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ARTICLE

RESEARCH ARTICLE

Effect of light, temperature, storage duration and conditions on the germination of two Mediterranean conifers: *Tetraclinis articulata* and *Cedrus atlantica*

Efecto de la luz, la temperatura, la duración y las condiciones de almacenamiento en la germinación de dos coníferas mediterráneas: *Tetraclinis articulata* y *Cedrus atlantica*

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Abstract: *Aim of study*: This research aims to determine the optimal germination and storage Conditions for the seeds of two vulnerable Mediterranean conifers, *Cedrus atlantica* Manetti ex Carrière and *Tetraclinis articulata* (Vahl) Masters. *Area of study*: The seeds of *C. atlantica* and *T. articulata* were collected in northwestern Algeria. *Material and methods*: The effect of light [alternation of daylight and darkness (night) *vs* continuous darkness] and temperature (5, 10, 15, 20, 25, 30, 35, 40 °C) on the germination behavior of the two species was examined. Subsequently, the variation of seeds viability under different storage Conditions (-20 °C, 5 °C, ambient temperature) and throughout various timeframes (6, 12, 18 and 24 months) was assessed. *Main results*: Daylight presence favored *C. atlantica* seed germination [final germination percentage (FGP) = 80%] whereas *T. articulata* germination was light-independent. Overall, temperature significantly affected the majority of the germination parameters of the two species ($p < 0.01$). The optimal temperature for seed germination of *T. articulata* and *C. atlantica* was 15 °C (FGP = 56%) and 20 °C (FGP =80%) respectively. The seeds of the two species were able to retain their viability after 24 months of storage, despite the decline in their germination percentage. The analysis of variance revealed a significant influence of storage Conditions on almost all the germination parameters of both species. *Research highlights*: The obtained results are crucial for the construction and management of seed banks, as they facilitate the effective conservation of the studied species. This involves the appropriate and well-scheduled renewal of accessions, which is essential to preserve their long-term integrity.

Keywords: conservation; *ex-situ* conservation; germination behaviour; photosensitivity; seeds; viability; 24 months.

Resumen: *Objetivo del estudio:* La presente investigación tiene como objetivo determinar las condiciones óptimas de germinación y almacenamiento para las semillas de dos coníferas mediterráneas vulnerables *Cedrus atlantica* Manetti ex Carrière y *Tetraclinis articulata* (Vahl) Masters. *Área del estudio:* Las semillas de *C. atlantica* y *T. articulata* fueron recolectadas en el noroeste de Argelia. *Material y métodos:* Se examinó el efecto de la luz [alternancia de luz diurna y oscuridad (noche) frente a oscuridad continua] y la temperatura (5, 10, 15, 20, 25, 30, 35, 40 °C) sobre el comportamiento germinativo de ambas especies. Posteriormente, se evaluó la variación de la viabilidad de las semillas bajo diferentes condiciones de almacenamiento (-20 °C, 5 °C, y temperatura ambiente) y a lo largo de diversos periodos (6, 12, 18 y 24 meses). *Resultados principales:* La presencia de luz favoreció la germinación de las semillas de *C. atlantica* (FGP = 80%), mientras que la germinación de *T. articulata* resultó ser independiente de la luz. En términos generales, la temperatura afectó significativamente a la mayoría de los parámetros de germinación de ambas especies ($p < 0.01$). La temperatura óptima para la germinación de las semillas de *T. articulata* y *C. atlantica* fue de 15 °C (FGP = 56 %) y 20 °C (FGP = 80 %), respectivamente. Las semillas de ambas especies lograron conservar su viabilidad tras 24 meses de almacenamiento, a pesar del descenso en su porcentaje de germinación. El análisis de varianza reveló una influencia significativa de las condiciones de almacenamiento sobre casi todos los parámetros de germinación de ambas especies. *Aspectos destacados de la investigación:* Los resultados obtenidos son fundamentales para la creación y gestión de bancos de germoplasma, ya que facilitan la conservación efectiva de las especies estudiadas. Esto implica la renovación adecuada y debidamente programada de las accesiones, lo cual resulta esencial para preservar su integridad a largo plazo.

Palabras clave: comportamiento germinativo; conservación; conservación *ex-situ*; fotosensibilidad; semillas; viabilidad; 24 meses.

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Supplementary information ↓

1. INTRODUCTION

Conifers, gymnosperms dominating phylum, are extensively distributed over the planet, particularly abundant in cold and temperate regions (Cassan et al., 2009). Coniferous forests are also found in North Africa (MAGRAMA, 2017). The relict populations of these forests are endemic and survive in small, isolated locations (Diaz-Sala et al., 2013). In recent decades, the Algerian forest area has been steadily declining. The geographical spread of this degradation, which is primarily caused by the consequences of climate change and irrational exploitation, puts Algeria's forest patrimonial and ecological balance at risk (Haichour & Benabdelli, 2022). Thus, the national attempts to extend the forest cover have failed to counteract this regression.

Two fundamental conservation strategies are typically used to conserve biodiversity, each of which consists of a variety of methods that allow the preservation of genetic diversity. The two strategies are *ex-situ* conservation (conservation of plant or animal species outside their habitats) and *in-situ* conservation (in their habitat). *Ex-situ* conservation of plant species refers to the sustainable preservation of genetic resources in the form of seeds, grafts, cuttings, or even tissues for in-vitro cultures outside of the location where they were collected.

Attributable to the extreme tolerance of seeds to storage Conditions, the conservation of more than 50,000 species has been achieved through seed banking, and the number of seed banks worldwide has consequently grown to over 1,750 (Walters & Pence, 2020).

