



After-Ripening–Induced Changes in Seed Water Status and Hormonal Balance Regulate Germination of Job’s Tears (*Coix lacryma-jobi* L. var. *ma-yuen*) at Different Maturity Levels and Storage Durations

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ABSTRACT

Freshly harvested Job's Tears seeds exhibit varying degrees of maturity and physiological dormancy. Dormancy breaking in the Poaceae family (Job's Tears) can occur during dry storage, resulting in seed maturation. Therefore, the impact of seed maturity and storage duration during the ripening period needs to be evaluated in relation to changes in physiological traits and seed germination. This experiment was arranged in a completely randomized design with seed maturity stages: immature (yellow), mature (light brown), overmature (white), and storage duration of 0, 2, 4, and 6 weeks after harvest. The results of the research indicate that the level of seed maturity at harvest and the duration of post-harvest dry storage play important roles in regulating physiological changes, dormancy release, and germination performance of Job's Tears (*Coix lacryma-jobi* var. *ma-yuen*) through an after-ripening process involving changes in seed water status, membrane integrity, and the balance of GA and ABA hormones. Mature seeds (brown) showed optimal viability and vigor, as reflected by moisture content (14.87%), the lowest imbibition duration (27.33 hours), an EC value of 55.33 μ S/cm/g, a higher germination percentages (89.00%), faster germination rates (6.77%/etmal), and a higher vigor index (88.89%) with the best storage for 2–4 weeks, while immature seeds required longer storage to overcome partial dormancy. The findings of this investigation emphasize the value of selecting appropriate harvest maturity and implementing short-term controlled storage as an effective, low-input strategy to improve seed quality, uniform germination, and field development.

Keywords: After-ripening, Germination, Job's Tears, Maturity, Storage.

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INTRODUCTION

Seed dormancy is an essential adaptive trait in cereal crops that prevents precocious germination under unfavorable environmental conditions and enables seeds to survive until conditions become suitable for seedling establishment (Nelson et al., 2023). From an agronomic perspective, dormancy must be carefully managed because both excessive dormancy and premature germination can reduce crop establishment uniformity and yield quality, particularly due to preharvest sprouting (Rehmani et al., 2022; Fu et al., 2024). In cereals, seed dormancy is

predominantly physiological and is primarily regulated by endogenous hormonal balance and metabolic status rather than by physical seed coat barriers (Nalwa & Seth, 2021; Jing et al., 2023). Dormancy release commonly occurs during a period of dry storage known as after-ripening (AR), a post-harvest physiological process that enables seeds to gradually lose dormancy and acquire germination capacity (Chandra et al., 2024).

After-ripening represents a critical phase during dry seed storage in which dormancy is progressively alleviated through coordinated physiological and biochemical changes within the seed (Chandra et al., 2024). The duration

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of AR varies widely among species and genotypes, ranging from several days to several months (Sweeney et al., 2022; Nelson et al., 2023). In cereal species such as rice (*Oryza sativa*), dry AR has been shown to reduce dormancy intensity and alter metabolic profiles, including changes in hormone levels and enzyme activities associated with germination processes (Yuan et al., 2023). Physiologically, AR involves modulation of key plant hormones, particularly abscisic acid (ABA), which promotes and maintains dormancy and gibberellins (GA), which stimulate dormancy release and germination (Ali et al., 2022). A common feature of after-ripened seeds is a reduction in both ABA content and sensitivity compared with freshly harvested seeds (Du et al., 2015). According to the hormone balance theory, when ABA signaling declines following seed maturation and dry storage, GA signaling becomes dominant, thereby promoting embryo growth and seed germination (Sohn et al., 2021). This hormonal antagonism represents a fundamental mechanism underlying the transition from dormancy to germination competence across cereal crops and model species.

Seed moisture content plays a critical role in regulating AR by influencing seed water status, membrane stability, metabolic activity, and dormancy release. Dormancy loss during drying is strongly dependent on storage temperature and embryo moisture content, with dormancy release generally occurring more rapidly at lower moisture levels under appropriate storage conditions (Abrantes et al., 2021; Hay et al., 2022). Excessive moisture during storage may accelerate seed deterioration, whereas overly dry conditions may slow the physiological processes required for effective AR (Sato & Köhler, 2022). Therefore, optimizing seed moisture content during storage is essential to balance dormancy alleviation and seed longevity.

Seed maturity at harvest substantially influences dormancy intensity and AR behavior. Seeds harvested prematurely often exhibit high moisture content, incomplete reserve accumulation, and stronger dormancy, resulting in delayed germination or poor seedling development (Matilla, 2024). In contrast, seeds harvested at optimal physiological maturity typically demonstrate improved viability, storability, and uniformity of germination (Sahromi et al., 2025). Over-mature or improperly stored seeds, however, are more susceptible to deterioration and loss of germination potential due to oxidative damage and membrane instability during storage (Corbineau, 2024). These general principles indicate that seed moisture content, hormonal balance and storage duration are critical determinants of dormancy release and germination behavior (Sato & Köhler, 2022).

Job's Tears (*Coix lacryma-jobi* L.) is a cereal crop belonging to the Poaceae family that has gained increasing attention due to its potential as a functional food and its richness in nutritional and bioactive compounds (Bhoomika & Suhas, 2025). The grains contain high levels of dietary fiber, carbohydrates, proteins, lipids, and diverse phytochemicals, including saponins, ferulic acid, coumaric acid, spermidine, gallic acid, catechin, chlorogenic acid, phenolic acid, quercetin, kaempferol, caffeic acid, and protocatechuic acid (Wang et al., 2016; Kaur et al., 2025). According to Yu et al. (2017), Job's Tears seeds contain 14%

protein, 5% fat, 65% carbohydrates, 3% fiber, 0.07% calcium, 0.242% phosphorus, and 0.001% iron. These compounds have been associated with antioxidant, anti-inflammatory, anticancer, and anti-obesity activities; stimulate reproductive hormones; increase uterine contractions; and modulate gut microbiota (Chen et al., 2016; Xi et al., 2016; Ruttanaporn et al., 2019; Devaraj et al., 2020).

