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ORIGINAL PAPER

The effect of peat substrate compaction on the macronutrient content of Scots pine *Pinus sylvestris* L. container seedlings

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ABSTRACT

Various factors, such as availability of light, water, nutrients and soil properties have impact on plant growth. Macroelement content in the seedlings affects their biometric features (such as height and weight) which in turn affects the likelihood that the seedling would survive and thrive later in the forest. This research focuses on analyzing how changes in bulk density of the substrate affect the selected biometric features and the content of macroelements in different parts of the Scots pine *Pinus sylvestris* L. seedlings (needles, shoot and root). This paper presents the results of research carried out using Scots pine seedlings grown in 120 cm^3 containers. The seedlings grew at 9 different peat substrate bulk densities (ranging from 0.208-0.342 $g \cdot cm^{-3}$). Here, we have determined the macroelements (N, P, K, S, Ca and Mg) content of individual parts of the seedlings (needles, shoot, root system) and substrate furthermore their selected biometric features (height of the above ground plant, dry weight of needles, shoot, root system, length of fine roots). It was found that higher bulk density of the substrate had a limiting effect on the uptake of most macroelements by seedlings and on the examined biometric features. The analysed macroelement content in the assimilation apparatus was compared to the optimal values given in the literature and it was shown that the best concentration of peat substrate for the cultivation of Scots pine seedlings, in terms of this criterion, is in the range of 0.103-0.117 $g \cdot cm^{-3}$ dry bulk density.

KEY WORDS

Pinus sylvestris, bulk density, macronutrients, fine roots, nursery container, seedling morphology

Introduction

The nutrient cycle is closely related to soil conditions, which play a key role in the good nutrition and proper growth of trees (Cambi *et al.*, 2015). The annual nutrient uptake by one-year-old seedlings of forest trees in nurseries depends on the species of plant. Scots pine *Pinus sylvestris* L. is an oligotrophic species, and its demand for nutrients varies depending on the stage of development and the moment in the vegetation cycle (Obmiński, 1970). Artificial fertilization, used

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to produce seedlings in container nurseries, is crucial for their growth and nutritional level (Salifu and Timmer, 2003; Oliet *et al.*, 2009). The optimal percentage of elements, expressed as a percentage of N, by weight in the fertilizer for Scots pine is, P 14, K 45, Ca 6, Mg 6, S 9, Na 0.03, Fe 0.70, Mn 0.40, B 0.20, Cu 0.03, Zn 0.03, Mo 0.07, Cl 0.03 (Wesoły *et al.*, 2009). To determine the fertilization needs, a chemical analysis of the concentration of elements is carried out during the plant's growth, and the most used method for this purpose is to analyse the assimilation apparatus for these elements. For one-year-old pine seedlings, the optimal content of macroelements expressed as a percentage of dry weight in the assimilation apparatus should be in the following ranges: N: 1.50-2.00; P: 0.15-0.25; K: 0.70-1.50; Mg: 0.10-0.15 (Szołtyk, 2003); Ca: 0.20-0.80, and S: 0.10-0.20 (Wesoły *et al.*, 2009).

In addition to the chemical properties of the soil, its physical parameters, particularly compaction, are also important. Low compaction of the substrate may limit plant growth due to limited root-soil contact and reduced nutrient uptake (Arvidsson, 1999). The negative effect of excessive compaction of the substrate is more often observed and is associated with a significant increase in substrate bulk density and decrease in porosity, which in turn reduces water permeability and flow, and consequently also reduces air capacity (Blouin *et al.*, 2008; Bejarano *et al.*, 2010; Boja and Boja, 2011; Lipiec *et al.*, 2012; Kormanek *et al.*, 2015a, b, c). Usually, the compaction of the substrate causes a reduction in space for the growth of roots which are responsible for the uptake of water and minerals, leading to inhibition of growth or even plant dieback (Kozlowski, 1999; Sinnett *et al.*, 2008; Shrestha and Lal, 2011). Plant metabolism depends on the availability of oxygen and water, which determine the active transport of ions and the allocation of elements to individual parts of the seedling. Limited nutrient uptake from compacted soil results in the reduced concentration of these elements in tree shoots (Kozłowski and Pallardy, 1997), and growing in an excessively compacted soil may have long-term negative consequences (Banach *et al.*, 2020). Excessive compaction also reduces water displacement in the deeper areas of the substrate, increasing the risk of stress in the case of drought, as well as the risk of excess water in the substrate leading to insufficient space for gas exchange (Cox and McFarlane, 1995; Startsev and McNabb, 2009). Additionally, excessive compaction may reduce C mineralization and cause denitrification. Strong soil compaction usually reduces the root absorption of primary nutrients (N, P, K, Ca, Mg) (Castilo *et al.*, 1982; Kozlowski, 1999). The uptake of chemical compounds by the plant is also dependent on the activity of soil microorganisms (Abigail *et al.*, 2005; Libudzisz *et al.*, 2010). Increased compaction encourages hypoxic soil conditions, which results in reduced activity of aerobic microorganisms and increased denitrification (Szember, 2001; Brzezińska, 2009).