Seed germination, a complex process starting with water absorption and ending with radicle emergence, is controlled by the interaction of dormancy-releasing factors (phytohormones, light, temperature, water, nutrients, humidity) and a balance between phytohormones (abcissic acid /gibberelic acid), light, and temperature, which induces dormancy release or radicle emergence (Bareke, 2018). While seed germination is fundamentally governed by factors such as the ones mentioned above, the physiological changes that seeds undergo during storage can either enhance or impair their ability to respond to these cues.

Seeds, based on their physiological responses during storage, are divided into two main categories: orthodox seeds which tolerate drying and can be stored for relatively long periods at sub-zero temperatures if their moisture content is reduced; and recalcitrant seeds which do not withstand drying and freezing and therefore cannot be stored even under optimal Conditions, their viability is limited to a few weeks, sometimes several months (Corbineau, 2024). During long-term storage, the Conditions under which seeds are conserved significantly affect their germination ability. Inadequate storage Conditions often result in seed deterioration and loss of viability. Low temperature storage restricts the fungal and bacterial activity, and reduces the rate of metabolic processes inside the seed, which minimizes the consumption of food reserves.

In the context of conserving endangered species and protecting forest biodiversity, we have undertaken a study on two conifer tree species characterizing the Algerian floristic composition, which are *Tetraclinis articulata* (Vahl) Masters and *Cedrus atlantica* Manetti ex Carrière. *Tetraclinis articulata*, formerly called *Callitris articulata* (Vahl) and commonly known under the names Atlas Cypress, Barbary Thuja, or even “Arar” in Arabic, is mainly distributed in the southern Mediterranean region (IUCN, 2011). This species plays an important socio-economic role in North Africa and is primarily used in artisanal products (Hadjadj & Letreuche Belaroussi, 2017). Likewise, the tree’s leaves, fruits, wood, resin and oil are economically valuable and are used for multiple purposes. In Algeria, anthropogenic activities have caused this species distribution area to considerably regress (Hadjadj & Letreuche Belaroussi, 2017). Illegal logging, overgrazing, and especially fires are the main threats to this forest species and are considered the primary causes of its population decline. Therefore, *T. articulata* is classified as a locally vulnerable species (JORA, 2012). *Cedrus atlantica*, commonly known under the names Atlas cedar, “Arz” or “Meddad” in Arabic, is an Algerian-Moroccan endemic species. This conifer tree has consistently received attention due to a number of crucial forestry qualities, including its ecological importance, quality wood, low flammability, and strong climatic stress tolerance (Rabhi et al., 2018). However, *C. atlantica* is currently classified by the IUCN (2013) as “Endangered” due to overexploitation, and the small populations of this species are threatened by various factors. In Algeria, it is classified as rare and threatened (FAO, 2012). The area covered by Atlas cedar forests in northern Algeria is actively in regression (Bouazza et al., 2018). If the regional climate continues becoming progressively arid, this population decline is likely to continue (IUCN, 2013).

This research aims to determine the optimal germination and storage Conditions for the seeds of two vulnerable Mediterranean conifers, *C. atlantica* and *T. articulata*. This knowledge will contribute to improving plant-production techniques for the two species in their natural habitat and will facilitate their *ex-situ* conservation.

2. MATERIAL AND METHODS

2.1. Harvest location, description, and preparation of seeds

The seeds of *C. atlantica* and *T. articulata* were collected in September 2021 in two sites in northwestern Algeria (Table 1). The seeds of both species were randomly collected from approximately 20 trees to optimize spatial and genetic representativeness. Following collection, seeds were stored for three months in paper bags under dark, dry Conditions, prior to germination experiments. Intact, undamaged, and mature seeds were selected for germination tests. The fresh weight of 100 seeds of each species was evaluated as well as their moisture content according to the following formula (Bonnet, 1981).

FW: Fresh seed weight the day of the harvest, DW: Seed dry weight.

Table 1. Geographical coordinates and bioclimatic characteristics of seed collection sites for *Cedrus atlantica* and *Tetraclinis articulata* in northwestern Algeria

Species	GPS coordinates	Harvest site	Bioclimatic zone
Cedrus atlantica	N: 35°51’56’’ W: 01°55’30’’ Alt: 1500 m	Theniet El Had National Park (province of Tiaret, Algeria)	Humid to semi-humid (Mairif et al., 2023)
Tetraclinis articulata	N: 35°29.426’; W: 001°11,724’ Alt: 597m	Sassel forest (province of Ain Témouchent, Algeria)	Semi-arid (Djemel, 2022)

N: north; W: west; Alt: altitude (meters); GPS: Global Positioning System.

Seed dry weight was determined following seed desiccation in silica gel. Seed weight was monitored periodically during silica gel drying. Final dry weight was recorded when no further weight change was observed.

Prior to every germination test, seeds were subjected to surface sterilization for 10 minutes using a 1% sodium hypochlorite solution and subsequently rinsed thoroughly with distilled water in order to remove all traces of chlorine. Following the disinfection, seeds were placed onto Petri dishes of 90 mm diameter and 14.2 mm height lined with a double layer of filter paper, constantly moistened with distilled water. Germination tests were performed on a replicate size of 100 seeds divided into 4 batches of 25 seeds each. The number of germinated seeds was recorded every 24 hours. The protrusion of the radicle through the seed coat served as the indicator of germination (Song & Choi, 2019).