Despite these promising attributes, the cultivation and utilization of Job's Tears remain constrained by seed-related problems, particularly inconsistent germination and poor stand establishment, which are closely linked to seed dormancy and AR behavior (Nautiyal et al., 2023)). Freshly harvested Job's Tears seeds generally exhibit varying degrees of maturity and physiological dormancy. According to Baskin (2020), physiological dormancy is characteristic of many Poaceae family, and is defined by the ability of seeds to lose dormancy during dry storage, indicating that maturation continues after harvest through AR. The degree of seed maturity at harvest strongly determines seed moisture content, endogenous hormone levels, and metabolic reserve accumulation (Wang et al., 2023).

Immature cereal seeds typically possess high moisture content of approximately 25–35%, as reported in rice (He et al., 2015), germinate failure which increases susceptibility to deterioration and loss of viability during storage (Pedrini et al., 2020). As a cereal species, Job's Tears (*Coix lacryma-jobi*) is expected to exhibit similar moisture-related physiological behavior at immature harvest stages. In contrast, seeds harvested at optimal physiological maturity exhibit higher viability, improved storability and more uniform germination (Magne'e et al., 2023). The interaction between seed maturity and AR duration is complex and genotype dependent, with significant variation in the length of AR required to achieve optimal germination potential among cereal species (Nelson et al., 2023). For example, rice seeds subjected to dry storage show progressive dormancy release accompanied by hormonal modulation and transcriptomic shifts during early AR stages (Yuan et al., 2023).

Despite extensive research on AR and dormancy in major cereals like rice (Liu et al., 2020), wheat (Nguyen et al., 2022; Yu et al., 2020) and barley (Nagel et al., 2019) there is a notable knowledge gap regarding these processes in Job's Tears. Specifically, systematic investigations on how different seed maturity levels at harvest interact with storage duration during AR to affect physiological properties, hormonal regulation, and germination performance in Job's Tears seeds are still limited. This lack of information constrains the ability to develop evidence-based seed handling and storage recommendations for Job's Tears, thereby limiting its agronomic potential and wider cultivation adoption. Therefore, this study aims to investigate the combined effects of seed maturity and storage duration during the AR period on the physiological and germination characteristics of *Coix lacryma-jobi* seeds.

MATERIALS & METHODS

Research Site

This research was conducted at the Genomics Laboratory of the National Research and Innovation Agency (BRIN) located at 6°29'50.478"S 106°50'42.505"E (Fig. 1), the Crop

Science Laboratory of the Faculty of Agriculture, Padjadjaran University 6°55'31.599"S 107°46'17.172"E (Fig. 2) and the Greenhouse in Nagrak District, Sukabumi Regency 6°51'13.267"S 106°48'6.5457"E (Fig. 3). The experiment took place from January 2024 to December 2024.

Research Design

The research was arranged in a 3x4 factorial completely randomized design. The first factor consisted of three treatment levels of seed maturity: 1. immature (yellow), 2. mature (light brown), and 3. overripe (white). The second factor consisted of four treatment levels of storage duration: 0, 2, 4, and 6 weeks after harvest (WAH), with three replications. Each experimental unit consists of 50g of seeds, so there are $3 \times 4 \times 3 \times 50 = 1,800$ g of seeds. The seeds of Job's Tears were sourced from the Faculty of Agriculture at Padjadjaran University and were propagated in Nagrak District, Sukabumi Regency.

Treatment and Measurement Stages

The harvested seeds were immediately cleaned and

sorted to select seeds of equal size, bright color, and fullness. Seeds of Job's Tears were selected based on their maturity level, which was grouped into three color categories: immature (yellow) at 25 days after pollination (DAP), fully mature (light brown) at 35 DAP, and overripe (white) at 50 DAP. Seeds with different maturity levels were weighed at 50g for each treatment. The seeds were placed in plastic containers and stored at room temperature (21-29°C) and humidity 95-98% for AR. The stored seeds were then soaked in water for 12 hours before sowing. The seeds were reweighed to determine the water absorption rate. The seed soaking water was used to measure electrical conductivity (EC). Before sowing, the seeds were soaked in a 0.5% sodium hypochlorite solution for 5 minutes to eliminate pathogens. Seeds were sown in a seedbed consisting of a mixture of sand and soil in a 1:1 ratio. Thirty seeds were scattered evenly on the seedbed to facilitate germination monitoring. After germination, five seed samples were planted in polybags/seedling trays to observe seed growth until 2 weeks after planting (WAP).

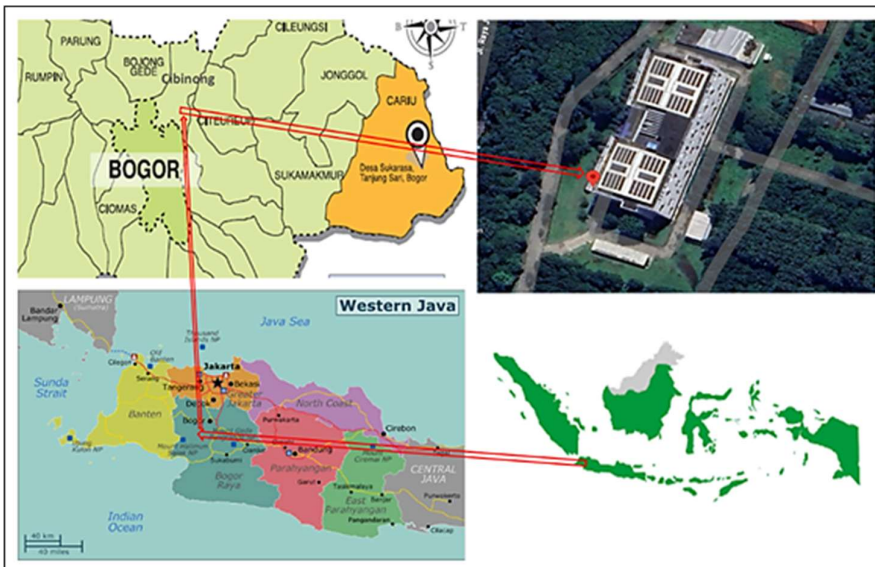


Fig. 1: Map of the National Research and Innovation Agency (BRIN) Genomics Laboratory research location.

