrity, reduced energy metabolism, protein synthesis, degradation of DNA, and impairment of RNA in the seed affected by declining seed viability and vigor (Shaban 2013). Many factors causing seed deterioration during storage are relative air humidity, temperature, oxygen, seed structure, and genetics. During storage, a number of physiological and chemical changes occur, termed aging. Improving the quality of deteriorated seed could be carried out by seed invigoration treatments, such as priming techniques (Raj and Raj 2019) and gamma irradiation (Zanzibar and Sudrajat 2016; Syamsuwida et al. 2020).

Table 1. Background geo climate information of *Neolamarckia cadamba* provenances and the seed's physical and chemical characteristics

Geoclimate and seed characteristics	Provenance				
	Alas Purwo	**Kampar**	**Batuhijau**	**Kapuas**	**Pomalaa**
Geoclimate:					
Latitude	08°38' S	00°18' N	08°58' S	01°00' S	04°03' S
Longitude	114°21' E	100°57' E	116°48' E	114°28' E	121°39'E
Altitude (m asl)	33	50	53	147	210
Precipitation (mm year^{-1})	1500	3000	2290	2970	1780
Climate type (Schmidt and Fergusson)	D-E	A	D	A	C
Seed characteristics:					
Seed length (μm)	584.4	567.4	586.4	607.5	623.9
Seed width (μm)	459.4	434.7	388.8	388.3	440.5
Weight of 1000 seed (mg)	37.7	39.3	46.1	35.8	46.9
Carbohydrate content (%)	72.89	72.55	74.54	73.42	73.01
Protein content (%)	14.05	14.88	15.01	14.53	14.40
Fat content (%)	0.68	0.50	0.60	0.16	1.80

Priming can partially improve the germination capability, uniform seedling emergence, seedling vigor, and growth of deteriorated poor-quality seed lots via some metabolic and physiological repairs within the seed. Priming can be carried out by several methods that rely on the type of priming agents. These include hydropriming, osmopriming, hormone priming, solid matrix, halopriming, hardening, humidification and stratification, and thermal shock (Lemarsky and Hasseini 2012; Abhilash et al. 2020). The effectivity of priming in improving seed germination was reported on some plant species, such as *Gmelina arborea* (Siregar et al. 2020) and *Albizia chinensis* (Sudrajat et al. 2022). Gamma irradiation in low doses is able to stimulate early germination by increasing enzyme activity, increasing cell division, and stimulation by activation of RNA/protein synthesis or the phenomenon that irradiation inhibited the population of bacteria/fungi carried inherently by the seeds so that the seed could germinate better (Iglesias-Andreu et al. 2012; Araújo et al. 2016). Gamma irradiation has been studied on several tropical tree species, such as *Magnolia champaca* and *Toona sureni* (Zanzibar and Sudrajat 2016; Zanzibar et al. 2021). However, in general, the application of invigoration in the practice of tropical forest tree nurseries in Indonesia is still limited (Syamsuwida et al. 2020). This research is aimed to evaluate the seed storability of 5 provenances of *N. cadamba* and their response to hydropriming, chemical priming (polyethylene glycol and gibberellin acid), and gamma irradiation treatments.

MATERIALS AND METHODS

Seed collection

Seeds were collected from 5 natural populations (provenances), i.e., Kampar (Sumatra), Alas Purwo (East Java), Kapuas (Central Kalimantan), Pomalaa (Southeast Sulawesi), dan Batuhijau (Sumbawa Island) (Table 1). The seed collection was conducted on the 10-20 dominant seed trees per provenance. Seed extraction was carried out by wet method and continuously by seed drying in ambient conditions for 2-3 days (Sudrajat 2016). The seeds collected from individual seed trees were equally sampled by weight and bulked by provenance, and some physical traits were measured for each provenance (Table 1).

Seed storage and testing

Seed testing and storage were carried out at the Seed Technology Laboratory, Forest Tree Seed Technology Research and Development Center (FTSTRDC), Bogor, West Java, Indonesia. Prior to seed storage, the seed moisture content was measured by low-temperature oven method at 103±2°C for 17 hours (Sudrajat 2016). Seed biochemical traits (carbohydrate, protein, and fat) were measured at the Laboratory of Plant and Nutrition, SEAMEO-BIOTROP, Bogor (Table 1). Seeds were stored in the refrigerator (temperature 0-4°C, relative humidity 40-50%) for 5 years. A germination test was carried out before and after storage using a test on sand-sowing media in a greenhouse. Prior to sowing, the sand media was sterilized by steaming it at 100ºC for 2 hours. The media also was treated with 0.2% fungicide (antracol) to avoid any chances of fungus infection attacking newly germinated seedlings.

A completely randomized design with provenance as a factor was used to test the storability of *N. cadamba* seeds from 5 provenances. The number of seeds sown was 100 seeds with 4 replications for each provenance. The seeds were sown evenly on the surface of the sand media, and the seedlings were watered with a fine sprayer to keep them wet and were maintained in the greenhouse. Testing of seeds after storage was carried out with the same method as the seeds before storage. Likewise, the observed germination parameters were the same as the observations in the initial test before the seeds were stored. The criteria for normal *N. cadamba* seedlings are the appearance of a pair of leaves perfectly. Germination was carried out for 28 days by observing and calculating several germination parameters, i.e., germination capacity, germination rate, mean germination time, and germination value (Sudrajat 2016). The following formula was used to perform the calculation (Gairola et al. 2011):

Germination capacity

$$\text{Germination capacity} = \frac{\text{Number of normal seedling}}{\text{Total Number of seeds}} \text{x100\%}$$

Germination rate

$$\text{Germination rate} = \frac{n_1}{d_1} + \frac{n_2}{d_2} + \frac{n_3}{d_3} + \cdots + n_{ni}/d_i$$

Where:
n = number of germination seed
d = number of days

Mean germination time

$$\text{Mean germination Time} = \frac{n_1 x d_1 + n_2 x d_2 + n_3 x d_3 + \cdots n_i x d_i}{\text{Total number of days}}$$

Where:
n = number of germination seed
d = number of days

Germination value

$$\text{Germination value} = \text{PV X MDG}$$

$$\text{Peak value (PV)} = \frac{\text{Highest seed germinated}}{\text{Total Number of days}}$$

$$\text{Mean daily germination (MDG)} = \frac{\text{Total number of germination seeds}}{\text{Total Number of seeds}} \text{x100\%}$$

