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Unraveling seed dormancy in *Tuberaria guttata* from the Maamora forest: Effects of physical, chemical, and morphological factors

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ABSTRACT

Tuberaria guttata, an herbaceous plant belonging to the *Cistaceae* family, occupies the Maamora forest bare spaces. It plays an important role in promoting fruiting of desert truffles, soil fertility, and also preventing erosion and desertification. This plant produces two categories of seeds that are distinguished by their size, weight, and color, as well as by their varying germination capacities. We assessed the viability of these seeds, the influence of their morphological characteristics, certain physical, physiological and chemical pre-treatments aimed at breaking the dormancy, as well as the lighting conditions on the rate and speed of their germination. Results show that the germination response is almost the same in light as in darkness. The highest germination percentages (98.33% for light brown seeds and 89.94% for dark brown) were achieved when seeds underwent mechanical scarification that overcame the physical barrier responsible for tegumentary dormancy. Pre-treatment of seeds by wet cold stratification for 74 days promoted also this germination (66.67% for light brown seeds and 58.89% for dark brown seeds). Immersion in gibberellic acid did not have any effect on both categories of seeds. Germination rates remain almost identical to those of untreated seeds, not exceeding 31.11% for light brown seeds and 14.44% for dark brown ones.

Keywords: *Cistaceae*, desert truffles, dormancy, germination, pre-treatment, seed heterogeneity.

INTRODUCTION

Seeds, arising from sexual reproduction, serve as the primary unit for plant propagation. The developmental environment of the plant embryo plays a crucial role in ensuring species continuity (Bentsink and Koornneef, 2008). Zygotic embryogenesis encompasses a series of phases strict embryogenesis, maturation, and desiccation (Bewley, 1997) involving morphological, structural, and genetic changes from zygote formation to the development of a fully mature, germination-ready embryo. Seed germination takes place only when internal factors align with suitable environmental conditions (Holdsworth et al., 1999).

Seed heterogeneity is reflected in several features, including morphological traits like color, size, and weight, as well as physiological factors influencing germination, such as dormancy level (Matilla et al., 2005). During the germination process, differences in seed characteristics can affect water uptake. For instance, seeds with darker coats tend to absorb water more slowly than those with lighter coloration (Puga-Hermida et al., 2003). Seed coat permeability is closely linked to its density and thickness, which are typically lower in light-colored seeds. In contrast, dark-colored seeds often exhibit reduced permeability due to the presence of multiple integumentary layers, higher cell density, and unique chemical processes like phenolic

oxidation, specific to this seed type (Matilla et al., 2005). Among reproductive traits, seed size is one of the most extensively studied (Leishman et al., 2000). Smaller seeds are typically associated with longer persistence in the soil and are more likely to be found in deeper soil layers. Darkness enhances the germination ability of seeds when they are buried in soil (Luna et al., 2022). On the other hand, the requirement for light during germination serves as an adaptive strategy, allowing seeds to focus on disturbed areas where competition from established plants is lower (Espinosa et al., 2024). Most species with hard seeds are capable of germinating across a range of temperatures, regardless of light conditions, as long as the seed coat remains permeable (Langa et al., 2024).

