SYLWAN 166 (8): 537-550, August 2022
https://doi.org/10.26202/sylwan.2022062
Journal homepage: https://sylwan-journal.pl

ORIGINAL PAPER

Effect of peat substrate compaction on growth parameters and root system morphology of Scots pine *Pinus sylvestris* L. seedlings

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ABSTRACT

Substrate compaction is one of the most important factors influencing plant growth. Seedling growth is influenced by the substrate's physical properties, including its compaction level, typically expressed as bulk density. Substrate compaction determines the air-water ratio, water and nutrients availability, and microbial activity. Several authors have studied the effect of soil compaction on the growth and development of various plants. However, the influence of a wide range of different levels of substrate compaction on the growth of Scots pine seedlings in container nurseries has yet to be investigated. This paper presents the results of a study of the influence of different levels of peat substrate compaction on the growth parameters of Scots pine seedlings. The seedlings were grown in 9 variants of bulk density, ranging from 0.208 to 0.342 g·cm^{-3} (dry bulk density: 0.083-0.137 g·cm^{-3}) in containers with multiple 120 cm^3 cells. Each variant was prepared in 3 replicates (a total of 1080 seeds was sown). The experiment lasted one growing season. The substrate density was found to affect seedling height, root collar diameter, needles' dry weight , shoots and roots, and total root length. The results showed that the growth parameters of Scots pine seedlings grown in nursery containers could be modified by selecting appropriate peat substrate density. Low (0.208-0.242 g·cm^{-3}) and high (0.308-0.342 g·cm^{-3}) substrate densities reduced seedling growth. In terms of the desirable seedling parameters, namely shoot-to-root ratio (S/R) and sturdiness quotient (SQ), the seedlings achieved the best values at medium substrate densities, *i.e.*, from 0.26 to 0.29 g·cm^{-3}. We conclude that peat substrate compaction in the range 0.26-0.29 g·cm^{-3} is recommended for growing Scots pine seedlings in 120 cm^3 containers.

KEY WORDS

bulk density, nursery container, root distribution, root-shoot ratio, seedling quality, sturdiness quotient

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Received: 7 September 2022; Revised: 24 October 2022; Accepted: 25 October 2022; Available online: 16 December 2022

Introduction

Forest tree seedlings can be grown in a traditional way in ground nurseries, or in special containers in so-called container nurseries. Regardless of the culture method, seedling growth depends on the availability of light, water, and mineral nutrients, and the type and physical properties of the substrate, including its density (Perez-Ramos *et al.*, 2010; Alameda *et al.*, 2012; Kormanek, 2013). The advantages of growing seedlings in containers include automatic filling of containers with substrate and controlled fertilization and irrigation (Szabla and Pabian, 2009). The nursery substrate must have high water retention capacity, good permeability, and high air capacity (Kormanek *et al.*, 2021). A substrate suitable for a container nursery should have an air capacity of 20-25% by volume, a water capacity of 800-1000% by weight, and a total porosity of at least 70% by volume (Szabla and Pabian, 2009). High moor peat is the main component of substrates used in a container nursery; an important property of high moor peat that affects its other parameters is the degree of decomposition, *i.e.*, the ratio of the organic part decomposed to the total weight of peat. Substrate compaction determines the air-water ratio properties of the substrate, and thus significantly affects the availability of water and nutrients for plants (Bilderback *et al.*, 2005; Kormanek, 2021). The shape of the container also influences the growth of tree seedlings (Xianhong *et al.*, 2019). However, the density of the substrate rather than the volume or shape of the cell in the container significantly affects the morphology of growing seedlings (Barnett and Brissette, 1986). In agriculture and horticulture, changes in soil physical, chemical, and biological properties as functions of compaction have been investigated in multiple field studies (Arvidsson, 1999; Lipiec and Hatano, 2003; Fernandes and Cora, 2004; Ferree *et al.*, 2004; Onweremadu *et al.*, 2008; Bartholomew and Williams, 2010; Alameda *et al.*, 2012). These authors indicated a negative effect of excessive soil compaction on plant growth, because compaction increases the bulk density and reduces the pore diameter of the soil, which in turn reduces permeability and water flow, and consequently air capacity (Blouin *et al.*, 2008; Bejarano *et al.*, 2010; Boja and Boja, 2011; Lipiec *et al.*, 2012a). In forestry, most of the studies and research on the effects of soil compaction on plant growth have been conducted in the field of forestry mechanization, mainly concerning the effects of machinery on soil, tree seedlings, and trees (Arvidsson, 2001; Boja and Boja, 2011; Kormanek, 2015a). Studies on the growth and quality of regeneration of Scots pine *Pinus sylvestris* L., European beech *Fagus sylvatica* L., and pedunculate oak *Quercus robur* L. involving sowing and growing the trees under the stand canopy showed that unit pressure exerted on the soil, and thus its compaction, affected the parameters of seedlings (Kormanek and Banach, 2011). Studies were also conducted under controlled soil compaction conditions in ground nurseries for seedlings of several forest tree species, including pedunculate oak (Maupin and Struve, 1997), lodgepole pine *Pinus contorta* Dougl. ex Loud. (Conlin and van den Driessche 1996), Austrian pine *Pinus nigra* Arn. (Zahreddine *et al.*, 2004), European beech and Scots pine (Kormanek, 2013; Kormanek *et al.*, 2013a,b), and sessile oak *Quercus petraea* (Matt.) Liebl. (Kormanek *et al.*, 2015b) and European beech (Pająk *et al.*, 2022a). These studies showed that a change in the bulk density of the substrate affects the development of root systems, total seedling height, diameter at the root collar (RCD), and dry weight of seedlings, while the strength of this relationship depends on the species and substrate density. In Poland, such studies have not yet been conducted for forest species grown in container nurseries. Although the total production area of container nurseries in Poland is small (98 ha) in comparison to 1900 ha of ground nurseries (as of December 31, 2019), they nevertheless produce annually 10-13% of the total number of seedlings, mainly coniferous species, including Scots pine. Planting of seedlings is most commonly performed in spring, but container cultivation also allows planting seedlings in autumn (in the same year they were sown). For economical and biological reasons (risk of root deformation), a shorter breeding cycle is more desirable in container nurseries . Therefore, it was decided to measure the seedlings immediately after cultivation. In container nursing, substrate density is usually selected intuitively, as there is little information on the effect of this factor on the growth parameters of seedlings of forest tree species grown in nursery containers.