Seed invigoration treatment

The invigoration methods applied in this research are hydropriming, hormone priming, osmo-conditioning and physical invigoration using gamma ray irradiation. In the priming technique, seeds were immersed in petri-dish for each method, hydropriming (soaking in distilled water), osmo-conditioning (soaking in PEG 6000) at osmotic potentials of 0, -0.4, -0.8 and -1.2 Mpa (Janmohammadi et al. 2008), and hormone priming (soaking in GA_3) doses of 0, 250, 500 and 750 ppm. Determination of the PEG dosage adopted the formula (Michel and Kaufman 1973). The soaking ratio between seed and priming solution was 1:5 (w/v) (Rustam et al. 2017). Immersion was carried out for 0, 12, 24 and 48 hours in a dark room, a temperature of 15-25°C and a relative humidity of 45% (Janmohammadi et al. 2008). Invigoration treatment with gamma irradiation was carried out with doses of 10 Gy, 20 Gy, 30 Gy, 40 Gy, and 50 Gy using Gamma Cell 220 with a radiation source of ^{60}Co (Cobalt-60) and a rate of 6645.7 Gy hour^{-1} in the Center for Application of Isotope and Radiation Technology, National Nuclear Energy Agency, Jakarta.

Completely randomized design was used to examine the effect of 27 seed invigoration treatments (control, 2 hydropriming treatments, 9 PEG 6000 treatments, 9 GA_3 treatments, and 6 gamma irradiation treatments) on several parameters of *N. cadamba* seed germination. Each treatment was repeated 4 times and each replicated 100 seeds. Germination testing was carried out using a test on sand that had been sterilized by steaming at 100ºC for 2 hours. The seeds were sown evenly on the surface of the sand media and the seedlings were watered with a fine sprayer to keep them wet and were maintained in the greenhouse. The germination parameters observed were germination capacity, germination rate, and germination value (Sudrajat 2016).

Seedling quality testing

Seedling quality testing is a continuation of germination testing in a greenhouse with the same treatment. The testing used completely randomized block design within 3 replications (blocks), involving 27 seed invigoration treatments, and each treatment consisted of 20 seedlings. Seedlings that had been germinated on sand media for 2 months and had grown into normal seedlings were transplanted to polybags sized 10 cm in diameter and 15 cm in height, containing media consisted of top soil, sand and compost in a ratio of 3:2:1 (volume) and were set up in nursery (Sudrajat 2016). Seedlings were grown at 50% light intensity using shading net and maintained by controlling weeds and watering regularly. Seedling height, root collar diameter and total biomass were carried out at the end of the observation (4 months after transplanting). Seedling height was measured using a ruler from the initial limit of stem growth to the end of the growing point. Stem diameter was measured using a digital caliper at the base of the stem. The seedling biomass was calculated by 3 seedlings (replications) per treatment. The measurement of the total seedling biomass was carried out by drying all parts of the seedlings (roots, stems and leaves) in an oven at 70°C for 48 hours (Sudrajat 2016).

Data analysis

The observation data were analyzed with SPSS software version 25. One-way analysis of variance was used to analyze the two part of research, i.e., *N. cadamba* seed storability in provenance level stored for 5 years and the effect of invigoration treatments on the seed vigor and seedling growth. If the results of the analysis of variance have a significant effect, then the Duncan Multiple Range Test (DMRT) test is continued at the 5% level. The relationship between seed characteristics and seed germination before and after storage was calculated using simple correlations (Pearson's) at $p < 0.05$.

RESULTS AND DISCUSSION

Provenances variation in seed germination and storability

Provenances significantly affected all germination parameters of *N. cadamba* seeds, both before and after storage for 5 years, except for moisture content before storage and mean germination time after storage. Seed germination varied between provenances and Pomalaa provenance seed had the highest germination capacity (82.8%), followed by Kapuas, Kampar, Batuhijau, and Alas Purwo provenances seeds. Germination capacity of all provenances decreased after 5 years of storage (Table 2). The moisture content of the seeds before storage ranged from 5.6-7.5%, with the lowest water content found in the Pomalaa provenance seed and the highest moisture content in the Kampar provenance seed. After 5 years of storage, the moisture content for all provenances ranged from 4.1-

6.3%, decreased by about 1.10-2.94% from the initial water content (Table 2).

In general, germination capacity decreased after storage. The low initial seed moisture content can increase the seed storability. Pomalaa provenance seed with lower moisture content had the highest germination capacity both before (82.8%) and after storage (79.0%). Judging from the level of moisture content and germination capacity after storage, *N. cadamba* seed can be categorized as orthodox seed. Seed vigor parameters such as germination rate, mean germination time, and germination value also decreased after storage. The mean germination time before storage was 13 days, and after being stored for 5 years become 15-18 days (Table 2). After storage, the Pomalaa provenance seed had a mean germination time of 15 days faster than other provenances. Pomalaa provenance seed experienced a relatively lower decrease in vigor compared to seeds from other provenances, while the highest decrease in seed vigor was experienced by Kampar provenance seed. Based on simple correlations (Pearson's), seed characteristics (Table 1) which showed a positive correlation with germination capacity were the correlation of initial seed moisture content with germination capacity after storage (r2 = -0.93), weight of 1000 seeds and germination capacity after storage (r2 = -0.93). (r2 = 0.86), and fat content with germination capacity after storage (r2 = 0.86) (Figure 1).

Effect of invigoration treatment on seed germination

Analysis of variance showed that the invigoration treatment significantly affected all parameters of seed germination (germination capacity, germination rate, and germination value) for all tested provenances, except for the germination value of seeds from the Kampar provenance (Figure 2, Table 3). The seeds with relatively high germination capacity before invigoration treatments, such as seeds from Pomalaa (79.0%) and Batuhijau (67.5%), hydropriming treatment (soaking in aquades for 48 hours) gave the best germination capacity and germination rate, with germination capacity was 97.3% and 85.0%, and germination rate were 6.6% day^{-1} and 5.7% day^{-1}, respectively. In addition, the hydropriming treatment for 48 hours was able to give the highest germination value in the Pomalaa provenance seed (12.8) (Table 3).

