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Article *in* Journal of Berry Research · July 2025

DOI: 10.1177/18785093251359032

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Research article

Effects of storage on the seed germination of *Vaccinium delavayi*: A promising nutraceutical species from China

Journal of Berry Research
1–12

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Abstract

Background: *Vaccinium delavayi* is a high-value nutraceutical berry. The species is rarely cultivated, and its demand is met through wild collection. The species has striking apparency and is suitable for landscaping.

Objectives: The present study aims to investigate the effects of storage, environmental factors (i.e., light and temperature), and the application of gibberellic acid (GA_3) on the seed germination of *V. delavayi*.

Methods: Fresh, 4, 8, and 16-month stored seeds at different storage conditions were kept in the incubators. The incubators were set at 3 different alternate temperature regimes (5/10°C, 10/20°C, and 20/30°C) in 24-h darkness (dark treatment) and/or 12 h light/12 h darkness (light treatment). Eight-month-old stored seeds were retrieved from different storage conditions and soaked in four different concentrations (0-, 500-, 1000-, and 1500- mM) of gibberellic acid (GA_3) for 24 h at room temperature to test the effect of GA_3 on seed germination.

Results: The species exhibits physiological seed dormancy. Wet-stored seeds kept at 4°C for 16 months exhibited the highest germination rate (37.0%), suggesting limited natural regeneration potential. The external use of GA_3 significantly enhanced the germination. Seeds treated with GA_3 showed a positive photoblastic response.

Conclusion: These findings provide insights for the cultivation and alleviating stress on wild populations, contributing to conservation and sustainable utilization of the species.

Keywords

berry, dormancy, mean germination time, photoblastism, synchrony

Received: 15 March 2025; accepted: 30 June 2025

Introduction

In recent years, nutritional food has become a top priority for healthy living. Berries can forestall several lifestyle diseases. They serve as an excellent source of bioactive compounds, including flavonoids, anthocyanins, and polyphenols.[1,2] Antioxidant protection against oxidative stress is highly beneficial in delaying the onset or progression of several degenerative diseases.[3] Due to their high nutritional value and consumers' acceptance, berries have gained significant importance in the food industry.

Blueberries and bilberries (*Vaccinium* spp.) are particularly rich in potassium, fiber, and bioactive compounds and are considered as superfruits.[4,5] *Vaccinium* species are cultivated worldwide due to their economic importance and positive health benefits.[6–8] About ninety species of

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Vaccinium are reported from China.[9] Among them, *V. angustifolium, V. ashei*, *V. corymbosum*, *V. uliginosum* and *V. vitis-idaea* are used for making jam, jelly, and juices.[10,11] Some other species like *V. conchophyllum*, *V. saxicola*, and *V. vacciniaceum* have ornamental importance and are used in landscaping.[12,13]

Vaccinium delavayi is an underutilized shrub distributed in southwestern Sichuan, southeastern Xizang, and Yunnan Province of China, at an altitude of 2400 to 3800 meters.[14] The species is commonly known as 'Yan Tan Xiang' in Chinese Herbal Medicine and is used to treat chest and abdominal distension, and digestive disorders.[15] However, the species is rarely cultivated, with its use primarily relying on wild collection.

Mass-scale cultivation of economically important species can reduce pressure from the wild and can be a viable source of income for local communities.[16–18] Propagation by seed is the most convenient and effective method for large-scale cultivation. Seed germination in *Vaccinium* seeds is influenced by temperature, light, media, and several other environmental factors.[19–21] Under natural conditions, germination in *Vaccinium* species is impeded by humidity, temperature shifts, and light variations, resulting in prolonged germination periods and limited seedling production.[21]

The *Vaccinium* genus is known to exhibit physiological dormancy.[22–26] This type of dormancy can be overcome by dry storage at room temperature,[18,27] cold-wet stratification,[28,29] or by gibberellic acid treatment.[30] However, germination requirements for *V. delavayi* are poorly explored. Therefore, the present study aimed to (i) determine the status of dormancy in the freshly collected seeds, and (ii) study the effects of varying temperature, light, storage, and GA_3 on seed germination.

Material and methods

Plant species

The ripe fruits of *V. delavayi* Franch. (Figure 1) were collected from Lanping Bai and Pumi Autonomous County in the Nujiang Lisu Autonomous Prefecture of Yunnan Province, China (26°25′22″N 99°24′57″E, 2431 m asl) in November 2021. The weather conditions varied considerably in the region. The rainfall varied from 0 mm (Jan-Feb, 2022) to 309.8 mm (Aug 2021) (Figure 2). The minimal air temperature ranged from −6°C (Jan-Feb 2022) to 12°C (July 2021) while the maximum air temperature ranged from 18°C (Feb 2022) to 32°C (Mar 2021).

Fruits were collected from 20–25 plants located more than 2 m apart from each other. The voucher specimens were deposited in the herbarium of Lushan Botanical Garden, China. After collection, fruits were rubbed in clean water to separate seeds from pulp. After repeated washing, the peel, pulp, and immature seeds were removed. The mature seeds were dried at room temperature for one week. The dried seeds were divided into four batches. One batch was immediately tested for germination (hereafter referred to as fresh seeds). The other three batches were: i) dry-stored in brown paper bags at 4°C in a refrigerator, ii) wet-stored at 4°C by placing them in moistened towels enclosed in plastic containers, and iii) stored in a sealed glass bottle at −18°C. The germination potential of stored seeds was tested after 4, 8, and 16 months.

