Herbaceous Peonies

Subjects: Biodiversity Conservation

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Herbaceous peonies are species with high ornamental, edible, medicinal, economic, and ecological values. Apart from their valuable roots and flowers, which contain various biologically active substances, their seeds also attract the attention of scientists.

Keywords: double dormancy release ; rare species

1. Introduction

The seeds are around 25% oil, which is rich in various unsaturated fatty acids, amino acids, and mineral elements [1][2][3]. The oil also has biologically active constituents that have several proven beneficial effects (antioxidant, anti-ageing, anti-UV and sunscreen, anti-tumour, etc.) [4]. 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 [5][6][7]. 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.) [8].

Herbaceous peonies represent the plant genus with the longest history of all flowering plants, *Paeonia* L. [9][10]. It is the only genus of the *Paeoniaceae* family and comprises about 34 species native to the northern hemisphere [11][12]. The genus is commonly divided into three sections [13][14], 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 [15].

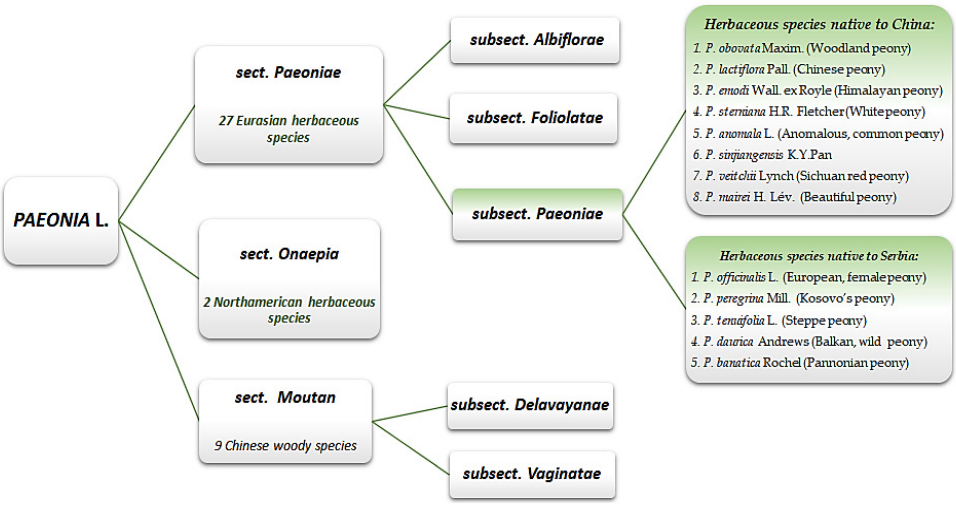

Figure 1. Division of genus *Paeonia*, with focus on herbaceous species native to Serbia and China.

All five herbaceous species native to Serbia [16][17] 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 [18][19]. 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 [20].

Although peonies are generally characterized as long-lived and relatively disease- and pest-resistant plants [21], 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 [22][23], although there could be several other reasons which contribute, such as loss of habitat, inadequate nature protection policies, susceptibility to diseases, etc. [3][23][24].

The loss of species is a risk associated with vegetation succession [24]. Apart from unsustainable wild collecting practice [25], the trade of wild herbaceous peonies and their seeds is becoming increasingly popular [26]. 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 [27] and/or increased the incidence of abnormal seedlings [28]. 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 [26][27].

Herbaceous peonies spontaneously grow and thrive in temperate and cold climates [9] and produce seeds that are double dormant as a key protection mechanism [23]. 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 [29], 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 [3][30]. The seeds mature slowly, ripen in late summer, and disperse in autumn [31]. The spatial grouping of seedlings near maternal plants indicates that their dispersal is spatially limited, as confirmed in an investigation conducted in France [32]. 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 [32]. 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 [32].

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. 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) [33]. In addition, it was also reported that the pollination process in herbaceous peony species *P. lactiflora* [33] and *P. officinalis* [32] 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 [34][35][36][37]. Such low interest could be attributed to the very slow germination procedure, which, in various natural conditions, can take up to 24 months [38].

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* [39].

