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Review

The Seed Traits Associated with Dormancy and Germination of Herbaceous Peonies, Focusing on Species Native in Serbia and China

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Abstract: Even though peonies are highly valued as ornamental, medicinal, and edible species and are also considered to be long-lived and relatively disease and pest resistant, they are becoming rare or endangered in their natural habitats. This could be primarily associated with climate change and unsustainable wild collecting practices. So far, in situ conservation efforts have received little attention. In addition, very little is known about the cultivation of herbaceous peonies, particularly their propagation from seeds. What is known is that their seeds possess double dormancy, often accompanied by a low germination rate, which, together, make the cultivation of herbaceous peonies more difficult. Based on a comprehensive analysis of relevant literature, this paper summarizes, analyzes, and discusses all available studies on the seed traits of herbaceous peonies associated with the effect of seed harvest time on dormancy and seed germination, with a strong focus on dormancy breaking procedures. Improving our understanding of dormancy release modalities (impacts of temperature, moisture, light, hormones, various pre-treatments, etc.) will aid the establishment and management of in situ and ex situ collections of valuable species of herbaceous peonies and enable further studies for their successful propagation, breeding, and cultivation.

Keywords: double dormancy release; rare species; endangered species; *Paeonia* L.

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1. Introduction

Herbaceous peonies are species with high ornamental [1,2], edible [3–5], medicinal [6,7], economic, and ecological values [8]. Apart from their valuable roots and flowers, which contain various biologically active substances [9], their seeds also attract the attention of scientists. The seeds are around 25% oil, which is rich in various unsaturated fatty acids, amino acids, and mineral elements [10–12]. The oil also has biologically active constituents that have several proven beneficial effects (antioxidant, anti-ageing, anti-UV and sunscreen, anti-tumour, etc.) [13]. About 30% of the dry seed weight is account for by the seed shell, which is the main co-product in peony seed oil production [14–16]. It contains cellulose, lignin, monoterpene glycosides, and crude protein and also has been proved to have several biological properties (strong antioxidant, antibacterial, anti-tumor, etc.) [17].

Herbaceous peonies represent the plant genus with the longest history of all flowering plants, *Paeonia* L. [8,18]. It is the only genus of the *Paeoniaceae* family and comprises about 34 species native to the northern hemisphere [19,20]. The genus is commonly divided into three sections [21,22], as presented in Figure 1, although recent study suggests reclassifying the subgenus *Moutan*, which includes only woody species, and the subgenus *Paeonia*, which includes only herbaceous species [23].

