








Sustainable Substrates for Containerized Scots Pine (*Pinus sylvestris* L.) Seedlings

Zarina Sergazinova ¹, Anton Chashin ², Assel Rakhmetova ¹, Gulmaira Amanova  and Kamshat Jumasheva ^{3,*}

¹Department Biology and Ecology, Toraighyrov University, Pavlodar, 140000, Kazakhstan

²Landscape Design Pavlodar", LLP, Pavlodar, 140000, Kazakhstan

³Department of Ecology and Geology, Yessenov University, Aktau, 130002, Kazakhstan

*Corresponding author: kamshat.dzhumasheva@mail.ru

ABSTRACT

The paper investigates the influence of different types of substrates on biometric characteristics of Scots pine (*Pinus sylvestris* L.) seedlings grown in containers with a closed root system (CRS). Container cassettes were developed according to the authors' own drawings, and five types of substrates with different structures and compositions, with the addition of organic and mineral components, were used for the experiment. Seedling growth and development were evaluated by key biometric parameters such as plant height and needle length. The germination percentage was also evaluated. As a result of the study, the most optimal composition of the developed substrate was identified. The developed substrate, including local organic components (coniferous fall and humus) and top peat, allowed to reduce the use of peat by 17.5-22.5%. Germination on the experimental substrate averaged 70.9%; seedling height was 3.80 ± 0.30 cm and needle length 1.70 ± 0.03 cm, comparable to commercial controls. Seedling height differed significantly between the experimental and less effective formulations ($p < 0.05$), and needle length differed significantly from industrial peat substrates ($p < 0.05$). By lowering peat consumption, the proposed mix can lessen pressures on peatland ecosystems and carbon stocks, thereby improving the environmental sustainability of reforestation nurseries. Local organic components were sourced from the Chaldai Forest in eastern Pavlodar Region, at the southern margin of the relict ribbon pine forest.

Keywords: Biometric parameters; Container cultivation; Germination rate; Organic additives; Peat reduction; Reforestation

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INTRODUCTION

Closed root system (CRS) cultivation is a modern nursery method in which seedlings are grown in containers and transplanted with an intact root plug. Its advantages include minimal root disturbance at lifting, which improves post-transplant rooting and early growth (Sapronova & Khuzhakhmetova, 2024). CRS can also shorten the production cycle, increase planting throughput and enable outplanting at any point in the growing season (Zaykova, 2014; Sapronova & Khuzhakhmetova, 2024). As a result, CRS-grown plants establish more readily under field conditions and exhibit higher survival (Pascual et al., 2018). The approach is widely applied in agriculture, forestry, and urban landscaping, and is particularly effective in regions

with unfavorable climates. The technology of cultivation with closed root system began to be applied in the middle of the XX century, namely in the countries of Northern Europe, such as Sweden and Finland. In these countries, experiments on growing seedlings with a closed root system were conducted for the first time, which demonstrated high safety of plants and their ability to successfully root and grow in new conditions (Stepanov & Zaitseva, 2016; Mukhortov et al., 2022). In Scandinavia, Canada, USA, Russian Federation, CRS technology is actively used in reforestation (Burtsev, 2014; Kostin, 2019).

Adoption of closed root system (CRS) technology in the Republic of Kazakhstan began relatively recently. Since 2016, the Complex of Forest Nursery and Forest Seed Station has operated in the village of Kara-Murza

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(Beskaragai District, Abai Region) under the Kanonersky Forestry Office of the State Forest Nature Reserve "Semei Ormany." The complex's primary activity is the production of planting stock using CRS technology; to date, it remains, to our knowledge, the only facility in the country implementing CRS for forest crops at industrial scale. For Scots pine (*Pinus sylvestris* L.), durable plastic containers are most commonly used because they combine strength and service life with root-favorable conditions (Zvyagintsev et al., 2020; Sakhnov et al., 2023). Perforated walls promote aeration and drainage, supporting normal root development and stable plug formation. As a traditional substrate for growing pine, spruce and larch seedlings in nurseries, top peat enriched with mineral fertilizers is used (Tebenkova et al., 2014). However, one of the problems of traditional substrates is the high dependence on peat, the extraction of which leads to the degradation of peat ecosystems, reduction of carbon stocks, reduction of biodiversity and disturbance of water balance in the regions of its extraction. This makes peat utilization unsustainable in the long term (Leifeld & Menichetti, 2018). Current research confirms that the addition of pulp and paper, forestry and mining wastes (e.g. in the form of composts and mixtures) reduces peat utilization, improves the physicochemical properties of substrates and increases the quality of standard planting material. In order to reduce the amount of waste and the integrated utilization of forest resources, technologies for processing tree biomass, also for the preparation of substrates, are being actively developed (Robonen et al., 2015).