The seed lots with relatively low initial germination such as Kapuas provenance seed, the soaking in GA_3 500 ppm for 48 hours gave the best germination capacity of 52.3% (control 38.8%), respectively (Figure 2). Improvement in seed germination parameters also occurred in the germination rate and germination value (Table 3). Soaking in PEG -1.2 MPa for 24 hours was able to improve viability and vigor of low-vigor *N. cadamba* seeds such as Alas Purwo and Kampar provenance seeds with initial germination capacity of 40.8% and 26.5%, respectively, to 52.3% and 35.5% after the treatment. The treatment was also able to increase the germination rate of Alas Purwo and Kampar provenance seeds, as well as the germination value of Alas Purwo provenance seed (Table 3).

Table 2. Moisture content and germination parameters of *Neolamarckia cadamba* seeds before and after storage for 4.5 years

Provenance	MC (%)		GC (%)		GR (% day^{-1})		MGT		GV	
	BS	AS	BS	AS	BS	AS	BS	AS	BS	AS
Alas Purwo	7.3 ab	4.5	53.3 e	40.8 c	4.3 d	2.6 c	13	17 abc	3.8 c	1.2 c
Kampar	7.5 a	4.9	69.0 c	26.5 d	5.6 b	1.6 d	13	18 abc	6.5 b	0.4 d
Batuhijau	6.9 b	4.1	63.0 b	62.5 b	4.2 d	4.1 b	13	17 abc	3.7 c	1.9 b
Kapuas	7.5 ab	4.9	75.3 b	38.8 c	6.0 b	2.4 c	13	17 abc	6.4 b	0.8 cd
Pomalaa	5.6 c	4.5	82.8 a	79.0 a	6.7 a	5.4 a	13	15 c	8.7 a	4.5 a
F-test	**	ns	**	**	**	**	ns	*	**	**

Note: MC: moiture content, GC: germination capacity, GR: germination rate, MGT: mean germination time, GV: germination value, BS= before seed storage, AS: after seed storage; **: significant at 1%, ns: ns= non-significant; Values followed by different letters in the same column indicate significant differences at P ≤ 0.05 based on Duncan Multiple Range Test

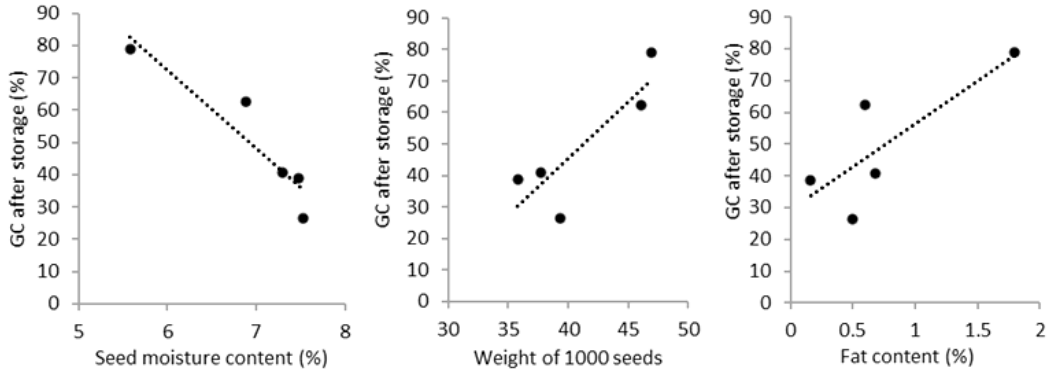

Figure 1. Correlation of *Neolamarckia cadamba* seed moisture content, weight of 1,000 seeds, and fat content with germination capacity (GC) after storage for 5 years