Various standards based on single trait values (*e.g.*, height, dry weight) are used to assess the suitability of seedlings for crop plantation. More recently, however, many authors suggest that synthetic indices such as seedling sturdiness quotient (SQ) and shoot-root index (S/R) better characterize the adaptive potential of seedlings (Haase, 2007; Grossnickle, 2012; Ivetić and Skorić, 2013; Banach *et al.*, 2020, 2021). SQ is a measure of seedling stability in the culture (resistance to wind and drought), with smaller values of SQ corresponding to more sturdy seedlings. The S/R value determines the balance between the transpiration area and the area of water absorption.

In the present study, the following hypothesis was tested for Scots pine seedlings grown in Hiko V120SS containers: there is an optimum density at which the seedlings will have the allometric growth parameters desirable for good adaptation, *i.e.*, the value of S/R should be <2 (S/R<2:1) and the SQ should be below <70.

Materials and methods

SUBSTRATE PREPARATION. Peat substrate produced by Nursery Farm in Nędza (GPS coordinates 50.167964 N, 18.3138334 E) was used in the experiment; the substrate composition was as follows: peat 93% and perlite 7% with the addition of dolomite (3 kg per m^3 of substrate) to obtain pH of 5.5. The peat used to prepare the substrate had the following characteristics: maximum degree of decomposition: 15%; organic matter content: >85%; granulometric composition: 10.1--20 mm – 2.5%, 4.1-10 mm – 12.5%, 2.1-4.0 mm – 12.5%, <2.0 mm – 72.5%; air capacity: 15-25% vol.; water capacity: 70-80% vol. at 10 cm H_2O (after squeezing loose gravity water – PN-EN 13041); total porosity: 85-95% vol.; relative humidity: approximately 65%; pH in H_2O: 3.0-4.5, and salinity (conductivity): up to 0.12 mS·cm-1.

In the experiment, nine variants of substrate compaction by the weight method were prepared in polypropylene HIKO V120SS containers 352 × 216 × 110 mm (length × width × height) with 40 square cells of 120 cm^3 volume, tapering to the bottom with guides for the root system. The minimum bulk density (variant V1) was obtained by pouring the substrate with approximately 60% moisture content loosely into a single cell, which was then poured out and weighed. The procedure was repeated three times, and after averaging, the substrate weight for this variant was 25 g. Similarly, the weight of the substrate for the maximum compaction variant (V9) was determined to be 41 g. In this case, the substrate in the cell was compacted using a wooden stamp until the cell was full. For variants V2 to V8, the substrate weight was calculated by dividing evenly the difference in substrate weight obtained for the variants with borderline compaction (Table 1). As a result, the weight difference between subsequent variants equalled 2 g. In each variant, three containers (total of 120 cells) were filled with the substrate by pouring into each cell the calculated substrate mass weighed on an analytical balance with an accuracy of ±0.2 g.

Plant growth

On the BCC AB nursery line, one pine seed (81% germination capacity) was sown into each cell in the nursery container in April. A total of 1080 seeds was sown, 120 pcs (40 cells × 3 repetitions) in each of the 9 variants of substrate density. The seed germination period lasted 4 weeks in the

Table 1.
Wet substrate weight and corresponding wet and dry bulk density for each experimental variant

Parameter	Variant								
	V1	V2	V3	V4	V5	V6	V7	V8	V9
Weight of wet substrate (60% H_2O) [g]	25	27	29	31	33	35	37	39	41
Wet bulk density [g·cm^{-3}]	0.208	0.225	0.242	0.258	0.275	0.292	0.308	0.325	0.342
Dry bulk density [g·cm^{-3}]	0.083	0.090	0.097	0.103	0.110	0.117	0.123	0.130	0.137

vegetation hall, after which the containers were transported to the production field. The 27 containers were randomly distributed on a rack placed among other seedlings of the species in the central part of the production field, where the seedlings were grown until they were collected for measurements. In the process of growing seedlings, foliar fertilization was carried out along with irrigation (2 times in the tent, 17 times in the production field, totalling 0.171dm^3·m^{-2} using Floralesad; Florasin K 500 was applied once, at the end of the vegetation season). Floralesad fertilizer consisted of (g·dm^{-3}), N=103.1, N-NO_2=0.0214, N-NO_3=16.369, N-NH_4^+=2.602, N-NH_2=84.107, P=17.231, K=47.423, Mg=3.567, Ca=0.737, Na=0.28, S=1.24, B=1.107, Cu=0.123, Fe=1.04, Mn=0.281, Mo=0.048, and Zn=0.231. Florasin K 500 consisted of (g·dm^{-3}), K=420.75, Na=2.2, and Ca=0.003. Throughout the vegetative season, the conductivity of the aqueous fertilizer solution was maintained at approximately 600 µS·cm-1. During the seedling cultivation period, natural precipitation was 78 mm, the plants were irrigated using automatic sprinkler ramps HAB-T1 BCC to supplement water deficit. Irrigation during the production season in the open field totalled 904 mm.