Seed traits

Seed shape, dimensions (length, width, and height), and color were assessed using a Nikon SMZ800N Stereo Microscope equipped with a microscope camera IMG-SC600C. Fifteen seeds were examined by affixing them ventrally to filter paper with double-sided sticky tape. Seed mass was determined at the time of collection from three 100-seed replicates using an electronic balance (Electronic balance, model CUBIS_II_PRECISION, Sartorius Co., Goettingen, Germany).

Water imbibition

The water imbibition test was performed by measuring the mass of 100-seed in three replicates. Fresh seed weight was measured before placing them in petri dishes. Petri dishes containing two Whatman No. 1 filter paper were moistened with 10 mL of distilled water for different duration (3, 6, 9, 12, 24, and 36 h) at room temperature (22 ± 2°C). The seeds were blotted with a paper towel and weighed using an electric balance. The absorbed water at each time was calculated using the equation: Water absorption (%) = [(W2 − W1)/W1] × 100, where W2 represents the mass of the seeds after 3, 6, 9, 12, 24, and 36 h of imbibition, and W1 is the initial seed mass as methodology established previously.[31] The values were plotted in a chart and a second-order potential curve was fitted to verify the data homogeneity.

Germination responses

Before the germination trials, the seeds were sterilized in 0.5% sodium hypochlorite for 1 min to avoid fungal infection. After sterilization, the seeds were washed with double distilled water to remove any traces of sodium hypochlorite. Fresh, 4, 8, and 16-month stored seeds at different storage conditions were kept in incubators (Kesheng incubators, Model- DRX-800C- LED, China). The incubators were set at 3 different alternate temperature regimes (5/10°C, 10/20°C, and 20/30°C) in 24-h darkness (dark treatment) and/or 12 h light/12 h darkness (light treatment). This arrangement helped us test the photoblastic response, i.e,

Figure 1. Berries of *Vaccinium delavayi*.

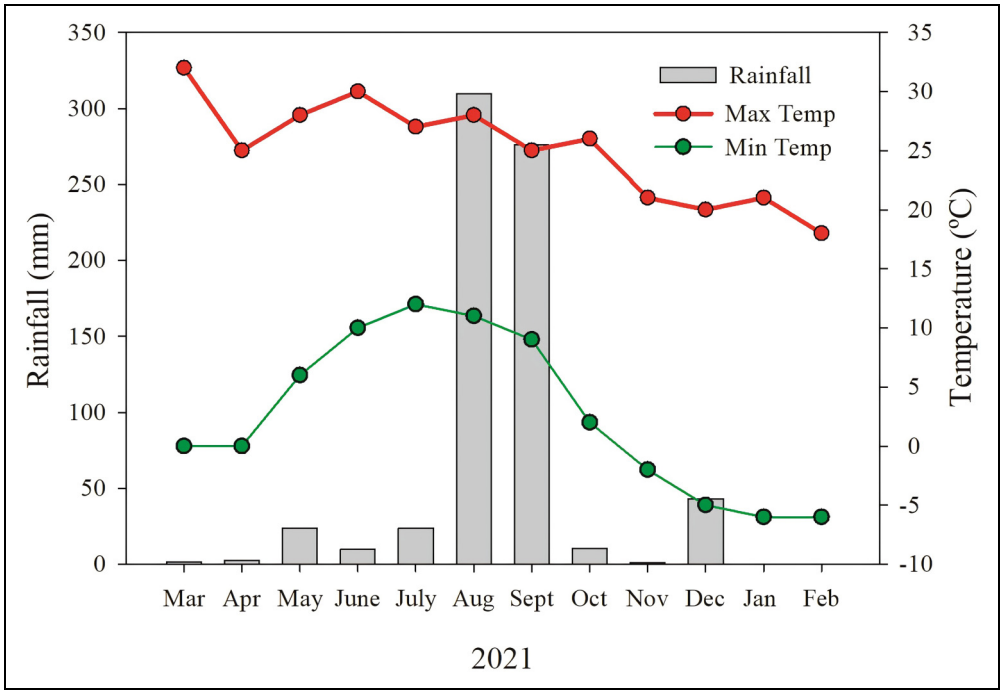

Figure 2. Rainfall, maximum and minimum temperatures measured from march 2021 to February 2022 in Lanping County China.

how seed respond to light during germination. Seeds may be positively photoblastic (requires light for germination), negatively photoblastic (germination is inhibited by light) or non-photoblastic (light has no germination) based on photoblastic responses.

The incubators were fitted with cool white fluorescent tubes (60 μ mol photons m−2s−1). Seeds were exposed to 12 h light at the highest temperature within each alternating temperature. These temperature regimes were chosen to simulate the average temperature of the natural habitat (seed collection site) for

Table 1. Seed morphology of Vaccinium delavayi.