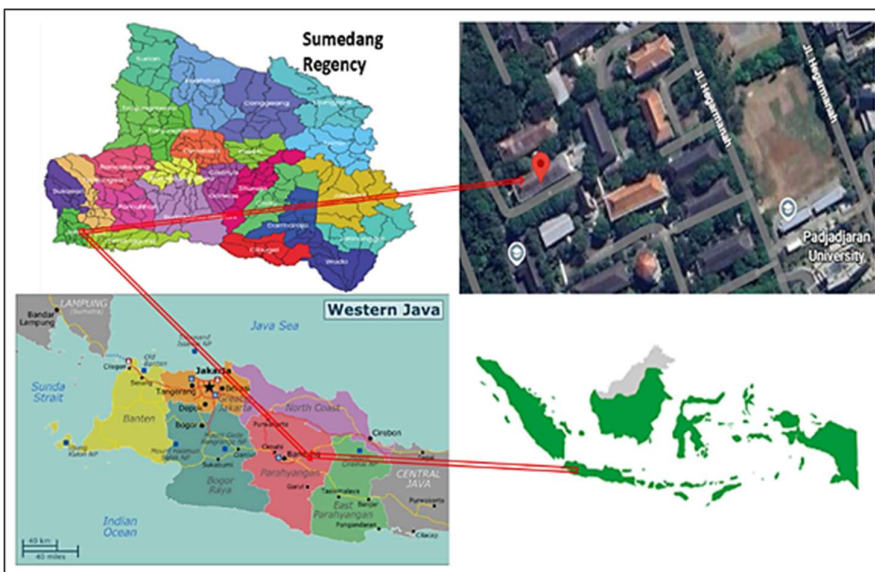


Fig. 2: Research location map of the Plant Science Laboratory, Faculty of Agriculture, Padjadjaran University.

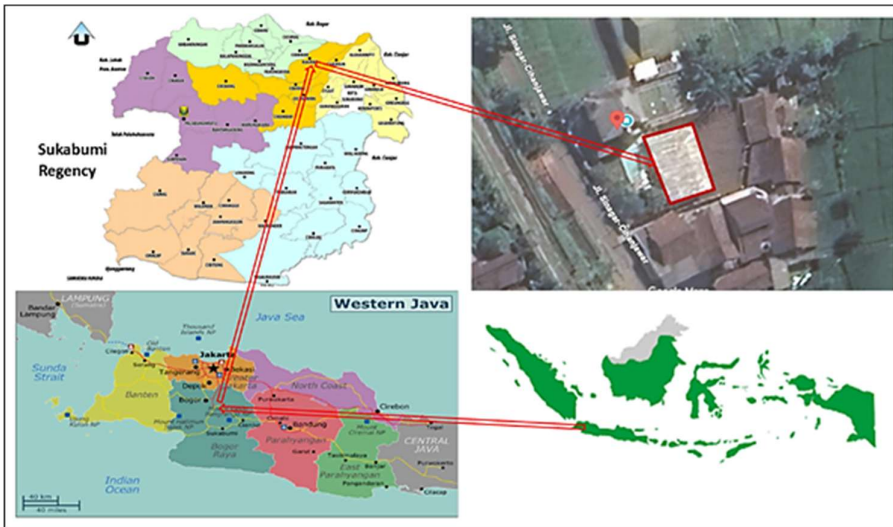


Fig. 3: Map of research locations in Nagrak District, Sukabumi Regency.

Observation parameters included: seed moisture content (MC), imbibition moisture content (IMC), imbibition duration (ID), germination percentage (GP), mean germination time (MGT), speed of germination (SG), vigor index (VI), seed vegetative performance, gibberellin (GA), abscisic acid (ABA), auxin (IAA), and electrical conductivity (EC).

Hormone analysis was carried out using High Performance Liquid Chromatography (HPLC) with mobile phase (A) methanol: (B) 0.1% formic acid pH 3.2, UV detector with wavelength 200nm (or 210-220nm; gibberellin), 250-300nm (ABA), 254-280nm (Auxin) on Phenomenex® Luna C18 column, 5 μ m (250 x 4.6mm), flow rate 1.44mL/min, gradient elution model (10:90) and injection volume 10 μ L (Li et al., 2016).

Data Analysis

Observation data on the response variables were statistically analyzed using Analysis of Variance (ANOVA) to determine the influence and interaction between factors using the F-test. If the F-test showed a significant influence, a Tukey's test was used for the parameters studied. A correlation test was then conducted to determine the relationship, the direction, and the strength of the observed parameters. The analysis used Asis stat software.

RESULTS

Job's Tears Seed Water Status

The effect of seed maturity and storage duration on seed moisture content are shown in Fig. 4. At harvest, immature seeds exhibited substantially higher moisture content than mature (brown) and overripe (white) seeds, indicating incomplete physiological development. Dry storage progressively reduced moisture content across all maturity stages, with mature seeds reaching the lowest levels for 4 WAH, reflecting improved desiccation tolerance.

Seed maturity and storage duration also significantly influenced imbibition moisture content after soaking (Fig. 5). In general, imbibition moisture content increased with longer storage periods, particularly in immature seeds, suggesting enhanced water uptake capacity following

dormancy alleviation. In contrast, mature and overripe seeds showed more moderate imbibition responses, indicating better membrane regulation during water absorption.

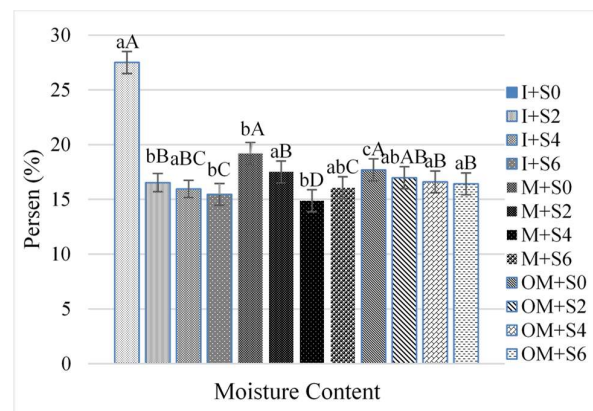


Fig. 4: The interaction effect of the seed maturity level and storage duration on seed moisture content. I: Immature, M: Mature, OM: Overripe, S0: no storage, S2: 2 WAH, S4: 4 WAH, S6: 6 WAH. Numbers followed by the same uppercase and lowercase letters indicate no significant difference according to Tukey's test at the 5% level.