Laboratory analysis. At the end of September, the number of viable seedlings was determined, their RCD was measured with an electronic caliper at an accuracy of ±0.01 mm, and height (SH) with a linear gauge at an accuracy of ±1 mm. The SQ was calculated as the ratio of seedling height to the diameter at the root collar (Skrzyszewska *et al.*, 2019; Banach *et al.*, 2020), while the S/R was taken as the ratio of the dry weight of the aboveground part to that of the underground part (Haase, 2007). In each variant in each replication, 3 seedlings closest to the mean height in the respective variant and replication were selected and subjected to detailed analyses. The selected seedlings were removed from the cells, and the root ball was divided (cut) into 3 equal parts: upper (a) 0-3.7 cm cell depth, middle (b) 3.8-7.4 cm, and lower (c) 7.5-11 cm to evaluate the uniformity of development of the root system throughout the whole profile of the root ball. The peat was separated from the roots manually and by rinsing the roots with water to remove peat fibres. The separated sections of the root system were scanned using an Epson V800 Photo scanner (800 dpi), and the resulting images were analysed using WinRhizo software (Regent Instruments Inc.). The length of the root system was determined by root diameter ranges of <0.5 mm (very fine roots), 0.5-2.0 (fine roots), and >2.0 mm (skeletal roots) (Makita *et al.*, 2011; Farahnak *et al.*, 2020). All parts of the seedlings (needles, shoots, and roots) were dried at 105°C for 48 h, and after cooling, dry weight was determined to an accuracy of ±0.1 mg.

Statistical analysis. One-way analysis of variance and Tukey's post-hoc multiple comparisons test were used to determine the effect of density variant on the parameters of the seedlings. Calculations were performed in Statistica 13.3 (TIBCO Software Inc.), using a significance level of p=0.01. We used nonlinear regression to model the influence of bulk density on selected features of seedlings.

Results

From the 1080 pine seeds sown, 737 seedlings were grown, *i.e.*, the total yield in the experiment was 68%. The highest percentage survival for all density variants from three replications was achieved by seedlings from the extreme density variants, *i.e.*, V1 and V9 (Fig. 1). A total of 76% of the variation in the seedling yield was explained by variation in substrate density. The difference in productivity per container between the density variants in the extreme case was 30%.

The F-value for the traits tested compared to the critical value, $F_{8.719}$=2.5 at p=0.01, showed a statistically significant effect of density variant on each biometric trait tested (Tables 2 and 3).

Seedling height, thickness at the root collar, and strength index showed statistically significant differences between the variants. Seedlings grown in the more compacted substrate (V5-V9) had greater aboveground height (with a maximum value of 20.1 cm for V5) compared to seedlings grown in substrate with the lower compaction (V1-V4). The largest thickness val-

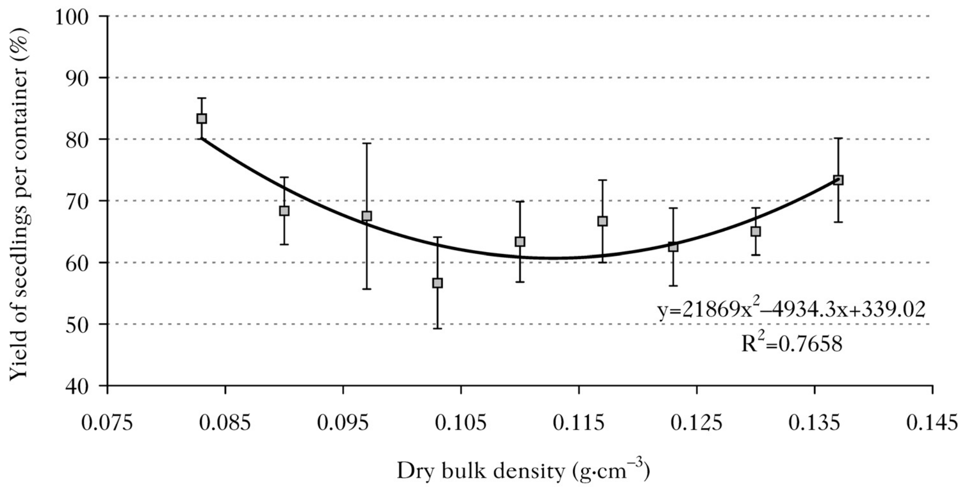

Fig. 1.

Average seedling yield (±SE) from a single container in variants of nursery substrate compaction. Dry bulk density values (in g·cm^{-3}) for each variant

Table 2.

Mean growth parameters (±SD) according to the density variant SH: height, RCD: thickness at the root collar, SQ: sturdiness quotient, abcd – statistically homogeneous groups

Density variant	Growth parameters		
	SH [cm]	RCD [mm]	SQ
V1	18.4 ±2.44ac	2.8 ±0.45ab	65.9 ±5.41ab
V2	17.6 ±2.34c	2.8 ±0.46ab	62.0 ±5.10a
V3	17.4 ±3.25c	2.7 ±0.57b	65.2 ±5.76ab
V4	18.0 ±3.41ac	3.0 ±0.44acd	60.5 ±7.73a
V5	20.1 ±2.66b	3.1 ±0.49d	63.6 ±5.48ab
V6	19.6 ±2.57b	3.1 ±0.47cd	63.3 ±5.51ab
V7	18.9±2.63ab	3.0 ±0.52acd	64.1 ±5.11ab
V8	19.2 ±2.39ab	2.8 ±0.54ab	67.4 ±4.46b
V9	19.1 ±2.11ab	2.9 ±0.52ac	65.6 ±4.03ab
Average	18.7 ±2.64	2.9 ±0.50	66.01 ±1.33

Table 3.