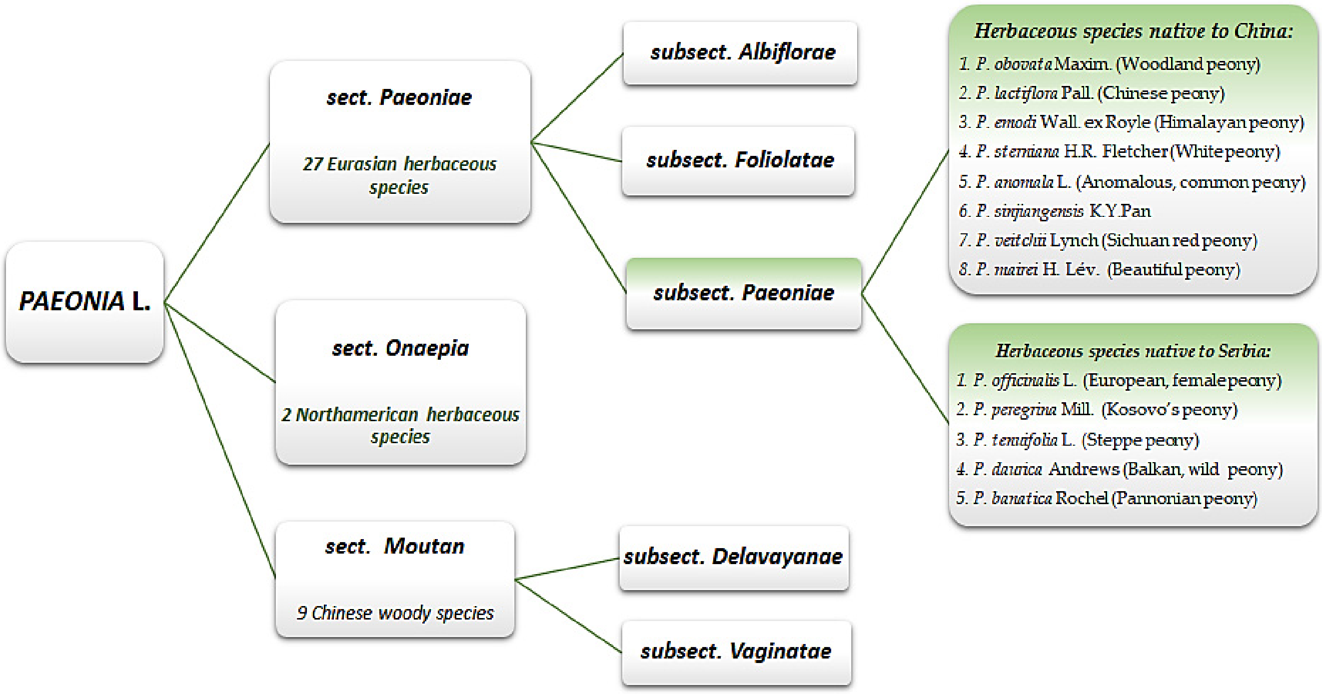

Figure 1. Division of genus *Paeonia*, with focus on herbaceous species native to Serbia and China.

All five herbaceous species native to Serbia [24,25] are rare and endangered, with the exception of the Pannonian peony (*P. banatica*), which is endemic, relict, and strictly protected and is, thus, listed in the Red Book of the Flora of Serbia [26,27]. Among the eight herbaceous species native to China, only the White peony (*P. sterniana*) is recorded in the List of National Protected Wild Plants of China as a Class II rare species [28].

Although peonies are generally characterized as long-lived and relatively disease- and pest-resistant plants [29], in many cases they are becoming rare or endangered in their natural habitats. This can mainly be attributed to climate change and/or reckless human activity [30,31], although there could be several other reasons which contribute, such as loss of habitat, inadequate nature protection policies, susceptibility to diseases, etc. [12,31,32].

The loss of species is a risk associated with vegetation succession [32]. Apart from unsustainable wild collecting practice [33], the trade of wild herbaceous peonies and their seeds is becoming increasingly popular [34]. In the last two decades, climate change has resulted in an increase in temperature, especially during the winter period, which has impacted the timing and success of germination [35] and/or increased the incidence of abnormal seedlings [36]. Plants which are not able to adapt to climate changes or shift to northern areas and/or to higher altitudes are lost from the population, making the species rare or endangered [34,35].

Herbaceous peonies spontaneously grow and thrive in temperate and cold climates [8] and produce seeds that are double dormant as a key protection mechanism [31]. To survive, plants depend on the ability to cope with changing environmental conditions. Of the different strategies that have evolved in this respect, dormancy is a widely distributed one. Double dormancy is a combination of the seed coat (external) and internal dormancy. Peony seeds require temperature variations to progress through the many stages of the germination cycle [37], and if they are not adequate, the survival of the entire peony population in its natural habitat is jeopardized.

Even more concerning is the low rate of peony seed dispersal in nature [12,38]. The seeds mature slowly, ripen in late summer, and disperse in autumn [39]. The spatial grouping of seedlings near maternal plants indicates that their dispersal is spatially limited, as confirmed in an investigation conducted in France [40]. The spatial aggregation of wild-growing seedlings of *P. officinalis* ssp. *macrocarpa*, their significantly greater abundance down the slope of flowering plants, and a small number of seedlings observed at distances > 1.5 m from flowering individuals all pointed to the conclusion that the species is primarily barochorous [40]. The data also suggest that long-distance dispersal in *P. officinalis* is extremely rare and that poor seed dispersal may limit colonization of the species at favorable sites [40].