Containerized (closed root system, CRS) substrates typically combine a primary organic base with structural and functional amendments: peat—raised (Sphagnum) or lowland (fen)—as the main matrix providing high water-holding capacity and favorable aeration (Kitir et al., 2018; Leifeld & Menichetti, 2018); wood-derived materials (wood fiber/flour, bark, hydrolyzed lignin) to improve structure and air-filled porosity (Chemetova et al., 2019); composts from biodegradable wastes to enhance fertility and microbial activity (Zhang et al., 2018); perlite and vermiculite to tune porosity and moisture retention; coconut coir to stabilize moisture dynamics and increase mix durability (Carlile et al., 2015; Mariotti et al., 2020); and biochar (also termed biocoal), a pyrolyzed carbon-rich material produced with limited oxygen, which can increase nutrient retention and support seedling performance when appropriately dosed (Seehausen et al., 2017). Substrates are often supplemented with controlled-release fertilizers, liming materials for pH adjustment, binders, wetting agents, hydrogels, biologicals/biostimulants, and plant protection products to optimize physical and chemical properties for nursery targets.

Current research (2021-2025) confirms the promising use of alternative organic and mineral components such as compost, wood waste and local organic materials to reduce the share of peat, improve the physicochemical properties of the substrate and improve the quality of planting material (Chemetova et al., 2021; Sabirzyanov et al., 2023; Stepanova et al., 2024). The introduction of additives such as coniferous fallow, humus, biocoal, coconut fiber improves aeration, water-holding capacity and plant nutrition, providing environmentally sustainable solutions (Carlile et al., 2015;

Seehausen et al., 2017; Mariotti et al., 2020). In the Kazakhstan context, there remains a significant research gap related to the development and evaluation of locally adapted substrates that use regionally organic resources to reduce the use of peat. At the moment, there are no systematic studies investigating the possibility of using coniferous fall and humus of relict ribbon forests as substrate components.

The purpose of this study is to evaluate the effect of different types of container substrates on biometric indicators of Scots pine (*Pinus sylvestris*) seedlings grown by closed root system technology, with the subsequent justification of the choice of the most effective and environmentally sustainable substrate for reforestation. For the first time in the conditions of Pavlodar region the substrate was tested on the basis of local organic resources taken from the territory of the ribbon boron—Chaldai forest, with minimization of peat use. It is assumed that the use of substrate with reduced peat content (the composition developed by the authors) will ensure the growth of Scots pine seedlings at the level of standard industrial substrates.

MATERIALS & METHODS

To grow seedlings of Scots pine (*Pinus sylvestris*) with a closed root system, cassette containers developed according to the personal drawings adapted to the morphology of the species under study were used (Fig. 1, Table 1). The container is made in the form of a rectangular cassette, on which 50 cells of the container are connected with each other by means of stiffening ribs. The volume of one cell is 148.72ml. The material of the cassette is polypropylene, resistant to moisture, fertilizers and temperature fluctuations.

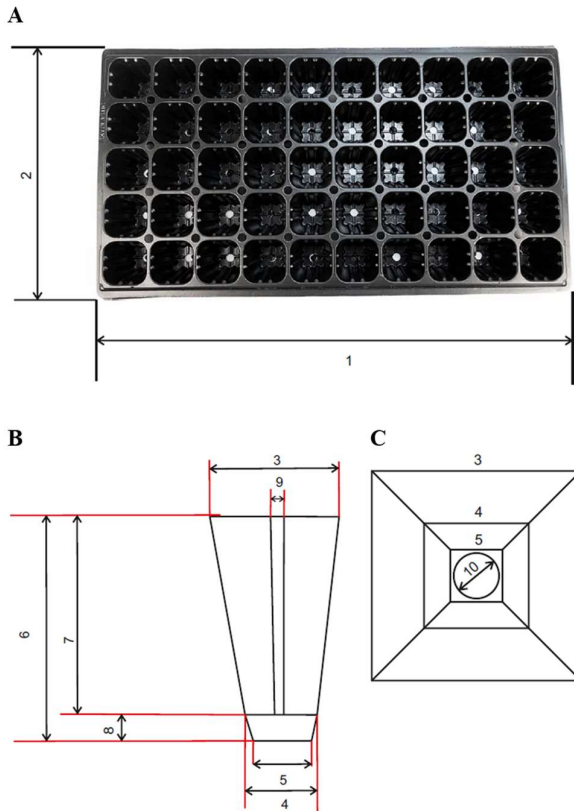
Table 1: Technical characteristics of container cassette with cells