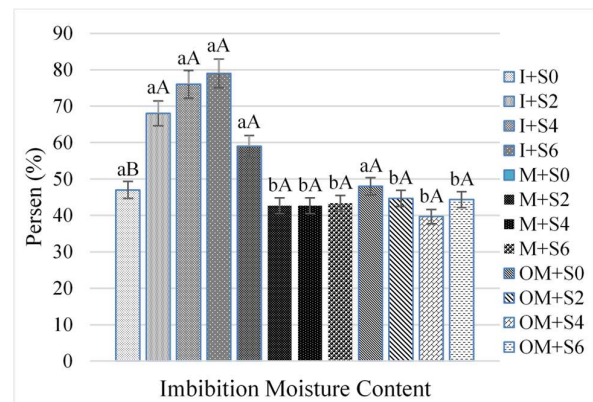


Fig. 5: The interaction effect of seed maturity level and storage duration on the moisture content during seed imbibition. I: Immature, M: Mature, OM: Overripe, S0: no storage, S2: 2 WAH, S4: 4 WAH, S6: 6 WAH. Numbers followed by the same uppercase and lowercase letters indicate no significant difference according to Tukey's test at the 5% level.

A significant interaction between seed maturity and storage duration was observed for imbibition duration (Fig. 6). Overripe seeds stored tended to require longer imbibition periods, especially after short-term storage, whereas mature seeds stored for 2 weeks exhibited the shortest imbibition duration. This pattern suggests that optimal AR promotes faster and more efficient water absorption during germination.

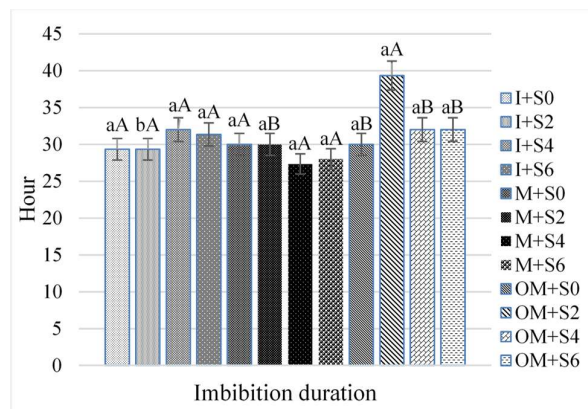


Fig. 6: The interaction effect of seed maturity level and storage duration on imbibition duration: I: Immature, M: Mature, OM: Overripe, S0: no storage, S2: 2 WAH, S4: 4 WAH, S6: 6 WAH. Numbers followed by the same uppercase and lowercase letters indicate no significant difference according to Tukey's test at the 5% level.

Electrical conductivity (EC), an indicator of membrane integrity, was significantly affected by the interaction between seed maturity and storage duration (Fig. 7). Immature seeds generally exhibited higher EC values, indicating greater membrane leakage. In contrast, mature seeds stored for mature and overripe seeds stored for 2 weeks showed the lowest EC values, reflecting improved membrane stability following short-term dry storage.

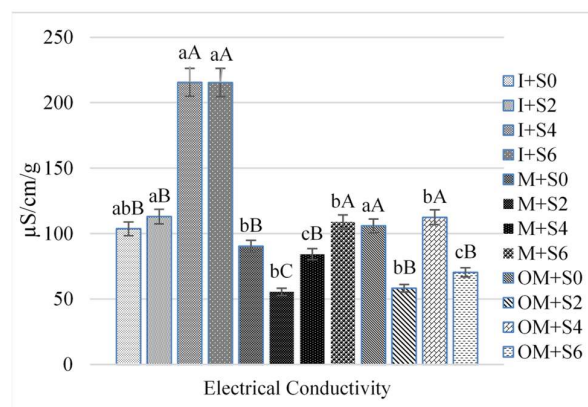


Fig. 7: The interaction effect of seed maturity level and storage duration on electrical conductivity. Immature, M: Mature, OM: Overripe, S0: no storage, S2: 2 WAH, S4: 4 WAH, S6: 6 WAH. Numbers followed by the same uppercase and lowercase letters indicate no significant difference according to Tukey's test at the 5% level.

Hormonal Changes in Job's Tears

The effect of seed maturity and storage duration on gibberellin (GA), abscisic acid (ABA), and indole-3-acetic acid (IAA) contents in Job's Tears seeds are summarized in

Table 1. The analysis results indicate a significant dynamic between the increase in GA and the decrease in ABA, which occurred specifically depending on the maturity level and storage duration. GA content increased markedly during AR, particularly in mature and immature seeds. Overripe seeds without storage exhibited the highest GA concentration (97.19ppm), while immature seeds stored for 6 WAH also showed elevated GA levels (70.76ppm). In mature seeds, GA accumulation peaked after 4 WAH at 56.82 and 6 WAH at 47.43ppm, indicating progressive dormancy release during dry storage. In contrast, freshly harvested mature seeds and those stored for only 2 WAH maintained very low GA levels at 1.54ppm and 1.95ppm, respectively. This reflecting limited germination readiness at early AR stages.