In container nurseries, both fertilization and irrigation, as well as soil compaction, are elements of a controlled process and can be matched to the needs of a given species. The production of high-quality seedlings, resistant to abiotic and biotic factors, requires the use of mineral fertilization. The peat substrate used in the container nursery does not contain the required amounts of macro- and microelements, therefore making the use of fertilizers necessary. The most common method of fertilization in container nurseries is with liquid fertilizers, delivered with irrigation. With irrigation, nutrients are quickly washed out from the substrate. Therefore, solid fertilizers are rarely used, and only as an auxiliary starter fertilizer. Usually, liquid fertilizers used during the irrigation of seedlings, have a low concentration, and have a foliar or foliar-soil effect (Szabla and Pabian, 2003).

Tree species are characterized by diverse ecological requirements, including nutritional and edaphic requirements (Puchalski and Prusinkiewicz, 1990; Jaworski, 2011), which should be considered when selecting the conditions for their cultivation in the nursery. Good growth and high vigour of trees can be achieved with a sufficient quantity and proportion of nutrients adapted to the species' requirements. Proper mineral fertilization enables better nourishment of seedlings, and the accumulated reserves of nutrients enable them to grow better, adapt to environmental conditions, and be resistant to stress in difficult periods after planting (Baule and Fricker, 1973). Thus far, the relationship between the level of peat substrate compaction in the nursery cassette cell and the content of elements in individual parts of seedlings has not been investigated.

The aim of this study was to analyse the effect of changes of bulk density of peat substrate on the content of macronutrients (N, P, K, Ca, Mg, S) in *Pinus sylvestris* seedlings fertilized by foliar fertilization in container cultures. The following hypotheses were put forward:

1. An increase in the bulk density of the substrate will affect the uptake of macroelements by seedlings, when the amount of these elements supplied with fertilization and irrigation is consistent;
2. For some bulk density of the substrate in the cells of the cassettes the content of macroelements in the needles of pine seedlings will be at the optimal level *i.e.*, content of each element will fall within range as defined by Szołtyk (2003) and Wesoły *et al.* (2009).

Material and methods

In this experiment, 9 different variants of substrate compaction were prepared, using the gravimetric method, in polypropylene containers (HIKO V120SS) with dimensions 352 × 216 × 110 mm, containing 40 square cells of volume 120 cm^3, tapering downwards with guides for the root system (BCC HIKO). The minimum substrate bulk density (variant V1) was obtained by loosely pouring the substrate, with a moisture content of approx. 60%, into a single cell, which was then poured out and weighed. The procedure was repeated three times and averaged, giving a substrate mass of 25 g for V1. Similarly, the mass of the maximum variant (V9) was determined by compacting the substrate in the cell in layers with a wooden punch, until filled (41 g) without deforming the cell. For variants V2 to V8, the mass of the substrate was calculated by evenly dividing the mass range from V1 to V9 (Table 1). Then, for each variant, three containers were filled with the calculated mass of the substrate and weighed on an analytical scale, with an accuracy of ±0.2 g.

On the BCC nursery line located in Rudy Raciborskie Forest District, one pine seed was sown in each cell on 10 March 2015. A total of 1080 seeds were sown; 120 (40 cells × 3 replicates) for each of the 9 variants of substrate compaction. For the period of seed germination, the containers were placed in a vegetation hall for 2 weeks and then transported to an external production field. The containers (27 pcs) were placed randomly on the rack, among other seedlings of this species in the central part of the production field. The seedlings were grown for a period of

Table 1.
The mass of the wet substrate and the corresponding actual and dry bulk density for each variant of the experiment

Variant	V1	V2	V3	V4	V5	V6	V7	V8	V9
Wet substrate weight (60% H_2O) [g]	25	27	29	31	33	35	37	39	41
Actual bulk density [g·cm^{-1}]	0.208	0.225	0.242	0.258	0.275	0.292	0.308	0.325	0.342
Dry bulk density [g·cm^{-1}]	0.083	0.090	0.097	0.103	0.110	0.117	0.123	0.130	0.137

5 months, in accordance with the production procedure carried out in the nursery, periodically changing the position of the cassettes on the pallet. During the seedling cultivation period, 78 mm of natural precipitation was recorded, and to replenish the water deficit, irrigation was carried out using automatic HAB-T1 BCC ramps. In total, during the production season, in open space, irrigation was carried out for 103 days, in the amount of 904 mm per m^2. The amount of each element (in $mg \cdot m^{-2}$) delivered with rainwater in the analysed period was: N – 120; P – 6.02; K – 6.73; Ca – 361.3; Mg – 3.87, with water used for irrigation: N – 1.5; P – 0.0074; K – 1.233; Ca – 12.66; Mg – 2.419. Fertilization was carried out by fertigation, with Floralesad fertilizer for most of the production period and with Florasin K once, at the end of seedling growth. Composition of the Floralesad fertilizer ($g \cdot dm^{-3}$): N – 103.1; $N\text{-}NO_2$ – 0.0214; $N\text{-}NO_3$ – 16.369; $N\text{-}NH_4$ – 2.602; $N\text{-}NH_2$ – 84.107; P – 17.231; K – 47.423; Mg – 3.567; Ca – 0.737; Na – 0.28;. Composition of fertilizer Florasin K 500: K – 420.75; Na – 2.21; Ca – 0.003. Throughout the entire vegetation cycle, the conductivity of the aqueous solution of foliar fertilizer was maintained at 0.6 $mS \cdot cm^{-1}$.