Herbaceous peonies are generally considered self-fertile, meaning that, when isolated, their flowers self-pollinate, and their seeds produce offspring that are a genetic match to the parent plant (for the appearance of herbaceous peony flowers, see the Figure S1 in the supplementary material). In the case of *P. lactiflora*, isolated self-pollination result in the lowest seed-setting rate of all other pollination models (natural pollination, hand cross-pollination, hand self-pollination, and natural cross-pollination) [41]. In addition, it was also reported that the pollination process in herbaceous peony species *P. lactiflora* [41] and *P. officinalis* [40] also requires insects or wind-mediated assistance.

Cultivating herbaceous peonies species is one of the most important strategies for preserving them. However, only a few studies have been conducted so far on the proper agronomic practices and conditions for their cultivation, particularly for propagation by seeds [42–45]. Such low interest could be attributed to the very slow germination procedure, which, in various natural conditions, can take up to 24 months [46].

The major goal of this review was to present up-to-date knowledge on the dormancy and seed germination of 13 herbaceous peony species native to Serbia and China, as this knowledge can contribute to the protection of their natural genetic resources and provide basic guidelines for their successful cultivation. Given the scarcity of literature on the seeds of the examined species, information that is currently available on seeds of other herbaceous peony species from the subsection *Paeoniae* is included in this review. This might aid researchers to narrow the field of the unknown and guide them to move towards successful propagation of these precious plant species by seeds.

2. Seed Properties

2.1. Physical and Morphological Properties

Despite the fact that morphological distinctions between the seeds of herbaceous peonies do exist (as evidenced by the literature data presented in Table 1 and supported by the seed images presented in Figure 2), it appears that they have been almost neglected in the systematics of the section *Paeoniae* [47].

Table 1. Summarized literature data on seeds of most herbaceous peony species.

Species	Seeds				Reference
	Testa Colour	Size (mm)	Shape	Maturation	
P. algeriensis	black	9.0 × 7.5	ovoid to oblong	August	[48]
P. anomala	black	6.6–8.8 × 5.1–6.0	ellipsoidal	August	[8,38,47]
P. banatica	black	6.0–8.0 × 5.0	ellipsoidal	late July to August	[49]
P. broteri	black	7.0–8.0	oblong	August to September	[49]
P. cambessdesii	black	5.0	globular	June to July	[49]
P. clusii	black	8.0 × 5.0	ovoid to ellipsoidal	August	[48]
P. coriacea	black	7.0–8.0 × 5.0–6.0	oblong	September	[48]
P. corsica	black	7.0 × 5.0–6.0	ovoid to globular	late July to September	[48]
P. daurica	black	6.1–7.5 × 4.2–7.0	globular	August to September	[38,50]
P. emodi	brownish black	2.0–3.5	globular	August to September	[51]
P. intermedia	black glossy	5.0–5.5 × 3.0–3.5	cylindrical to ovoid	August to September	[48]
P. lactiflora	brownish black	5.5–10.0 × 4.1–6.8	ellipsoidal or globular to rhomboid, flattish	late July to September	[8,38,48,50]
P. mairei	black with blue shine	7.0–8.0 × 4.0–5.0	irregular, round	July to August	[48]

