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Using Extreme Physical Impacts to Study Properties of Hard Seeds of Legume Plants

A. Yu. Belyaev[a], **N. A. Kruglikov**[b, *], **I. V. Kochev**[b], **and D. A. Krylova**[b, c]

[a] *Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia*
[b] *Mikheev Institute of Metal Physics, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620108 Russia*
[c] *Ural Federal University, Yekaterinburg, 620202 Russia*
**e-mail: nick@imp.uran.ru*

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Abstract—Different physical impacts are used to overcome the hard-seededness of legumes. The germination of yellow melilot and meadow clover seeds is shown to grow after cryotreatment. In licorice and astragalus, germination increases only after treating their seeds with hydrostatic pressure. It is assumed that liquid oxygen stimulates the development of yellow melilot seedlings. The origin of licorice seeds is found to affect their deformation: resistance to deformation (hardening) is determined by the seed coat (in arid areas) or by cotyledons (if excess moisture).

Keywords: legume plants, hard-seededness, cryoprocessing, high pressure treatment, hydrostatic pressure, mechanical tests

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INTRODUCTION

The impact consequences of different physical (physicochemical) factors on plant seeds have long been studied for various purposes, due mainly to the development of ways to improve the sowing qualities of seeds, the long-term preservation of their viability, and reliable germination [1]. There has recently been an increase in data obtained in the field of seed biophysics using advanced physical techniques and high-tech equipment [2]. Results from these studies are used to develop ways of using new plant species in cultivation, preserving and reproducing the genetic resources of cultivated plants and their wild relatives, and solving current problems of agricultural production and environmental protection.

Many species of leguminous plants belonging to such genera as yellow melilot, clover, astragalus, and licorice are valuable forage and honey plants, used to obtain medicine and technical raw materials. They are also widely used for the phytomelioration (recultivation) of disturbed grounds. Of particular value are the natural populations of these plants, which (in addition to the above areas of use) provide gene pools for obtaining new cultivars [3]. The expanded reproduction of such plants under cultural conditions is therefore needed, along with improving the sowing qualities of their seeds. With regard to a number of species of wild leguminous plants (e.g., species of licorice and astragalus), it is of interest to develop technologies for the mass propagation of their seeds in order to cultivate them [4, 5]. A solution to the problem of hard-seededness is in this case needed, since 70–100% of the seeds of many wild leguminous plants do not germinate even under favorable conditions of moisture and temperature because of the special structure of their seed coats, in which there is a layer of specialized thick-walled cells tightly bound together. In combination with other components, this layer ensures the high strength of the seed coat and its impermeability to water. Such seeds are referred to as hard, and their germination requires scarification (damage to the seed coat) [6, 7]. Hard seeds are quite viable, a characteristic property retained for a very long time, so long as their resistance to water is maintained [8]. The hardness of seeds is largely determined by the genotype of the plant on which they form [9]. The resistance to water displayed by the seed coats of hard seeds is provided by a complex combination (interaction) of many morphological (special cellular structure), biochemical (special organic substances), and physicochemical characteristics, plus properties of the outer layer of seed coat [6, 7, 10, 11]. This property takes a variety of forms in different species from the above genera (taxa) of leguminous plants. It is expressed in different proportions of hard seeds in the seed material, and in these seeds' degree of resistance of to extreme physical and chemical impacts [6, 12, 13]. In light of this, we chose to study seeds of several species of legume plants that differ significantly in their hereditary ecologicaly determined characteristics.

Identifying physical factors that upset the resistance to water of the coats of hard seeds can provide information about their properties, along with the resistance of different species of legume plants to the effects of extreme external factors. Methods of scarification differ greatly. They particularly include various mechanical and thermal impacts on seeds [6, 13]. At the same time, high seed germination is not always achieved, and some of them lose viability. Morphological anomalies and defects develop in some sprouts, and for the most part they are not viable [5]. Since existing means do not always ensure sufficient germination while preserving the embryo, the search continues for effective ways of overcoming hard-seededness that ensure sufficient germination and the subsequent normal development of sprouts.