Traits	Average	Standard error	Max.	Min.	Range (-fold)
Length (mm)	1.75	0.04	1.98	1.50	1.32
Width (mm)	1.05	0.03	1.23	0.84	1.47
Height (mm)	0.45	0.01	0.57	0.38	1.50
L: W ratio	1.69	0.06	2.24	1.45	1.55
Seed shape index	0.09	0.00	0.11	0.07	1.50
1000-grain weight (g)	0.31	0.01	0.32	0.28	1.14

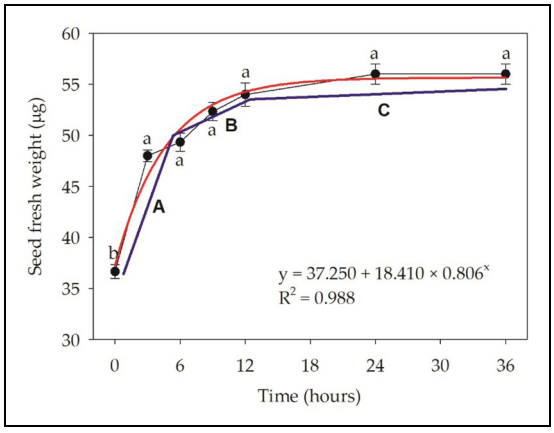

Figure 3. Imbibition curve of *Vaccinium delavayi* seeds along 36 h in distilled water. All values denote the mean (± SE) of 5 repetitions. Means followed by different small case letters denote statistical differences (Statistical Newman-Keuls; $P \leq 0.05$) between the time of imbibition. Red highlighted the theoretical curve at $R^2 = 0.988$. Blue highlights the curve tendency to distinct three distinct portion on seed imbibition curve.

different months (Figure 2) and to test the thermotolerance of the species, i.e, the ability of seed to germinate and maintain physiological function across a range of temperatures. The germination was conducted in 9-cm tight-fitting petri dishes containing one disk of Whatman No. 1 filter paper, moistened with 10 mL of distilled water. During the dark treatment, the petri dishes were wrapped in double layers of aluminum foil to prevent exposure to light. Four replicates of 25 seeds were used for each treatment. The number of germinated seeds was counted and removed every day for 40 days. A seed was considered to have germinated when the emerging radicle reached a length of 2 mm.[32] Seeds incubated under dark conditions were counted after 40 days.

Effect of gibberellic acid on seed germination

Eight-month-old stored seeds were retrieved from different storage conditions and soaked in four concentrations (0-, 500-, 1000-, and 1500- mM) of gibberellic acid (Sigma-Aldrich, UK, part number G1025) for 24 h at room temperature. They were then air-dried for 4 h before being used in the test. After treatment, pre-treated seeds from each storage condition were tested for germination separately at three alternate temperature regimes (5/10, 10/20, and 20/30°C) in 24-h darkness (dark treatment) and/or 12 h light/12 h darkness (light treatment). Four replicates of 25 seeds were used for each treatment and seed germination was recorded. The germination percentage, mean germination time (MGT), and germination synchrony (SYN) were calculated using the GerminaR Package.[33]

Experimental design and statistical analyses

The experiment was designed in a completely randomized design with four replicates having 25 seeds each. The data was analysed by using the ANOVA procedure. The means were compared by using a Statistical Newman-Keuls (SNK) test ($p < 0.05$) using Statistic version 14.0 (StatSoft, Tulsa, OK, USA).

Results

Seed morphology and imbibition

Seeds of *V. delavayi* are longer than wide (Table 1). The seed length ranged from 1.50 mm to 1.98 mm and the seed width ranged from 0.84 mm to 1.23 mm. The ratio of length to width was 1.69 indicating elongated or disc-shaped seeds with a seed shape index of 0.09 (Table 1). The weight of 1000 seeds was approximately 0.31 g. Fresh seeds (36.7 ± 0.7 mg) absorbed 19.5 mg of water after 36 h, having a final weight of about 56.2 mg (Figure 3).

Seed germination responses

Effect of storage time on seed germination. The germination increased with the increase in storage time. Interactions between storage time and temperature ($P \leq 0.01$), and between storage condition, storage time, and temperature ($P \leq 0.05$) were significant (Table 2). The germination in fresh seeds was low in all temperature ranges. The seeds stored at 4°C (wet) exhibited higher germination than

Table 2. ANOVA table of germination seed parameters of *Vaccinium delavayi* germinated without- (up panel) or with gibberellic acid (GA_3; down panel). SS, sum of squares; MS, mean square; LG, light germination; DG, dark germination; MGT, mean germination time.

Source of Variation	DF	SS-LG	MS-LG	SS-DG	MS-DG	SS-MGT	MS-MGT
Storage condition	2	2973.630	1486.815 ***	122.074	61.037 ***	162.238	81.119 ^{ns}
Storage time	2	1352.296	676.148 ***	156.741	78.370 ***	554.515	277.258 *
Temperature	2	4857.185	2428.593 ***	37.630	18.815 **	3654.937	1827.468 ***
Storage condition × Storage time	4	907.259	226.815 ***	123.259	30.815 ***	307.245	76.811 ^{ns}
Storage condition × Temperature	4	1991.704	497.926 ***	98.370	24.593 ***	459.850	114.963 ^{ns}
Storage time × Temperature	4	282.370	70.593 **	29.037	7.259 *	1297.391	324.348 **
Storage condition × Storage time × Temperature	8	1130.074	141.259 ***	72.296	9.037 **	1083.537	135.442 *
Residual	81	1776.000	21.926	244.000	3.012	7016.328	86.621
Total	107	15,270.519	142.715	883.407	8.256	14,536.042	135.851
Source of Variation	DF	SS -LG	MS-LG	SS-DG	MS-DG	SS-MGT	MS-MGT
Storage condition	2	250.889	125.444 ^{ns}	469.556	234.778 *	59.156	29.578 ^{ns}
Giberelic acid (GA_3)	3	47,993.222	15,997.741***	49,762.667	16,587.556 ***	1732.774	577.591 ***
Temperature	2	108,422.889	54211.444 ***	75,949.556	37,974.778 ***	5109.097	2554.548 ***
Storage condition × GA_3	6	2154.444	359.074 ***	1275.333	212.556 **	109.718	18.286 ^{ns}
Storage condition × Temperature	4	180.444	45.111 ^{ns}	405.111	101.278 ^{ns}	56.929	14.232 ^{ns}
GA_3 × Temperature	6	26,547.778	4424.630 ***	25,464.667	4244.111 ***	599.431	99.905 *
Storage condition × GA_3 × Temperature	12	1723.556	143.630 **	1647.333	137.278 **	631.297	52.608 *
Residual	108	7916.000	73.296	6784.000	62.815	5074.056	46.982
Total	143	195,189.222	1364.960	161,758.222	1131.176	13,372.458	93.514