Nº	Parameters	Parameter values, cm
	Overall size of the cassette	
1	Length	55.5
2	Width	29.2
	Cellsize	
3	Width of top square cross-section	4.9×4.9
4	Width of middle square cross-section	2.4×2.4
5	Width of bottom square cross-section	1.2×1.2
6	Total height	11.5
7	Height between top and middle cross section	10.5
8	Height between bottom and middle cross-section	1
9	Width of stiffening ribs	0.5
10	Diameter of bottom hole	0.11

Within the framework of the experiment, 5 variants of substrates with different composition were investigated, from which the optimal one was selected in comparison with the control peat substrate (Table 2). The first two represented ready mixes. The third and fourth substrates were composed of the most common components. The fifth substrate was a substrate that was developed on the basis of a mixture of top peat and organic additives (crushed coniferous fall of Scots pine and humus of local natural resources of Chaldai forest of Pavlodar region) that improve plant nutrition. Coniferous fall and humus were selected in October, after which they were dried and treated with potassium permanganate and phytosporin-M solution. The latter substrate allows increasing the ecological

Table 2: Substrates used for Scots pine cultivation

Substrate variant	Substrate name	Repetitions(n)	Substrate composition
Var 1	Soil for conifer plants «Agrobalt»	150	Consists of a mixture of peat of various degrees of decomposition, limestone, flour, complex mineral fertilizers
Var 2	Readysubstrate «Generous Land»	150	transitional peat, coarse, colored sand, dolomite flour, complex mineral fertilizers
Var 3	Substrate with perlite	150	Is based on a mixture of peat and perlite, with the addition of dolomite flour.
Var 4	Substrate with mineral additives «Bona Forte»	150	Includes peat, dolomite flour and mineral fertilizers «Bona Forte»
Var 5	Developedsubstrate	450	Peat: coniferous litter (Scots pine needle litter): perlite = 77.5–82.5: 7.5–12.5: 7.5–12.5 (% v/v); dolomite flour at 1 g per 10 g substrate; mycorrhizal fertilizer. Substrate acidity is maintained in the range of pH 4.0–4.5.

**Fig. 1:** Sizes of used container cassette and cell: A - container cassette, top view; B - cell, side view; C - cell, bottom view.

efficiency of growing Scots pine (*Pinus sylvestris*) seedlings with a closed root system by using a combined substrate and reducing the use of peat.

The acidity of all substrates was pH 4.5–5.5. The addition of perlite helps to increase air permeability and substrate resistance to compaction. The introduction of dolomite flour helps to regulate acidity, and complex mineral fertilizers provide the substrate with necessary nutrients, contributing to the improvement of plant growth and development. The obtained substrate was poured into container cassettes. Cultivation was carried out under greenhouse conditions with the maintenance of temperature 19–21°C and relative humidity 70%. The photoperiod (16h light/8h dark) was maintained using supplemental artificial light. Prior to sowing seeds, the substrate was treated with phytosporin-M solution and moistened to full saturation, providing optimal conditions for germination and seedling development. The seeds were treated in potassium permanganate solution. Biometric measurements (seedling height, needle length) were taken on day 25 after sprouting. In addition, the total %

germination of the total number of plantings was estimated. The germination percentage was calculated as the ratio of the number of germinated seeds to the total number of sown seeds in the variant, followed by multiplication by 100 to convert to percentages. For each trait, mean values and mean error, coefficient of variation, and reliability of differences were calculated. Before applying Student's t-criterion, the normality of the data distribution was checked using the Shapiro-Wilk criterion, and the homogeneity of dispersions was checked using the F-test (Lakin, 1990; Sokolov et al., 2018). Statistical analyses were performed in STATISTICA 12.0, and graphs were prepared in PAST and STATISTICA 12.0. Differences between groups were evaluated using Student's t-test (two-tailed), with the t statistic (t) and degrees of freedom (df) reported; results were considered significant at $P < 0.05$.