Table 1. *Cont.*

Species	Seeds				Reference
	Testa Colour	Size (mm)	Shape	Maturation	
P. mascula	first red than black	7.0–8.5 × 5.0–7.0	ellipsoidal to globular	late July to August	[50]
P. obovata	black	6.0–7.0 × 5.0–6.0	ovoid to globular	August to September	[48]
P. officinalis	black	6.0–9.0 × 4.5–6.5	obovate to ellipsoidal	late July to August	[50]
P. peregrina	black	7.5–10.0 × 5.0–6.0	ellipsoidal	late July to August	[48,50]
P. sterniana	indigo blue	7.0–8.0 × 5.0	ellipsoidal	August to September	[48]
P. tenuifolia	brownish black	5.9–8.0 × 3.5–4.9	cylindrical to ellipsoidal	July to August	[8,38,50]
P. veitchii	dark blue	6.0 × 4.0	ellipsoidal to oval	July	[8]
P. kesrouanensis	black	6.0–10.0 × 6.0–8.0	ovoid to globular	July to September	[48]

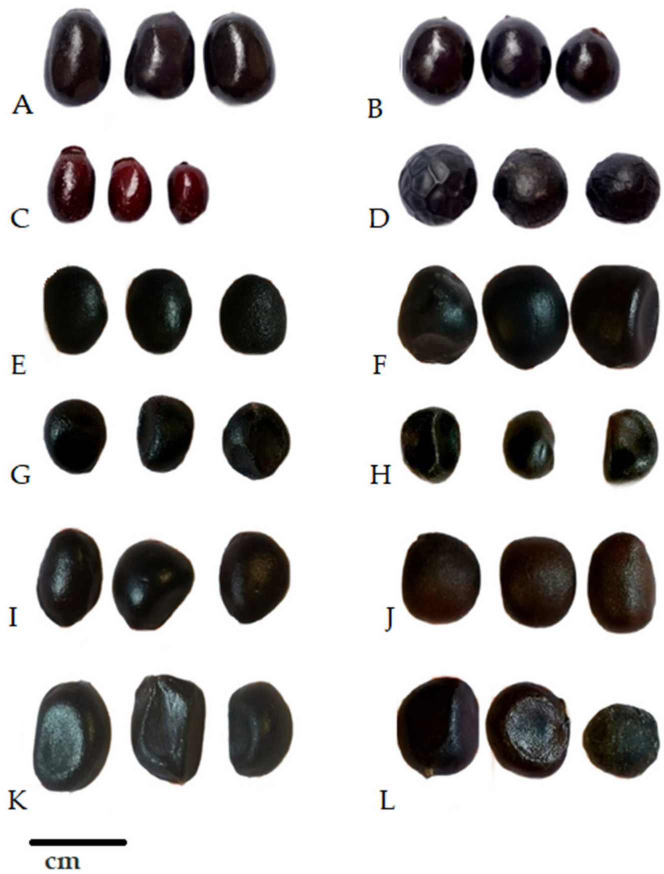

Figure 2. Ripe seeds of several herbaceous peony species (seed collection, 2021); (**A**) *P. peregrina*, (**B**) *P. banatica*, (**C**) *P. tenuifolia*, (**D**) *P. daurica*, (**E**) *P. veitchii*, (**F**) *P. mairei*, (**G**) *P. emodi*, (**H**) *P. anomala*, (**I**) *P. sterniana*, (**J**) *P. obovata*, (**K**) *P. lactiflora*, and (**L**) *P. sinjiangensis*.

Figure 2 shows images of the seeds of all herbaceous peony species native to Serbia and China with the exception of *P. officinalis*.

Species of herbaceous peonies differ in the number, size, and shape of their seed follicles which, in turn, affect the number and size of seeds [38,46]. They also differ in seed shape and in colour of testa, which is caused by the oxidation of various polyphenolic compounds in its palisade layers during maturation. The color of the seed testa in ripe seeds can range from brown to dark (Figure 2) and, in most cases, is smooth [46,52]. In addition, the seed size also depends on the locality, plant position at the locality, and year [43]. Given that the seeds of herbaceous peonies are large and dark and are not preferential rodent food (chipmunks, mice, etc.), their natural dissemination is thought to be rather low and close to the maternal plants [40,53]. On the other hand, due to their size and mass, they are less dependent on light to germinate [53] and, in harsh environmental conditions, are capable of providing enough energy to ensure survival of the species [31].