Table 1: Interaction Effect of Seed Maturity Level and Storage Duration on Job's Tears Seed Hormones

Hormone (ppm)	Seed maturity	Storage duration (WAH)			
		0	2	4	6
GA	Immature	5.69 ^{bb}	8.75 ^{bb}	7.15 ^{ba}	70.76 ^{aa}
	Mature	1.54 ^{bb}	1.95 ^{bb}	47.43 ^{aa}	56.82 ^{ba}
	Overripe	97.20 ^{aa}	47.23 ^{ab}	39.41 ^{ab}	2.42 ^{cc}
ABA	Immature	11.57 ^{ba}	7.44 ^{bb}	13.11 ^{aa}	2.68 ^{cc}
	Mature	1.56 ^{cb}	1.34 ^{cb}	1.20 ^{bd}	13.61 ^{ba}
	Overripe	28.55 ^{ab}	23.30 ^{ac}	11.96 ^{ad}	39.43 ^{aa}
IAA	Immature	8.997 ^{aa}	3.520 ^{ab}	2.553 ^{ab}	0.147 ^{bc}
	Mature	0.077 ^{bb}	1.067 ^{ba}	0.200 ^{bb}	0.067 ^{bb}
	Overripe	0.277 ^{ba}	0.590 ^{ba}	0.377 ^{ba}	0.610 ^{aa}

Note: According to Tukey's test at the 5% level, numbers that are followed by the same capital letter horizontally and the same lowercase letter vertically do not significantly vary.

ABA content varied significantly across treatments, showing a less uniform trend than GA. The highest ABA concentration was detected in overripe seeds stored for 6 WAH (39.43ppm), suggesting delayed hormonal rebalancing in this maturity class. Conversely, consistently low. The lowest ABA levels were found in mature seeds without storage (1.56ppm), 2 WAH (1.34ppm), 4 WAH (1.2ppm), and immature seeds stored for 6 WAH, supporting the role of ABA decline in dormancy alleviation. IAA levels were primarily influenced by seed maturity rather than storage duration. Immature seeds without storage exhibited the highest IAA content, which declined sharply following dry storage. In contrast, mature and overripe seeds maintained relatively low IAA concentrations across most storage periods, with the lowest level recorded in mature seeds stored for 6 WAH (2.68ppm). These patterns suggest that IAA plays a limited role in dormancy release compared to GA-ABA regulation and may be more closely associated with early seed developmental status.

Job's Tears Seed Germination

Seed maturity level and storage duration significantly interacted to influence germination percentage (GP) and mean germination time (MGT), speed of germination (SG) and vigor index (VI) (Table 2). Overall, mature seeds consistently exhibited superior germination performance compared to immature and overripe seeds, particularly following short to moderate AR periods. The highest GP was recorded in mature seeds stored for 6 WAH (89%) and 4 WAH (87.67%), indicating optimal dormancy release and physiological readiness at these storage durations. Overripe

seeds achieved the highest GP at 4 WAH (83.33%), while immature seeds required longer storage to reach comparable performance, with the highest GP observed at 2 WAH (76.67%) and 6 WAH and 88%). In contrast, freshly harvested immature seeds showed the lowest GP (41%), reflecting incomplete physiological development and persistent dormancy.

Table 2: Effect of interaction between seed maturity level and storage duration on germination percentage, mean germination time, speed of germination, and vigor index of Job's Tears

Parameter	Seed maturity	Storage duration (WAH)			
		0	2	4	6
Germination percentage (%)	Immature	41.00 ^{bc}	76.67 ^{aAB}	62.33 ^{bb}	88.00 ^{aA}
	Mature	53.33 ^{bb}	50.00 ^{bb}	87.67 ^{aA}	89.00 ^{aA}
	Overripe	72.00 ^{aAB}	65.67 ^{abAB}	83.33 ^{aA}	56.67 ^{bb}
Mean germination time (day)	Immature	12.21 ^{aA}	7.71 ^{bb}	6.59 ^{ab}	7.79 ^{abB}
	Mature	9.88 ^{bA}	7.71 ^{bb}	5.03 ^{bc}	6.81 ^{bb}
	Overripe	8.30 ^{cb}	11.01 ^{aA}	6.86 ^{ac}	8.55 ^{ab}
Speed of germination (%/etmal)	Immature	3.52 ^{bb}	10.72 ^{aA}	9.85 ^{cA}	11.57 ^{aA}
	Mature	5.60 ^{bc}	6.77 ^{bc}	18.10 ^{aA}	13.56 ^{ab}
	Overripe	9.30 ^{ab}	7.08 ^{bb}	12.67 ^{bA}	6.69 ^{bb}
Vigor Index (%)	Immature	28.89 ^{cc}	75.55 ^{aAB}	62.22 ^{bb}	87.78 ^{aA}
	Mature	53.33 ^{bb}	48.89 ^{bb}	87.78 ^{aA}	88.89 ^{aA}
	Overripe	71.11 ^{aAB}	51.11 ^{bc}	82.22 ^{aA}	56.67 ^{bbC}

Note: According to Tukey's test at the 5% level, numbers that are followed by the same capital letter horizontally and the same lowercase letter vertically do not significantly vary.

Mean germination time was significantly reduced by AR across all maturity levels. Mature seeds stored for 4 WAH exhibited the fastest MGT (5.03 days), followed by immature and overripe seeds at the same storage duration (6.59 and 6.86 days respectively). All stored seeds germinated significantly faster than non-stored seeds, particularly immature seeds without storage, which showed the longest MGT (12.21 days), indicating delayed and uneven germination. Similar trends were observed for speed of germination (SG) and vigor index (VI) (Table 2). The highest SG occurred in mature seeds stored for 4 WAH (18.10%/etmal) and 6 WAH (13.56%/etmal) exceeding those of overripe seeds at their optimal storage duration (12.67%/etmal at 4 WAH). The lowest SG (3.52%/etmal) was for immature seeds without storage, consistent with poor germination capacity. Vigor index followed the same pattern, with the highest values recorded in mature seeds at 6 WAH (88.89%) and 4 WAH (87.8%), and in immature seeds after prolonged storage at 6 WAH (87.78%). In contrast, immature seeds without storage showed the lowest VI (28.89). Meanwhile, overripe seeds displayed fluctuating vigor responses during storage, peaking at 4 WAH (82.22%) and declining at 2 WAH (51.11%).