Scarification based on the cryotreatment of seeds with liquid nitrogen are promising. They include exposing seeds to ultra-low temperatures (77 K) in various modes and conditions of freezing and thawing. The effectiveness of such impacts varies for different plant species. Effective ways of overcoming the hardness of seeds have thus been developed for some species and varieties of forage legume grasses, based on experiments on freezing seeds with liquid nitrogen [14]. Cryotreatment with liquid nitrogen to overcome hard-seededness combines well with their cryopreservation. For many species of wild leguminous plants, a considerable drop in the proportion of hard seeds has been observed after storing the seeds in liquid nitrogen for one month [12]. It should be noted that both hard and "soft" seeds germinate normally later on [12, 15, 16]. However, there is evidence that the short-term treatment and cryopreservation of seeds of some species of astragalus in liquid nitrogen did not ensure an appreciable increase in germination [5, 12, 15].

Exposure to high hydrostatic pressure in order to increase the germination of legume seeds began in the first half of the twentieth century. In experiments performed by Davies [17, 18], the germination of alfalfa and *Melilotus alba* seeds (with hard seed fractions of 50% or more) grew considerably after exposure to high hydrostatic pressures (up to 200 MPa). However, these works provided no data on the subsequent development of sprouts. Interest in using high hydrostatic pressure to improve seed germination and parameters of the development of legume sprouts remains among many of today's researchers, but such works deal mainly with solving problems of the production of food products based on microgreens [19, 20]. Data from our earlier works testify to the prospects for using high hydrostatic pressure to overcome hard-seededness in Ural licorice for the purpose of its mass seed propagation and obtaining valuable medical raw materials [21, 22]. Works by other authors also show that in order to overcome hard-seededness with high hydrostatic pressure and ensure the subsequent normal development of sprouts, we must determine the best options for treating seeds of specific plant species [19, 20].

The aim of this work was to assess the effect treating seeds with liquefied gases at ultra-low temperatures and by high hydrostatic pressures has on the properties of hard seeds, the germination of the treated seeds, and the subsequent development of sprouts for different types of wild legume plants from natural populations and ones that are cultivated.

EXPERIMENTAL

We used seeds of several species of wild leguminous plants, taken directly from natural populations or grown in a botanical garden. They consisted of population samples (a mixture of seeds from many plants in a population), and familial samples of seeds from individuals and clones from populations. Samples of seeds were taken for licorice (*Glycyrrhiza glabra* L.) (a population sample and two familial samples, clones 1 and 2 from the same population) collected in the Astrakhan region in 2008; a hybrid clone of licorice from the population of the southern Urals now being cultivated in the medicinal plant plot at the Ural Branch Botanical Garden (seed harvest of 2022); yellow melilot and astragalus (*Astragalus falcatus* Lam.) from the collection of the Ural Branch's Botanical Garden (population sample harvest of 2021); and meadow clover (a population sample and familial samples from three different individuals) from the natural population of Sverdlovsk Oblast.

Licorice (the four indicated samples), astragalus, and yellow melilot seeds were treated with hydrostatic pressure of 100 MPa for three times each. Additional yellow melilot was treated once at 200 MPa in a laboratory hydrostat, according to the procedure in [21–23]. Samples of seeds of the above species were treated in a special cryostat inside a Dewar vessel containing liquid nitrogen [24]. The duration of treatment in liquid gases (oxygen, argon) was as long as 24 h [21], which corresponds to the regime of seed treatment in [14] using fabric bags with rapid freezing and subsequent gradual thawing at room temperature. Seeds were treated with liquid oxygen and liquid argon in a cryostat at the temperature of liquid nitrogen (77 K) in order to identify the possible effect of oxygen as a biologically active substance. Along with pressure treatment, a population sample of licorice glabra seeds was exposed to liquefied argon for 24 h.

Each experimental option was repeated three times using 35–50 seeds. They germinated in Petri dishes under fluorescent lamps (12 h light, 12 h dark) at 23°C. The germination of seeds was studied, the conditions of sprout growth were assessed, and a quantitative count was made of rotten seeds and normal and abnormal sprouts.