RESULTS

A total of 1050 Scots pine (*Pinus sylvestris*) seedlings were planted using closed root system technology. The planting was carried out on November 30, 2024. Seeding was carried out in individual cells filled with different types of substrates, including both ready-made soil mixtures and experimental compositions with the addition of mineral and organic components. On day 14 after sowing, the first seedlings appeared. The average germination rate for all substrates was 67%. The condition of Scots pine *Pinus sylvestris* 25 days after planting (Fig. 2).

**Fig. 2:** Condition of Scots pine *Pinussylvestris* 25 days after planting out.

Evaluation of seed germination and biometric indicators. The results of research on the influence of the type of substrate on seed germination, seedling height and needle length are presented in Table 3, here are reflected the average values of the studied indicators. Viable seedlings with uniform development were selected for biometric analysis, which resulted in a reduced number of analyzed specimens compared to the total number of plants that grew up.

Table 3: Influence of peat substrate type on seed germination of Scots pine *Pinussylvestris* seeds under the closed root system technology

Substrate variant	Substrate(trade name)	Germination%	Seedling height (cm)			Needle length (cm)		
			n	mean±SE	CV	n	Mean±SE	CV
Var1	Soil for conifer plants «Agrobalt»	61.3	46	3.97±0.19	0.33	40	1.49±0.06	0.26
Var2	Readysubstrate «GenerousLand»	78	99	4.05±0.15	0.36	99	1.50±0.04	0.28
Var3	Substratewithperlite	53.3	61	3.39±0.13	0.31	61	1.57±0.05	0.23
Var4	Substrate with mineral additives «Bona Forte»	70.7	88	3.86±0.12	0.28	88	1.74±0.04	0.24
Var5	Developedsubstrate	70.9	257	3.80±0.07	0.30	257	1.70±0.03	0.29

Note: n = sample size; CV = coefficient of variation

By the end of observations, the highest percentage of germination was recorded in seedlings grown on ready-made substrate «Generous Land» – 78% (variant 2), as well as on developed substrate with mineral additives – 70.9% (variant 5) and developed substrate with mineral additives «Bona Forte» – 70.7% (variant 4). The minimum germination was observed on the substrate with perlite – 53.3% (variant 3). The highest average height of seedlings was observed in seedlings grown on substrate «Generous Land» – 4.05 cm, with coefficient of variation (CV) 0.36, indicating stable growth. Somewhat lower values of height were observed in seedlings grown on the soil for coniferous trees «Agrobalt»– 3.97, developed substrate – 3.80 cm, and on the substrate with mineral additives «Bona Forte»– 3.86 cm. The minimum height of sprouts was recorded on substrate with perlite - 3.39 cm.

The average length of needles varied from 1.49 cm (variant 2) to 1.74 cm (variant 4). At the same time, on all substrates, the coefficient of variation remained within the range of 0.23–0.29, indicating the homogeneity of needle length values within each group. The analysis of experimental data showed that the best results in terms of seed germination (78%) and average height of sprouts (4.05cm) were demonstrated by the ready-made substrate «Generous Land». Despite the slightly shorter length of needles compared to other variants, this substrate provides optimal conditions for germination and growth of seedlings. Considering the totality of indicators, «Generous Land» shows biologically better result, but contains 100% peat, which can be a disadvantage of sustainable development. The developed substrate is slightly inferior to the ready-made substrate «Generous Land» in terms of biometrics, but has alternative components, which makes it the most balanced from an ecological and practical point of view.