*** significative at $P \leq 0.001$; ** significative at $P \leq 0.01$; * significative at $P \leq 0.05$; ns, non-significative.

other treatments (Table 3). The maximum germination was reported in seeds stored for 16 months (Figure 4).

Effect of gibberellic acid (GA_3) on seed germination. Even after treatment with GA_3, the seed germination at 5/10°C was almost nil (Table 4). Seed germination with higher GA_3 treatment improved significantly, particularly at 10/20°C and 20/30°C. At higher temperatures (10/20°C and 20/30° C), wet-stored seeds showed better germination than those seeds stored in dry conditions (Table 4). GA_3 treatment significantly reduced MGT while it improved synchrony (SYN) at optimal temperature (10/20°C).

Effect of temperature on seed germination. The seed germination was almost nil at 5/10°C, low-to-moderate at 20/30°C, and higher at 10/20°C (Figure 4). All regression coefficients were greater than 0.750 and all were significant at $p \leq 0.01$, except for 16-month-old seeds stored at 4°C dry (Figure 3A).

In fresh, 4- and 8-month stored seeds, the thermotolerance indicates a preference for germination at 10/20°C. Seeds stored at −20 °C had the most stable germination across all temperatures and duration. The application of GA_3 at higher concentrations did not enhance the germination (Table 5). The findings show that −20°C storage is optimal for maintaining the seed viability.

Effect of light on seed germination. The light (12-h light/ 12-h darkness) exhibited a weak influence on seed germination (Table 3 and 4). At temperature 5/10°C there was no significant difference between seed germination on a 12-h light/12-h darkness or full darkness, however in 10/20°C there was a statistical difference between seed germination on a 12-h light/12-h darkness or full darkness. Similarly, at 20/30°C, there is no statistical difference between treatments. However, relative light germination (RLG) values favored the positive photoblastic effects in comparison to neutral or non-photoblastic (Table 5).

Discussion

Seed dormancy is a protective mechanism ensuring the survival of seeds in adverse or uncertain environmental conditions.[30] Studying the nature of seed dormancy is important for understanding the species' reproduction and developing effective cultivation methods. In this study, the seed mass increased after water imbibition, confirming that the seed coat of *V. delavayi* is water-permeable, indicating absence of physical dormancy and suggesting that physiological dormancy may be prominent. Water imbibition is an important criterion to distinguish physical dormancy from other types of dormancy.[34] The findings are consistent with the physiological dormancy species type,

Table 3. Effect of storage conditions (fresh, 4°C dry, 4°C wet, and −20°C), storage time (0, 4, 8, and 16 months), and germination temperatures (5/10°C, 10/20°C, and 20/30°C) on light (12-h light /12-h darkness) and dark (full darkness) germination, mean germination time (MGT), and synchrony (SYN) of Vaccinium delavayi seeds. Means followed by different small-case letters denote the difference between storage conditions in the same storage time and temperature, and different upper-case letters denote the difference between storage times in the same storage condition and temperature. The Newman-Keuls Test (SNK; $p \leq 0.05$) was used to characterize statistical differences. Asterisks (*) denote the statistical difference between light and dark germination (Bonferroni's Test; $p \leq 0.05$). All values denote the mean (± SE) of 4 repetitions. n.d. non-determined.