2.2. Seed Collection Period

Peony seed maturation is a complex process that includes numerous physiological and biochemical alterations [1]. In herbaceous peonies, it is considered very slow [39]. For instance, the entire development of *P. lactiflora* 'Hangshao' seeds lasts about 85–90 days [39,54], during which physiological maturation occurs between the 70th and 75th day following flowering [54]. The seeds of herbaceous peonies ripen in summer and disperse in autumn [39]. Depending on species, locality (altitude, shading, etc.), and year, the seed harvest time ranges from July to the end of October (Table 1); *P. tenuifolia*, *P. cambessdesii*, and *P. veitchii* mature earlier, whereas *P. peregrina*, *P. banatica*, *P. mascula*, *P. officinalis*, *P. sinjiangensis*, *P. anomala*, *P. emodi*, *P. obovata*, and *P. sterniana* mature a bit later. However, the optimum time to collect the seeds is when the follicle begins to open and the seed testa starts to darken [37,39]. The optimum time for collecting seeds is important as it significantly affects germination. If the seeds are collected too early, they do not reach maturity and are not fertile [37], while if they are collected too late, their coat hardens and this reduces germination [37,39]. To date, there is currently no data within the literature regarding the germination rate of seeds collected after maturation has peaked; however, it can only be assumed that it would decline, as was the case with the seeds of some tree peonies [55]. When the seeds are collected at the optimum time, the rate of germination can be as high as 90%, as already confirmed in the case of *P. lactiflora* [52].

2.3. Seed Dormancy

Seed dormancy is an important adaptational trait of higher plant species. It prevents seeds from germination during unfavorable ecological conditions (temperature, humidity, light, rainfall, drought, heat waves, etc.) or incidents (fire, etc.) [56]. Optimal dormancy release conditions are defined as those in which high-quality plants are produced in a short period of time [57].

Indicating its great diversity and complexity, seed dormancy is classified by the developmental status of its embryo, its water absorption capacity, and the interrelationships of its phytohormones, into many distinct categories [58]. There are two major categories of seed dormancy: exogenous and endogenous. At present, exogenous dormancy includes only physical dormancy, while endogenous dormancy includes several types: (1) morphological, (2) physiological, (3) morpho-physiological, and (4) combinational (physical + physiological). In herbaceous peonies, only two types have been confirmed so far: physical dormancy and morpho-physiological dormancy [36,59,60].

Physical seed dormancy is influenced by environmental stimulus [49] and is enabled by seed coat layer(s) which provide(s) a mechanical barrier for water and gas uptake. Thus, the seed coat is considered a major modulator of interactions between the internal seed structures and the surrounding environment, maintaining the viable status of embryos for a long period of time [36]. The mature seed of *P. lactiflora* is composed of the seed coat, endosperm, and embryo [52]. Its coat is made of tightly packed palisade cells with gaps between them [61]. If the seeds are exposed to appropriate dormancy breaking conditions, they became water permeable (i.e., a gap in the seed coat opens, and water reaches the embryo). Otherwise, the coat remains hard and impervious to water and gases, making germination difficult unless physically altered [37]. The alteration can be induced by dry, warm stratification or warm-water stratification, either with or without scarification. During warm stratification, the temperature should resemble that of the corresponding natural habitat, which ranges from 20 °C to 25 °C, for 1–3 months, until the radicle reaches sufficient length, which is species specific; for *P. lactiflora* it is about 3–4 cm [62,63], while, for *P. corsica*, it is 4 cm [42,54]. In nature, dry, warm stratification for physical dormancy release occurs during summer. For instance, seeds of *P. tenuifolia* experienced spontaneous, dry, warm stratification after a fire in Russia's forest-steppe zone (the Khvalynsky National Park), and the post-fire community had a higher recovery and replacement rate with juvenile individuals than the intact environment [64].