2.2. Preliminary germination tests

To verify the viability of *C. atlantica* and *T. articulata* seeds, preliminary germination tests were conducted in an incubator (Memmert IPP 200) under a constant temperature of 20 °C and two light regimes: alternating daylight/night darkness (photoperiod =15h) and continuous darkness. The effect of light on the germination of the two studied species was assessed through these tests. The light condition that produced the highest germination percentage was used for the subsequent experiments.

The temperature 20 °C was selected for preliminary testing as it is widely regarded as optimal for the germination of most Mediterranean seed species (Bertsouklis et al., 2022).

2.3. Effect of temperature on germination

In order to determine the optimal thermal Conditions for seed germination of the studied species, germination tests were performed at the following constant temperatures: 5, 10, 15, 20, 25, 30, 35, and 40 °C.

2.4. Effect of storage Conditions on seed viability

Periodic germination tests (every 6 months) were employed to evaluate and track seed viability of the studied species stored in different Conditions: at ambient temperature of the laboratory (20~25 °C), at 5 °C, and at -20 °C. Germination tests conducted immediately post-harvest and prior to storage (Control tests) were labeled T_0. Storage Durations for the aforementioned Conditions were: 0 months (Control tests), 6 months, 12 months, 18 months, and 24 months. Under all experimental storage Conditions and Durations, seeds of each species were stored in airtight glass bottles and covered with cotton on which a few Silica gel pellets were placed.

2.5. Data processing

The germination kinetics of both studied species was graphically depicted by curves representing the cumulative germination percentage as a function of time, expressed in days. The following germination parameters were determined (ISTA, 2023):

The final germination percentage (FGP) or germination capacity, which represents the maximum average percentage of germinated seeds:

FGP (%) = (Number of germinated seeds / Total number of seeds)× 100

The germination rate or velocity coefficient (VC), which describes the germination speed as a function of the total number of seeds germinating within a specified period:

Where N_1 is the number of seeds germinated on the first day (t1); N2 is the number of seeds germinated on the second day (t2); …*NnTn*.

This formula takes into account the number of seeds germinating on each day of the experiment. As a result, when a larger proportion of seeds germinate in the early days, the calculated rate is higher, reflecting the faster germination speed. Conversely, when germination is delayed and only few seeds germinate each day, the rate is lower, indicating a slower germination process. The unit for this germination rate is “average percentage of seeds germinated each day”.”

Mean Germination Time (MGT), is a measure of the average number of days it takes for the seeds in a batch to germinate:

Latency time (LT) is the number of days required for the first seed in the batch to germinate.

The effect of light and temperature on germination parameters was verified by one-way analysis of variance (ANOVA I) using IBM SPSS software version 22. The pairwise comparison of the means was carried out by the Tukey test. The two-way analysis of variance (ANOVA II) was performed to investigate the influence of storage Duration and Conditions, as well as their interaction on seed viability.

3. RESULTS

3.1. Description and seed morphometry

The description of the seeds of the studied species, including their morphometric characteristics and their moisture content, is presented in Table 2 and Figure 1.

Table 2. Physical and morphological characteristics of seeds from *Cedrus atlantica* and *Tetraclinis articulata* collected in northwestern Algeria

Species	**Form**	**Color**	**Ornamentation**	**W (g)**	**MC (%)**	**L(mm)**	**W (mm)**	**T (mm)**
Tetraclinis articulata	Obovate	Brown	Wing	0.62	2.66	5.75±0.48	2.28±0.58	2.13±0.78
Cedrus atlantica	Obovate	Brown	Wing	7.72	0.30	13.11±0.58	5.40±0.24	3±0.35

W: weight of 100 seeds; MC: Moisture content; L: Length; W: Width; T: Thickness

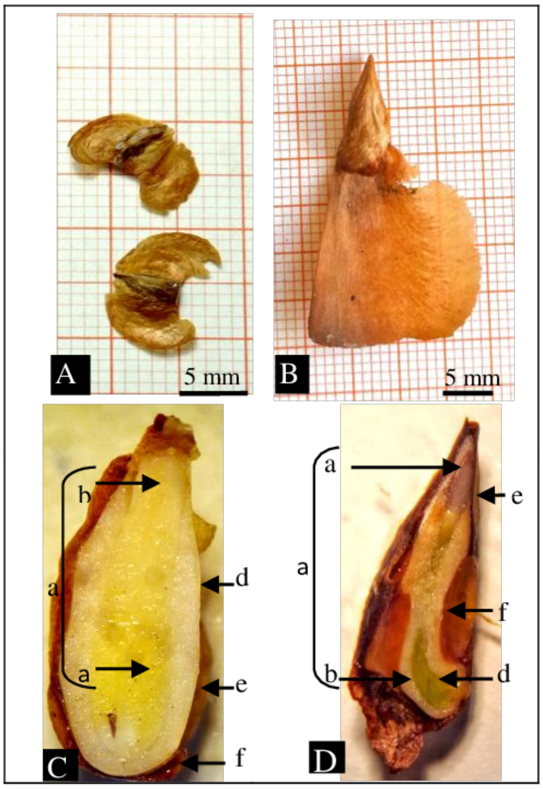

Figure 1. Longitudinal sections of *Tetraclinis articulata* and *Cedrus atlantica* seeds from Northwestern Algeria (photo by Meriem Bentekhici, 2024).A: seeds of *Tetraclinis articulata*; B: seeds of *Cedrus atlantica*; C: internal seed morphology of *Tetraclinis articulata* (×30) [a: cotyledon; b: radical; c: embryo; d: megagametophyte; e: seed coat; f: resin vesicle]; D: internal seed morphology of *Cedrus atlantica* (×20) [a: cotyledon; b: radical; c: embryo; d: megagametophyte; e: seed coat; f: resin vesicle].