		Light Germination												Dark Germination											
		Temperatures (°C)												Temperatures (°C)											
Storage condition	Storage time	5/10				10/20				20/30				5/10				10/20				20/30			
Fresh	0	0.0	±	0.0	n.d.	5.0	±	3.0	n.d.	1.0	±	1.0	n.d.	1.0	±	1.0	n.d.	2.0	±	2.0	n.d.	0.0	±	0.0	n.d.
4°C (Dry)	4	0.0	±	0.0	Aa	8.0	±	2.8	Ab*	4.0	±	0.0	Aa*	0.0	±	0.0	Aa	0.0	±	0.0	Aa	0.0	±	0.0	Aa
4°C (Wet)	4	0.0	±	0.0	Aa	31.0	±	1.9	Aa*	2.0	±	1.2	Ba	0.0	±	0.0	Aa	2.0	±	1.2	Ba	0.0	±	0.0	Ba
−20°C	4	2.0	±	1.2	Aa	11.0	±	5.7	Bb	2.0	±	1.2	Ba	0.0	±	0.0	Aa	0.0	±	0.0	Aa	0.0	±	0.0	Aa
4°C (Dry)	8	1.0	±	1.0	Aa	10.0	±	2.0	Ab*	3.0	±	1.0	Aa*	0.0	±	0.0	Aa	0.0	±	0.0	Aa	0.0	±	0.0	Aa
4°C (Wet)	8	3.0	±	1.9	Aa	30.0	±	2.6	Aa*	8.0	±	1.6	Ba*	0.0	±	0.0	Aa	2.0	±	1.2	Ba	0.0	±	0.0	Ba
−20°C	8	2.0	±	1.2	Aa	11.0	±	5.7	Bb	2.0	±	1.2	Ba	0.0	±	0.0	Aa	0.0	±	0.0	Aa	0.0	±	0.0	Aa
4°C (Dry)	16	4.0	±	0.0	Aa*	5.0	±	1.9	Ac*	1.0	±	1.0	Ac	1.0	±	1.0	Aa	0.0	±	0.0	Ab	0.0	±	0.0	Aa
4°C (Wet)	16	4.0	±	1.6	Aa	37.0	±	3.0	Aa*	35.0	±	1.9	Aa*	1.0	±	1.0	Aa	11.0	±	3.0	Aa	7.0	±	1.0	Aa
−20°C	16	9.0	±	1.9	Aa*	26.0	±	4.2	Ab*	11.0	±	1.9	Ab*	1.0	±	1.0	Aa	1.0	±	1.0	Ab	3.0	±	1.9	Aa
		Mean Germination Time (MGT)												Synchrony (SYN)											
		Temperatures (°C)												Temperatures (°C)											
Storage condition	Storage time	5/10				10/20				20/30				5/10				10/20				20/30			
Fresh	0	0.0	±	0.0	n.d.	29.3	±	2.3	n.d.	n.d.				n.d.				0.17	±	0.12	n.d.	n.d.			
4°C (Dry)	4	n.d.				27.9	±	1.3	Aa	19.3	±	3.3	Ba	n.d.				0.11	±	0.10	Aa	n.d.			
4°C (Wet)	4	n.d.				19.8	±	0.7	Ab	14.0	±	0.7	Aa	n.d.				0.07	±	0.03	Aa	n.d.			
−20°C	4	31.0	±	0.0	Aa	29.4	±	0.2	Aa	10.0	±	0.0	Bb	n.d.				0.02	±	0.02	Aa	n.d.			
4°C (Dry)	8	30.0	±	0.0	Aa	0.0	±	0.0	Bb	n.d.				n.d.				0.00	±	0.00	Ba	n.d.			
4°C (Wet)	8	30.0	±	0.0	Aa	24.6	±	2.0	Aa	15.4	±	4.0	Aa	1.0	±	0.00	n.d.	0.18	±	0.07	Aa	0.33	±	0.29	n.d.
−20°C	8	31.0	±	0.0	Aa	29.4	±	0.2	Aa	10.0	±	0.0	Ba	n.d.				0.02	±	0.02	Aa	n.d.			
4°C (Dry)	16	23.5	±	2.4	Ba	26.3	±	0.5	Aa	27.0	±	0.0	Aa	n.d.				0.00	±	0.00	Bb	n.d.			
4°C (Wet)	16	28.0	±	1.7	Aa	21.0	±	0.4	Ab	12.4	±	0.7	Ab	1.0	±	0.00	n.d.	0.23	±	0.04	Aa	0.09	±	0.02	n.d.
−20°C	16	20.3	±	1.2	Bb	24.4	±	1.2	Ba	16.0	±	1.6	Bb	0.0	±	0.00	n.d.	0.07	±	0.03	Ab	0.13	±	0.08	n.d.

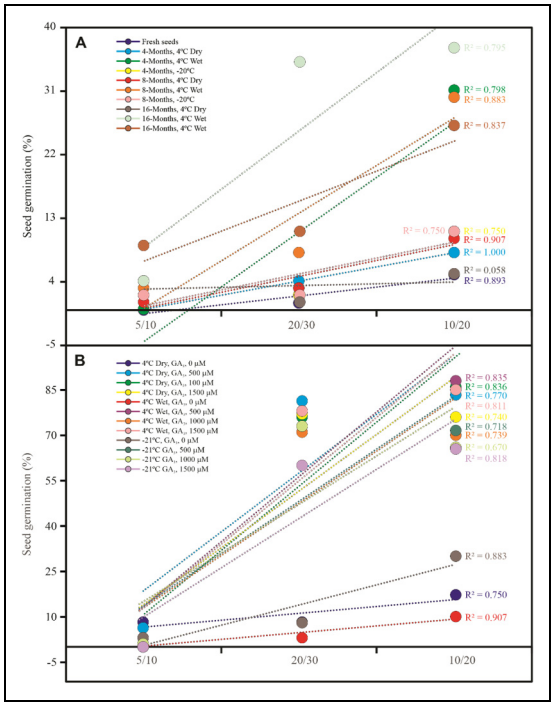

Figure 4. Regression curves of seed germination on light (12-h light/12-h darkness) of *Vaccinium delavayi* under three different temperatures (5/10°C, 10/20°C, and 20/30°C) and in presence (A) or absence (B) of gibberellic acid (GA_3). All regressions were followed by its coefficient of regression (R^2).

in which the seed coat does not act as a barrier for water absorption.