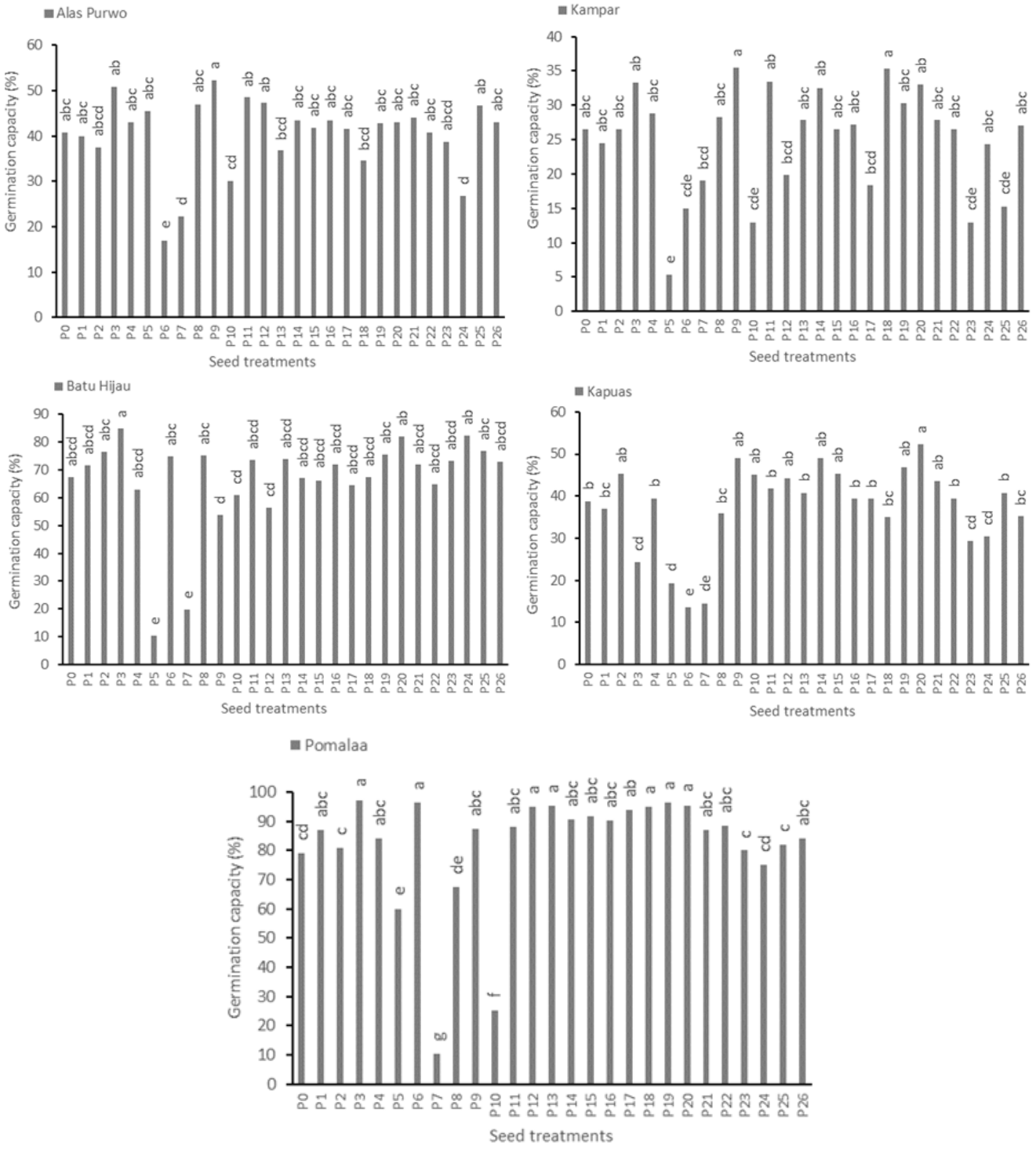

Figure 2. Effect of hydro-chemical priming and gamma irradiation on the germination capacity of *Neolamarckia cadamba* seeds from 5 provenances. Note: P0: control, P1: soaking in aquades for 12 hours, P2: soaking in aquades for 24 hours, P3: soaking in aquades for 48 hours, P4: PEG 6000 -0.4 Mpa for 12 hours, P5: PEG 6000 -0.8 Mpa for 12 hours, P6: PEG 6000 -1.2 Mpa for 12 hours, P7: PEG 6000 -0.4 Mpa for 24 hours, P8: PEG 6000 -0.8 Mpa for 24 hours, P9: PEG 6000 -0.4 Mpa for 48 hours, P10: PEG 6000 -0.4 Mpa for 48

Table 3. Effect of hydro-chemical priming and gamma irradiation on the germination rate and germination value of *Neolamarckia cadamba* seeds from 5 provenances

Seed treatment	Provenance				
	Alas Purwo	**Kampar**	**Batuhijau**	**Kapuas**	**Pomalaa**
Germination rate (% day^{-1})					
Control	2.6 b-e	1.6 abc	4.5 a-e	2.4 ab	5.4 bcd
Soaking in aquades for 12 hours	2.7 b-e	1.4 abc	5.2 ab	2.4 ab	6.2 ab
Soaking in aquades for 24 hours	2.4 c-f	1.5 abc	4.7 a-e	2.6 ab	5.5 bcd
Soaking in aquades for 48 hours	3.3 ab	2.0 ab	5.7 a	1.5 cde	6.6 a
PEG 6000 -0.4 Mpa for 12 hours	2.8 b-e	1.6 abc	4.3 a-e	2.5 ab	5.4 bcd
PEG 6000 -0.8 Mpa for 12 hours	2.9 a-d	2.0 ab	0.7 f	1.3 de	4.0 e
PEG 6000 -1.2 Mpa for 12 hours	0.5 g	0.9 cde	5.1 abc	0.8 ef	6.2 ab
PEG 6000 -0.4 Mpa for 24 hours	1.4 f	0.5 de	1.3 f	0.3 f	0.6 g
PEG 6000 -0.8 MPa for 24 hours	3.2 abc	1.8 abc	4.9 a-d	2.3 abc	4.8 de
PEG 6000 -1.2 MPa for 24 hours	3.9 a	2.4 a	3.7 cde	2.9 ab	5.9 abc
PEG 6000 -0.4 MPa for 48 hours	1.9 ef	0.8 e	3.9 b-e	2.7 ab	1.5 f
PEG 6000 -0.8 MPa for 48 hours	2.9 a-d	1.2 bcd	4.3 a-e	2.5 ab	5.6 a-d
PEG 6000 -1.2 MPa for 48 hours	2.8 b-e	1.1 bcd	3.4 e	2.7 ab	5.6 a-d
GA_3 250 ppm for 12 hours	1.9 ef	1.5 abc	4.3 a-e	2.1 bc	5.5 bcd
GA_3 500 ppm for 12 hours	2.2 c-f	1.7 abc	3.6 de	2.1 bc	5.2 bcd
GA_3 750 ppm for 12 hours	2.3 c-f	1.4 bcd	3.7 cde	2.5 ab	5.2 bcd
GA_3 250 ppm for 24 hours	2.5 b-e	1.5 abc	4.3 a-e	2.3 abc	5.5 bcd
GA_3 500 ppm for 24 hours	2.4 b-e	1.3 bcd	3.9 b-e	2.9 ab	5.6 bcd
GA_3 750 ppm for 24 hours	1.9 def	2.0 ab	4.1 b-e	2.0 bcd	5.5 bcd
GA_3 250 ppm for 48 hours	2.4 b-e	1.6 abc	4.5 a-e	2.5 ab	5.6 a-d
GA_3 500 ppm for 48 hours	2.3 b-e	1.9 ab	4.6 a-e	**3.1 a**	5.50bcd
GA_3 750 ppm for 48 hours	2.5 b-e	1.5 abc	4.2 a-e	2.3 abc	4.9 cd