The positive effects of laboratory-induced mechanical scarification of the seed coat of *P. lactiflora* have also been recorded; the germination rate of the seeds scraped and left at 25 °C for 70 days increased by about 50% compared to control [65]. This could be due to the enhanced speed of water uptake caused by the increased permeability of the seed coats [39,66,67] which resulted in increased seed germination [68,69].

In an attempt to understand the mechanism of breaking physical dormancy, scientists found that larger, physically dormant seeds become water permeable earlier than the smaller ones, which explains why they show faster dormancy release [62]. When compared to small seeds, large seeds show high water content and a low ratio between the palisade layer thickness and seed mass. As a result, the barrier in large seeds can be broken earlier, and, thus, they germinate faster [62]. This shows that the physical mechanism for breaking dormancy is far more complex than just the retraction and expansion of the seed coat and should be researched further for the seeds of herbaceous peonies.

Morpho-physiological seed dormancy is a combination of *physiological* and *morphological dormancy*. *Morphological dormancy* is present in seeds, the embryos of which are not fully developed (undifferentiated embryos) at seed dispersal. Prior to germination, the embryo within the seed has to be fully developed [58]. When it fills more than half of the seed, the embryo can continue to expand, but the radicle emerges only if the environmental conditions are favorable [36]. Such conditions are species specific and may vary even among varieties of the same peony species [37]. On the other hand, *physiological dormancy* is caused by the physiological state of the embryo [70]. It prevents embryo growth and further germination until chemical changes occur. Seeds may have one of the following seed dormancy levels: deep, intermediate, or non-deep [36,59,60]. According to the literature [71,72], ≥90% of physiologically dormant seeds in the world are characterized by a non-deep dormancy level, accounting for about 41% of all species. However, herbaceous peonies are not among them.

For seeds with *morpho-physiological dormancy*, it is believed that they cannot germinate unless their embryo elongates enough and morphologically develops inside the seed (which is expressed through the embryo-to-seed ratio), as well as overcomes any physiological limitations [36]. For herbaceous peonies, there are no data on the critical embryo:seed ratio, except for in the case of *P. corsica* (Sieber) ex. Tausch (syn. *P. mascula* ssp. *russoi*), which is 0.58 ± 0.09 [42]. Research on seed dormancy in herbaceous peonies revealed that the seeds of *P. officinalis* have an intermediate, simple dormancy [65], which means that, following the embryos' full development, further dormancy release treatment is required. On the other hand, it confirmed that the seeds of *P. corsica* [42], *P. tenuifolia*, *P. caucasica* [62], *P. veitchii* [31], *P. lactiflora* [73,74], *P. intermedia*, and *P. anomala* [75] have deep, simple, epicotyl morpho-physiological dormancy. This indicates that, although the growth of an underdeveloped embryo in the seed begins in the I (warm) phase of dormancy release, it also continues into the II phase, in which seed exposure to cold is essential for full embryo development [58]. In natural habitats, after a warm dormancy breaking period, the seeds of peony species with deep, simple, epicotyl morpho-physiological dormancy do not emerge until the next season. In other words, the peony shoots do not emerge until the second spring unless the roots do not pass cold stratification, which happens during winter [58]. The peony seeds are sensitive to cold stratification only after the radicle length exceeds 3 cm; for *P. lactiflora*, the critical length is between 3 and 4 cm [63,64], while, for *P. corsica*, it is 4 cm [42]. If the low temperatures are missing, the radicle can grow further, but the epicotyl cannot extend the seed coat [76]. It is still unclear how the radicle length affects epicotyl dormancy release, but it is suggested that it probably depends on the content of hormones in the epicotyl of the seed from which the radicle emerged [39].

3. Seed Germination

Seed germination is the result of the equilibrium between the degree of dormancy and the ability of the embryo to overcome it [77]. Almost all herbaceous peonies experience hypogeal seed germination, where the epicotyl elongates and the cotyledons remain below the soil [46]. However, *P. tenuifolia* experiences epigeal germination, in which the hypocotyl rapidly elongates, pulling the cotyledon above the ground [78].