3.2. Effect of light on seed germination

The results obtained from the germination tests performed in alternating daylight and night darkness (15 h light/9 h dark), as well as in continuous darkness are summarized in Table 3. The analysis of variance indicated that the mean values of the germination parameters (FGP, VC, MGT and LT) for *T. articulata* did not exhibit statistically significant variations in the two experimental Conditions (Table 3). On the other hand, a statistically significant enhancement in *C. atlantica* seeds FGP was observed under alternating daylight and night darkness Conditions compared to continuous darkness. However, the other parameters (VC, MGT and LT) were identical in both germination Conditions (Table 3).

Table 3. Photoblastic responses of *Tetraclinis articulata* and *Cedrus atlantica* seeds collected in northwestern Algeria

	Photoperiod	FGP (%)	VC (%)	MGT (days)	LT (days)
Tetraclinis articulata	Daylight/Night darkness	55 ± 1.73	25.15 ± 1.74	5.25 ± 3.7	1.5 ± 0.7
	Continuous darkness	65 ± 1	26.77 ± 0.67	3.8 ± 0.99	1.5 ± 0.7
	F value	2.0^{ns}	0.015^{ns}	0.28^{ns}	0.0^{ns}
Cedrus atlantica	Daylight/Night darkness	80 ± 0	15.09 ± 2.42	6.6 ± 1.17	2.3 ± 1.15
	Continuous darkness	53 ± 1.52	21.31 ± 4.06	4.8 ± 1.18	3
	F value	9.143*	3.78^{ns}	3.90^{ns}	1.00^{ns}

ns: non-significant (p>0.05); *: significant (p<0.05); FGP: final germination percentage; VC: velocity coefficient; MGT: mean germination time; LT: latency time.

3.3. Effect of temperature on germination parameters

As shown in Figure 2, the germination of *T.articulata* occurred within the temperature range of 5 °C to 40 °C, with the highest FGP obtained at 10 and 15 °C (56%). Analysis of variance revealed a significant effect of temperature on FGP (F5, 20 = 4.22, p < 0.05). The temperature did not have a significant effect on VC (Figure 3). The MGT values of *T. articulata* seeds were significantly influenced by temperature (F7, 20 = 3.91, $p < 0.05$), whereas LT values remained unaffected (F7, 20= 2.68, p > 0.05). The longest and shortest MGT occurred at the temperatures 5 °C and 40 °C respectively. The longest LT was obtained at 15 °C (3.75 days) (Figure 3). According to Figure 2, the germination of *C. atlantica* seeds occurred within a temperature spectrum extending from 5 °C to 35 °C, with the highest FGP observed at 20 °C (80%). MGT and LT values declined progressively with elevating temperature (Figure 3); in contrast, VC values increased with temperature (Figure 3). The slowest germination proceeded at 5 °C, resulting in a low VC and a longer MGT and LT. Analysis of variance revealed a significant effect of temperature on all *C. atlantica* seed germination parameters.

3.4. Effect of storage Conditions and Durations on seed viability

The two-way analysis of variance examining the impact of storage Conditions and Durations on *T. articulata* seed viability revealed a non-significant effect of storage Durations and Conditions on the FGP of *T. articulata* seeds (Table 4). On the other hand, a significant effect of storage Conditions on VC, MGT and LT was noted (Table 4). Compared to T_0, regardless of storage Conditions employed, a decrease in VC was observed throughout all storage Durations, with a more pronounced decline observed in seeds stored at 5 °C and at room temperature. Furthermore, the MGT and the LT values remarkably and progressively increased over time under all storage Conditions (Figure 4).