Gamma ray irradiation 10 Gy	1.9 ef	1.3 bcd	3.6 de	1.3 de	5.4 bcd
Gamma ray irradiation 20 Gy	2.1 def	0.7 cde	4.0 b-e	2.1 bc	5.4 bcd
Gamma ray irradiation 30 Gy	1.6 ef	1.3 bcd	4.4 a-e	2.2 bc	4.2 def
Gamma ray irradiation 40 Gy	2.7 b-e	0.7 cde	4.5 a-e	2.3 ab	4.7 de
Gamma ray irradiation 50 Gy	2.4 c-f	1.5 abc	4.3 a-e	1.8 bcd	4.8 de
F-test	**	**	**	**	**
Germination value					
Control	1.16 cde	0.41	1.90 def	0.76 fgh	4.52 ghi
Soaking in aquades for 12 hours	1.19 cde	0.27	2.86 def	0.92 e-h	5.07 fgh
Soaking in aquades for 24 hours	1.20 cde	0.39	3.05 def	1.22 c-g	3.99 hij
Soaking in aquades for 48 hours	3.71 ab	0.92	6.95 ab	2.73 ab	12.75 a
PEG 6000 -0.4 MPa for 12 hours	2.27 bcd	0.63	4.89 bcd	1.92 b-e	5.38 fgh
PEG 6000 -0.8 MPa for 12 hours	2.88 bc	1.10	0.20 f	0.65 fgh	4.97 gh
PEG 6000 -1.2 MPa for 12 hours	0.14 e	0.25	3.29 def	0.21 gh	12.32 abc
PEG 6000 -0.4 MPa for 24 hours	0.58 de	0.08	0.77 ef	0.02 h	0.25 j
PEG 6000 -0.8 MPa for 24 hours	2.95 bc	0.80	6.66 abc	1.12 d-g	8.23 c-h
PEG 6000 -1.2 MPa for 24 hours	5.34 a	2.53	2.93 def	2.23 bc	8.68 a-f
PEG 6000 -0.4 MPa for 48 hours	0.76 de	0.01	3.56 c-f	1.15 d-g	0.86 ij
PEG 6000 -0.8 MPa for 48 hours	1.76 cde	0.81	4.59 bcd	1.16 d-g	8.52 a-f
PEG 6000 -1.2 MPa for 48 hours	1.43 cde	0.30	3.76 b-e	2.01 bcd	9.47 a-f
GA_3 250 ppm for 12 hours	1.32 cde	0.42	3.89 b-e	1.63 c-f	9.84 a-e
GA_3 500 ppm for 12 hours	1.22 cde	0.39	3.18 def	1.23 c-g	8.42 b-h
GA_3 750 ppm for 12 hours	1.30 cde	0.62	2.75 def	1.32 c-f	7.52 d-h
GA_3 250 ppm for 24 hours	1.29 cde	0.41	3.38 def	1.29 c-f	6.89 d-h
GA_3 500 ppm for 24 hours	2.21 bcd	0.84	6.93 ab	0.63 fgh	6.46 e-h
GA_3 750 ppm for 24 hours	1.62 cde	1.52	6.96 ab	1.96 b-e	10.95 a-d
GA_3 250 ppm for 48 hours	2.10 b-e	0.78	8.50 a	1.62 c-f	12.67 ab
GA_3 500 ppm for 48 hours	1.66 cde	1.30	6.91 ab	3.30 a	12.87 a
GA_3 750 ppm for 48 hours	2.26 bcd	0.68	6.87 ab	1.46 c-f	7.46 d-h
Gamma ray irradiation 10 Gy	0.76 de	0.42	3.76 b-e	0.30 gh	8.22 c-h
Gamma ray irradiation 20 Gy	0.91 de	0.16	3.14 def	0.92 e-h	6.78 e-h
Gamma ray irradiation 30 Gy	0.55 de	0.36	3.38 def	0.95 e-h	5.14 fgh
Gamma ray irradiation 40 Gy	1.53 cde	0.23	3.54 c-f	1.07 d-g	3.79 hij
Gamma ray irradiation 50 Gy	1.31 cde	0.46	4.72 bcd	0.76 fgh	3.64 hij
F-test	**	ns	**	**	**