For a deeper understanding of the nature of hard-seededness, we must study the deformation of seeds for certain types of legume plants using modern methods of materials science [22]. To study the deformation

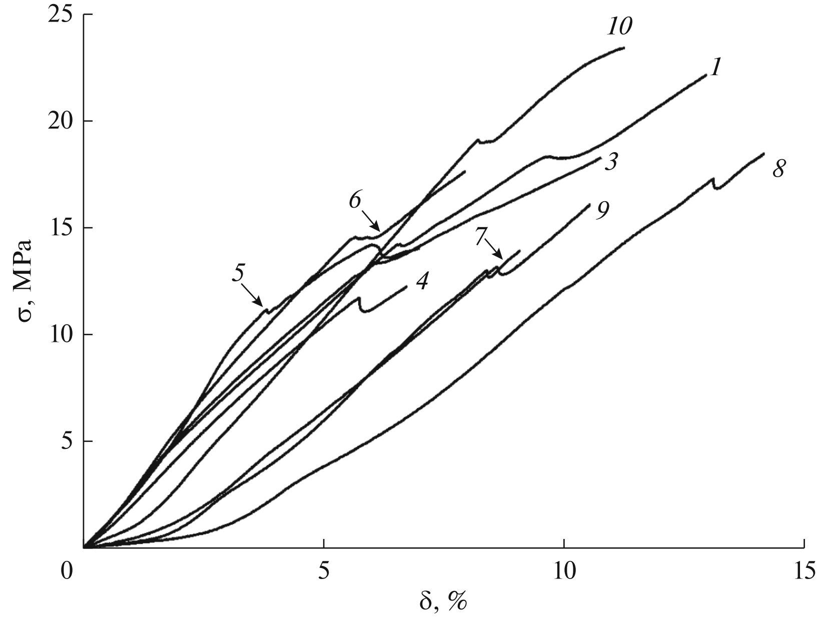

Fig. 1. Deformation curves for seeds of hybrid clone of licorice (*Glycyrrhiza glabra* L.) from the southern Urals.

of licorice glabra seeds according to the procedure tested in [22], they were subjected to individual uniaxial compression on a Shimadzu AGS-X mechanical testing machine while recording the deformation curves in coordinates of force (*P*, N)—absolute deformation (Δ, mm). We examined ten seeds taken from each of two familial samples of licorice (from the Astrakhan region, clones 1 and 2) and a hybrid clone sample of licorice from the southern Urals.

To obtain deformation curves in coordinates of stress (σ, MPa) and relative strain (δ, %), we used a technique similar to the one described in [25]. The geometric dimensions of seeds were determined in three directions using a micrometer with divisions of 0.01 mm, the cross-section area of each seed was calculated (the midsection perpendicular to the axis of compression), and the stress was obtained as the force-to-area ratio. To determine the relative deformation, the absolute deformation obtained at each point of the deformation curve was divided by the initial height of the seed and multiplied by 100%. This approach allowed us to unify the curves and compare them better. The resulting curves, numbered in order of testing, are shown in Figs. 1–3. It was important for us to determine the effect the origin and conditions of plant development had on the qualitative difference in the deformation of seeds between different familial samples, and when comparing seeds obtained from different fruits of the same plant (among clones). Absolute values of the seed coat strengths can be obtained using the more complex procedure we described in [22] and require more detailed study.

Prior to our experiments, the seeds were stored under laboratory conditions of room temperature and low relative humidity (dry storage mode). We used undamaged seeds, cleansed of mechanical impurities and completely mature in appearance [8]. Reference samples of seeds were prepared and included in our experiments, allowing us to clearly assess the proportion of hard seeds in the studied samples and the effect of overcoming hard-seededness from exposure to extreme physical factors [21]. This was an exploratory study with regard to selecting the objects and options for extreme physical impacts. We also considered earlier data of our own and other researchers in order to minimize expenses, so not all seed samples were subjected to identical treatment.

RESULTS AND DISCUSSION

The aim of this work was to find ways of using extreme physical impacts to appreciably reduce or completely overcome hard-seededness in samples of seeds of wild legume plants used to create crops for various purposes. It was therefore necessary to study features of seed development after treatment.

The germination of seeds in reference variants (without treatment) showed a high level of hard-seededness in all studied samples. The proportion of hard seeds was ~95% in licorice (all four samples) and yellow melilot, 92% in astragalus, and 70% in meadow clover from the natural population.