At seed maturity, the embryo in herbaceous peonies is differentiated but underdeveloped (rudimentary), so it must grow inside the seed until the radicle develops [36]. Fresh peony seeds are recommended for the best germination results as they germinate faster and do not require any pre-soaking treatment before planting [45]. Although germination of perennial species *P. corsica* started one week after seed collection [42], the rate of germination observed after 100 days was still less than 10%. One of the possible reasons for such a low germination capacity is the low activity of the peroxidase enzyme [8]. A seed can also maintain its high viability if stored for 1–2 years in a ventilated, non-soil, sterile, wet place with up to 10% moisture, either at a temperature that corresponds to its natural habitat [37] or in a refrigerator (4–6 °C) covered with wet moss [45] or sand [31]. Moisture content is one of the most important factors affecting seed viability, especially after long-term seed conservation such as cryopreservation. In the case of *P. emodi*, 8.77% of the seed moisture was suggested [79].

To the best of our knowledge, there are no published data on the effect of seed moisture on the germination of herbaceous peonies. A pre-soaking seed treatment is required if the seeds are air-stored or dry or if the content of germination inhibiting substances needs to be reduced. Imbibition initiates the germination process as it activates the seed respiratory metabolism, as well as transcriptional and translational activities [79]. The European Peony Society suggests soaking the seeds of herbaceous peonies at room temperature in sterile water for 3–4 days [78], whereas other authors suggest up to 7 days [39]. In particular, pre-soaking seed treatment for *P. tenuifolia* should last no more than one day [78] and two days for *P. emodi* [45] and *P. lactiflora* [76]. In any case, the seed absorption rate should be in the "slow–fast–slow" order [76].

Peonies have a long germination period in general. Germination of *P. lactiflora* seeds takes 6–7 months in controlled, optimal conditions [76], whereas, in the natural environment, it takes 8–9 months, with low seedling survival [66]. Wild peonies in Russia require 10–16 months [8], which can be extended to 2 years if the environmental conditions are harsh [77].

4. Pre-Treatments for Dormancy Release Process

4.1. Temperature

Peonies have adapted to the temperate zones of the northern hemisphere [31]. Their adaptation to the climatic cycle resulted in the development of unique growth patterns that allow them to avoid unfavorable periods and resume plant growth during favorable ones. As a result, their temperature requirements vary not only between different species but also among their varieties. In addition, peonies from warmer regions require a lower sum of temperatures to break dormancy than those from colder ones; hence, their adaptation is linked to their natural habitats.

The dormancy of peony species is temperature dependent [42]. So far, it has been tested in several herbaceous species. During warm stratification, the temperature should resemble that of the corresponding natural habitat (20 °C–25 °C) for 1–3 months until the radicle reaches sufficient length, which is species specific; for *P. lactiflora* it is about 3–4 cm [49,50], while, for *P. corsica*, it is 4 cm [42,54].

P. veitchii seeds require two months of warm stratification (15–20 °C) for embryo development, followed by three months of cold stratification (0–10 °C) for epicotyl growth [31]; *P. corsica* seeds require three months of warm stratification (25 °C) for embryo development, followed by two months of cold stratification (5 °C) for epicotyl growth [42]; and *P. lactifora* needs four months at 15 °C [80] or one month at 25 °C [39] of warm stratification for embryo development and another three months of cold stratification (4 °C) for epicotyl growth [80]. For *P. tenuifolia*, the EU Peony Society has no precise data but states that its seeds require cool but not very low temperatures to germinate [81].

4.2. Light

The majority of herbaceous peony species experience hypogeal seed germination [46,51], which means that the germinating seeds' cotyledons remains below ground (i.e., is non-photosynthetic). Although the seeds germinate spontaneously in the dark [31,47], it is unknown whether and how light and its quality affect their dormancy release.

The application of red light had a positive effect on hypocotyl dormancy release as a dark condition on tree peony, whereas blue LEDs had a positive effect on epicotyl dormancy release [78].