Note: **: significant at 1%, *: significant at 5%; Values followed by different letters in the same column indicate significant differences at $P \leq 0.05$ based on Duncan Multiple Range Test

Table 4. Effect of hydro-chemical priming and gamma ray irradiation on the seedling height, root collar diameter and biomass of five *Neolamarckia cadamba* provenances

Seed treatments	Provenance				
	Alas Purwo	**Kampar**	**Batuhijau**	**Kapuas**	**Pomalaa**
Seedling height (cm)					
Control	40.8 abc	26.5 abc	67.5 a-d	38.8 b	79.0 cd
Soaking in aquades for 12 hours	40.0 abc	24.5 abc	71.5 a-d	37.0 bc	87.0 abc
Soaking in aquades for 24 hours	37.5 a-d	26.5 abc	76.5 abc	45.3 ab	80.8 c
Soaking in aquades for 48 hours	50.8 ab	33.3 ab	85.0 a	24.3 cd	97.3 a
PEG 6000 -0.4 MPa for 12 hours	43.0 abc	28.8 abc	63.0 a-d	39.5 b	84.0 abc
PEG 6000 -0.8 MPa for 12 hours	45.5 abc	5.3 e	10.3 e	19.3 d	60.0 e
PEG 6000 -1.2 MPa for 12 hours	7.0 e	15.0 cde	75.0 a-d	13.5 de	96.3 a
PEG 6000 -0.4 MPa for 24 hours	22.3 d	9.0 de	19.8 e	4.5 e	10.5 g
PEG 6000 -0.8 MPa for 24 hours	47.0 abc	28.3 abc	75.3 a-d	35.8 bc	67.5 de
PEG 6000 -1.2 MPa for 24 hours	52.3 a	35.5 a	53.8 d	49.0 ab	87.3 abc
PEG 6000 -0.4 MPa for 48 hours	30.0 cd	3.0 e	61.0 cd	45.0 ab	25.3 f
PEG 6000 -0.8 MPa for 48 hours	48.5 ab	33.5 ab	73.5 a-d	41.8 ab	88.0 abc
PEG 6000 -1.2 MPa for 48 hours	47.3 ab	19.8 bcd	56.5 cd	44.3 ab	95.0 a
GA_3 250 ppm for 12 hours	36.8 bcd	27.8 abc	73.8 a-d	40.8 ab	95.3 a
GA_3 500 ppm for 12 hours	43.5 abc	32.5 ab	67.0 a-d	49.0 ab	90.5 abc
GA_3 750 ppm for 12 hours	41.8 abc	26.5 abc	66.0 a-d	45.3 ab	91.8 abc
GA_3 250 ppm for 24 hours	43.5 abc	27.2 abc	71.8 a-d	39.3 b	90.3 abc
GA_3 500 ppm for 24 hours	41.5 abc	18.3 bcd	64.5 a-d	39.3 b	94.0 ab
GA_3 750 ppm for 24 hours	34.5 bcd	35.3 a	67.3 a-d	35.0 bc	95.0 a
GA_3 250 ppm for 48 hours	42.8 abc	30.3 abc	75.5 a-d	46.8 ab	96.3 a
GA_3 500 ppm for 48 hours	43.0 abc	33.0 ab	82.0 ab	52.3 a	95.5 a
GA_3 750 ppm for 48 hours	44.0 abc	27.8 abc	72.0 a-d	43.5 ab	87.0 abc
Gamma ray irradiation 10 Gy	40.8 abc	26.5 abc	64.8 a-d	39.5 b	88.3 abc
Gamma ray irradiation 20 Gy	38.8 a-d	13.0 cde	73.3 a-d	29.3 cd	80.0 c
Gamma ray irradiation 30 Gy	26.8 d	24.3 abc	82.3 ab	30.5 cd	75.0 cd
Gamma ray irradiation 40 Gy	46.8 ab	15.3 cde	76.8 abc	40.8 ab	82.0 c
Gamma ray irradiation 50 Gy	43.0 abc	27.0 abc	72.8 a-d	35.3 bc	84.0 abc
F-test	**	**	**	**	**
Root collar diameter (mm)					
Control	2.77 c-f	2.79 a-d	2.90 c-h	2.47 c-g	2.87 bcd
Soaking in aquades for 12 hours	1.85 j	1.84 de	2.33 e-h	1.77 hij	1.99 e
Soaking in aquades for 24 hours	2.43 d-j	2.73 a-d	2.35 e-h	1.69 hij	2.62 cde
Soaking in aquades for 48 hours	2.34 e-j	2.18 b-e	2.89 c-g	1.67 ij	2.56 cde
PEG 6000 -0.4 Mpa for 12 hours	1.95 ij	2.48 bcd	1.94 h	1.50 j	2.29 de
PEG 6000 -0.8 Mpa for 12 hours	2.49 c-i	2.96 abc	2.89 c-g	2.98 cd	2.95 bcd
PEG 6000 -1.2 Mpa for 12 hours	3.39 ab	3.05 abc	2.29 e-h	2.25 e-i	2.44 cde
PEG 6000 -0.4 Mpa for 24 hours	2.02 hij	-	3.04 cd	2.74 b-f	2.00 e
PEG 6000 -0.8 Mpa for 24 hours	2.16 f-j	2.59 bcd	2.27 fgh	1.71 hij	2.38 cde
PEG 6000 -1.2 Mpa for 24 hours	2.74 c-f	2.30 b-e	2.21 gh	2.17 f-i	2.17 de
PEG 6000 -0.4 Mpa for 48 hours	2.06 g-j	3.08 bc	3.76 ab	3.17 ab	3.62 bc
PEG 6000 -0.8 Mpa for 48 hours	1.21 k	1.96 de	2.77 c-g	2.03 g-j	3.15 bc
PEG 6000 -1.2 Mpa for 48 hours	1.25 k	2.43 bcd	1.88 h	1.90 g-j	2.16 de
GA_3 250 ppm for 12 hours	-	2.09 b-e	3.25 bc	1.53 j	2.52 cde
GA_3 500 ppm for 12 hours	3.65 a	2.51 bcd	3.07 c	3.60 a	2.50 cde
GA_3 750 ppm for 12 hours	3.12 abc	3.63 a	4.18 a	2.80 b-e	4.17 a
GA_3 250 ppm for 24 hours	2.67 c-g	-	3.04 cd	2.86 bcd	-
GA_3 500 ppm for 24 hours	2.70 c-f	1.43 ef	2.38 d-h	2.28 d-h	2.62 cde
GA_3 750 ppm for 24 hours	2.96 b-e	2.08 cde	2.93 c-f	2.69 b-f	4.16 a
GA_3 250 ppm for 48 hours	3.05 bcd	0.85 f	2.97 cde	2.48 c-g	3.53 ab
GA_3 500 ppm for 48 hours	1.97 ij	2.63 b-e	2.87 c-g	1.93 g-j	2.97 bcd
GA_3 750 ppm for 48 hours	2.61 c-h	2.36 b-e	2.32 e-h	1.90 g-j	2.66 cde
Gamma ray irradiation 10 Gy	1.73 ijk	1.78 de	2.56 d-h	2.13 f-i	3.13 bc
Gamma ray irradiation 20 Gy	1.98 ij	3.17 abc	2.50 d-h	2.51 c-g	2.70 cde
Gamma ray irradiation 30 Gy	2.87 c-f	2.39 b-e	2.74 c-g	3.35 ab	2.53 cde
Gamma ray irradiation 40 Gy	3.05 bcd	3.43 ab	2.92 c-h	3.04 abc	2.98 bcd
Gamma ray irradiation 50 Gy	2.13 g-j	3.00 bc	2.71 c-g	2.32 d-h	3.12 bc
F-test	**	**	**	**	**

Seedling biomass (gram)					
Control	4.88 jkl	5.15 fgh	5.14 c-f	4.69 gh	5.79 e
Soaking in aquades for 12 hours	5.50 f-i	4.94 ghi	6.52 bcd	5.23 efg	6.52 b-e
Soaking in aquades for 24 hours	5.85 def	4.86 ghi	6.30 b-e	5.08 fg	5.94 de
Soaking in aquades for 48 hours	5.33 g-j	5.39 efg	4.86 ef	4.74 gh	4.37 f
PEG 6000 -0.4 Mpa for 12 hours	4.93 ijk	4.69 ghi	6.32 be	5.40 efg	6.75 bcd
PEG 6000 -0.8 Mpa for 12 hours	4.37 lm	6.03 b-e	5.33 c-f	4.71 gh	6.02 cde
PEG 6000 -1.2 Mpa for 12 hours	6.09 bcd	4.46 hi	6.28 b-e	5.00 g	6.00 cde
PEG 6000 -0.4 Mpa for 24 hours	6.37 bcd	-	6.43 b-e	6.80 c	7.00 abc
PEG 6000 -0.8 Mpa for 24 hours	5.33 g-j	7.57 a	6.07 b-e	6.97 bc	3.70 fg
PEG 6000 -1.2 Mpa for 24 hours	6.03 c-f	6.76 bc	6.21 b-e	5.95 de	7.00 abc
PEG 6000 -0.4 Mpa for 48 hours	5.37 g-j	6.60 bc	6.17 b-e	8.09 a	6.22 b-e
PEG 6000 -0.8 Mpa for 48 hours	4.53 klm	5.50 d-g	4.96 def	3.55 i	7.10 ab
PEG 6000 -1.2 Mpa for 48 hours	6.87 b	6.09 b-e	6.48 bcd	6.05 de	6.40 cde
GA_3 250 ppm for 12 hours	-	5.93 c-f	5.88 be	5.86 ef	5.98 bcd
GA_3 500 ppm for 12 hours	8.04 a	6.86 gh	5.75 b-e	7.62 ab	6.80 bcd
GA_3 750 ppm for 12 hours	8.04 a	5.41 efg	9.23 a	4.14 hi	5.50 e
GA_3 250 ppm for 24 hours	5.24 hij	-	5.12 c-f	6.67 cd	-
GA_3 500 ppm for 24 hours	5.79 e-h	5.00 bcd	6.59 bc	5.47 efg	7.79 a
GA_3 750 ppm for 24 hours	5.79 e-h	4.80 ghi	6.59 bc	5.95 de	5.89 de
GA_3 250 ppm for 48 hours	4.90 jkl	6.31 bcd	4.22 f	3.72 i	5.70 e
GA_3 500 ppm for 48 hours	6.06 b-f	4.12 i	5.90 b-e	5.14 fg	5.56 e
GA**3** 750 ppm for 48 hours	6.50 bc	4.33 hi	7.02 b	6.00 de	6.48 b-e
Gamma ray irradiation 10 Gy	3.15 m	4.62 ghi	5.42 c-f	3.60 i	5.72 e
Gamma ray irradiation 20 Gy	4.80 jkl	5.13 fgh	3.68 f	5.92 de	5.40 e
Gamma ray irradiation 30 Gy	5.58 f-i	5.33 efg	4.62 sf	3.75 i	3.12 g
Gamma ray irradiation 40 Gy	5.85 def	5.83 c-f	9.85 a	9.94 a	7.88 a
Gamma ray irradiation 50 Gy	5.23 hij	5.38 efg	6.11 b-e	4.27 hi	4.00 efg
F-test	**	**	**	**	**