Comparative Analysis of Biometric Parameters of *Pinus sylvestris* Seedlings Grown on Different Substrates

The study included pairwise comparative evaluation of sprouts height and needle length of five experimental substrate variants (Var1-Var5) by means of paired Student's t-test. Differences were considered statistically significant at a significance level of $P < 0.05$. Comparative analysis of sprouts height revealed statistically significant differences between some variants. Var2 substrate showed the highest height values (4.05cm), and the differences from Var3 and Var5 were statistically significant ($P < 0.05$). The average height of seedlings on the developed substrate Var5 was 3.80cm, which is comparable to the industrial substrates Var1 and Var4, but significantly higher than the value of Var3 (3.39cm). Furthermore, the analysis of the results shows that Var2 substrate is superior to Var5, although the difference is less pronounced. The developed alternative

substrate Var5 showed a significant advantage over the Var3 substrate ($P < 0.05$), demonstrating its promising performance compared to the perlite variant. Moreover, Var5 was not statistically different from the commercially used Var1 and Var4, confirming its comparability with them. Var1 substrate (Agrobalt) has a significant advantage over Var3 substrate ($P < 0.05$). Thus, the substrate with perlite (Var3) was the weakest, whereas Var2 provided the best results in terms of shoot height. The developed substrate Var5 proved to be a stable alternative. These data are confirmed by the graph (Fig. 3), where Var2 substrate is visually leading, and Var5 occupies a stable intermediate position between the industrial samples and the least efficient Var3.

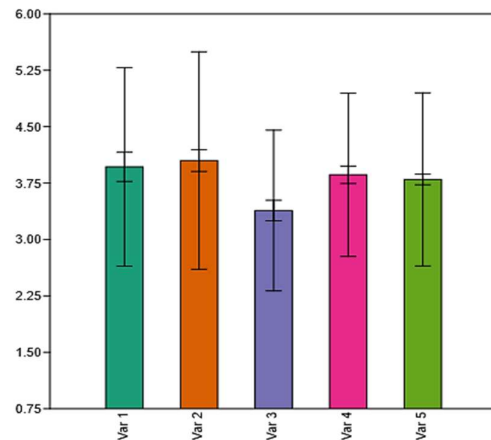


Fig. 3: Comparative growth dynamics of seedlings grown on five different substrates by sprout height (cm).

The values of t-criteria for significant differences are in the range of 2.5–3.1cm, which indicates the average strength of the effect between the substrate variants. From a practical point of view, the Var2 substrate is recommended for industrial cultivation, and the developed Var5 substrate can be considered as a promising, environmentally friendly alternative. The substrate with perlite (Var3) showed the worst results in terms of seedling height and biometric parameters, which makes it unpromising for use. Needle length differed significantly among substrates. The greatest values were observed for Variant 4 (1.74 ± 0.04 cm) and Variant 5 (1.70 ± 0.03 cm), both exceeding the remaining mixes in pairwise two-tailed Student's t-tests: Variant 4 was higher than Variants 1, 2, and 3 ($p < 0.01$), and Variant 5 was higher than Variants 1 and 2 ($P < 0.05$). Conversely, Variants 1 and 2 showed the shortest needles (1.49 ± 0.06 and 1.50 ± 0.04 cm, respectively). These results indicate that the formulations in Variants 4 and 5 favor early needle morphogenesis. Fig. 4 illustrates this trend, with Variants 4–5 at the upper range and Variants 1–2 at the lower.

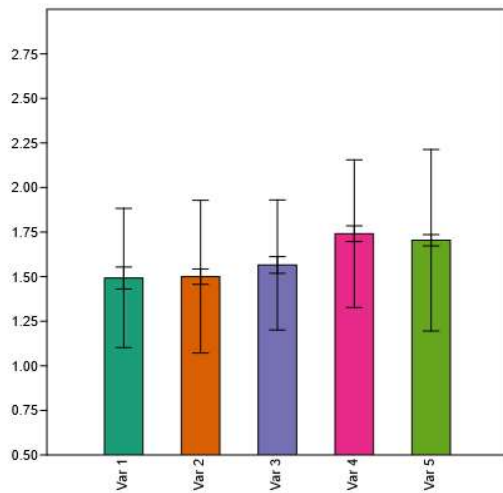


Fig. 4: Comparative dynamics of needle length in seedlings grown on five different substrates. Modify Figures 3, in Var1-5, Y-Axis upto 1.5 are common and can be deleted and start Y-Axis from 1.5. Similarly, in Figure 4, start Y-Axis from 0.75.