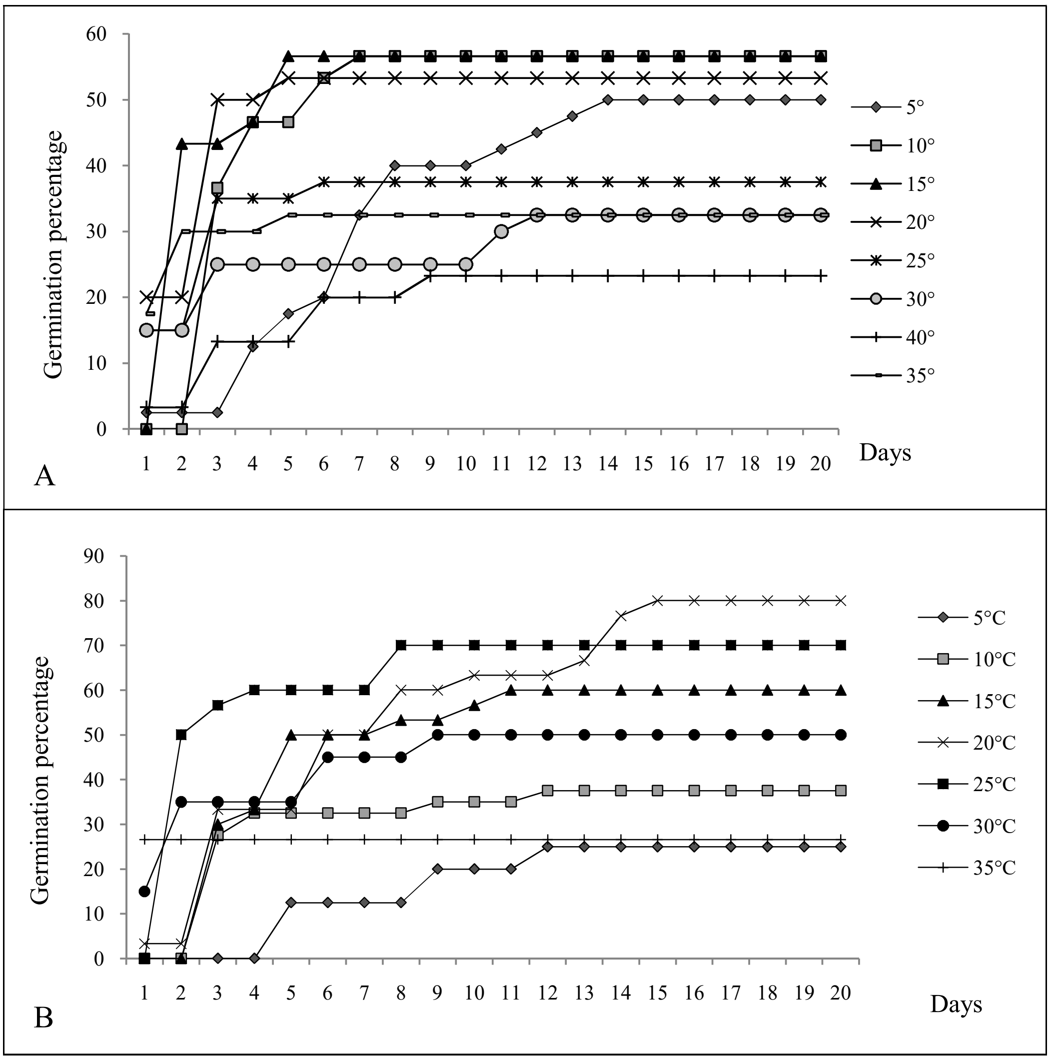

Figure 2. Germination kinetic curves of *Tetraclinis articulata* (A) and *Cedrus atlantica* (B) seeds at different temperatures.

The significant effect of storage Conditions on FGP, VC and MGT of *C. atlantica* seeds was confirmed by ANOVA II. The significant influence of storage Duration and the interaction between storage Durations and Conditions on the LT were also confirmed by the same test (Table 4). Compared to T_0, the FGP of seeds stored at 5 °C and at room temperature showed a gradual decline over time. Conversely, an acceleration of germination was observed under all the Conditions tested, characterized by an increase in VC and a decrease in MGT values (Figure 5).

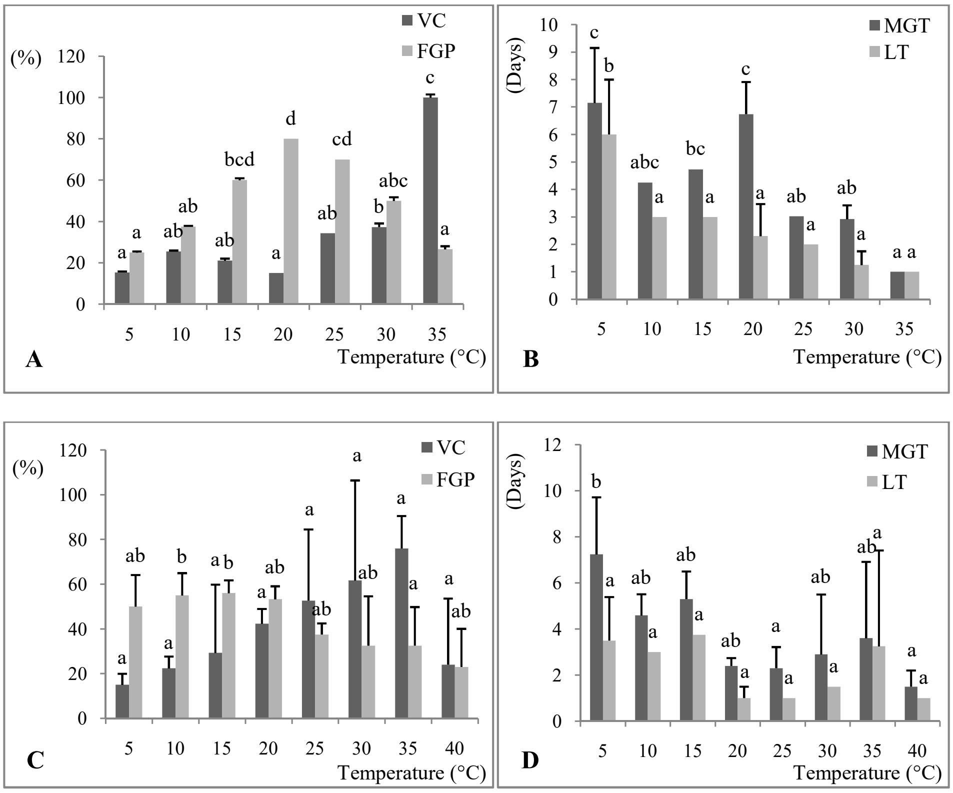

Figure 3. Variation of final germination percentage (FGP), velocity coefficient (VC), mean germination time (MGT) and latency time (LT) of *Cedrus atlantica* (A, B) and *Tetraclinis articulata* (C, D) seeds at different temperatures. Different letters indicate a significant difference between means by Tukey's test ($p \leq 0.05$), error bars display standard deviation

Table 4. Effect of storage Duration and Conditions on seed germination parameters (two-way ANOVA) of *Tetraclinis articulata* and *Cedrus atlantica*