After keeping seeds of yellow melilot in different liquid gases (nitrogen, oxygen, argon) with a variety of exposures (including a minimum of 15 min in liquid argon), germination was 95–98% and sprouts grew normally. The highest germination energy of yellow melilot seeds was 95% after treating them with liquid

Table 1. Laboratory germination and the proportion of hard seeds in the studied samples, in reference groups and after exposure to hydrostatic pressure (average values are shown as a percentage of the number of seeds in the samples)

Seed sample and harvest year	Reference (no treatment)		Pressure treatment: 100 MPa × 3 times	
	germination	hard seed fraction	germination	hard seed fraction
Licorice (*Glycyrrhiza glabra* L.). Population sample, Astrakhan region, 2008	5	94	14	78
Licorice (*Glycyrrhiza glabra* L.), clone 1, Astrakhan region, 2008	2	97	5	93
Licorice (*Glycyrrhiza glabra* L.), clone 2, Astrakhan region, 2008	3	96	8	86
Licorice (*Glycyrrhiza glabra* L.), hybrid clone from the Southern Urals, Botanical Garden (UB RAS), 2022	3	95	49	30
Astragalus (*Astragalus falcatus* Lam.). Population sample, Botanical Garden (UB RAS), 2021	6	92	45	40
Yellow melilot *Melilotus officinalis* (L.) Lam. Population sample, Botanical Garden (UB RAS), 2021	4	96	50	8

oxygen (24 h), which is consistent with results on the germination of *oxytropis* seeds after 100 days of cryostorage in liquid nitrogen [16]. The authors of that work noted a high germination energy of seeds and ~98% germination after cryostorage with an initial germination of 12% (reference group). Note that according to the data of [14], the proportion of hard seeds in samples of *Melilotus alba* and yellow melilot was reduced appreciably only for the latter after cryotreatment in liquid nitrogen at the same high content of hard seeds (98–99%). This testifies to the species-specific response of hard melilot seeds to cryotreatment.

Treating the seeds of meadow clover samples with liquefied gases (oxygen and argon) greatly improved germination with a corresponding drop in the proportion of solid seeds. Germination of reference group seeds of the population sample (a mixture of seeds from 26 clover plants) yielded a value of 17%. Germination reached 53% after keeping the seeds in liquid oxygen for 24 h. At the same time, the fraction of hard seeds fell from 70 to 20%. Seeds of each of the three familial samples of meadow clover were also tested for germination after 1 h of storage in liquid argon. The results from analysis were similar to ones obtained after treating a population sample of seeds in liquid oxygen. However, considerable variation in seed germination was found between familial samples (41–77%), testifying to the great role of the genotype of the mother plant (on which the seeds of one family were formed) in shaping the special morphophysiological properties of seed coats [3] that determine the hard-seededness of wild meadow clover in particular.

When germinating meadow clover seeds in all sample options after treatment with liquefied gases, many sprouts had breaking of the cotyledons at one-quarter of their length from the base. A similar phenomenon has been noted by other researchers after exposing the seeds of wild leguminous plants to liquid nitrogen [12]. The reason for this phenomenon has yet to be established, due possibly to strong deformation of certain areas of the seed coat or embryo tissue when the seeds are immersed in liquid gases. The sprouts in this case continued to develop with roots, the first true leaf, and subsequent juvenile leaves. In other words, such sprouts can be used to produce seprouts for reproducing collection samples of meadow clover seeds from natural populations. Results from these experiments provide additional information about possible changes in the properties of wild meadow clover seeds after treatment with liquefied gases and during cryostorage.

Treating seeds from population samples of licorice and astragalus with liquefied gases did not noticeably reduce the proportion of hard seeds in the studied samples. After 24 h of exposure in liquid oxygen, the licorice seeds did not differ from the reference sample in terms of germination. The fraction of hard seeds in astragalus fell slightly after 24 h of cryotreatment in liquid oxygen and liquid nitrogen.