Extended analysis of the results confirms that Var4 substrate provides maximum needle length, significantly superior to Var1 ($P < 0.01$), Var2 ($P < 0.001$) and Var3 ($P < 0.01$). Also, Var5 substrate shows significant differences compared to Var1 ($P < 0.05$), Var2 ($P < 0.001$) and Var3 ($P < 0.05$), emphasizing its positive effect on needle formation. At the same time, no statistically significant differences were found between Var4 and Var5 substrates, indicating their comparable effectiveness in ensuring morphological development of seedlings. The lowest values of needle length were recorded for Var1 and Var2 substrates, which practically do not differ from each other and do not provide optimal conditions for needle growth. Thus, substrates Var4 and Var5 can be considered the most effective for stimulating needle development. The developed Var5 substrate demonstrates similar efficiency to the industrial Var4 substrate, which allows recommending it as an environmentally sustainable alternative. Thus, in the comparative analysis of statistical data of biometric indices of Scots pine seedlings *Pinus sylvestris* with closed root system, it is possible to see pairs of variables with $P < 0.05$, indicating statistically significant differences between groups. In some cases, p is significantly less than 0.01, indicating high reliability of differences. Analyzing the growth of CRS seedlings under different conditions (e.g. substrate type, growing conditions) shows that there are significant differences between groups. It can be concluded that growth conditions significantly affect the development of pine seedlings, which is confirmed by significant differences in t-test. Hierarchical cluster analysis using single linkage and Euclidean distances was performed to assess the overall similarity of substrate variants based on a set of biometric parameters (seedling height, needle length) (Fig. 5).

Cluster analysis showed that the developed substrate (Var5) significantly differs from the industrial variants and forms a separate group (Fig. 5). Substrates Var3 and Var4 are the closest to each other in terms of biometric parameters, with Var2 partially adjoining them. Var1 occupies an intermediate position. These data confirm the

uniqueness of the developed substrate by a set of characteristics.

Complex analysis of the obtained data allows us to identify two substrates – Var2 and Var5 – as the most effective in terms of agrobiological traits. Var2 provides maximum germination and sprouts height, but contains 100% peat, which reduces its sustainability from the ecological point of view. In contrast, the developed Var5 substrate contains alternative organic components and provides high performance in all key parameters, including needle length: seed germination was 70.9%, which is comparable to the best industrial substrates, while sprouts height (3.80cm) and needle length (1.70cm) indicate good plant development. Thus, the developed substrate combines high agrobiological characteristics and environmental sustainability, which makes it the most preferable for use in reforestation technologies. The use of alternative substrates reduces the negative environmental impact, reduces carbon emissions and conserves natural resources. Organic and inorganic materials provide plants with optimal conditions for growth, helping to reduce dependence on traditional resources such as peat and chemical fertilizers. The introduction of these alternative substrates contributes to the development of sustainable agriculture and the adaptation of agro-systems to changing climatic conditions.

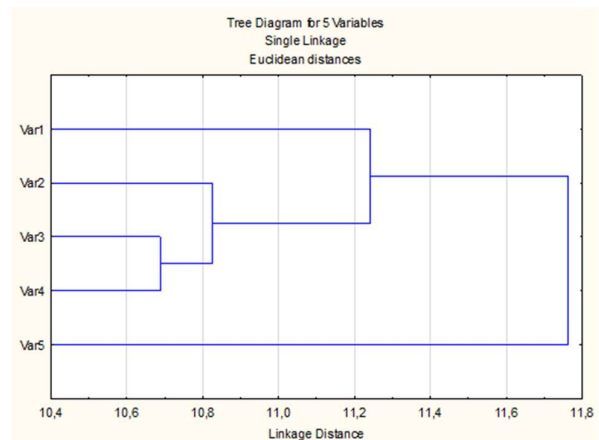


Fig. 5: Comparative cluster analysis of substrates by biometric parameters of *Pinus sylvestris* seedlings.

DISCUSSION

In recent years, global practice has shown a targeted reduction in the dependence on peat in substrate production. According to the European strategy to reduce the use of peat in horticulture (Nordbeck and Høgl, 2024), the main directions are the use of renewable organic materials (wood fibers, bark, coconut fiber, biochar) as well as recycled agricultural and forestry waste (Growing Media Europe, 2021; Lewandowski et al., 2025; Leopard et al., 2025; Hirschler and Osterburg, 2025). Canada and Nordic countries are adopting technologies using substrates based on Miscanthus fibers and paper waste (Carlile et al., 2015; Zhang et al., 2018). China is actively using organic composts and biochar as peat substitutes (Seehausen et al., 2017; Mariotti et al., 2020). In the context of these global studies, the