Mean (±SD) dry weight of needles, shoots, and root [g] divided into three parts according to cell height (upper (a) 0-3.7 cm cell depth, middle (b) 3.8-7.4 cm, and lower (c) 7.5-11 cm) and ratio of mean dry weight of the aboveground to underground parts (S/R) depending on substrate compaction variant, abcd – statistically homogeneous groups

Density variant	Dry weight [g]					S/R
	needles	shoots	Root parts			
			a	b	c	
V1	0.486 ±0.16ab	0.712 ±0.22a	0.277 ±0.09c	0.177 ±0.07a	0.152 ±0.06ab	2.09 ±0.70b
V2	0.459 ±0.15a	0.719 ±0.23a	0.302 ±0.10ac	0.208 ±0.08ab	0.177 ±0.08abc	1.78 ±0.54a
V3	0.448 ±0.18ab	0.700 ±0.24a	0.278 ±0.10c	0.188 ±0.09a	0.177 ±0.08 abc	1.91 ±0.77ab
V4	0.523 ±0.18abc	0.773 ±0.25ab	0.340 ±0.10ab	0.199 ±0.08abc	0.186 ±0.09bcd	1.87 ±0.57ab
V5	0.622 ±0.18d	0.874 ±0.26b	0.414 ±0.14d	0.237 ±0.09c	0.194 ±0.09cd	1.878 ±0.66ab
V6	0.608 ±0.18cd	0.874 ±0.28b	0.352 ±0.10ab	0.231 ±0.08bc	0.215 ±0.08d	1.91 ±0.57ab
V7	0.549 ±0.15bcd	0.761 ±0.25ab	0.334 ±0.10ab	0.197 ±0.07abc	0.169 ±0.06 abc	1.95 ±0.65ab
V8	0.531 ±0.18abc	0.741 ±0.26a	0.343 ±0.13ab	0.205 ±0.08abc	0.146 ±0.08a	1.92 ±0.63ab
V9	0.544 ±0.17bcd	0.718 ±0.23a	0.369 ±0.13bd	0.201 ±0.08abc	0.152 ±0.05ab	1.79 ±0.49a
Average	0.530 ±0.17	0.765 ±0.25	0.335 ±0.11	0.205 ±0.08	0.174 ±0.07	1.90 ±0.63

Table 4.

Mean length (cm) (±SD) of roots from each cell height (upper (a) 0-3.7 cm cell depth, middle (b) 3.8-7.4 cm and lower (c) 7.5-11 cm) grouped by root diameter (mm) along with mean total root length (cm) from all levels for the variant, ab – statistically homogeneous groups

	Skeletal roots (diameter >2 mm)			Fine roots (diameter ≤2-0.5> mm)			Very fine roots (diameter ≤0.5 mm)			Total root length
	a	b	c	a	b	c	a	b	c	
V1	3.8 ±2.6a	0.3 ±0.7a	0.0 ±0.0a	29.6 ±15.7a	23.2 ±9.7a	27.5 ±22.0ab	630.0 ±288.9a	556.6 ±196.1ab	416.2 ±206.6a	1687.1 ±594.5
V2	4.1 ±2.3a	0.5 ±0.7a	0.0 ±0.0a	38.0 ±21.7a	32.5 ±12.7a	26.2 ±9.4ab	635.0 ±394.0a	621.4 ±276.4b	463.5 ±197.7a	1766.9 ±405.7
V3	1.4 ±1.2a	0.2 ±0.6a	0.0 ±0.0a	29.0 ±10.0a	16.7 ±8.8a	18. 9 ±10.8ab	447.4 ±109.6a	317.3 ±134.1a	366.1 ±147.5a	1197.1 ±337.8
V4	2.7 ±2.9a	0.8 ±1.7a	0.0 ±0.1a	24.8 ±6.8a	22.2 ±8.4a	20.7 ±16.0ab	384.9 ±182.6a	354.9 ±109.8a	353.1 ±159.8a	1155.7 ±357.9
V5	2.5 ±2.3a	0.5 ±0.7a	0.1 ±0.1ab	50.6 ±39.9a	33.5 ±19.3a	22.9 ±13.1ab	550.7 ±207.3a	400.3 ±211.2ab	361.2 ±165.0a	1422.3 ±396.3
V6	3.6 ±3.3a	0.2 ±0.2a	0.3 ±0.4b	36.2 ±22.6a	31.3 ±14.0a	35.8 ±14.0b	464.7 ±209.0a	489.1 ±127.0a	544.9 ±156.0a	1590.8 ±316.7
V7	5.1 ±3.5a	0.4 ±0.6a	0.0 ±0.1a	40.3 ±15.9a	17.2 ±6.7a	17.7 ±5.4ab	490.0 ±178.9a	345.2 ±156.1ab	418.6 ±111.2a	1334.6 ±346.8
V8	5.2 ±2.7a	0.4 ±0.4a	0.0 ±0.0a	31.6 ±8.3a	23.7 ±10.0a	11.9 ±6.4a	728.7 ±334.2a	509.9 ±192.6ab	337.6 ±173.4a	1538. 5 ±73.7
V9	5.4 ±2.6a	1.1 ±1.8a	0.0 ±0.0a	34.4 ±12.6a	27.4 ±11.3a	18.4 ±11.2ab	707.1 ±303.3a	441.4 ±170.2ab	392.0 ±192.1a	1581.7 ±483.0

ues at the root collar were for variants with medium compaction (V4-V6), with a maximum value of 3.2 cm obtained for V5. The most beneficial ratio between aboveground height to thickness at the root collar (SQ) was obtained for variant V4 (60.5) and the least beneficial for V8 (67.4) (see Table 2).