Storage has a positive effect on the germination of *V. delavayi* seeds suggesting that dormancy was alleviated over time, a characteristic of species with non-deep physiological dormancy.[35] The findings contradict the commonly observed fact that seed viability generally decline during long-term storage.[27] Storage at a low temperature (3°C) was effective in breaking the physiological dormancy and improving the germination in *Lotus corniculatus* var. *japonicas* seeds.[36] Our findings are consistent with regional studies, such as on *Primula florindae*, endemic to eastern Tibet, South-West China, where wet-chilled seeds showed better germination due to overwintering cues.[37]

Wet stored seeds at 4°C for different time duration (*i.e.*, 4, 8, and 16 months) had higher germination as compared to those stored under other conditions. It suggests that low temperature and moisture prior to germination are essential requirement for germination of *V. delavayi* in nature. Moist chilling is effective in overcoming physiological seed dormancy and enhancing the germination of many species.[38–41] In nature, seeds of *V. delavayi* likely to experience snow cover and cold soil temperature which stimulate overwintering and promoting germination.

GA_3 plays an important role in overcoming dormancy by promoting the synthesis of hydrolytic enzymes, such as α-amylase, which mobilizes the reserved food in seeds. Exogenous application of gibberellic acid is effective in releasing physiological dormancy of seeds via hydrolytic enzyme induction in various species.[30,40,42,43] In this study, concentrations of GA_3 significantly enhance the germination of stored seeds of *V. delavayi* under different storage conditions, especially at 10/20°C and 20/30°C. However, variations in germination among temperatures after GA_3 application could be due to differences in signal transduction and ABA suppression, which are temperature dependent.[44–46] The enhanced seed germination with the application of GA_3 further suggests that physiological dormancy is primarily responsible for seed dormancy in *V. delavayi* which can be broken by hormonal priming.

At molecular level, GA_3 modulates seed dormancy by promoting the degradation of DELLA proteins.[47] The activation of GA-responsible genes lead to down-regulation of ABA biosynthesis and unregulation of ABA-catabolic genes.[48] GA_3 also activates transcription factors such as GAMYB, which stimulates, germination-related gene network.[49] These hormonal interaction are well known in model species like *Arabidopsis thaliana* and may apply to *V. delavayi.*

Our findings revealed that the exogenous application of GA_3 facilitated the dark germination (i.e., the ability of seeds to germinate in the absence of light) of *V. delavayi* seeds. Increased germination in positive photoblastic seeds when exposed to GA_3 in darkness highlights the effectiveness of GA_3 in overcoming photo-dormancy by inducing transcriptional cascades similar to those triggered by light.[50] These results align with previous research demonstrating the GA_3 ability to simulate dark germination in light-sensitive seeds.[51–53]

Fresh seeds of *V. delavayi* showed poor germination (< 6%), indicating the presence of primary dormancy at fruit maturation time to prevent precocious germination during unfavorable winter conditions. This strategy might help the species to survive the harsh environmental conditions during winter. Similar ecological adaptations have been reported in the temperate flora including *Primula* and *Viola* species.[54,55]

Stored seeds of *V. delavayi* germinated better at 10/20°C, irrespective of storage conditions, suggesting that this is the optimal temperature for germination of the species. Seeds of *V. delavayi* mature during winter, and encounter adverse winter conditions, leading them to remain dormant until conditions become optimal for germination. This may serve as an adaptation strategy for survival, as these conditions may not provide sufficient support for seedling growth.[56,57] The temperatures above or below the optimum range resulted in poor germination.

In natural conditions, seeds of the species germinate in July-September, when soil moisture is high due to snow melt, and temperatures range from 10°C to 26°C, with a high probability of rainfall. These findings are similar to those reported in other species of temperate regions.[57,58]

Table 4. Effect of storage conditions (4°C dry, 4°C wet, and −20°C), gibberellic acid (GA_3) concentration (0, 500, 1000, and 1500 μM L^{-1}), and germination temperatures (5/10°C, 10/20°C, and 20/30°C) on light (12-h light /12-h darkness) and dark (full darkness) germination, mean germination time (MGT), and synchrony (SYN) of *Vaccinium delavayi* seeds. Means followed by different small-case letters denote the difference between GA_3 concentrations in the same condition and temperature. Mean followed by different upper-case letters denotes the difference between storage conditions in the same GA_3 concentrations and temperature. The Newman-Keuls Test (SNK; $p \leq 0.05$) was used to characterize statistical differences. Asterisks (*) denote the statistical difference between light and dark germination (Bonferroni's Test; $p \leq 0.05$). All values denote the mean (± SE) of 4 repetitions. n.d. non-determined.