After the end of the production cycle, the number of alive seedlings was determined. The height of the above-ground part of the seedling was measured (±1 mm). The material obtained from all seedlings was dried (assimilation apparatus at 70°C, roots and stems at 105°C for 48 h). After drying, each part of the seedling (needles, shoots, and roots) was weighed on an analytical balance with an accuracy of 0.1 mg. The length of the root system was measured with WinRhizo (Regent Instruments Inc.) after the roots had been scanned with an Epson V800 Photo scanner, using a resolution of 800 dpi. The substrate samples and plant material from each compaction variant were analysed for the content of N and S elements using the CNS TruMac analyser by LECO, and P, K, Ca, Mg, using the ICP-OES iCAP 6500DUO emission spectrometer by Thermo, after mineralization in 65% HNO_3 and 38% HCl (in a ratio 7:3). The analyses were performed at the Laboratory of Forest Environment Geochemistry and Land Intended for Reclamation of the Department of Ecology and Silviculture, Faculty of Forestry, University of Agriculture in Kraków.

The data were statistically analysed with one-way ANOVA and Tukey's *post-hoc* multiple comparison test in Statistica 13.3 (TIBCO Software Inc.) with a significance threshold of $p<0.01$. The aim of the test was to check, for the individual parts of seedlings, which variants of substrate compaction produced a significant difference in the selected biometric features and the content of elements. Non-linear regression was used to visualize the variability of the average height and dry weight of seedlings, the length of the roots with a diameter of <0.05 mm (fine roots) and the content of elements in individual parts of the seedlings, dependent on the density of the nursery substrate.

Results

From 1080 pine seeds sown, 737 seedlings were grown, making the total yield in the experiment 68%. The highest percentage survival rates were achieved by seedlings from the extreme variants of density, V1 (80%) and V9 (over 70%). The dry weight of seedlings initially increased with greater compaction of the substrate, reaching the maximum values at V5 and V6, after which the dry weight decreased for compaction variants V7 to V9 (Fig. 1). The average height of seedlings (Fig. 2) showed similar results, with maximum values for V5 and V6, and minimum at V1 and V9. The coefficient of determination (R^2) was 50% and 40%, respectively.

The length of the finest roots (responsible for nutrient uptake) with a diameter <0.05 mm increased with the compaction of the substrate, from V1 to a maximum at V6 and V7, and then

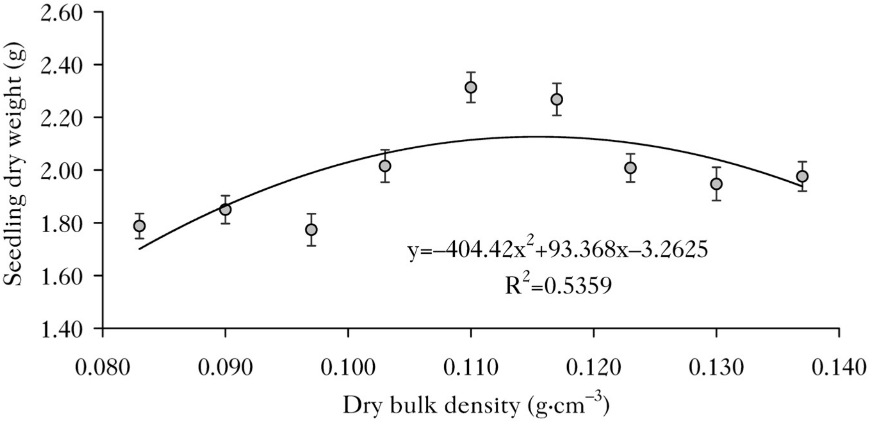

Fig. 1.
Mean value of Scots pine seedling dry weight (±SE) dependent on the substrate compaction variant

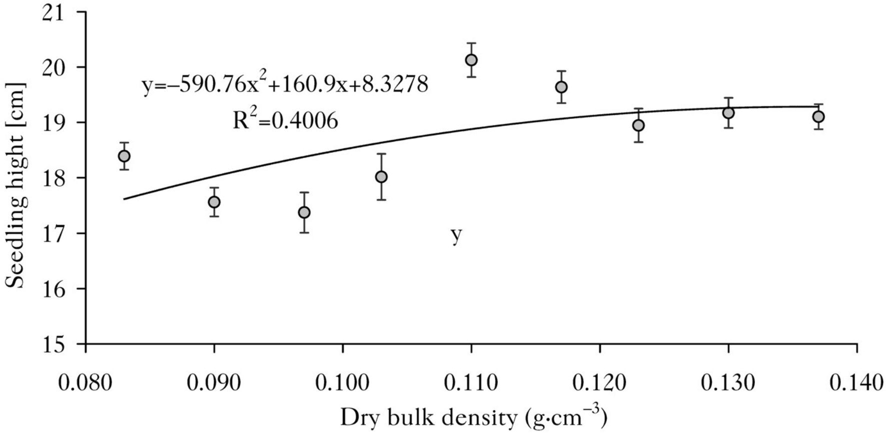

Fig. 2.
The mean value of the height of Scots pine seedlings (±SE) dependent on the variant of substrate compaction

decreased drastically to V9 (Fig. 3). According to non-linear regression analysis, 80% of the variability in the length of the smallest roots was explained by the variability in substrate compaction.