developed substrate using conifer fall and humus from relict ribbon forests represents a regionally adapted alternative similar to global practices to utilize local organic resources to reduce dependence on peat. The results obtained by the authors confirm that it is possible to efficiently grow common pine seedlings while reducing the proportion of peat by 17.5-22.5%, which is in line with international trends in sustainable nursery production (Carlile et al., 2015; Leifeld & Menichetti, 2018; Growing Media Europe, 2021). From a practical point of view, the developed substrate can be recommended for industrial implementation in forestry nurseries of the Republic of Kazakhstan. The use of available local organic components will reduce the cost of production of planting material and reduce the environmental load while maintaining the high quality of growing seedlings. In addition, it should be emphasized that the developed substrate and the container cassette used in this study are protected by patents of the Republic of Kazakhstan № KZ 10562 and № KZ 10807, respectively, the owners of which are the authors of the article Z. Sergazinova and A. Chashin. The patented technologies provide legal protection of the author's method, which contributes to its widespread implementation.

The ecological advantage of reducing the share of peat is not only in the conservation of natural resources, but also in the protection of biodiversity of wetland ecosystems and reducing the carbon footprint of nursery production. Substitution of peat with local organic components directly contributes to the formation of climate-resilient reforestation technologies by preserving natural carbon stocks and minimizing the destruction of peatlands (Jokanović et al., 2024). It should be noted that the observation period in this study was 25 days after the emergence of seedlings. Despite its relative short duration, this period is sufficient to assess the starting biometric indicators (germination, seedling height, needle length) under nursery production conditions. It is at this stage that the key characteristics of seedlings that determine their further development are formed. Evaluation of plants in the early period allows timely identification of substrate efficiency and correction of technology at the initial stages. Nevertheless, for a more complete assessment of the potential of the developed substrate in the conditions of reforestation, it is recommended to conduct further studies with an extended observation period (60-90 days) and analysis of rooting after planting in the open ground (Heiskanen et al., 2024). Thus, this study demonstrates compliance with global trends in the development of closed-root cultivation technologies and environmentally sustainable substrates, emphasizing the practical significance of integrating local organic components into container substrates for reforestation. The results obtained indicate that the developed substrate based on organic components of local origin (coniferous fall and humus from the territory of Chaldai relict ribbon forest) in combination with top peat and perlite can be an effective alternative to traditional peat substrates. Despite the fact that ready-made industrial substrates (e.g., «Generous Earth») showed higher values for some biometric indicators, the developed composition demonstrated balanced results for all criteria (germination, shoot height, needle length), while ensuring

environmental sustainability by reducing the share of peat (Socha et al., 2022). In general, the results obtained contribute both to global research in the field of sustainable containerized planting and to the development of applied reforestation technologies in Kazakhstan, filling the existing deficit of research on the development of substrates using local organic resources.

Conclusion

The developed substrate Var5 with the addition of coniferous fall and humus from relict ribbon pine forests is a balanced combination of high agrobiological efficiency and environmental sustainability. Its application provides stable indicators of germination (70.9 %), seedling height and needle length comparable to industrial peat substrates (Var1 and Var4). At the same time, reducing the share of peat by 17.5-22.5 % contributes to reducing the carbon footprint and preserving peatland ecosystems. The obtained results allow recommending Var5 substrate for industrial introduction in forest nurseries of the Republic of Kazakhstan as an environmentally sound alternative to traditional substrates. The use of local organic resources reduces dependence on imported peat and promotes the development of sustainable nursery production. To scale up the technology, it is necessary to conduct further research, including assessment of seedling survival after planting in the open ground and optimization of technological parameters of cultivation. Implementation of the developed substrate is possible within the framework of national programs of reforestation and landscaping of territories of the Republic of Kazakhstan. It should be emphasized that the developed substrate and applied container cassette are protected by patents of the Republic of Kazakhstan (№ KZ 10562 and № KZ 10807), which provides legal protection of technologies and contributes to their wide practical application

DECLARATIONS

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Ethics Statement: No humans or animals were involved in the study; thus, it needs no ethical approval.

Author's Contribution: SZ: Directed the study, conducted experimental work, conducted literature review, prepared the manuscript. ACh: conducted experimental work. AG, RA: conducted literature review, interpreted and analyzed data. KJ: proofread the manuscript.

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