The Cistaceae family is represented at the Maamora forest, Morocco, by three genera: Cistus, Halimium, and Tuberaria (Afi et al., 2005). Their different species occupy poor and slightly acidic soils and are considered opportunistic because they have the ability to colonize disturbed areas and degraded forests (Trabaud,1995). The ability to colonize disturbed areas and degraded forests (Trabaud, 1995) stems from the capacity of their seeds to germinate under diverse environmental conditions once physical dormancy is overcome (Thanos and Georghiou, 1988). Seed heterogeneity within this family has been noted in only four species of the genus *Cistus* (Imbert, 2002) and one species of the genus *Tuberaria* (Zaidi et al., 2010). Seed dormancy in many species of Cistaceae is mainly attributed to the hardness of their integument (Thanos et al., 1992). This hardness inhibits seed germination until the seed coat is disrupted (Baskin and Baskin, 2014). In these situations, mechanical scarification is typically employed to enhance water uptake and trigger the initiation of germination (Perez-Perez et al., 2005a) and (Milotić and Hoffmann, 2016). In addition, *Cistaceae* do not require cold stratification, as optimal germination occurs rapidly at different temperatures, once the integument has become permeable (Thanos and Georghiou, 1988). *Tuberaria guttata* is an annual herbaceous plant that produces very tiny, light-weight seeds (Kay and John, 1995). It forms mycorrhizal associations with desert truffles (Figure 1) in the Maamora forest (Dafri and Beddiar, 2018) and probably with other endomycorrhizal fungi. These symbioses improve the resilience of plant communities in the face of environmental stresses, notably drought, nutrient deficiencies and soil disturbance (Barea et al., 2011). Since it is a xerothermophilic plant, its planting can help preserve the land from desertification and degradation (Henkrar et al., 2022). Seed germination of *Tuberaria guttata* occurs under sufficiently moist conditions in late summer or early fall and, to a lesser extent, in winter and early spring (Proctor, 1960). Young plants form overwintering rosettes about 5 cm in diameter, although usually rather small. The main flowering period is around the third week of May. The initial seeds mature and drop before the end of the flowering period, although the length of this phase and the timing of seed dispersal are mainly influenced by weather conditions (Proctor, 1960). Since this plant is self-compatible, seeds should be fertile and generally viable (Proctor, 1960). So, the weakness of the germinative power of the seeds would be of physical origin, namely, integumentary structures, physiological aspects intervening in the emergence of dormancy and even morphological properties of the seed. In this sense, the precise aims of this work were: (1) to analyze the appearance, weight and size of seeds, and (2) to determine the rates of their germination under lighting and in the dark. This study aims to investigate the impact of various physico-chemical pretreatments on seed germination. Understanding the germination process of *Tuberaria guttata* is essential for the sustainability of truffles in the Maamora region, as this plant likely plays a critical role in the mycorrhizal ecosystem supporting their growth. By identifying optimal germination conditions, it would be possible to create an environment that fosters truffle production, ultimately aiding in their long-term conservation.

MATERIALS AND METHODS

Plant

Tuberaria guttata fruits were harvested during the senescence phase of the plant in June, in Morocco's Maamora forest. After being cleaned, the capsules were opened to extract the seeds, which were then air-dried and stored in a cool, dark environment at 4 °C to maintain their germination potential.

Seed sorting

Seed lots were first sorted for their colour. For each colour type, two samples of 50 seeds each were used to assess their size and weight averages.

Viability evaluation of seeds

Seed viability was assessed using the tetrazolium (TTZ) colorimetric method. This procedure involves longitudinally cutting the seeds into two halves and incubating them for 48 hours at room temperature, in darkness, within a 1% solution of 2,3,5-Tetrazolium chloride. Viable seeds develop a red coloration, whereas non-viable ones show no visible change (Paiva et al., 2017). This test provides an indirect evaluation of seed viability by detecting mitochondrial respiratory activity in living tissues (França-Neto and Krzyzanowski, 2019).

Effect of seed colour and light on germination in order to study the germinative power, a first test with 720 seeds divided into 2 colours, and subdivided into 24 lots (12 lots of light brown seeds and 12 lots of dark brown seeds), then arranged under two lighting regimes (16 h photoperiod and total darkness), was performed. Seeds were put in germination on sheets of sterile filter paper, previously hydrated with distilled water, situated in glass Petri dishes (9 cm of diameter), and positioned in a culture chamber at a 20 °C of temperature. The filter paper was kept adequately moist by rehydrating it as required. Throughout the germination period, Petri dishes were inspected on a daily basis, and any germinated seeds were counted and taken out. A seed was deemed to have germinated once a clearly emerging radicle of 1 to 1.5 mm was visible.