The macronutrient of highest concentration, among the considered elements, both in the starting substrate (before cultivation) and after the seedling growth period was determined to be Ca. The content of N, P, K and S after the cultivation period was higher than in the starting substrate. The calcium content for the most compacted substrates (V8 and V9) was higher than the initial content, and in the other variants was lower. Only the content of Mg in the substrate was lower after cultivation for all variants compared to the starting substrate (Table 2). The substrates with middle density values (V3-V6) were characterized by the lowest content of N after the cultivation period. The content of P and K was lowest for the densest variants (V8 and V9), which differed significantly from the other variants. The content of Ca was highest in the densest variants (V6-V9), differing significantly from the other variants, with the difference between the lowest (V2) and the highest content being 59%. The content of Mg significantly increased for variants V6 to V9, reaching the highest content in the most compacted variant which was 157%

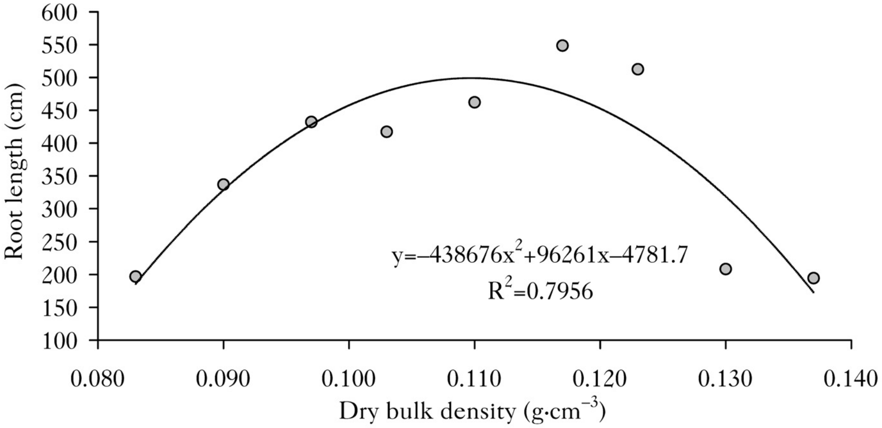

Fig. 3.
Average total root length for fine roots of the Scots pine seedling less than 0.05 mm in diameter

Table 2.
The concentration of macronutrients in the starting substrate and in the substrate after the cultivation period for each substrate compaction variant (± SD)

Variant	N [%]	P [%]	K [%]	Ca [%]	Mg [%]	S [%]
Starting substrate	0,609	0,014	0,069	1,131	0,528	0,058
V1	0.926±0.008b	0.044±0.004ac	0.110±0.003a	0.835±0.115a	0.214±0.065a	0.140±0.007ab
V2	0.904±0.028ab	0.050±0.007a	0.112±0.045a	0.705±0.087a	0.175±0.023a	0.156±0.041ab
V3	0.850±0.034a	0.043±0.008abc	0.092±0.007ab	0.826±0.018a	0.223±0.030a	0.157±0.003ab
V4	0.844±0.023a	0.050±0.007a	0.127±0.019a	0.747±0.078a	0.207±0.034a	0.169±0.008b
V5	0.866±0.015ab	0.048±0.004a	0.116±0.013a	0.877±0.169a	0.224±0.043a	0.157±0.012ab
V6	0.855±0.026a	0.052±0.004a	0.121±0.024a	1.141±0.087b	0.338±0.065b	0.153±0.008ab
V7	0.862±0.043ab	0.042±0.010abc	0.092±0.038ab	1.100±0.092b	0.381±0.057bc	0.142±0.022ab
V8	0.898±0.013ab	0.032±0.001b	0.059±0.003b	1.191±0.041b	0.420±0.017bc	0.122±0.002a
V9	0.911±0.009ab	0.034±0.001bc	0.056±0.005b	1.151±0.049b	0.449±0.063c	0.126±0.003ab
Mean	0.880±0.035	0.044±0.009	0.098±0.032	0.953±0.199	0.292±0.108	0.147±0.020

higher than in the low-density variant V2. We observed increase of the content of S with increasing compaction up to variant V4, followed by decrease for variants V5-V9. (Table 2).

Despite the differences in the content of individual macronutrients in the Scots pine assimilation apparatus (Table 3), the proportions of these elements (K, Ca, Mg, P, S) in the needles compared to N were similar in all variants, and amounted to a ratio of 1-0.5-0.3-0.1-0.1-0.1 (N-K-Ca-Mg-P-S). P, Mg and S, in relation to nitrogen, differed in individual variants by 1-2% (Table 4).