Early Growth Phase of Job's Tears

The interaction between seed maturity level and storage duration influenced early vegetative growth for Job's Tears, highlighting the importance of harvest maturity and AR in determining seedling establishment and initial vigor. Stem diameter varied with both factors, with the largest value observed in mature seeds stored for 6 WAH and overripe seeds stored for 2 WAH (0.37cm) (Table 3). This value were not significantly different from those of overripe seeds stored for 4-6 WAH, mature seeds stored for 0-4 WAH, or immature seeds without storage and stored for 4 and 6 WAH. Whereas the smallest stem

diameter was recorded in overripe seeds without storage (0.23cm), indicating reduced early growth performance in the absence of AR.

Table 3: Effect of interaction between seed maturity level and storage duration on stem diameter, leaf length, and leaf width of Job's Tears at 2 WAP

Parameter	Seed maturity	Storage duration (WAH)			
		0	2	4	6
Stem diameter (mm)	Immature	0.34 ^{aA}	0.28 ^{bA}	0.28 ^{aA}	0.30 ^{aA}
	Mature	0.35 ^{aA}	0.35 ^{abA}	0.33 ^{aA}	0.37 ^{aA}
	Overripe	0.23 ^{bb}	0.37 ^{aA}	0.35 ^{aA}	0.36 ^{aA}
Leaf length (cm)	Immature	20.09 ^{aA}	17.38 ^{aA}	18.17 ^{bA}	22.03 ^{bA}
	Mature	21.55 ^{ab}	21.53 ^{ab}	20.51 ^{abB}	28.62 ^{aA}
	Overripe	19.93 ^{aA}	18.96 ^{aA}	23.21 ^{aA}	21.02 ^{bA}
Leaf width (cm)	Immature	1.36 ^{aA}	0.94 ^{bc}	1.10 ^{bBC}	1.17 ^{bb}
	Mature	1.21 ^{ab}	1.19 ^{ab}	1.13 ^{abB}	1.49 ^{aA}
	Overripe	1.33 ^{aA}	1.18 ^{aA}	1.28 ^{aA}	1.18 ^{bA}

Note: According to Tukey's test at the 5% level, numbers that are followed by the same capital letter horizontally and the same lowercase letter vertically do not significantly vary.

Leaf growth parameters showed clearer differentiation among treatments. The longest leaves were produced by mature seeds stored for 6 WAH (28.62cm), whereas the shortest leaves occurred in immature seeds stored for 2 WAH (17.38cm). Leaf width followed a similar trend, with the highest values recorded in mature seeds at 6 WAH (1.49cm) and immature seeds without storage (1.36cm). The narrowest leaves were observed in immature seeds stored for 2 WAH (0.94cm), suggesting suboptimal physiological readiness at this storage duration.

Plant biomass accumulation was also significantly affected by the interaction of seed maturity and storage duration in Table 4. The highest shoot dry weight was recorded in overripe seeds stored for 2 WAH had (0.37g), while immature seeds stored for 4 WAH and mature seeds without storage exhibited the lower value (0.27g). A pronounced decline in biomass was observed in overripe seeds stored for 4 WAH, which showed the lowest shoot dry weight (0.14g). Root dry weights followed a comparable pattern, with the highest value in overripe seeds stored for 2 WAH (0.15g), followed by mature seeds across all storage duration (0-6 WAH). The lowest root dry weight was again found in overripe seeds stored for 4 WAH (0.07g). Consequently, total dry weight peaked in overripe seeds for 2 WAH (0.53g), followed by mature seeds without storage (0.47g) and those stored for 2 WAH (0.37g), while the lowest total dry weight occurred in overripe seeds at 4 WAH (0.21g).

Table 4: The interaction effect of seed maturity level and storage duration on the shoot and root of Job's Tears plants at 2 WAP

Parameter	Seed maturity	Storage duration (WAH)			
		0	2	4	6
Shoot dry weight (g)	Immature	0.17 ^{bb}	0.17 ^{bb}	0.27 ^{aA}	0.18 ^{ab}
	Mature	0.27 ^{aA}	0.23 ^{bA}	0.22 ^{aA}	0.23 ^{aA}
	Overripe	0.24 ^{ab}	0.37 ^{aA}	0.14 ^{bc}	0.19 ^{abC}
Root dry weight (g)	Immature	0.10 ^{aA}	0.10 ^{bA}	0.11 ^{aA}	0.10 ^{aA}
	Mature	0.13 ^{aA}	0.14 ^{aA}	0.13 ^{aA}	0.11 ^{aA}
	Overripe	0.11 ^{ab}	0.15 ^{aA}	0.07 ^{bc}	0.08 ^{abC}
Total dry weight (g)	Immature	0.27 ^{bA}	0.26 ^{bA}	0.38 ^{aA}	0.28 ^{aA}
	Mature	0.47 ^{aA}	0.37 ^{baB}	0.34 ^{ab}	0.34 ^{ab}
	Overripe	0.35 ^{bb}	0.53 ^{aA}	0.21 ^{bc}	0.27 ^{abC}
Root volume (cm ³)	Immature	3.91 ^{aA}	4.00 ^{aA}	3.98 ^{aA}	3.96 ^{aA}
	Mature	3.17 ^{bb}	4.31 ^{aA}	4.29 ^{aA}	3.94 ^{aA}
	Overripe	3.95 ^{aA}	3.99 ^{aA}	3.89 ^{aA}	3.93 ^{aA}

Note: According to Tukey's test at the 5% level, numbers that are followed by the same capital letter horizontally and the same lowercase letter vertically do not significantly vary.

Root volume at 2 WAP was strongly influenced by the interaction between seed maturity and storage duration in Table 4. The largest root volumes were obtained from mature seeds stored for 2 WAH (4.31cm³) and 4 WAH (4.29cm³), followed by immature seeds stored for 2 WAH (4.00cm³) and overripe seeds stored for 2 WAH (3.99cm³). In contrast, mature without storage exhibited the lowest root volume, indicating delayed root system development in non-after-ripened seeds. Independent effects of seed maturity and storage duration on root shoot ratio (RSR), plant height, and leaf number at 2 WAP are presented in Table 5. Seed maturity alone did not significantly affect these parameters. However, storage duration significantly influenced plant height and leaf number. Seeds without storage produced the shortest plants (21.76cm), whereas seeds stored for 6 WAH resulted in tallest plants (26.99cm). Leaf number was highest at 6 WAH (3.86) and lowest at 2 WAH (3.15) while no significant difference was observed between seeds without storage and those stored for 4 WAH. Across all treatments, RSR value ranged from 1.77 to 2.31, indicating relatively stable biomass allocation patterns during early growth.