Table 1 presents data characterizing changes in seed properties (germination, proportion of hard seeds) in the studied samples after treating them three times with hydrostatic pressure (100 MPa). Pressure treatment of a population sample of licorice seeds resulted in only 14% of hard seeds germinating after 17 days. The same pressure treatment of seeds of two familial samples (clones 1 and 2) from the same pop-

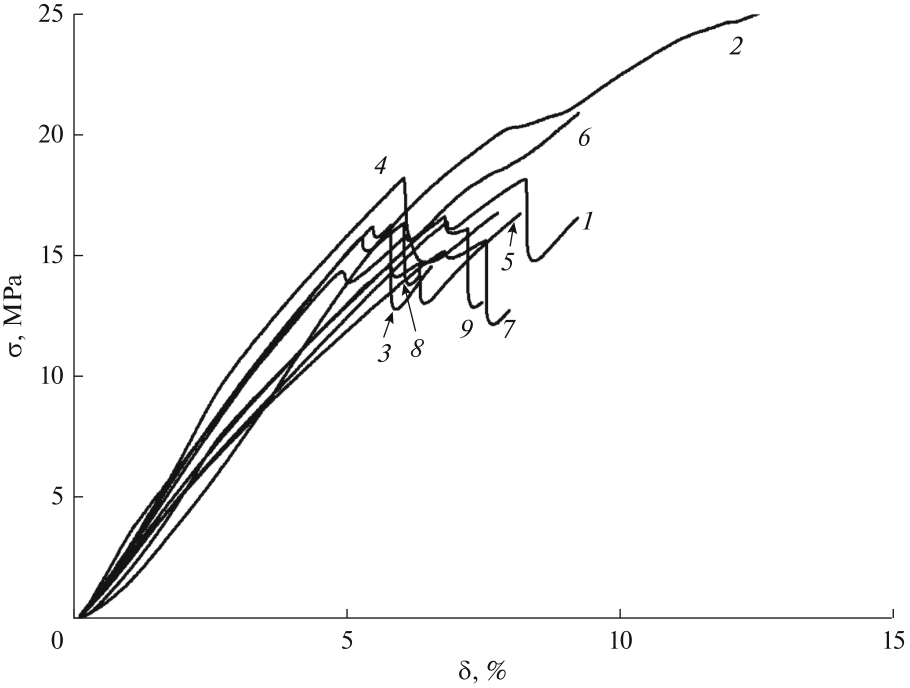

Fig. 2. Deformation curves for seeds of a hybrid clone of licorice (*Glycyrrhiza glabra* L.) (clone 1 from the Astrakhan region). Curve *2* was obtained after unsuccessfully positioning the traverse of the testing machine and has an anomalous shape.

ulation produced a slight increase in seed germination and a corresponding small drop in the proportion of hard seeds (relative to reference groups). However, it was shown in [21] that three times as many seeds sprouted in a sample of *Glycyrrhiza uralensis* Fisch. seeds from the Karaganda region of Kazakhstan after triple exposure to a hydrostatic pressure of 100 MPa. A similar good rate of germination (~50%) was observed after identical pressure treatment of seeds collected from plants of a hybrid clone of cultivated licorice (*Glycyrrhiza glabra* L.) from the southern Ural population (seed harvest 2022). Triple exposure of astragalus seeds to a pressure of 100 MPa also raised their germination to 40–50%. Seeds of a population sample of licorice subjected to pressure treatment and additionally kept in liquid argon for 24 h showed a slight increase in germination, relative to the rate for the same sample of seeds after simple pressure treatment. In other words, the cryotreatment of licorice seeds after pressure treatment did not enhance the scarification effect caused by hydrostatic pressure. Note that after all the above types of extreme impacts, normal sprouts formed from the germinating seeds of licorice and astragalus without anomalies in their further development. The pressure and number of cycles can therefore probably be increased.

In this sense, the pressure treatment of yellow melilot seeds produced a negative result. Sweet clover seeds after triple pressure treatment at 100 MPa displayed around 50 and 80% germination after exposure to a pressure of 200 MPa. After such impacts, however, more than half the sprouts were abnormal and nonviable, while many of the seeds swelled and did not germinate at all.