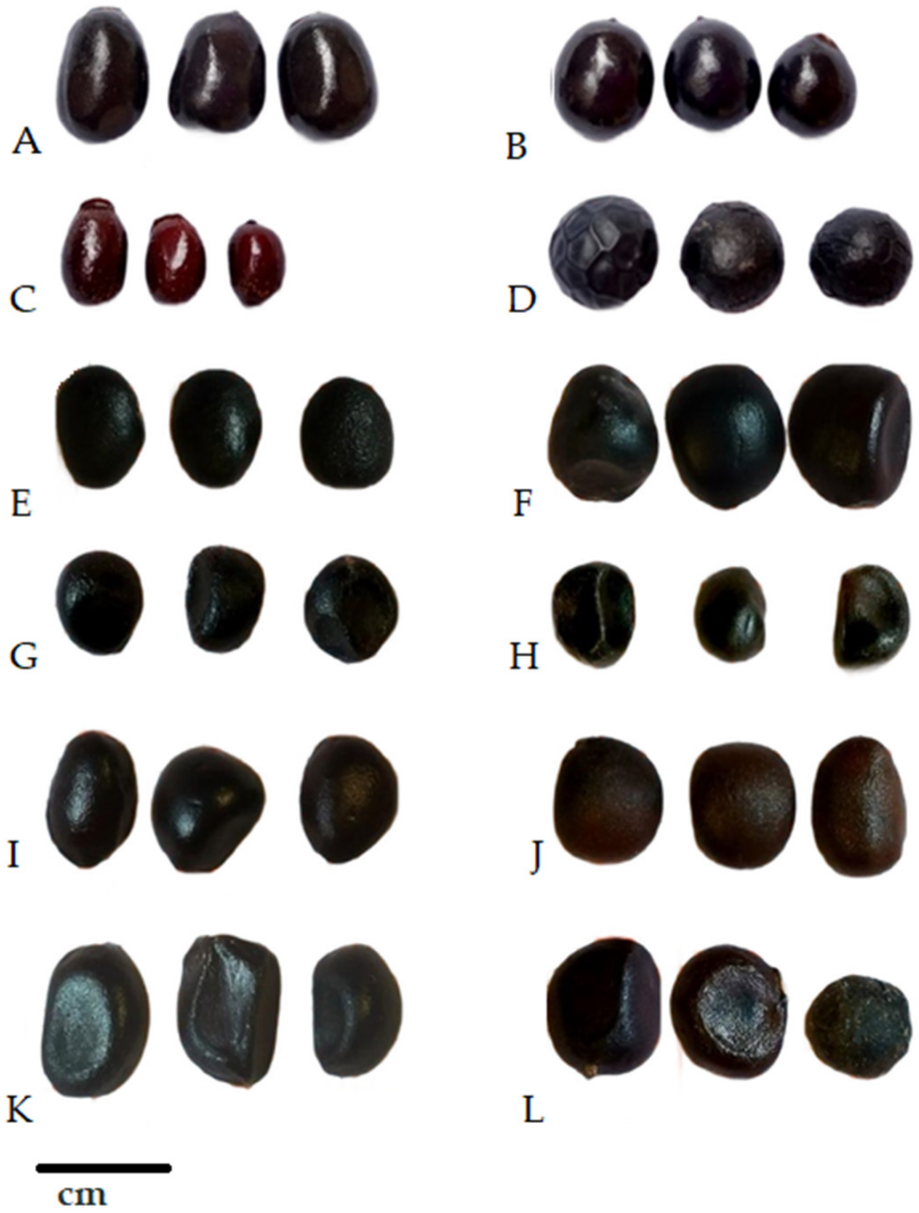

Figure 2. Ripe seeds of several herbaceous peony species (seed collection, 2021); (**A**) *P. peregrina*, (**B**) *P. banatica*, (**C**) *P. tenuifolia*, (**D**) *P. daurica*, (**E**) *P. veitchii*, (**F**) *P. mairei*, (**G**) *P. emodi*, (**H**) *P. anomala*, (**I**) *P. sterniana*, (**J**) *P. obovata*,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