Table 5: Independent effects of seed maturity level and storage duration on root shoot ratio, plant height, and number of leaves of Job's Tears at 2 WAP

	Plant height (cm)	Number of leaves	RSR
Seed maturity			
Immature (yellow)	23.90 ^a	3.44 ^a	2.12 ^a
Mature (brown)	25.20 ^a	3.50 ^a	1.77 ^a
Overripe (white)	23.58 ^a	3.67 ^a	2.23 ^a
Storage duration (WAH)			
0	21.76 ^b	3.63 ^a	1.82 ^a
2	23.61 ^b	3.15 ^b	2.07 ^a
4	24.55 ^{ab}	3.56 ^{ab}	1.96 ^a
6	26.99 ^a	3.82 ^a	2.31 ^a

Note: RSR: root shoot ratio; WAH: weeks after harvest. According to Tukey's test, values that were followed by the same letter did not differ substantially ($p < 0.05$).

Correlation of Water Status, Hormones and Germination Parameters

The relationship among water status, hormones, and germination-related parameters of Job's Tears seeds across different maturity levels and storage durations is presented in Table 6. Correlation analysis was employed to elucidate key physiological factors governing seed vigor and early growth performance. Seed moisture content exhibited a strong and highly significant negative correlation with GP ($r = -0.641^{**}$), VI ($r = -0.715^{**}$), and SG ($r = -0.653^{**}$), while showing a positive correlation with MGT ($r = 0.742^{**}$). These relationships indicate that elevated seed moisture content is associated with delayed and reduced germination performance, reflecting impaired physiological readiness of seeds with insufficient AR.

Germination percentage was strongly and positively correlated with SG ($r = 0.879^{**}$), VI ($r = 0.967^{**}$), confirming that rapid and synchronized germination is a key determinant of overall seed vigor. In addition, germination showed a significant positive correlation with gibberellin content (GA: $r = 0.612^{**}$), underscoring the promotive role of GA in dormancy release and germination processes. Mean germination time was significantly negatively correlated with SG ($r = -0.833^{**}$) and VI ($r = -0.736^{**}$),

indicating that seeds with faster germination rates and higher vigor tend to emerge earlier and more uniformly. Similarly, speed of germination was positively associated with vigor index ($r = 0.892^{**}$) and GA content ($r = 0.468^{*}$), further supporting the involvement of GA in enhancing germination dynamics during AR. Vigor index also exhibited a significant positive correlation with GA ($r = 0.557^{**}$), reinforcing the contribution of gibberellin-mediated metabolic activation to improved seed performance. In contrast, total dry weight (TDW) showed no significant correlation with other measured parameters, suggesting that early biomass accumulation was less directly linked to initial seed physiological status. RSR displayed a positive correlation with ABA content ($r = 0.344^{*}$), indicating a potential role of ABA in regulating biomass partitioning during early seedling growth. Meanwhile, the relationship between GA and ABA was weakly positive ($r = 0.158$), reflecting a dynamic but non-linear hormonal balance during AR and germination.

Table 6: Pearson correlation analysis of selected water status, hormone, and germination at maturity level and storage duration of Job's Tears seeds

	GP	MGT	SG	VI	TDW	RSR	GA	ABA
MC	-.641**	.742**	-.653**	-.715**	-0.101	-0.268	-0.322	-0.015
GP		-.610**	.879**	.967**	-0.186	0.242	.612**	-0.137
MGT			-.833**	-.736**	0.227	0.050	-0.225	0.238
SG				.892**	-0.167	0.033	.468**	-0.265
VI					-0.265	0.182	.557**	-0.169
TDW						0.051	0.082	0.040
RSR							0.237	.344*
GA								0.158

**significant correlation at 0.01 level, *significant correlation at 0.05 level, MC; moisture content, GP; germination percentage, MGT; mean germination time, SG; speed of germination, VI; vigor index, TDW; total dry weight, RSR; root-shoot ratio, GA; gibberellin, ABA; Abscisic acid.

DISCUSSION

Seed color is widely recognized as a visual indicator of seed maturity and physiological condition, reflecting internal biochemical status and developmental progression. Storage duration during the AR period also plays a decisive role in determining seed quality, dormancy release, and subsequent germination performance. Among the governing factors, seed moisture content is central because it regulates the biophysical and biochemical state of cellular structures during storage and strongly influences seed aging dynamics (Hay et al., 2022). In this study, moisture content declined significantly across all maturity levels following storage, confirming that dry storage promotes progressive dehydration associated with AR.

The most pronounced moisture reduction occurred in immature seeds stored for 2 WAH (I+S2) decreasing from an initial moisture content (I+S0) of 10.97%. This pattern is consistent with cereal studies showing that early dry storage induces rapid moisture equilibration and accelerates dormancy release (Chandra et al., 2024). During AR, moisture content values for immature and mature seeds at 2, 4, and 6 WAH, as well as overripe seeds without storage up to 6 WAH, ranged from 14.87 to 17.51%, which falls within the optimal moisture window 5–18% reported for cereal AR. This range allows biochemical reprogramming while limiting oxidative damage (Hay et al., 2022). Immature

seeds harvested before physiological maturity typically retain higher moisture content. Physiological maturity is closely associated with declining seed moisture concentration, with elevated values indicating immature developmental status (Menendez et al., 2019). High moisture in immature seeds enhances respiratory metabolism, accelerates reserve depletion, and increases susceptibility to aging if drying is not properly controlled (Kameswara et al., 2017). Recent evidence indicates that elevated moisture intensifies enzymatic and oxidative reactions, thereby exacerbating deterioration during storage (Hay et al., 2023). These mechanisms explain why immature seeds in this study required longer storage to reach acceptable physiological quality.