A comparison of the deformation curves of hard seeds from familial samples of licorice (clones 1 and 2 and a hybrid clone), subjected separately to uniaxial compression, allowed us to determine the effect the origin of the seed material had on the deformation of seed coats. It should be noted that the destruction of the seed coats of clones 1 and 2 was similar. Figures 2 and 3 in particular show a sharp drop in stress after destruction of the coat and some additional hardening (an increase in deformation stress σ). Seeds obtained from a hybrid clone cultivated in the Botanical Garden of the Ural Branch of the Russian Academy of Sciences (UB RAS) do not have a segment of the deformation curve with a sharp drop. This difference can be explained by the existence of microcavities between the embryo and the coats in seeds obtained from plants that growed in and adapted to a drier climatic zone. The seeds of clones 1 and 2 were also stored in the laboratory much longer than the hybrid clone, which could also have contributed to the slow evaporation of water from cotyledons. The scatter in the values of fracture stress and relative deformation at the moment of destruction could be due to the existence and size of such microcavities, and to the heterogeneity of the cellular structure of the seed coat [7, 10].

Under repeated stress during hydrostatic compression, such inhomogeneities can also result in cracks (defects) in the seed coat, thereby upsetting its resis-

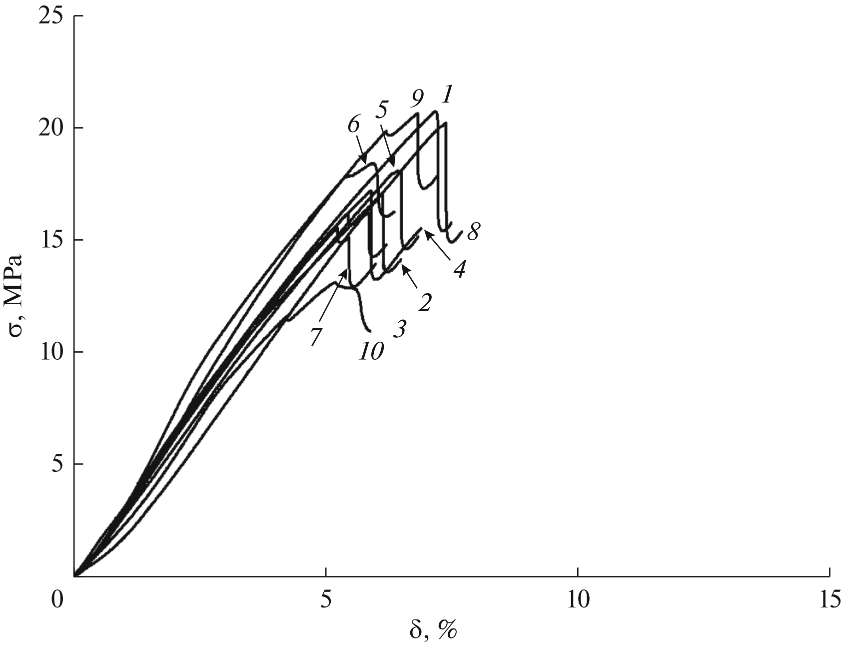

Fig. 3. Deformation curves for seeds of our licorice (*Glycyrrhiza glabra* L.) hybrid clone (clone 2 from the Astrakhan region).

tance to water. Electron microscopy was used in [11] to identify such microcracks in the seed of *Glycyrrhiza uralensis* Fisch.

The deformation curves of the seeds of the hybrid clone differ mainly in shape. In Fig. 1, we can clearly distinguish two main segments with different slopes (coefficients of hardening) on deformation curves *7–10*, indicating different mechanisms of deformation in each of them. The first segment is apparently associated with deformation of the soft seed coat and has a different length, depending on when the cotyledons start to participate in deformation. As a result, the total deformation grows for both segments. Such segments can also be seen on the remaining curves, but they are less expressed and also masked by an increase in the area of the contact spot between the seed and the plate of the testing machine.