Factors		Mean square		Df		F value		*p* value	
		T.A	*C.A*	*T.A*	*C.A*	*T.A*	*C.A*	*T.A*	*C.A*
FGP	Duration	0.818	0.830	6	7	1.284	1.159	0.297	0.353
	Conditions	0.582	2.111	4	4	0.914	2.948	0.496	**0.035**
	Duration*Conditions	0.532	0.647	11	4	0.835	0.903	0.608	0.516
VC	Duration	175.226	23.41	6	7	1.428	0.438	0.239	0.871
	Conditions	474.80	413.21	4	4	3.869	7.726	**0.013**	**0.0001**
	Duration*Conditions	91.93	123.47	11	7	0.749	2.309	0.684	0.050
MGT	Duration	1.243	0.677	6	7	0.765	0.886	0.604	0.529
	Conditions	17.382	12.76	4	4	10.689	16.69	**0.0001**	**0.0001**
	Duration*Conditions	1.820	1.95	11	7	1.119	2.55	0.383	0.03
LT	Duration	1.237	1.190	6	7	0.852	4.079	0.542	**0.003**
	Conditions	15.086	0.255	4	4	10.387	0.876	**0.0001**	0.489
	Duration*Conditions	0.604	1.086	11	7	0.416	3.722	0.937	**0.005**

T.A: *Tetraclinis articulata*; C.A: Cedrus atlantica; Df: Degrees of freedom; *p* value: borderline significance level; *p*<0.05: significant; *p*>0.05: non-significant; Values in bold: significant difference.

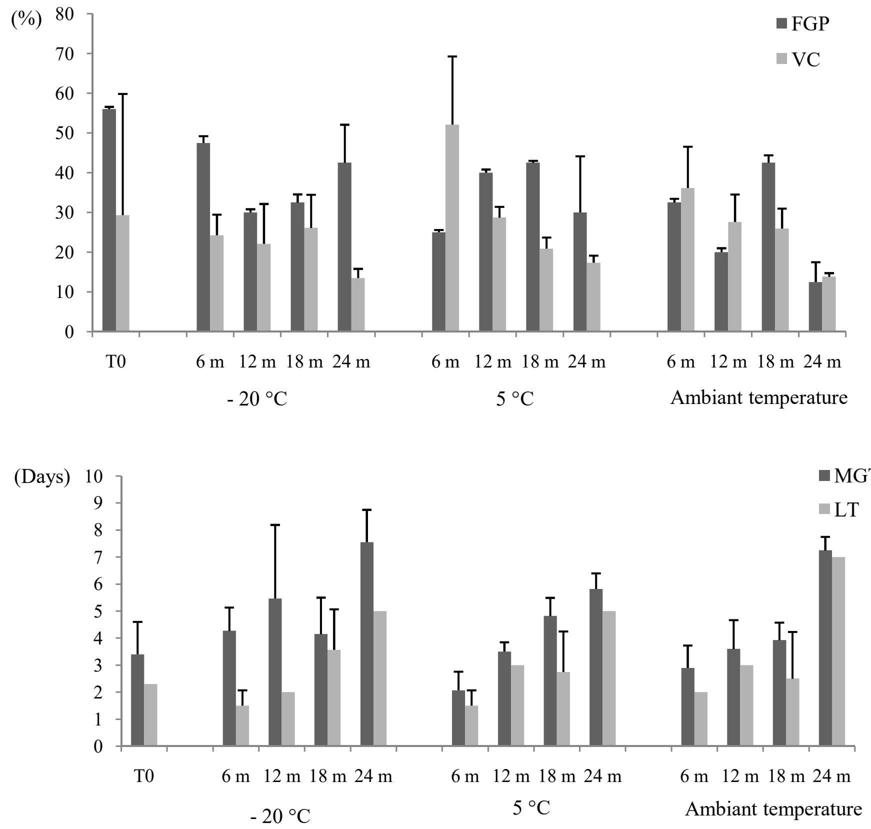

Figure 4. Variation of final germination percentage (FGP), velocity coefficient (VC), mean germination time (MGT) and latency time (LT) of *Tetraclinis articulata* seeds under different storage Durations and Conditions. m: months; T_0: Control tests.

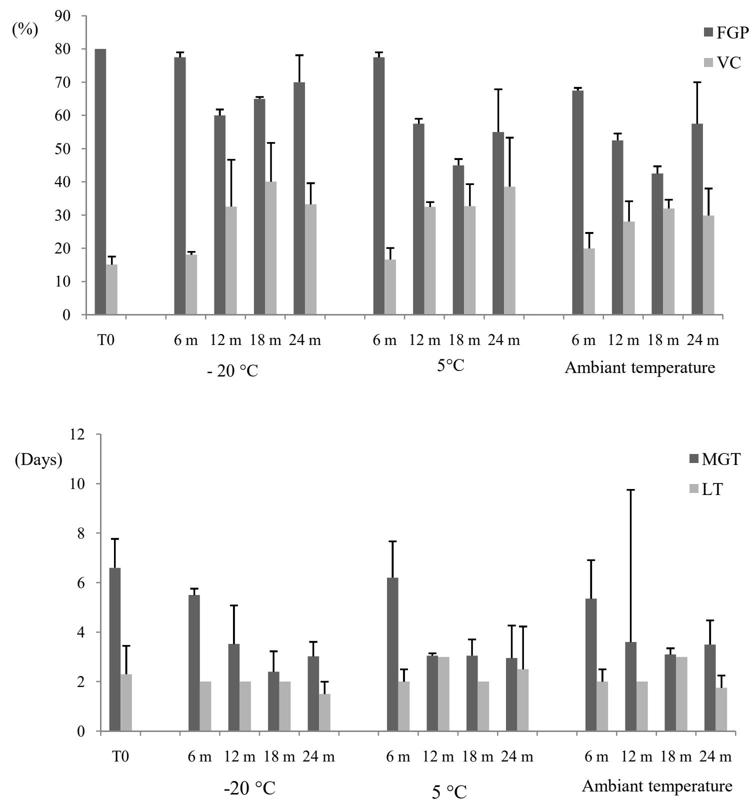

Figure 5. Variation of final germination percentage (FGP), velocity coefficient (VC), mean germination time (MGT) and latency time (LT) of *Cedrus atlantica* seeds under different storage Duration and Conditions. m: months; T_0: Control tests