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**	[40]
P. anomala	**black**	**6.6–8.8 × 5.1–6.0**	**ellipsoidal**	**August**	[9][30][39]
P. banatica	**black**	**6.0–8.0 × 5.0**	**ellipsoidal**	**late July to August**	[41]
P. broteri	**black**	**7.0–8.0**	**oblong**	**August to September**	[41]
P. cambessdesii	**black**	**5.0**	**globular**	**June to July**	[41]
P. clusii	**black**	**8.0 × 5.0**	**ovoid to ellipsoidal**	**August**	[40]
P. coriacea	**black**	**7.0–8.0 × 5.0–6.0**	**oblong**	**September**	[40]
P. corsica	**black**	**7.0 × 5.0–6.0**	**ovoid to globular**	**late July to September**	[40]

Species	Seeds				Reference
	Testa Colour	Size (mm)	Shape	Maturation	
P. daurica	**black**	**6.1–7.5 × 4.2–7.0**	**globular**	**August to September**	[30][42]
P. emodi	**brownish black**	**2.0–3.5**	**globular**	**August to September**	[43]
P. intermedia	**black glossy**	**5.0–5.5 × 3.0–3.5**	**cylindrical to ovoid**	**August to September**	[40]
P. lactiflora	**brownish black**	**5.5–10.0 × 4.1–6.8**	**ellipsoidal or globular to rhomboid, flattish**	**late July to September**	[9][30][40][42]
P. mairei	**black with blue shine**	**7.0–8.0 × 4.0–5.0**	**irregular, round**	**July to August**	[40]
P. mascula	**first red than black**	**7.0–8.5 × 5.0–7.0**	**ellipsoidal to globular**	**late July to August**	[42]
P. obovata	**black**	**6.0–7.0 × 5.0–6.0**	**ovoid to globular**	**August to September**	[40]
P. officinalis	**black**	**6.0–9.0 × 4.5–6.5**	**obovate to ellipsoidal**	**late July to August**	[42]
P. peregrina	**black**	**7.5–10.0 × 5.0–6.0**	**ellipsoidal**	**late July to August**	[40][42]
P. sterniana	**indigo blue**	**7.0–8.0 × 5.0**	**ellipsoidal**	**August to September**	[40]
P. tenuifolia	**brownish black**	**5.9–8.0 × 3.5–4.9**	**cylindrical to ellipsoidal**	**July to August**	[9][30][42]
P. veitchii	**dark blue**	**6.0 × 4.0**	**ellipsoidal to oval**	**July**	[9]
P. kesrouanensis	**black**	**6.0–10.0 × 6.0–8.0**	**ovoid to globular**	**July to September**	[40]

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 [30][38]. 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 [38][44]. In addition, the seed size also depends on the locality, plant position at the locality, and year [35]. 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 [32][45]. On the other hand, due to their size and mass, they are less dependent on light to germinate [45] and, in harsh environmental conditions, are capable of providing enough energy to ensure survival of the species [23].

2.2. Seed Collection Period

Peony seed maturation is a complex process that includes numerous physiological and biochemical alterations [46]. In herbaceous peonies, it is considered very slow [31]. For instance, the entire development of *P. lactiflora* ‘Hangshao’ seeds lasts about 85–90 days [31][47], during which physiological maturation occurs between the 70th and 75th day following flowering [47]. The seeds of herbaceous peonies ripen in summer and disperse in autumn [31]. 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 [29][31]. 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 [29], while if they are collected too late, their coat hardens and this reduces germination [29][31]. 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 [48].

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* [44].

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.) [49]. Optimal dormancy release conditions are defined as those in which high-quality plants are produced in a short period of time [50].

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 [51]. 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 [28][52][53].

Physical seed dormancy is influenced by environmental stimulus [41] 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 [28]. The mature seed of *P. lactiflora* is composed of the seed coat, endosperm, and embryo [44]. Its coat is made of tightly packed palisade cells with gaps between them [54]. 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 [29]. 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 [55][56], while, for *P. corsica*, it is 4 cm [34][47]. 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 [57].

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 [58]. This could be due to the enhanced speed of water uptake caused by the increased permeability of the seed coats [31][59][60] which resulted in increased seed germination [61][62].

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 [55]. 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 [55]. 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.

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