Effect of physicochemical pretreatments

A total of 2880 seeds of both colour is divided into eight large batches of 360 seeds each. Six, three of light brown and three of dark brown seeds, were exposed to three distinct pre-treatment methods. (1) scarification carried out by mechanically rubbing the seeds with fine-grained sandpaper; (2) moist cold stratification for 74 days, by placing the seeds, lined with water- soaked filter paper, in Petri dishes and storing them in a refrigerator at 4 °C; and (3) soaking the seeds in a 1 g/l GA_3 solution for 24 h. Two batches, one of each color, are kept as controls. Thus, for each of these treatments, 360 seeds of each colour category were distributed equally in 12 boxes at a rate of 30 seeds per box. Six were placed under a 16 photoperiod and six in continuous darkness. The temperature was set at 20 °C.

Germinated seeds were counted daily throughout the trials. The germination percentage (GP) was calculated using the following formula (Khalaki et al., 2019):

$$FPG\ (\%) = (Number\ of\ germinated\ seeds / Total\ number\ of\ seeds\ tested) \times 100 \quad (1)$$

The germination energy is expressed by the following formula (Pawłat et al., 2022):

$$MGT\ (Day) = \sum(dn)/N \quad (2)$$

where: MGT – mean germination time of seeds;
n – the number that germinated each day;
d – number of days since the test started;
N – total number of seeds that sprouted at the end of test.

Statistical analysis

PFG and MGT were submitted to an ANOVA using the SPSS software. The Tukey test was used for multiple mean comparisons to detect significant differences in germination rates at the 5% threshold.

RESULTS

Seed morphometric characteristics

Tuberaria guttata seeds are very tiny and characterized by two different coat colours: light brown (78 ± 5.86%) and dark brown (22 ± 5.86%). Their size and weight varied, respectively, from 587.9 ± 23.50 µm and 0.020 ± 0.001 mg for the first category to 495.1 ± 21.72 µm and 0.040 ± 0.001 mg for the second (Table 1). Light brown seeds are significantly larger than dark brown ones ($P < 0.001$), but, curiously, their weight is lower.

The mean values of seed size and weight (± standard error) are followed by the minimum and maximum values. Mean values followed by the same letter in a column are not significantly different ($P > 0.05$) as determined by a least significant difference test.

Seed viability

Seeds that had not germinated at the test end and analysed with tetrazolium were all viable.

Seed colour effect on germination

The influence of the colour of *Tuberaria guttata* seeds on their germination rate, without any pre-treatments and under darkness, is presented

Table 1. *Tuberaria guttata* seed size and weight

Colour	Size (µm)	Weight (mg)
Light brown	587.90[a] ± 23.50	0.020[c] ± 0.001
Dark brown	495.10[b] ± 21.72	0.040[d] ± 0.001

in Table 2. The highest germination (31.11 ± 0.70 %) is achieved by brown seeds, which recorded more than double the percentage noted for dark brown seeds (14.44 ± 0.70 %).

Mean values within a column followed by the same letters are not significantly different ($P > 0.05$) as determined by a least significant difference test.

Light effect on germination

Generally, seeds with the same colour had similar germination percentages under the light as in the dark. In fact, no significant difference ($P > 0.05$) was found between the two lighting regimes (Figure 1).

Pre-treatment effects on germination rate

All pre-treatments improved the germination rate average of the two seed categories. However, scarification and stratification showed more germination rates than soaking in GA_3; 94.14, 62.78 and 24.44 %, respectively (Figure 2).

Following 21 days of observation, germination was significantly greater in scarified light brown seeds (98.33 %) than in their dark brown counterparts (89.94 %), highlighting the strong effect of scarification (Figure 2).

Cold stratification also improved the germination rate, especially of light brown seeds, which reached a maximum rate of 66.67 % after 74 days. The effect of this pre-treatment had a very highly significant impact (Figure 2).

GA_3 treatment had a highly significant impact on the germination of light brown seeds, which reached a final germination rate of 33.88%. In contrast, the germination percentage of treated dark brown seeds (14.99 %) was nearly identical to that of the untreated control (14.44 %) (Figure 2).