The greatest value of dry bulk mass was obtained in variants with medium compaction: V5-V7 in the case of the shoot and V4-V6 in the case of the needles. In both cases, the lowest values were observed for variant V3, which differed significantly from seedlings grown in substrate from variants V5 and V6. The average dry mass of level *a* (closest to the root collar) and level *b* (in the middle of the cell) had the highest value in variant V5. In contrast, for part *c* (the farthest from the root collar) the highest value was obtained for variant V6 (see Table 3).

The ratio of seedlings aboveground to underground dry weight (S/R) ranged from 1.78 (V2) to 2.09 (V1) (Table 3). For all seedlings, except those from variant V1, this ratio was below 2. Variant V1 showed statistically significant differences from variants V2 and V9, where S/R reached the lowest values (recall that lower values of S/R are better). For seedlings growing in variant V4, for which the lowest SQ value was obtained, the S/R value was 1.87. In this variant and in variant V2, the number of seedlings simultaneously meeting both the assumed criteria for SQ and S/R constituted the largest share, *i.e.*, 50%. The smallest share of seedlings meeting both criteria was noted in variants V7, V8, and V1 (Fig. 2).

Nonlinear regression was used to illustrate the influence of substrate compaction on dry weight of each part of the seedlings (Fig. 3) and each part of the root ball (Fig. 4). For the parts of the seedling, in all three cases, namely root, shoot, and needle dry weight, the coefficient of determination was approximately 50%, *i.e.*, 50% of variation in seedling dry weight was explained by the variation in substrate compaction (Fig. 3), similar to that in roots; considering the division into individual parts of the root ball, R^2 was approximately 50% on average (Fig. 4). The largest influence of the density was observed on part *c* of the root.

The mean length of skeletal roots was significantly different between the variants in the lowest part of the root ball (level *c*). Similarly, differences in the lowest part were observed for

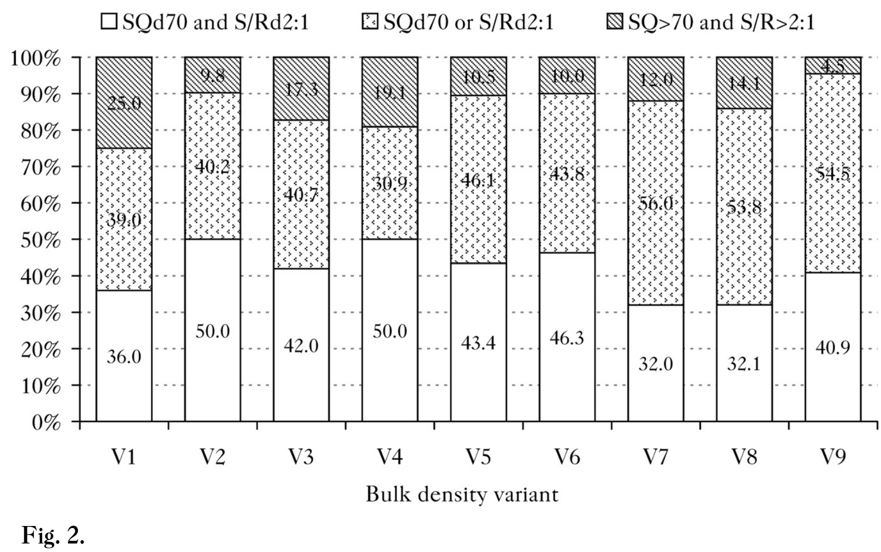

Fig. 2.

Proportion of Scots pine seedlings meeting both criteria (SQ<0 and S/R<2:1), only one, (SQ<70 and S/R<2:1) and not meeting either criterion (SQ>70 and S/R>2:1) (χ^2=36.263, *p*<0.003)

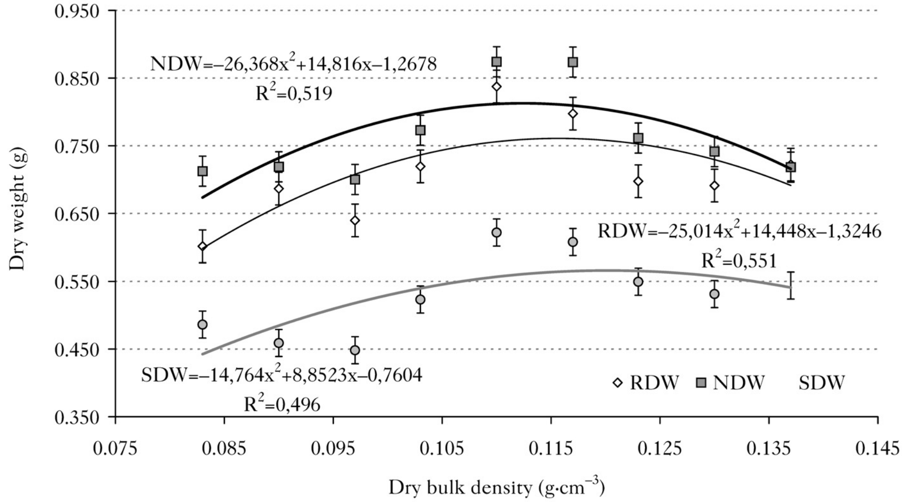

Fig. 3.