		Light Germination												Dark Germination											
		Temperatures (°C)												Temperatures (°C)											
Storage condition	GA_3 (μM L^{-1})	5/10				10/20				20/30				5/10				10/20				20/30			
4°C (Dry)	0	1.0	±	1.0	Aa	10.0	±	2.0	Bc*	3.0	±	1.0	Ab	0.0	±	0.0	Aa	0.0	±	0.0	Ab	0.0	±	0.0	Ab
4°C (Dry)	500	1.0	±	1.0	Aa	88.0	±	2.8	Aa*	78.0	±	4.2	Aa*	0.0	±	0.0	Aa	63.0	±	5.3	Aa	50.0	±	5.3	Aa
4°C (Dry)	1000	0.0	±	0.0	Aa	70.0	±	3.8	Bb	71.0	±	7.5	Aa	0.0	±	0.0	Aa	77.0	±	6.6	Aa	69.0	±	2.5	Aa
4°C (Dry)	1500	0.0	±	0.0	Aa	85.0	±	1.0	Aa	78.0	±	5.0	Aa	0.0	±	0.0	Aa	82.0	±	5.3	Aa	70.0	±	10.5	Aa
4°C (Wet)	0	3.0	±	1.9	Aa	30.0	±	2.6	Ab*	8.0	±	1.6	Ac*	0.0	±	0.0	Aa	2.0	±	1.2	Ab	0.0	±	0.0	Ac
4°C (Wet)	500	0.0	±	0.0	Aa	70.0	±	10.4	Aa	73.0	±	6.8	Aa*	0.0	±	0.0	Aa	73.0	±	4.7	Aa	45.0	±	6.0	Ab
4°C (Wet)	1000	1.0	±	1.0	Aa	66.0	±	1.2	Ba	73.0	±	4.1	Aa	1.0	±	1.0	Aa	72.0	±	4.9	Aa	74.0	±	2.6	Aa
4°C (Wet)	1500	0.0	±	0.0	Aa	66.0	±	3.5	Aa	60.0	±	0.0	Ab	2.0	±	2.0	Aa	65.0	±	2.5	Aa	53.0	±	5.3	Ab
−20°C	0	2.0	±	1.2	Aa	11.0	±	5.7	Bb	2.0	±	1.2	Ab	0.0	±	0.0	Aa	0.0	±	0.0	Ab	0.0	±	0.0	Ab
−20°C	500	0.0	±	0.0	Aa	77.0	±	5.3	Aa	75.0	±	8.7	Aa	0.0	±	0.0	Aa	65.0	±	3.0	Aa	51.0	±	7.2	Aa
−20°C	1000	0.0	±	0.0	Aa	86.0	±	1.2	Aa*	76.0	±	7.7	Aa*	0.0	±	0.0	Aa	69.0	±	4.1	Aa	44.0	±	5.2	Ba
−20°C	1500	0.0	±	0.0	Aa	76.0	±	5.9	Aa	77.0	±	9.8	Aa	0.0	±	0.0	Aa	74.0	±	4.8	Aa	55.0	±	8.1	Aa
		Mean Germination Time (MGT)												Synchrony (SYN)											
		Temperatures (°C)												Temperatures (°C)											
Storage condition	Storage time	5/10				10/20				20/30				5/10				10/20				20/30			
4°C (Dry)	0	30.0	±	0.0	n.d.	28.8	±	1.7	Aa	15.3	±	3.9	Aa	n.d.				0.00	±	0.00	Bc	n.d.			
4°C (Dry)	500	30.0	±	0.0	n.d.	15.9	±	0.2	Ab	9.5	±	0.4	Aa	n.d.				0.14	±	0.02	Ab	0.21	±	0.04	Ab
4°C (Dry)	1000	n.d.				15.9	±	0.4	Ab	8.6	±	0.3	Aa	n.d.				0.16	±	0.00	Aa	0.29	±	0.02	Aa
4°C (Dry)	1500	n.d.				15.7	±	0.4	Ab	8.5	±	0.1	Aa	n.d.				0.12	±	0.01	Ab	0.23	±	0.02	Ab
4°C (Wet)	0	30.0	±	0.0	n.d.	24.6	±	2.0	Aa	15.4	±	4.0	Aa	1.00	±	0.00	n.d.	0.18	±	0.07	Aa	0.33	±	0.29	Aa
4°C (Wet)	500	n.d.				17.9	±	1.2	Ab	9.1	±	0.6	Aa	n.d.				0.09	±	0.01	Bc	0.21	±	0.05	Ab
4°C (Wet)	1000	39.0	±	0.0	n.d.	15.7	±	0.4	Ab	9.1	±	0.3	Aa	n.d.				0.14	±	0.01	Ab	0.27	±	0.03	Bab
4°C (Wet)	1500	n.d.				16.7	±	0.8	Ab	9.3	±	0.5	Aa	n.d.				0.10	±	0.01	Ac	0.15	±	0.03	Ab
−20°C	0	31.0	±	0.0	n.d.	29.4	±	0.2	Aa	10.0	±	0.0	Aa	n.d.				0.02	±	0.02	Bb	n.d.			
−20°C	500	n.d.				16.0	±	0.2	Ab	10.2	±	0.6	Aa	n.d.				0.15	±	0.02	Aa	0.26	±	0.07	Aa
−20°C	1000	n.d.				15.6	±	0.3	Ab	8.4	±	0.2	Aa	n.d.				0.15	±	0.02	Aa	0.21	±	0.02	Ba
−20°C	1500	n.d.				15.3	±	0.4	Ab	8.9	±	0.2	Aa	n.d.				0.15	±	0.02	Aa	0.21	±	0.03	Aa

Table 5. Effect of storage conditions (4°C dry, 4°C wet, and -20°C), storage time (0, 4, 8, and 16 months), gibberellic acid (GA_3) concentration (0, 500, 1000, and 1500 μM L^{-1}), and germination temperatures (5/10°C, 10/20°C, and 20/30°C) on relative light germination index (RLG) of *Vaccinium delavayi* seeds. In **A.** Means followed by different small-case letters denote the difference between storage conditions in the same storage time and temperature, and different upper-case letters denote the difference between temperatures in the same storage conditions and storage time. In **B.** Means followed by different small-case letters denote the difference between GA_3 concentrations in the same storage condition and temperature. Mean followed by different upper-case letters denotes the difference between storage conditions in the same GA_3 concentrations and temperature. Different Greek letters denote the difference between thermotolerance between storage conditions in the same storage time in experiment A and between GA_3 concentrations in the same storage condition in experiment B. The Newman-Keuls Test (SNK; $p \leq 0.05$) was used to characterize all statistical differences. All values denote the mean (± SE) of 4 repetitions. n.d. non-determined.