Notes: -: no data (the germination capacity was low and many seedlings die so that the data are not adequate for observation); Values followed by different letters in the same column indicate significant differences at $P \leq 0.05$ based on Duncan Multiple Range Test , **: significant at 1%

Effect of seed invigoration on the seedling growth

Invigoration treatment significantly affected all seedling growth parameters of the 5 *N. cadamba* provenances. In general, GA_3 and gamma irradiation treatments gave the best seedling growth, although other treatments such as PEG -0.8 MPa for 24 hours were also able to increase seedling height and biomass of Kampar provenance. Soaking the seeds in GA_3 500 ppm for 12 hours was able to increase the seedling height and root collar diameter of Kapuas provenance with 33.79 cm (control 18.85 cm) and 3.60 mm (control 2.77 mm), respectively. This treatment also increased the root collar diameter and biomass of the Alas Purwo provenance seedling. Meanwhile, soaking the seeds in GA_3 750 ppm for 12 hours was able to increase the seedling root collar diameter of Kampar, Batuhijau and Pomalaa provenances, as well as increase the seedling biomass of Alas Purwo and Batuhijau provenances (Table 4).

Another treatment that gave the best *N. cadamba* seedling growth was gamma irradiation at a dose of 40 Gy. This treatment was able to increase the growth of seedling height in Alas Purwo provenance from 15.37 cm (control) to 27.49 cm, Batuhijau provenance from 17.01 cm (control) to 28.89 cm, Pomalaa provenance from 13.62 cm (control) to 28.70 cm. In addition, the gamma ray irradiation at 40 Gy also produced the highest seed biomass in the Batuhijau, Kapuas, and Pomalaa provenances, at 9.85 g, 9.94 g, and 7.88 g, respectively (Table 4).

Discussion

The germination characteristics of a species are adapted to the site where the species grows (Sudrajat et al. 2014). Intra-population variation in seed germination is a common occurrence in forest tree species, as a result of genetic factors and different climatic conditions during seed ripening (Sudrajat 2016). In this study, the diversity of seed germination capacity between provenances was very high, ranging from 53.5% to 82.8%. High variability in germination between populations was also reported in *Nothofagus glauca* (Moya et al. 2017) and *Sterculia foetida* (Sudrajat et al. 2018).

Germination diversity between provenances also occurred after 5 years storage of *N. cadamba* seeds. Seed storage is influenced by seed quality at the time of storage, seed maturity level, moisture content, storage conditions (temperature and humidity), storage time, biotic agents, and genetic characteristics (Arif et al. 2012; Hay et al. 2019). *N. cadamba* seeds can be categorized as orthodox seeds (Yuniarti and Nurhasybi 2015) with initial moisture content ranging from 5.6-7.5%. Seed moisture content is the most important factor in increasing the storability of orthodox seeds, where at 4-8% moisture content, the seeds have safe conditions to be stored in an airtight container with a cold dry storage environment (Duong et al. 2013; Jyoti and Malik 2013; Syamsuwida et al. 2020).

In this study, seed storage caused a decrease in seed germination traits in all provenances. Germination capacity before and after storage was quite varied between

provenances. Diversity of seed germination and storability among provenances were also reported in *Swertia chirayita* (Pradhan and Badola 2012) and *S. foetida* (Sudrajat et al. 2018). Seed germination after storage for 5 years was significantly negatively correlated with initial seed moisture content (r^2 = -0.933). The Pomalaa provenance seed had the lowest initial moisture content, the highest germination and relatively lower vigor reduction during storage compared to seeds from other provenances, while the Kampar provenance seed had the highest seed moisture content and experienced the highest decline in germination. The higher the water content in the seeds, the faster the respiration and the more CO_2, water and heat are produced when the seeds are stored (Syamsuwida et al. 2020). High water content, temperature, and humidity can accelerate seed damage (Jyoti and Malik 2013). Low seed moisture content is also able to reduce seed pathogen attacks (Mukkun et al. 2018). Seed viability, vigor and storability are not only influenced by seed handling (Khatun et al. 2009), but are also related to genetic and environmental factors in which they are grown (Arif et al. 2012; Sudrajat 2016; Li et al. 2017; Hay et al. 2019). The seeds used in this study came from genetically diverse populations (Sudrajat et al. 2015) and varied growing conditions ranging from submerged to dry conditions which will affect water content and germination (Sudrajat 2016).