4. DISCUSSION

4.1. Seeds photosensitivity

Light is one of the crucial factors that contribute in regulating seed germination. Phytochromes, a class of photoreceptors, play a major role in light perception. This perception triggers a cycle of enzymatic and chemical interactions that ultimately stimulates the seed germination (Wei et al., 2023). Based on their responses to light, seeds are classified into three categories: seeds that require light to germinate, seeds necessitating continuous darkness to germinate, and indifferent seeds. Indifferent seeds are capable of germinating in both light and dark Conditions. Nevertheless, some of these seeds may exhibit a slight preference for one condition over the other.

Regarding the photoblastic response of seeds of the two studied species, results revealed that *T. articulata* seeds are indifferent to light since the values of FGP, VC, MGT and LT did not show significant differences in presence or absence of light. According to Navarro-Cerrillo & Galvez-Ramirez (2001), *T. articulata* seeds germinate better in the presence of light. This does not agree with our results where this species seeds presented an indifferent photoblastism. Khaddari et al. (2019) studied the variation in germination capacity of seeds from different provenances of the western Mediterranean region and concluded that seed origin considerably influences plant development. The results of this study hypothesize that the reaction of *T. articulata* seeds to light may likewise vary depending on the collection site or harvest season.

Cedrus atlantica seeds FGP was significantly better in alternating daylight and night darkness. Similar results have been reported in several *Pinaceae* species such as *Pinus sylvestris* L and *Picea excelsa* (Lam.) Link (Sarvas, 1950). Furthermore, Garcia-Fayos (2001) recommended a photoperiod of at least 12h for *Pinaceae* seeds germination, based on the assumption that continuous darkness induces a profound dormancy in these seeds.

4.2. Effect of temperature on germination

The observation of germination at 40 °C (FGP= 23%) suggests a remarkable thermo-tolerance in *T. articulata* during the germination stage compared to other Mediterranean species seeds. Additionally, the high FGPs obtained at temperatures below 20 °C reflect the ability of these seeds to germinate better at low temperatures. According to Ghazouani et al. (2021), the thermal optimum for the germination of *T. articulata* seeds was 25 °C. The thermal optimum for germination within a species can be attributed to its provenance and origin, specifically the habitat characteristics associated with each provenance (Khaddari et al., 2019). Moreover, compared to the germination observed at temperatures below 20 °C, the germination of *T. articulata* seeds at temperatures above this threshold was faster. At 20, 25, 30 and 35 °C, the MGT did not exceed 2.4 days, with a VC ranging between 42.3 and 76%. In contrast, at 5, 10 and 15 °C, the MGT values ranged between 5 and 7.24 days, while the corresponding VC values ranged between 15 and 29.32%. The observed reduction in MGT at elevated temperatures aligns with a survival strategy commonly employed by Mediterranean seeds originating from arid and semi-arid environments. This strategy, characterized by rapid germination, maximizes the chances of radicle emergence and establishment under unpredictable Conditions (Gairola et al., 2019).

The thermal optimum for the germination of *C. atlantica* seeds was 20 °C, where the highest FGP (80%) was obtained. The same thermal optimum is reported by Hafidou et al. (2021) in the same species. In the natural habitat of *C. atlantica*, winters now persists until the arrival of spring. Longer snow cover can help maintain higher soil water potential, and snowmelt can increase it further (Kacha, 2018). Therefore, seed germination is typically delayed until spring to avoid excess water and cold temperatures caused by the gradual melting of snow, which can negatively influence or even hinder the establishment of the new seedling. This explains the high FGPs (between 60 and 80%), obtained at 15, 20 and 25 °C. These temperatures align with those of spring season of the *C. atlantica* native environment (Loukkas, 2001). The elevation of the temperature appears to accelerate the germination of cedar seeds, as evidenced by the progressive augmentation in VC and the concomitant reduction in MGT and LT. This rapid germination strategy allows new seedlings to benefit from soil moisture and moderate temperatures effectively before the dry season begins.

4.3. Effect of storage Duration and Conditions on germination

Under all tested storage Conditions and Durations, the FGP of *C. atlantica* seeds underwent a progressive decrease, which was more pronounced in seeds stored at 5 °C and at ambient temperature. The temperature of -20 °C appears to be optimal for maintaining the viability of *C. atlantica* seeds after 24 months of storage.

Hawkins et al. (2003) recommended storing conifer seeds at low temperatures (3 °C to -18 °C). Likewise, Takos & Merou (2001) found that the short-term storage of *Cedrus libani* (L.) A. Rich and *Cedrus deodara* (Roxb. ex D.Don) G.Don seeds in airtight containers at 5 °C to -10 °C successfully maintained seed viability. Seeds of most conifers can be stored effectively under such Conditions for 3 to 30 years. Trotter et al. (2001) considered the storage at -18 °C or -20 °C to be the most suitable, which agrees with our findings.