Mean (±SD) dry weight of root (RDW), shoot (SDW), and needle (NDW) of Scots pine seedlings as a function of substrate compaction value. Dry bulk density values (in g·cm^{-3}) for each variant

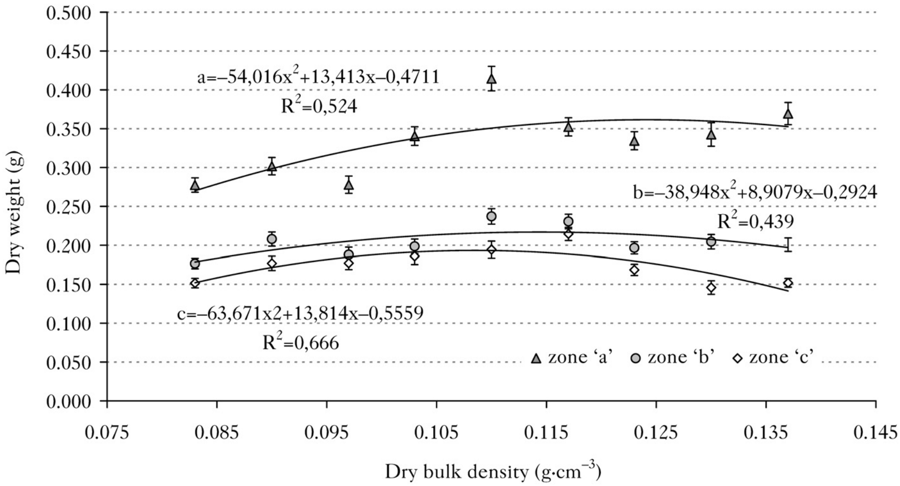

Fig. 4.

Mean value (±SD) of root dry weight of Scots pine seedlings in root ball zones (upper (a) 0-3.7 cm of cell depth, middle (b) 3.8-7.4 cm, and lower (c) 7.5-11 cm) depending on soil compaction values. Dry bulk density values (in g·cm^{-3}) for each variant

fine roots. However, in the case of the very fine roots, significant differences in mean length between the variants were observed in the middle part of the root ball (level *b*) No significant differences were noted between the total sum of root lengths from all cell levels for the variants (Table 4).

Discussion

In the present study, the seedling success rate was highest in the substrate density variant V1 (0.21 g·cm^{-3}) and V9 (0.34 g·cm^{-3}), while the fewest seedlings developed in variant V4 (0.26 g·cm^{-3}). A similar negative relationship between density and the seedling success rate was reported in studies for Scots pine and European beech seedlings (Kormanek *et al*., 2013a,b). Most of the analysed seedling parameters, *i.e*., SH, RCD, dry weight of individual seedling parts, and total length of fine roots, had the largest values in variants V5 (0.275 $g \cdot cm^{-3}$) and V6 (0.29 $g \cdot cm^{-3}$), *i.e*., at slightly higher than average densities. In variant V4, *i.e*., at the density of 0.26 $g \cdot cm^{-3}$, the pine seedlings achieved a very good SQ (60.5) and S/R (1.87). The results are consistent with the observations reported in the literature (Arvidsson, 1999), where it is indicated that low density can have a positive effect on plant growth because of better root-soil contact that allows better nutrient transport. An increase in bulk density is also associated with an increase in nutrients per unit volume of substrate. In the present study, the seedling height was highest when the average density (V5) was applied, while an increase in density much above the average (V7-V9) resulted in a decrease in seedling height. In similar studies, but with a substrate composition of 90% peat and 10% perlite, the length of whole Scots pine seedlings (shoot+root system) decreased with increasing peat substrate density, while their height increased slightly (Kormanek *et al*., 2013a). For sessile oak growing on sandy soil (75% sand, 14% clay, and 11% silt) (Kormanek *et al*., 2015b) and European beech growing on soil sampled from fresh mixed coniferous forest habitat (without organic fraction) (Kormanek *et al*., 2013b), the highest seedling height values were obtained for the lowest and medium densities with a range of 0.81-1.32 $g \cdot cm^{-3}$ for beech and 1.0-1.7 $g \cdot cm^{-3}$ for oak. Hatchell *et al*. (1970) showed that loblolly pine *Pinus taeda* L. seedlings grown under laboratory conditions grew less on highly compacted soil than on uncompacted soil. According to Maupin and Struve (1997), the growth of red oak *Quercus rubra* L. seedlings in containers was reduced at substrate densities above 1.75 $g \cdot cm^{-3}$, while Conlin and van den Driessche (1996) showed that bulk density higher than 1.7 $g \cdot cm^{-3}$ reduced the growth and dry weight of lodgepole pine *P. contorta* seedlings. For Douglas fir *Pseudotsuga menziesii* (Mirb.) Franco, growth inhibition was observed with an increase in bulk density above 0.72 $g \cdot cm^{-3}$ (Zhao *et al*., 2010). A negative correlation between increasing soil density and total seedling length was also reported by Cubera *et al*. (2009) for holly oak *Quercus ilex* L. seedlings.

The dry weight of the assimilation apparatus and the dry weight of shoots reached the highest values at medium density of the substrate, *i.e*., for variants V5 and V6. Similarly, dry weight of roots showed the highest value in the middle variants, for parts *a* and *b* in variant V5, and part *c* in variant V6. In a study on Scots pine, needle, shoot, and root weight increased with soil compaction (Kormanek *et al*., 2013a), while in European silver fir *Abies alba* Mill., the dry weight of the root system correlated negatively with soil compaction (r=–0.29), while the shoot dry weight correlated positively (r=0.26) (Kormanek *et al*., 2015c). Results for European beech (Kormanek *et al*., 2013b) are consistent with those for Scots pine presented in this paper, *i.e*., the highest dry weight of the assimilative apparatus and shoot occurred at the middle soil densities. In sessile oak, soil compaction significantly affected the dry weight of the whole seedling, with the lowest value at the bulk density of 1.23 $g \cdot cm^{-3}$ and the highest at 1.10 $g \cdot cm^{-3}$ (Kormanek *et al*., 2015b). A positive effect of substrate compaction of 0.71-1.01 $g \cdot cm^{-3}$ on the dry weight of Austrian pine *P. nigra* seedlings, compared to uncompacted substrate, was demonstrated by Zahreddine *et al*. (2004).