Morpho-physiology and biochemical content of *N. cadamba* seeds between provenances is quite diverse which also affects the storability of seeds. Seed germination after storage was also positively correlated with the weight of 1000 seeds (r^2 = 0.862) and fat content (r^2 = 0.859). Seed weight was also reported to be positively correlated with seed germination, as in *Triticum aestivum* (Moshatati and Gharineh 2012), and *Intsia palembanica* (Wulandari et al. 2015). Heavier seeds have more food reserves so that germination and storability are higher. Meanwhile, the fat accumulated in the seeds is in the form of triglycerides, and at the beginning of germination the fat is hydrolyzed with the help of lipase enzymes (Barros et al. 2021). Seeds from Pomalaa have size and weight as well as biochemical content (fat, protein, carbohydrates) which is higher (Table 1) and relatively low initial moisture content (Table 2) so that it is possible to have a longer seed storability.

In general, seed invigoration treatment with priming treatment and gamma irradiation gave a significant effect on seed germination. The effectiveness of each treatment depends on the condition of the seed, for seeds with high enough germination capacity, such as seeds from Pomalaa and Batuhijau, hydropriming treatment (soaking in aquadest for 48 hours) is effective enough to improve seed germination with an increase in germination capacity of 35% and 23%, respectively. The hydropriming for 48 hours was also effective in increasing the seed germination of *Momordica charantia* (Adhikari et al. 2021). The positive effect of hydropriming on seed germination was also reported in *Vicia faba* (Damalas et al. 2019), *Carum carvi* (Mirmazloum et al. 2020), and *Solanum melongena* (Forti et al. 2021). Seed storage in the long term can cause the seed coat to become drier and the seed moisture content to be lower (Table 2). Hydropriming treatment allows seeds to reach high humidity levels quickly and a constant supply of oxygen thereby activating enzymes that play a role in seed metabolism (Meena et al. 2013). This technique is also able to increase imbibition under controlled conditions, increase antioxidants and repair DNA when pre-germinative metabolism begins, while avoiding loss of desiccation tolerance (Paparella et al. 2015).

Meanwhile, for seeds with relatively low germination, such as seeds from Alas Purwo and Kampar, PEG -1.2 MPa for 24 hours was able to increase germination capacity, germination rate and germination value. Improved seed germination by PEG treatment was also reported in *Sorghum bicolor* (Zhang et al. 2015), *Vigna mungo* (Aryal et al. 2020), and *C. carvi* (Mirmazloum et al. 2020). PEG is a low potential osmotic solution. Soaking the seeds in PEG solution causes the environmental potential of the seeds to be low, so that the rate of water absorption is slowed and the duration of water absorption is extended which causes a strengthening (improvement) of the permeability of the plasma membrane and reduces the loss of cell electrolytes. The seeds can improve metabolism by optimizing internal factors to initiate germination. Recovery in seeds is in the form of membrane integrity, cell and enzyme activities as well as increased cellular respiration (Meena et al. 2013; Zhang et al. 2015) which causes the seed to germinate simultaneously and speed up.

Seeds with low germination capacity were also able to increase their germination with GA_3 treatments, such as soaking in GA_3 750 ppm for 24 hours and GA_3 500 ppm for 48 hours which improve the germination capacity of Kampar and Kapuas provenance seeds, respectively. For the Kapuas provenance seed, this treatment also improved germination rate and germination value. Improvements in seed viability and vigor with GA_3 treatment were also reported in *Eriobotrya japonica* (Al-Hawezy 2013), *Calopogonium caeruleum* (Asra 2014), and *Cyclamen* spp. (Cornea-Cipcigan et al. 2020). GA_3 is a hormone that is capable of being produced by seeds, but storage of seeds for too long causes the endogenous GA_3 content to degrade (Asra 2014). Soaking seeds with GA_3 can increase the availability of hormones for the germination process (Al-Hawezy 2013; Miransari and Smith 2014). During germination, GA_3 is released by the embryo and stimulates specific genes for mRNA transcription by a-amylase (Balaguera-López et al. 2009). GA_3 functions to stimulate growth and encourage the activity of hydrolytic enzymes (bonuktase, amylase and protease) in the endosperm and hydrolyze starch and proteins that will provide energy for embryonic development, including the radicle breaking down the endosperm and seed coat which limits seed germination (Miransari and Smith 2014).

The diversity of seedling growth occurred between provenances and invigoration treatments. Differences in seedling growth between genotypes also occurred in *Oryza sativa* (Harding et al. 2021) and *Antocephalus cadamba* (Sudrajat 2016). The response of seedling growth of each provenance to the invigoration treatment was different. Seeds from Kampar had the best growth in PEG -0.8 Mpa treatment for 24 hours, while seeds from Kapuas had the best seedling growth (height and root collar diameter) in

GA_3 500 ppm for 12 hours. In addition, the GA_3 treatment of 750 ppm for 12 hours gave the best seedling diameter growth in the Kampar and Batuhijau provenances and also the seed biomass in the Alas Purwo and Batuhijau provenances.

The effectiveness of PEG in increasing seedling growth was also reported in *T. aestivum* (Faijunnahar et al. 2017) and *Glycine max* (Hidayati et al. 2018). Osmo-priming with PEG had significantly improved root viability and chlorophyll content, and supported seedlings to maintain relative water content under adverse soil moisture environments (Zhang et al. 2015). While, GA_3 is a growth hormone that can accelerate the process of stem elongation, leaf growth, roots, affect growth, and root differentiation (Huang et al. 2014; Yunus et al. 2020). GA_3 treatment was able to increase the plant height, stem and total dry matter, leaf and root fresh matter and net assimilation (Al-Hawezy et al. 2013; Dilip et al. 2017).

Meanwhile, the gamma irradiation treatment with a dose of 40 Gy was able to increase the growth of seedlings from Alas Purwo, Batuhijau and Pomalaa, as well as increase the seedling biomass of the provenances of Batuhijau, Kapuas and Pomalaa. Improving seedling growth of gamma irradiation was also reported on *Lactuca sativa* (Marcu et al. 2013), *Terminalia arjuna* (Akshantha et. al. 2013), *Datura innoxia* (Aref et al. 2015), and *M. champaca* (Zanzibar and Sudrajat 2016). The beneficial effects of low dose gamma irradiation on the physiological parameters of seedlings were probably related to the increase in photosynthesis effectiveness, which was indicated by increasing of chlorophyll content in leaves (Marcu et al. 2013; Akshantha et al. 2013; Hadley and Woodwell 2014; Aref et al. 2015).

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