The 90% increase in the Mg and Ca content of the needles was explained by the increase in substrate compaction (Fig. 4). The contents of the remaining elements in the needles showed neither increase nor decrease with the change of the substrate density. The content of all tested elements in the shoots decreased with the increase of substrate compaction (Table 5). For N, P, K and Mg, a weak increase in content was observed at middle densities (N in V5, and P, K and Mg in V6). On average, 80% of the variability in the content of elements in the shoots was explained by the variability of the substrate compaction. In the roots, a decrease in the content of most elements (P, K, Mg, S) was also seen with the increase in substrate compaction (Table 6).

Table 3.

The concentration of macronutrients in the Scots pine seedling needles for each substrate density variant (± SD)

Variant	N [%]	P [%]	K [%]	Ca [%]	Mg [%]	S [%]
V1	1.580±0.111a	0.168±0.010a	0.806±0.039d	0.463±0.011a	0.203±0.004ab	0.137±0.010ab
V2	1.480±0.009a	0.162±0.004ab	0.613±0.031a	0.484±0.027ab	0.206±0.002abc	0.127±0.004ab
V3	1.380±0.075a	0.161±0.007ab	0.672±0.050abc	0.452±0.013a	0.196±0.004a	0.129±0.008ab
V4	1.465±0.174a	0.157±0.014ab	0.653±0.063ab	0.442±0.021c	0.197±0.006a	0.131±0.009ab
V5	1.557±0.119a	0.163±0.012ab	0.747±0.022bcd	0.465±0.014a	0.195±0.007a	0.137±0.010ab
V6	1.584±0.079a	0.170±0.007a	0.715±0.069abcd	0.464±0.014a	0.200±0.007ab	0.141±0.006b
V7	1.554±0.099a	0.159±0.016ab	0.664±0.094ab	0.496±0.053ab	0.201±0.006ab	0.135±0.009ab
V8	1.404±0.066a	0.145±0.006b	0.647±0.103ab	0.512±0.064ab	0.212±0.017bc	0.118±0.003a
V9	1.446±0.070a	0.158±0.005ab	0.783±0.023cd	0.539±0.017b	0.220±0.002c	0.125±0.006ab
Mean	1.495±0.109	0.160±0.011	0.700±0.084	0.480±0.041	0.203±0.010	0.131±0.009

Table 4.

The concentration of macronutrients in relation to N in needles for different variants of substrate density

Variant	N [%]	P [%]	K [%]	Ca [%]	Mg [%]	S [%]
V1	100	11	51	29	13	9
V2	100	11	41	33	14	9
V3	100	12	49	33	14	9
V4	100	11	45	30	13	9
V5	100	10	48	30	13	9
V6	100	11	45	29	13	9
V7	100	10	43	32	13	9
V8	100	10	46	36	15	8
V9	100	11	54	37	15	9

N showed a similar relationship, however, there were no statistically significant differences between the variants. The coefficient of determination for these elements was very high (R^2=0.9 for N and P, and 0.8 for K, S and Mg). Calcium content showed no significant changes in the roots (Fig. 4).

Discussion

The growth of small roots responsible for the uptake of minerals in high substrate densities was limited. In the most compacted variants, a decrease in the dry weight and height of seedlings was also observed (V7-V9). Concentrations of N, P, K and S in the needles of most variants remained at the lower limit of the optimal ranges given by Szołtyk (2003) and Wesoły *et al.* (2009), and were below in some cases (in V3, V8 and V9 for N, and V2 and V8 for K). The cultivation of pine seedlings was completed in October when chemical analyses were carried out on seedlings preparing for dormancy, which may have resulted in them maintaining the concentration of elements in the lower limits of the optimum range in the needles, with similar proportions of elements in relation to N, for all variants despite continuous fertilization. A decrease in the content of N, P and K in needles at the end of the growing season was also observed in mature pine stands, as reported by Jonczak (2011). In all variants, the magnesium content exceeded the upper limit of the optimum range. Calcium concentrations were within the optimum range in all variants of substrate compaction. As substrate compaction increased, the N, P, K and S content in shoots and roots decreased. High values of Ca and Mg (resulting from the