The dry weight ratio of the aboveground part to the root system exceeded the limiting value only in variant V1. These seedlings could easily adapt to cultivation, because the root zone is sufficiently well developed to provide adequate water for the seedlings. Our results were consistent with those for seedlings of other forest tree species growing under controlled levels of compaction (Sands and Bowen, 1978; Corns, 1988), but were different when compared with the growth of Scots pine regeneration under different levels of forest soil compaction, where seedlings with an abnormal ratio, which far exceeded the permissible level of 3:1 for seedlings growing in the ground, predominated (Banach *et al.*, 2020).

The total root length for each of the root ball fragments (*a-c*) showed low variability with changes in bulk density. The number of skeletal roots increased with substrate density: the number of fine roots showed an initial increase, peaking with variants V5 and V6 and then decreasing, while the length of very fine roots was not affected by the change in density. In the study of Kormanek *et al.* (2015b), soil compaction in the range of 0.81-1.32 g·cm^{-3} inhibited the root growth of sessile oak seedlings and limited their maximum penetration depth into the soil profile. Similar results were obtained by Tworkoski *et al.* (1983), who showed a reduction in the growth of white oak *Quercus alba* Liebm. with a change in soil bulk density from 1.0 to 1.5 g·cm^{-3}. A reduction in root length with an increase in soil bulk density was observed by Sands and Bowden (1978) for radiate pine *Pinus radiata* D. Don seedlings and by Corns (1988) for lodgepole pine and white spruce *Picea glauca* (Moench) Voss. Other studies have shown a reduction in the root system of Austrian pine seedlings grown on ash with the bulk density of 1.4 g·cm^{-3} and on clayey sand with the bulk density of 1.6 g·cm^{-3} (Zisa *et al.*, 1980). Reductions in root growth and root system dry weight in response to high soil density were also reported in studies on seedlings of Brazilian pine *Araucaria angustifolia* (Bertol.) Kuntze (Mosena and Dillenburg, 2004).

The results obtained in the present study can be associated with the effect of compaction on the physical and mechanical parameters of the substrate. As can be seen from the cited studies, the strength of the impact of the soil compaction differs for various species of trees and also depends on the composition of the substrate. Additional confirmation is found in studies conducted at the same time on one-year-old European beech seedlings, on the same peat-perlite substrate, where the best values of SQ and S/R were observed for seedlings that grew in soil with 0.196 g·cm^{-3} wet bulk density (Pająk *et al.*, 2022a). According to Kormanek *et al.* (2021), substrate compaction affects seedling growth by changing the air-water relationship in the substrate. In the variant with a high level of substrate compaction compared to that with a low level of compaction, less variation in substrate parameter values was observed throughout the growth period of Scots pine seedlings. The compactness increased with time, in relation to the growth of the root system. The capillary water holding capacity decreased, while the air holding capacity increased, which subsequently caused an increase in the noncapillary water holding capacity, resulting in faster water drainage from the substrate. Fernandes and Cora (2004) showed that as substrate compaction increases, total porosity and air capacity decrease, while water capacity increases because large pores are converted to small pores, increasing capillary water holding capacity. Similar studies conducted for agriculturally important species showed that excessive soil compaction reduces nutrient uptake and transport, decreases soil oxygen level, resulting in stunted plant growth and poor root growth (Lipiec and Hatano, 2003; Hamza and Anderson, 2005; Lipiec *et al.*, 2012a, b), and negatively affects soil microbial activity (Clark *et al.*, 2003). These findings were confirmed by a study on exactly the same samples as in this work, which showed that high substrate compaction limits uptake of macro-elements (N, P, K, Ca, Mg, S) by Scots pine seedlings (Pająk *et al.*, 2022b).

Conclusions

Two main conclusions can be drawn based on the results of this study.

First, substrate compaction has a significant influence on growth parameters and dry weight for Scots pine seedlings grown in 120 cm^3 cell containers. Seedlings from medium substrate density (wet bulk density 0.258-0.292 g·cm^{-3}) achieved the best morphological parameters (height, diameter at the root collar, dry weight). However, we assumed that synthetic indices such as seedling sturdiness quotient (SQ) and shoot-root index (S/R) better characterize the adaptive potential of the seedlings. For Scots pine, it was established that to secure a high adaptation potential in the environment, S/R should be <2 and SQ should be <70 (properties of the seedlings improve with decreasing S/R and SQ). Apart from the seedlings grown at the lowest density (wet bulk density 0.292 g·cm^{-3}), all seedlings met both criteria. The best value of SQ (60.5) was obtained at peat substrate density of 0.258 g·cm^{-3} (variant V4) with S/R of 1.87. Moreover, this variant had the highest proportion, *i.e.*, 50% of seedlings meeting both criteria simultaneously (SQ <70 and S/R <2).

Taking into account our results for both single traits and synthetic values, the second conclusion is that bulk density in the range of 0.258-0.292 g·cm^{-3} (dry bulk density of 0.103-0.117 g·cm^{-3}) can be considered optimal for the culture of Scots pine seedlings on peat substrate with the addition of perlite (93:7%).

Authors' contributions

Conceptualization – K.P., S.M, M.K.; Data curation – K.P., S.M, M.K.; Formal analysis – K.P.; Methodology – K.P., S.M, M.K.; Project administration – S.M., M.K.; Software – K.P., J.B.; Supervision – S.M, M.K.; Visualization – K.P., J.B.; Writing-original draft – K.P., J.B.; Writing--review and editing – K.P., S.M, M.K., J.B.

Conflicts of interest

The authors declare, that they have no conflict of interest.