It is likely that the load in other cases (curves *1–6* in Fig. 1) is almost immediately assumed by the cotyledons, which display greater elasticity and plasticity than the seed coats. The seeds of the hybrid clone were the least resistant to hydrostatic compression, though they showed the greatest plasticity under uniaxial compression. This was evidently due to different conditions of the formation of seed coats in the arid Volga region and the middle Urals with a considerable amount of precipitation during the formation of seed coats. In addition, the thickness of the seed coats in the sample of a hybrid clone was likely affected by the shorter summer period. Increased humidity of the coats led to greater plasticity. This is quite understandable, since the plasticity of cellulose, which is the reinforcing frame of a seed coat, depends strongly on the moisture content of its fibers. The matrix of such a natural composite is made up of amorphous hemicelluloses whose properties also depend on the content of water. A comparison of data on the uniaxial compression of seeds and indicators of changes in the fraction of hard seeds in the studied samples after hydrostatic compression and information on the origin of seeds suggests that the deformation of licorice seed coats is associated with the hereditary characteristics of mother plants and the conditions of seed formation.

CONCLUSIONS

It was established that hard seeds of ecologically different species of legume plants (and from different familial samples of licorice) respond differently to the extreme physical impacts used in our experiments. Complete elimination of hard-seededness in yellow melilot, and a considerable reduction in the fraction of hard seeds in meadow clover from the natural population, were achieved by treating seeds with liquefied gases (at a liquid nitrogen temperature of 77 K). An important factor in obtaining a clear scarification effect (eliminating the waterproofness of the seed coat) is the mode of freezing and thawing (i.e., rapid cooling at ultra-low temperatures with subsequent slow heating at room temperature), which was used with positive results in [12, 14, 16]. Our data indicate that the period of keeping seed samples at ultra-low temperatures has no appreciable effect on scarification, as was also noted in [14, 26]. However, an important role can be played by the chemical nature of liquefied gas, as experiments with yellow melilot seeds have shown. Liquid oxygen (when exposed for 24 h) stimulated the germination of melilot seeds. The natural presence of oxygen in liquid nitrogen can also explain the activation of seed germination of wild legume plants after cryotreatment and cryostorage in liquid nitrogen [12, 15, 16]. It is likely that the permeability of the coats of hard seeds of some leguminous plants toward liquid oxygen, which can affect seed germination, can already be improved at the stage of the rapid freezing of seeds at ultra-low temperatures (77 K).

Most clover sprouts and all those of melilot developed normally after exposure to liquefied gases. Normal development of the sprouts of many wild legume plants after cryopreservation of their seeds in liquid nitrogen was noted in [12, 16]. We observed damage (the breaking off of cotyledons in some meadow clover sprouts) after the cryotreatment of seeds. This damage slowed (but did not stop) the subsequent development of sprouts under laboratory conditions, since some of the photosynthetic organs (the bases of cotyledon leaves) were preserved.

Germination grew considerably in a sample of seeds from a hybrid clone of licorice and astragalus (the fraction of hard seeds was reduced) only after they were treated three times with high hydrostatic pressure (100 MPa). Different options for the cryotreatment of population samples of licorice and astragalus seeds were not effective in overcoming hard-seededness.

We therefore found that hard seeds of the studied species of legume plants had different resistance to extreme factors of different physical nature. At the same time, resistance was characterized by a set of properties of hard seeds: the ability to maintain the impermeability of the seed coat toward water under different options and impact modes, and to preserve the integrity of the embryo and its normal physiological state.

In terms of the mechanisms of influence on biological objects, freezing in liquefied gases and hydrostatic compression, which we used as extreme physical effects on legume seeds, differ qualitatively [1, 27]. Our investigations revealed a variety of responses from the studied seeds to these physical impacts, testifying to the complex nature of hard-seededness. It was also shown that hard seeds of ecologically different wild and cultivated species of legume plants differ considerably in their ability to maintain the impermeability of a seed coat to water under the effects of liquefied gases (oxygen, nitrogen, argon) at ultra-low temperatures (77 K) and high hydrostatic pressure treatment.

Based on our results, we recommend the staged testing of seed samples in order to choose the best conditions and modes of treating legume seeds to overcome hard-seededness, starting with cryotreatment in liquefied gases and a subsequent transition (if necessary) to treating seeds with high hydrostatic pressure.

It is of interest to study combined options for treating hard seeds that include cryotreatment and the pressure treatment of seeds. Our results can serve as a basis for developing effective means for the pre-sowing treatment of seeds from the natural populations of many species of leguminous plants with high contents of a hard seed fraction.

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CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

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