The negative effect of storage Duration on germination capacity under all Conditions may be further explained by the presence of resin vesicles in their seed coats. *Cedrus atlantica* seeds contain resin vesicles within their seed coats (Keeling et al., 2018). Resin is composed essentially of terpenoids which are characterized by germination-inhibiting properties (Keeling & Bohlmann, 2006). Keeling et al. (2018) and Navas & Sánchez-Romero (2021) reported that damaged resin vesicles are capable of reducing seed germination percentage. These vesicles are present between the outer and inner layer of the seed coat. If storage effect induces cracks in the seed coat, the vesicles will be damaged and consequently germination will be influenced (Kshatriya et al., 2018).

Furthermore, increased storage Duration significantly accelerated the germination as evidenced by the corresponding VC, MGT and LT values. The accelerated germination of *C. atlantica* seeds may be attributed to the continued maturation achieved by the seeds during the storage period. This was demonstrated in a study by Shibata et al. (2020) on the variation in germination behavior of the conifer species *Araucaria angustifolia* (Bertol.) Kuntze seeds throughout their different life stages. Indeed, the fastest germination was obtained at the stage of their complete maturity, where the contents of soluble proteins and carbohydrates were high.

Regarding *T. articulata*, the ANOVA II test revealed that neither Durations nor Conditions had a significant effect on seeds FGP. However, all the FGPs obtained after storage under all the Conditions employed, were lower compared to T_0. Several studies have found that the viability of *T. articulata* seeds declines rapidly after 24 or 32 months of storage (Peman Garcia et al., 2014; MAGRAMA, 2017). According to Juan-Vicedo et al. (2022), it is only possible to store them for medium-term Duration. For Peman-Garcia et al. (2014), it is recommended to store them at low temperatures. A marked similarity was observed between the germination patterns of *T. articulata* seeds under the employed experimental storage Conditions and those of *Quercus robur* L recalcitrant seeds, which exhibit declining viability after 24 months of storage near 0 °C. This decline is attributed to a slowdown in metabolism, leading to nutrient depletion and subsequent seed deterioration (Suszka, 1998).

The decline in *T. articulata* seeds FGP may also be due to the presence of resinous vesicles in their seed coats. A similar study on *Abies pinsapo* Boiss seeds (Navas & Sánchez-Romero, 2021) revealed that the damage to their resinous vesicles severely impaired seedling development and germination, this effect manifested as a significant reduction in germination percentage, decreased root length, and total inhibition of shoot development.

The VC, MGT and LT of *T.articulata* seeds were significantly influenced by storage Conditions. Seeds stored at 5 °C and at room temperature showed the slowest germination. As previously explained, the slow germination may be due to the effect of the resin. Damage to resin vesicles during storage allows volatile constituents to evaporate, enabling some types of terpenoids to polymerize (Keeling et al., 2018). Consequently, this chemical change hinders water imbibition, which in turn reduces the seeds germination speeds and capacities.

Overall, based on our findings, the temperature -20 °C is considered the most appropriate for maintaining *C. atlantica* and *T. articulata* seeds viability during storage for 24 months. Additionally, both species presented an orthodox storage behavior.

Prolonged storage Durations certainly result in seed aging and biochemical changes in seeds, which reduce their germination energy, leading to a reduction in the vigor with which the radicle pierces the seed coat (Olosunde et al., 2017). Thus, seeds stored for long periods gradually lose their viability. In general, the effect of storage Duration on seed viability is irreversible and inevitable. The Duration factor often causes protein degradation and affects DNA function, leading to a loss of seed viability (Nadarajan et al., 2023). Conditions represented mainly by temperature and moisture content influence the rate at which these processes take place (Liu et al., 2022).

5. CONCLUSIONS

The findings of this study define the optimal germination and storage Conditions for both *C. atlantica* and *T. articulata*. Our work confirms that *C. atlantica* seeds exhibits a positive photoblastic response as evidenced by their high FGP obtained in alternating daylight/night darkness Conditions, whereas *T. articulata* germination is indifferent to light.

Seeds of both species demonstrated an important tolerance to high and low temperatures as the germination was possible between 5 and 40 °C for *T. articulata*, and between 5 and 35 °C for *C. atlantica*. The thermal optima for germination of *C. atlantica* and *T. articulata* seeds are 20 °C and 15 °C respectively. Seeds of both species maintained their viability after 24 months of storage under all Conditions, although their germination capacity declined during this period. To effectively retain their viability, it is recommended to store seeds of both species at –20 °C. Findings on the germination behavior of seeds from the two studied species can improve plant breeding strategies in controlled environments. These strategies are intended to be used within operational frameworks for the reinforcement of threatened populations in their natural habitats. Recorded data on seed viability are likewise crucial in the context of the construction and management of seed banks, as they will facilitate an effective conservation of the studied species which involve appropriate and timely renewal and regeneration of accessions to safeguard its long-term integrity.

Seed storage classification (e.g., orthodox, recalcitrant) is an intrinsic physiological trait of a species that is not expected to change significantly from year to year. However, future research should incorporateseed lots from multiple collection years to quantify annual variation in initial seed quality and how these differences influence subsequent storage longevity. It would also be interesting to monitor the growth of young seedlings in controlled (*ex-situ*) and natural (*in-situ*) Conditions. Comparative growth studies of young seedlings in both *ex-situ* and *in-situ* environments would be important. The control of these parameters will be useful in conservation programs and will certainly ensure the survival of these plant genetic resources.

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Supplementary material

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Data availability

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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Authorship contribution statement

Meriem Bentekhici: Conceptualization, Data curation, Formal analysis, Methodology, Resources, Software, Visualization, Writing– original draft.

Zoheir Mehdadi: Conceptualization, Data curation, Formal analysis, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – review & editing.

Competing interests

The authors have declared that no competing interests exist.

Statement on the use of Artificial Intelligence

Not applicable.

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