Acknowledgments

We would like to thank the staff of the Rudy Raciborskie Forest District and the management and employees of the Nędza Nursery Farm for allowing and assisting us in the performance of this research work, as well as Hubert Bladziak, M.Sc., for providing help in conducting experiments.

Funding source

The research was conducted under the topic 'Optimization of production of seedlings with covered root system in selected container nurseries' (topic no. ER-2717-4/14) and funded by the State Forests National Forest Holding.

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STRESZCZENIE

Wpływ zagęszczenia substratu torfowego na parametry wzrostowe i morfologię systemu korzeniowego sadzonek sosny zwyczajnej *Pinus sylvestris* L.

Zagęszczenie podłoża jest jednym z ważnych czynników oddziałujących na wzrost roślin. Wpływa ono na właściwości powietrzno-wodne substratu, a tym samym na dostępność wody i składników

mineralnych dla roślin. W artykule przedstawiono wyniki badań wpływu różnych poziomów zagęszczenia substratu torfowego w komórkach kontenerów szkółkarskich na pojedyncze parametry wzrostowe sadzonek sosny zwyczajnej oraz wskaźniki syntetyczne, tj. współczynnik pędowo-korzeniowy (S/R) i współczynnik wytrzymałości (SQ). Im niższa jest wartość współczynnika S/R, czyli im niższa proporcja suchej masy części nadziemnej do podziemnej oraz im niższa proporcja wysokości części nadziemnej do grubości w szyjce korzeniowej SQ, tym lepsza adaptacja i wzrost sadzonek w terenie. Założono, że istnieje zagęszczenie optymalne, przy którym wyhodowane sadzonki będą miały pożądane parametry umożlwiające dobry wzrost na uprawie, tj. współczynnik S/R osiągnie wartość poniżej 2, a współczynnik SQ poniżej 70. Gęstość nasypową zawierającą się w przedziale 0,208-0,342 $g \cdot cm^{-3}$ (gęstość objętościowa sucha 0,083-0,137 $g \cdot cm^{-3}$) uzyskano przez indywidualne wypełnianie komórek w kontenerach HIKO V120SS odważoną masą substratu (uzyskano 9 wariantów, oznaczonych od V1 do V9, z których każdy kolejny różnił się od poprzedniego o 2 g) (tab. 1). Każdy z 9 wariantów zagęszczenia podłoża szkółkarskiego przygotowano w 3 powtórzeniach (3 kontenery po 40 cel), w których hodowano sadzonki przez jeden cykl produkcyjny. Po zakończonej hodowli określono udatność oraz zmierzono pojedyncze parametry sadzonek: ich wysokość, grubość w szyjce korzeniowej, suchą masę igieł, pędu i korzeni podzielonych na 3 części (a – górna część bryłki, najbliżej szyjki korzeniowej; b – środkowa; c – dolna) oraz długość korzeni (z podziałem na szkieletowe, drobne i bardzo drobne). Dodatkowo policzono wartość syntetycznych wskaźników S/R i SQ. Całkowita wydajność siewek w doświadczeniu wyniosła 68% (ryc. 1). Wyniki dotyczące wysokości sadzonek, grubości w szyjce korzeniowej oraz współczynnika wytrzymałości różniły się istotnie statystycznie między wariantami (tab. 2). Sadzonki rosnące w podłożu zagęszczonym (V5-V9) osiągnęły wyższe wysokości części nadziemnej, natomiast najwyższe wartości grubości w szyjce korzeniowej uzyskano dla wariantów ze średniego przedziału zagęszczenia substratu, tj. od V4 do V6. Najkorzystniejszą proporcję wysokości części nadziemnej do grubości w szyjce korzeniowej (SQ) stwierdzono dla sadzonek z wariantu V4 (tab. 2). Średnia sucha masa poszczególnych części sadzonek różniła się istotnie statystycznie pomiędzy wariantami doświadczenia (tab. 3). Najwyższe wartości suchej masy poszczególnych części sadzonek uzyskano w średnich wariantach zagęszczenia (tab. 3). Współczynnik S/R osiągnął najlepszy wynik w wariantach V4 i V5 (tab. 3). Przedstawiono procentowy udział sadzonek spełniających założone kryteria S/R<2:1 i SQ<70 (ryc. 2), na podstawie czego stwierdzono, że w wariantach V4 i V2 liczba sadzonek spełniających jednocześnie dwa przyjęte kryteria stanowiła największy udział, tj. 50%. Najmniejszy udział sadzonek spełniających oba kryteria wystąpił w wariantach V7, V8 i V1. Za pomocą regresji nieliniowej zobrazowano zależność średniej suchej masy sadzonek od wariantu zagęszczenia substratu dla każdej części sadzonki (ryc. 3) oraz zależność długości poszczególnych części korzeni od suchej masy (ryc. 4). Nie stwierdzono statystycznie istotnych różnic pomiędzy całkowitą długością korzeni, natomiast różnice statystyczne występowały pomiędzy częściami korzeni (a, b, c) wyróżnionymi w zależności od ich średnicy (tab. 4). Uzyskane wyniki dowiodły, że dobierając zagęszczenie substratu torfowego, można kształtować parametry wzrostowe sadzonek sosny zwyczajnej hodowanych w kontenerach szkółkarskich o pojemności celi 120 cm^3. Ze względu na pożądane wartości parametrów S/R (współczynnik pędowo-korzeniowy) i SQ (współczynnik wytrzymałości) oraz mierzone pojedyncze cechy wzrostowe gęstość nasypowa w zakresie 0,258-0,292 $g \cdot cm^{-3}$ (gęstość objętościowa sucha 0,103-0,117 $g \cdot cm^{-3}$) jest rekomendowana do hodowli sadzonek sosny zwyczajnej w pojemnikach o objętości 120 cm^3.