Table 2. Final germination percentages of seeds of different colours

Colour	PFG (%)
Light brown	31.11[a] ± 0.70
Dark brown	14.44[b] ± 0.70

Pre-treatments effect on mean germination time

The mean germination time (MGT) was significantly reduced ($P < 0.05$) by mechanical scarification in both seed color categories when compared to the controls (Table 3). Cold-stratified seeds showed an increase in MGT for light brown and dark brown seeds (39 and 38 days respectively) compared to untreated seeds (26 and 31 days, respectively) (Table 3). The results showed that GA_3 did not have a promoting effect on seed germination speed. The MGT value of light brown and dark brown seeds treated with GA3 was almost similar (26 and 32 days, respectively) to that of untreated seeds (Table 3).

DISCUSSION

Seed size and weight are strongly related to germination mechanisms in some species (Matilla et al., 2005). Most research has shown that, for the same species, heavier seeds generally have higher germination rates than lighter seeds (Moles et al., 2005). However, our study showed that darker brown seeds, smaller and heavier than light brown seeds, have lower germination percentages compared to those of the latter. This could be explained by the fact that the integument of the first category is may be thicker and consequently increases water impermeability (Matilla et al., 2005). This study also revealed that *Tuberaria guttata* produces seeds of different colours, with different germination rates and therefore different levels of physical dormancy. Thus, this variation in phenotype is associated with different germinative responses.

Light requirement for germination tends to be more prevalent among species with smaller seeds compared to those with larger seeds (Milberg et al., 2000). This trait is thought to function as a strategy that prevents small seeds, which have limited energy reserves, from germinating too deeply in the soil (Fenner and Thompson, 2005). In many plant species, seeds that require light to germinate typically contain phytochrome in its inactive form, which becomes active upon light exposure (Quail, 2010). Conversely, seeds capable of germinating in darkness usually possess a sufficient proportion of active phytochrome (Yan and Chen, 2020). This pattern appears to be consistent with the seeds examined in our study.

The findings of this study indicate that untreated seeds exhibited low germination rates

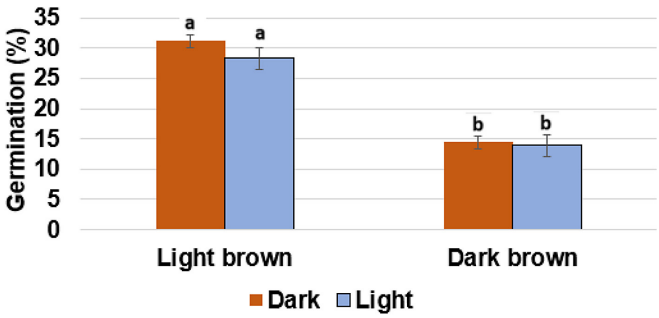

Figure 1. Influence of the lighting regime on the germination percentage of seed types

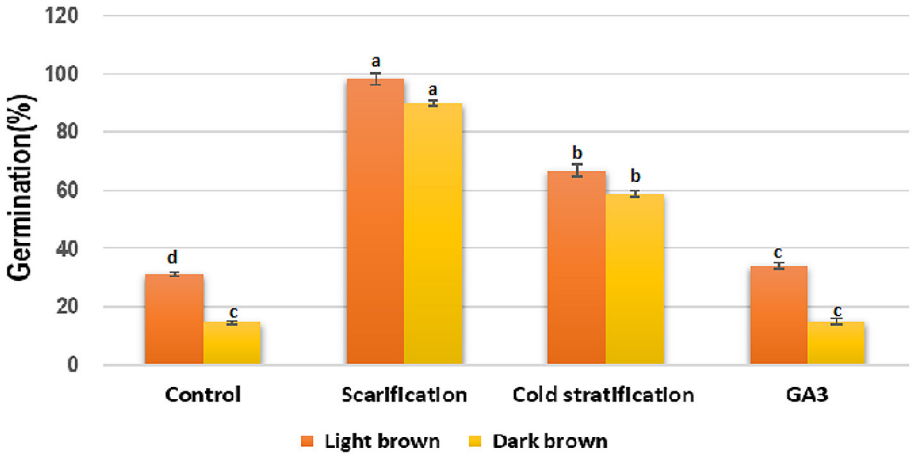

Figure 2. Germination percentage of *Tuberaria guttata* seeds submitted to different pre-treatments