In fact, dormancy in peonies is a self-contained process that is unaffected by photoperiod, regardless of whether the species is herbaceous or woody [82].

4.3. Hormones, Enzymes, and Genes

Seed endogenous factors, such as plant hormones, genetics, enzymes, and various physiological, biochemical, and molecular processes within the seed, are crucial in regulating its dormancy and germination [77]. The exogenous environmental factors (temperature, moisture, light, etc.) are also involved [44,78,83].

The application of the plant growth regulator GA_3, alone, with/without warm stratification, has been shown to accelerate embryo growth and germination in seeds of *P. corsica* [42]. However, application of GA_3 alone only gave a small increase in germination rate in the case of *P. officinalis* [84].

In a recent study of the seeds of *P. lactiflora* conducted under natural conditions, it was found that both natural growth regulators, abscisic acid (ABA) and gibberellic acid (GA_3), are involved in regulating the seed changeover from dormancy to germination, and their activities are antagonistic [76]. Additionally, it was reported that 30 mg/L ABA had a significant inhibitory effect on the seed germination of herbaceous peony hybrid 'Fen Yu Nu' × 'Fen Yu Lou' [85]. The activities of ABA and GA_3 in the seeds of various peonies were shown to be dependent on given environmental factors [60,64]; winter or low temperatures led to the accumulation of ABA in seeds, which induced dormancy, whereas spring or warm temperatures led to ABA degradation and the accumulation of GA_3, which triggered dormancy release and germination [44,72,86]. In herbaceous peonies, the following optimal concentrations of GA_3 for radicle emergence were reported: 250 mg L^{-1} for *P. corsica* [42] and 300 mg L^{-1} for *P. lactiflora* [76].

The impact of exogenous hormones on herbaceous peonies seeds has also been studied, and it was found that the application of 6-benzylaminopurine (BA) on seeds of *P. lactiflora* positively influenced the release of double dormancy [37], while the application of indole-3-acetic acid (IAA) and indole-3-butyric acid (IBA), in the case of *P. veitchii*, promoted root initiation and lateral root development [31,44].

Although seed dormancy and germination studies have made significant progress in the last two decades, it is still largely unknown how such complex signal transduction and gene expression regulation pathways are controlled in a coordinated and sequential manner during seed dormancy release [76,81]. Studies on the 'Fen Yu Nu' cultivar of the most studied herbaceous peony species *P. lactiflora* revealed that the expression of ABA 8′-hydroxylase genes *PlCYP70A1* and *PlCYP70A2* increased its seed germination, influencing ABA degradation and dormancy release [46]. The expression of genes associated with the development of the hypocotyl (the auxin response gene *PlSAUR1*) and epicotyl (genes *PlSAUR2* and *PlSAUR3*) of the same species was also observed [44,78].

The germination protocol for peony species is complex and demanding as most of them have double dormancy (in hypocotyls and in epicotyls), which has to be released separately by using different methods [78]. Several methods have been described so far as effective in stimulating germination and dormancy breaking for herbaceous peonies [36,42], but they can only guide researchers in the direction of possible dormancy breaking procedures that lead to germination and seedling development in other, less studied herbaceous peony species.

5. Conclusions

We are witnessing climatic changes in temperature and rainfalls patterns, which, in combination with reckless human activities towards nature, lead to the extinction of many valuable ornamental, edible, and medicinal plant species, including herbaceous peonies. Among them, most are already rare or endangered. As the seeds of most herbaceous peonies have double dormancy, the changes in environmental factors certainly impact their spontaneous resources, jeopardizing their survival. In order to preserve those valuable plant species, it is crucial to understand the specificity of their seeds, including requirements for their dormancy release, as this will further enable the establishment of in situ and ex situ collections and studies leading towards their successful propagation, breeding, and cultivation.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/horticulturae8070585/s1, Figure S1: The flowers of the herbaceous peony species of the *Paeonia* L., subsection *Paeoniae*.

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