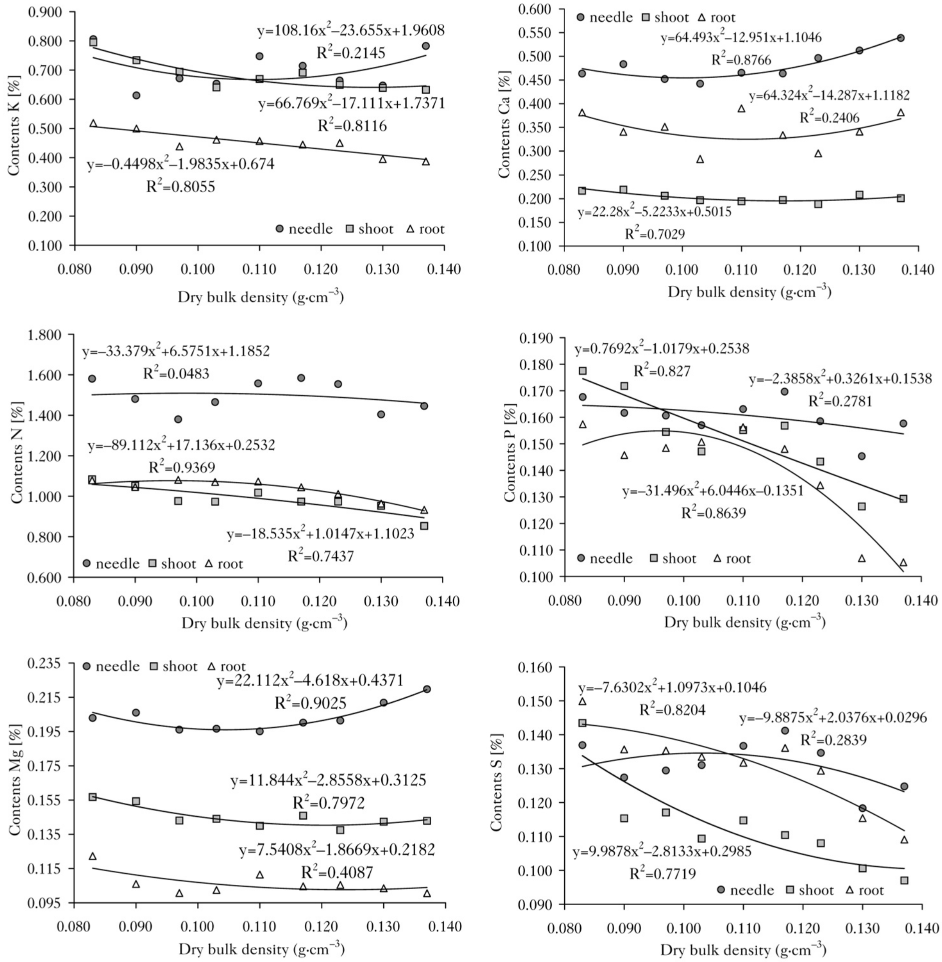

Fig. 4.

Average content of elements in specific parts of Scots pine seedlings dependent on the compaction variant of the nursery substrate

Table 5.

The concentration of macronutrients in the stems of the Scots pine seedling for each substrate density variant (± SD)

Variant	N [%]	P [%]	K [%]	Ca [%]	Mg [%]	S [%]
V1	1.084±0.030b	0.178±0.007e	0.795±0.025c	0.217±0.005bc	0.157±0.004c	0.143±0.020b
V2	1.052±0.030b	0.172±0.014bc	0.734±0.043bc	0.219±0.008c	0.154±0.010bc	0.115±0.005a
V3	0.976±0.066ab	0.154±0.006ab	0.694±0.032ab	0.206±0.015abc	0.143±0.008abc	0.117±0.007ab
V4	0.973±0.091ab	0.147±0.008ad	0.641±0.067a	0.197±0.009ab	0.144±0.008abc	0.109±0.006a
V5	1.018±0.030b	0.155±0.008ab	0.670±0.033ab	0.195±0.010a	0.140±0.009a	0.115±0.008a
V6	0.973±0.045ab	0.157±0.007ab	0.691±0.047ab	0.197±0.011ab	0.146±0.009abc	0.110±0.004a
V7	0.973±0.053ab	0.143±0.018acd	0.649±0.042a	0.189±0.016a	0.137±0.005a	0.108±0.003a
V8	0.953±0.069ab	0.126±0.009c	0.639±0.033a	0.209±0.013abc	0.142±0.007ab	0.101±0.007a
V9	0.853±0.033b	0.129±0.009cd	0.632±0.034a	0.201±0.010abc	0.143±0.004abc	0.097±0.002a
Mean	0.984±0.076	0.151±0.019	0.683±0.063	0.203±0.014	0.145±0.009	0.113±0.015

Table 6.
The concentration of macronutrients in the roots of the Scots pine seedling for each substrate density variant (± SD)

Variant	N [%]	P [%]	K [%]	Ca [%]	Mg [%]	S [%]
V1	1.078±0.106a	0.157±0.008b	0.519±0.049d	0.381±0.024ab	0.122±0.009b	0.150±0.019b
V2	1.045±0.115a	0.146±0.008ab	0.500±0.026cd	0.341±0.012abc	0.106±0.002a	0.136±0.023ab
V3	1.081±0.115a	0.148±0.017ab	0.439±0.038abc	0.351±0.038ab	0.101±0.005a	0.135±0.020ab
V4	1.070±0.135a	0.151±0.014ab	0.461±0.032bcd	0.283±0.044d	0.102±0.009a	0.133±0.020ab
V5	1.073±0.164a	0.156±0.010ab	0.457±0.023abcd	0.390±0.033b	0.111±0.008ab	0.132±0.022ab
V6	1.044±0.120a	0.148±0.009ab	0.445±0.064abc	0.464±0.014acd	0.105±0.011a	0.136±0.023ab
V7	1.011±0.146a	0.134±0.022a	0.450±0.039abcd	0.295±0.022cd	0.105±0.004a	0.129±0.022ab
V8	0.963±0.090a	0.107±0.004c	0.395±0.015ab	0.341±0.011abc	0.104±0.004a	0.115±0.013a
V9	0.963±0.086a	0.105±0.004c	0.387±0.022a	0.382±0.033ab	0.101±0.002a	0.115±0.016a
Mean	1.037±0.131	0.139±0.022	0.450±0.053	0.344±0.044	0.106±0.009	0.131±0.023