Table 3. Pre-treatments effects on mean germination time

Colour	Scarification (Day)	Stratification (Day)	GA_3 (Day)	Control (Day)
Light brown	10.94 ± 0.43	39.46 ± 98.72	26.21 ± 9.45	26.21 ± 9.45
Dark brown	10.74 ± 0.21	37.90 ± 10.99	32 ± 12.83	31.03 ± 3.70

across both seed types (Table 1). In *T. guttata*, this limited germination is likely due to primary dormancy, primarily maintained by the seed coat (Thanos and Georghiou, 1988). The physical hardness of the seed coat and its resistance to water uptake are known to hinder germination in many species within the Cistaceae family (Perez-Perez et al., 2005b). Additionally, water absorption occurs more slowly in dark-colored seeds compared to light-colored ones (Vidak et al., 2022).

Soltani et al., (2020) and Baskin and Baskin, (2004) described physical dormancy as being caused by the presence of water-impermeable layers in the seed coat, a barrier that can be overcome through mechanical scarification. In this study, *T. guttata* seeds showed a strong germination response to such treatment, achieving the highest germination rates (Table 3). As noted by Thanos et al., (1992) and Benabderrahim et al., (2024), once seeds are physically softened, regardless of the method, germination can proceed independently of external factors such as temperature or light availability.

Despite being viable, a portion of the seeds from this species failed to germinate. This suggests that physical dormancy may not be fully overcome in all individuals. These findings align with previous studies by Martínez-Baniela et al., (2016); Siles et al., (2017); and Luna et al., (2019). The incomplete germination may reflect an adaptive strategy aimed at avoiding the simultaneous emergence of all individuals, thereby reducing the risk of population loss under unfavorable conditions (Ooi et al., 2014). By maintaining dormancy in part of the seed bank, the species enhances its long-term persistence and lowers the likelihood of extinction (Luna et al., 2022).

Cold stratification also had a notable positive effect on germination. This process is believed to stimulate the activation of hydrolytic

and proteolytic enzymes, which aid in mobilizing nutrient reserves stored in the cotyledons or endosperm (Adkins et al., 2002; Kwon et al., 2025). Ultrastructural analyses by Chen et al., (2015) demonstrated a gradual breakdown of lipid and protein bodies in embryos of cold-treated seeds. Furthermore, stratification under moist and low-temperature conditions has proven effective in overcoming seed dormancy in various species, likely through the degradation of germination-inhibiting compounds (Benvenuti et al., 2016; Wang et al., 2024).

The application of a GA_3 solution at a concentration of 1 g/L did not significantly enhance the germination of *T. guttata* seeds. This outcome is in line with earlier findings reported for other members of the Cistaceae family (Nadal et al., 2002).

Mechanical scarification led to a marked decrease in mean germination time (MGT), suggesting a general enhancement in germination speed across all tested seeds. This improvement is likely due to increased permeability of the seed coat as a result of the mechanical treatment. These observations are consistent with those reported by Zaidi et al., (2010); and Debouza et al., (2024). In contrast, seeds treated with GA_3 showed germination speeds comparable to the untreated control, indicating that gibberellic acid had little to no effect on this parameter, as similarly noted by Zaidi et al., (2010).

CONCLUSION

Tuberaria guttata seeds have a high viability rate, but their germination is limited by the hardness of the integument and probably by the degree of embryo maturation. Mechanical scarification is necessary to break their dormancy. To better understand the germination mechanisms, it would be important to examine the effects of combined treatments. Furthermore, studying the physiology of seedling growth would be crucial, particularly for the production of plants intended to form mycorrhizal symbioses with desert truffles.

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