A – Relative light germination index in seeds germinated without GA_3

Storage condition	Storage time	Temperatures (°C) 5/10				10/20				20/30				Thermotolerance
Fresh	0	n.d.				0.67	±	0.33	n.d.	1.00	±	0.00	n.d.	1.00 ± 0.00 $^{n.d.}$
4°C (Dry)	4	n.d.				0.81	±	0.10	Aa	1.00	±	0.00	Aa	0.72 ± 0.03 α
4°C (Wet)	4	n.d.				0.95	±	0.03	Aa	1.00	±	0.00	Aa	0.94 ± 0.03 α
−20°C	4	1.00	±	0.00	n.d.	1.00	±	0.00	Aa	1.00	±	0.00	Aa	0.78 ± 0.16 α
4°C (Dry)	8	1.00	±	0.00	Aa	1.00	±	0.00	Aa	1.00	±	0.00	Aa	0.69 ± 0.06 α
4°C (Wet)	8	1.00	±	0.00	Aa	0.94	±	0.04	Aa	1.00	±	0.00	Aa	0.74 ± 0.04 α
−20°C	8	1.00	±	0.00	Aa	1.00	±	0.00	Aa	1.00	±	0.00	Aa	0.78 ± 0.16 α
4°C (Dry)	16	0.88	±	0.13	Aa	1.00	±	0.00	Aa	1.00	±	0.00	Aa	0.42 ± 0.16 α
4°C (Wet)	16	0.83	±	0.17	Aa	0.77	±	0.06	Bb	0.84	±	0.02	Bb	0.49 ± 0.03 α
−20°C	16	0.94	±	0.06	Aa	0.98	±	0.03	Aa	0.85	±	0.09	Aa	0.57 ± 0.07 α

B – Relative light germination index in seeds germinated with GA_3

Storage condition	GA_3 (μM L^{-1})	Temperatures (°C) 5/10				10/20				20/30				Termotolerance
4°C (Dry)	0	1.00	±	0.00	n.d.	1.00	±	0.00	Aa	1.00	±	0.00	Aa	0.78 ± 0.16 α
4°C (Dry)	500	1.00	±	0.00	n.d.	0.58	±	0.01	Ab	0.61	±	0.04	Ab	0.51 ± 0.03 α
4°C (Dry)	1000	n.d.				0.48	±	0.02	Ac	0.50	±	0.03	Bb	0.53 ± 0.03 α
4°C (Dry)	1500	n.d.				0.51	±	0.02	Ac	0.53	±	0.04	Ab	0.50 ± 0.04 α
4°C (Wet)	0	1.00	±	0.00	a	0.94	±	0.04	Aa	1.00	±	0.00	Aa	0.69 ± 0.06 α
4°C (Wet)	500	n.d.				0.48	±	0.03	Bb	0.62	±	0.04	Ab	0.53 ± 0.02 β
4°C (Wet)	1000	0.50	±	0.00	b	0.48	±	0.01	Ab	0.50	±	0.02	Bb	0.50 ± 0.03 β
4°C (Wet)	1500	0.00	±	0.00	c	0.50	±	0.01	Ab	0.53	±	0.02	Ab	0.52 ± 0.02 β
−20°C	0	1.00	±	0.00	nd	1.00	±	0.00	Aa	1.00	±	0.00	Aa	0.74 ± 0.04 α
−20°C	500	n.d.				0.54	±	0.03	Ab	0.60	±	0.05	Ab	0.48 ± 0.06 β
−20°C	1000	n.d.				0.56	±	0.02	Ab	0.63	±	0.04	Ab	0.47 ± 0.01 β
−20°C	1500	n.d.				0.51	±	0.01	Ab	0.58	±	0.05	Ab	0.52 ± 0.01 β

Most seeds germinated better germination in light than in dark. This light requirement for germination indicates that the seeds of *V. delavayi* are light-sensitive and, thus will germinate successfully on or near the soil surface when other conditions are suitable.

Conclusion

This study shows that seed dormancy in *V. delavayi* at maturity protects against harsh winter conditions, ensuring survival until ideal germination conditions arise. Seeds stored under wet condition at 4°C for 16 months showed a germination rate of up to 37%, indicating relative lower regeneration potential in natural conditions. The use of gibberellic acid (GA_3) significantly increased the germination rate. Understanding the dormancy breaking mechanism can facilitate the large scale cultivation, which may support local economies through its potential in nutraceutical and horticulture. Future studies should explore field trails and molecular mechanisms linked to dormancy to support the breeding strategies of the species.

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Author contributions

XC and AB conceived and conducted the research. AB, MFP and HKC drafted the manuscript, while BL and XC collected the seed samples. JDJ, YYP, LAR analyzed the data and edited the manuscript. All authors reviewed and approved the final manuscript.

Funding

The authors disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: AB received funding to carry this research through the Talents Program of Jiangxi Province (PR China) (Grants jxsq2020104003).

Declaration of conflicting interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

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