presence of dolomite in the substrate used), which increased with compaction, could be the cause of the observed drops in the content of P, K and S in seedlings, due to elemental antagonisms (Mg and K, Ca and P, and Ca and S) (Baule and Fricker, 1973).

The effect of substrate density on the content of elements and biometric features of various plants has been observed in several studies. Often, the uptake of elements by the plants is inhibited by high density substrates. As with our results, Arvidsson (1999) observed a decrease in plant biomass and uptake of elements when examining barley growing in both the field and in the laboratory. The cited experiment proved that both low and high soil bulk densities decreased biomass production and nutrient uptake (N, P, K) compared to medium bulk densities under field conditions. A decrease in the uptake of K and P, due to a reduction in the oxygen level of soil cavities in compacted substrates, was also noted in the species of conifers and deciduous trees, *Pinus elliottii* Engelm. and *Prunus* L. (Kozlowski, 1999). Apple trees (*Malus × domestica* Borkh.) growing in containers with a high clay-loam soil bulk density, above 1.5 $g \cdot cm^{-3}$, had lower concentrations of N, Ca, Mg, Mn, Na and Zn and increased P, K, B and Fe in leaves (Ferree *et al.*, 2004). As demonstrated by Jordan *et al.* (2003) in a greenhouse study, strong soil compaction reduced seedling height and dry weight in red oak *Quercus rubra* L. and scarlet oak *Quercus coccinea* Muenchh and reduced nitrogen fertilization. These seedlings were grown on loamy-skeletal, mixed, mesic Typic Paleudults (Ultisol), compacted (1.8 $g \cdot cm^{-3}$) and uncompacted (1.3 $g \cdot cm^{-3}$), in PVC pots for 6 months. The likely cause of nitrogen loss was due to denitrification and a small amount of leaching.

As with this paper, other studies have found that the concentration of calcium was highest in plants cultivated at the lowest densities, since calcium uptake by plants is considered to occur by passive transport through mass flow (Mengel and Kirkby, 1987). Contrastingly, in an experiment carried out in pots filled with clay soil with woolly vetch *Vicia villosa* Roth., common vetch *Vicia sativa* L., Italian ryegrass *Lolium italicum* Lam. and barley *Hordeum vulgare* L., using four substrate compaction variants, plants were found to have generally lower N, Ca and Mg contents and higher P content as substrate bulk density increased (Parlak and Parlak, 2011). In field trials with Stagnic Luvisol, the nitrogen uptake of spring wheat *Triticum aestivum* L. decreased by almost 30%, and barley *Hordeum vulgare* L. by 40% in the case of high soil compaction. As a result of six-fold substrate compaction, the content of N, P, K and Ca in barley (*H. vulgare*) and N, Ca, and Mg in spring wheat (*T. aestivum*) decreased compared to the non-compacted substrate (Kuht and Reintam, 2004).

Low aeration reduces the mineralization of organic matter, which can reduce the availability of nitrogen and other nutrients. The physical and chemical properties of the substrate also influence the uptake of mineral N and other nutrients. When the elongation of the roots in the substrate is inhibited by poor soil properties, the mineral N that accumulates in the substrate cannot be absorbed and can be washed away (Saito and Ishii, 1987). Nutrients are transported to the plant roots in the soil by two mechanisms – mass flow and diffusion. Those carried by diffusion are more prone to bulk density than ions transported by mass flow (Barber, 1962). According to Arvidsson (1999), the reason for the reduced uptake of elements at low densities is reduced root-soil contact, a low nutrient diffusion coefficient and reduced water transport to the roots, while in high densities, it is caused by oxygen deficiency and inhibited root growth. The author states that the lower concentration of nitrogen may have been caused in part by denitrification, while the lower concentrations of phosphorus and potassium were caused by disturbances in root development and function.

In addition to the reasons given by Arvidsson (1999) for the reduced uptake of elements in high density substrates, it is also possible to add impeded penetration of the substrate by the roots. Strong soil compaction makes it impossible to grow roots, limiting access to water and nutrients, and reducing the amount of oxygen in soil solutions, which affects the activity of microorganisms (Clark *et al.*, 2003). The activity of microorganisms is especially important for the availability of N when using fertigation.