In contrast, mature seeds exhibited lower harvest moisture content, confirming attainment of physiological maturity. Low moisture at harvest is widely accepted as an indicator of maturity and storage readiness (Ellis, 2019). Monitoring seed water status therefore provides a practical basis for optimizing harvest timing and minimizing post-harvest losses (Hay et al., 2023). However, excessive moisture during prolonged storage remains detrimental even for mature seeds, as increased oxygen availability promotes lipid peroxidation, disrupts membrane integrity, and accelerates viability loss (Tahir et al., 2023; Corbineau, 2024). Imbibition moisture content further reflected differences in seed structural integrity. Immature seeds consistently showed higher imbibition moisture content across storage durations than mature and overripe seeds. This increased water uptake is likely associated with looser tissue organization and incomplete cell wall development, facilitating rapid water entry (Kolo & Tefa, 2016). Such structural fragility compromises storability and vigor, as excessive water uptake during rehydration can disrupt membranes and impose high metabolic demand (Xing et al., 2025). With increasing storage duration, immature seeds required greater water input to re-establish hydration, placing additional strain on limited energy reserves.

Mature and overripe seeds exhibited lower imbibition moisture content, reflecting denser tissue structure and hardened cell walls. In cereals, increased dry matter accumulation including starch, proteins, and lipids is positively associated with higher seed density, membrane robustness, and storage stability (Saied et al., 2023). This advantage includes longer storage life, greater vigor, and optimal germination. Meanwhile, overripe seeds experience physiological aging in the plant (field weathering), and food reserves begin to degrade. The tissue can loosen or form air pockets due to internal damage (Choudhury & Bordolui, 2023; Ranganathan & Groot, 2023). Imbibition duration provided additional insight into membrane permeability. Across all maturity levels, imbibition duration increased with prolonged storage, reflecting reduced moisture content, denser tissue organization, and lower permeability (Hay et al., 2022). Extremely short imbibition duration may indicate membrane damage, whereas excessively long imbibition duration often signal physiological decline and reduced metabolic responsiveness (Cruz & Lobato, 2023; Dhaliwal et al., 2025). Immature seeds exhibited shorter imbibition duration due to thinner seed coats and less compact

tissues (Lin et al., 2019), but rapid water uptake did not translate into efficient germination because enzymatic systems and nutrient reserves were not fully developed (Obura & Lamo, 2024).

Electrical conductivity (EC) measurements supported these observations. EC increased markedly in immature seeds extended storage, indicating progressive membrane damage and electrolyte leakage. Mature seeds without storage showed EC values 90.33 $\mu\text{S}/\text{cm}/\text{g}$, comparable to values reported for oat seeds after 24 hours soaking (Sponchiado et al., 2014). Elevated EC is a recognized indicator of seed aging and compromised membrane semi-permeability (Bičárová et al., 2023). In very young seeds, high EC may also reflect incomplete membrane development rather than true deterioration (Hanapiah et al., 2022). Hormonal regulation during AR revealed strong antagonism between gibberellins (GA) and abscisic acid (ABA), modulated by seed maturity and storage duration. Immature seeds exhibited increasing GA activity from 0 to 6 WAP, consistent with activation of AR mechanisms promoting dormancy release. Similar GA increases during dry AR have been reported in rice and Arabidopsis, where GA stimulates α -amylase production and reserve mobilization (Nelson et al., 2023; Yuan et al., 2023). In contrast, overripe seeds showed declining GA levels after prolonged storage, reflecting hormonal degradation associated with physiological aging.

ABA levels were highest in overripe seeds and increased with storage duration, reinforced dormancy and aging-related stress responses. Has been physiologically reduced. While ABA is essential during seed development, excessive accumulation suppresses germination (Ali et al., 2022). In mature seeds, ABA declined during early storage before increasing again under prolonged storage, suggesting effective dormancy release followed by hormonal rebound linked to aging. These GA-ABA interactions align with current models identifying hormonal balance as the central regulator of dormancy-germination transitions (Sohn et al., 2021; T. Nguyen et al., 2025). Indole-3-acetic acid (IAA) also showed maturity-dependent dynamics. Immature seeds exhibited the highest IAA levels prior to storage, followed by a sharp decline, reflecting reduced auxin activity post-harvest. Similar auxin redistribution during late seed maturation has been reported in cereals (Cao et al., 2020; Pellizzaro et al., 2020). Overall, germination outcomes confirmed that mature seeds stored for 4 WAH achieved the most favorable balance of moisture status, hormonal regulation, vigor index, and germination performance. Immature seeds required extended storage (6 WAH) to reach comparable viability, indicating continued physiological maturation during AR. Correlation analyses further demonstrated that reduced moisture content and elevated GA were positively associated with germination percentage, vigor index, and germination speed, highlighting the central role of GA-mediated reserve mobilization in successful germination (Betts et al., 2020; Li et al., 2020; Hedden, 2025). Conversely, elevated ABA was associated with increased root-shoot ratio, consistent with its inhibitory effects on shoot elongation under stress conditions (Xie et al., 2019).

Conclusion

Seed maturity and storage duration significantly influence physiological changes Job's Tears seeds during AR, including hormone dynamics, water status, and germination performance. After-ripening effectively occurs in physiologically mature (brown) seeds stored 2 and 4 weeks after harvest, resulting in high viability and vigor, while immature (yellow) seeds require extended storage of up to 6 weeks to achieve comparable physiological quality. Seed moisture content emerged as a key determinant of germination, vigor, and early seedling growth, acting in concert with the hormonal balance of gibberellin (GA), abscisic acid (ABA), and indole-3-acetic acid (IAA) in regulating dormancy release and germination capacity. From a practical perspective, these findings provide a scientific basis for seed producers and breeders to optimize harvest timing and post-harvest storage strategies. Harvesting seeds at physiological maturity and applying appropriate AR periods can enhance seed quality, reduce variability in germination, and improve stand establishment. For breeding programs, understanding maturity-dependent hormonal regulation offers opportunities to select genotypes with superior dormancy control and storage performance, thereby supporting more reliable seed production and crop establishment.

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