Conclusion

The increase in the bulk density of the substrate influenced the content of elements in Scots pine seedlings by reducing N, P, K and S, especially in the shoots and the roots. In the high volumetric densities of peat substrate, ranging from 0.308 to 0.342 $g{\cdot}cm^{-3}$ (0.123-1.137 $g{\cdot}cm^{-3}$ dry bulk density), a decrease was seen in the height, dry weight and length of fine roots (<0.05 mm in diameter) of seedlings. The limited uptake of elements in high substrate densities could explain the reduction in the measured biometric characteristics of these seedlings. Due to the optimal content of the analysed elements in the pine assimilation apparatus, substrate volume density in the range of 0.258 to 0.292 $g{\cdot}cm^{-3}$ (0.103-1.110 $g{\cdot}cm^{-3}$ dry bulk density) is recommended for producing Scots pine in containers with a cell volume of 120 cm^3.

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. M.J.; Supervision – S.M, M.K.; Visualization – K.P., M.J.; Writing – original draft K.P., M.J.; Writing – review and editing – K.P., S.M, M.K., M.J.

Conflicts of interest

The authors declare that they have no conflict of interest.

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STRESZCZENIE

Wpływ zagęszczenia podłoża torfowego na zawartość makroelementów w różnych częściach sadzonek sosny zwyczajnej *Pinus sylvestris* L. (korzeń, pęd, igły) produkowanych w kontenerach

Obieg składników odżywczych jest ściśle powiązany z glebą. Roczny pobór składników pokarmowych przez jednoroczne sadzonki drzew leśnych w szkółkach zależy od gatunku. Sosna zwyczajna należy do gatunków oligotroficznych. Nawożenie stosowane w trakcie produkcji sadzonek ma kluczowe znaczenie dla ich wzrostu i poziomu odżywienia. W celu określenia potrzeb nawożeniowych przeprowadza się w trakcie wzrostu rośliny analizę chemiczną stężenia pierwiastków w aparacie asymilacyjnym. Jednym z ważnych parametrów fizycznych gleby jest jej zagęszczenie. Niskie zagęszczenie może ograniczać wzrost roślin ze względu na niedostateczną zawartość składników pokarmowych w podłożu. Częściej jednak obserwowany jest negatywny wpływ nadmiernego zagęszczenia podłoża. Zazwyczaj kompakcja podłoża powoduje zmniejszenie przestrzeni i brak ciągłości przestworów dla wzrostu korzeni, odpowiedzialnych za pobór wody i składników mineralnych, prowadząc do zahamowania wzrostu czy nawet zamierania roślin. Ograniczone pobieranie składników odżywczych z ubitej gleby powoduje ich zmniejszoną koncentrację w pędach drzew. Dodatkowo nadmierne zagęszczenie może zmniejszyć mineralizację węgla oraz powodować procesy denitryfikacyjne.

W pracy przedstawiono wyniki badań przeprowadzonych z wykorzystaniem sadzonek sosny zwyczajnej *Pinus silvestris* L. hodowanych w pojemnikach o objętości 120 cm^3. Sadzonki wzrastały w 9 różnych poziomach gęstości nasypowej substratu torfowego, w przedziale 0,208--0,342 $g \cdot cm^{-3}$ (tab. 1). W pracy określono zawartość makropierwiastków (N, P, K, S, Ca i Mg) w poszczególnych częściach sadzonek (igły, pęd, system korzeniowy) i substracie oraz ich wybrane cechy biometryczne (wysokość części nadziemnej, suchą masę, długość korzeni drobnych). Sucha masa sadzonek wzrastała wraz ze wzrostem zagęszczenia substratu, a następnie spadała (ryc. 1), podobny przebieg stwierdzono dla średniej wysokości sadzonek (ryc. 2) oraz ilości najdrobniejszych korzeni (odpowiedzialnych za pobór składników odżywczych) o średnicy <0,05 mm (ryc. 3). Najwyższą zawartość procentową spośród badanych makroelementów w substracie wyjściowym (przed hodowlą) oraz po okresie wzrostu sadzonek oznaczono dla Ca. Zawartość N, P, K i S po okresie hodowli była większa niż w substracie wyjściowym (tab. 2). Mimo różnic w zawartości poszczególnych makroelementów w aparacie asymilacyjnym sosny (tab. 3 i 4) proporcje tych pierwiastków w igłach w stosunku do azotu dla poszczególnych wariantów były zbliżone. Oprócz Mg i Ca, których zawartość zwiększała się wraz ze wzrostem zagęszczenia substratu, zawartość pozostałych pierwiastków w igłach nie przejawiała ani wzrostowych, ani spadkowych tendencji wraz ze zmianą zagęszczenia substratu (ryc. 4). Zawartość wszystkich badanych pierwiastków w łodydze zmniejszała się wraz ze wzrostem zagęszczenia substratu (tab. 5). Średnio 80% zmienności zawartości pierwiastków wyjaśniono zmiennością zagęszczenia. W korzeniach był również widoczny spadek zawartości większości pierwiastków: P, K, Mg, S, N wraz ze wzrostem zagęszczenia substratu (tab. 6). Zawartość wapnia w systemach korzeniowych nie wykazywała ani spadkowych, ani wzrostowych tendencji zawartości wraz ze wzrostem zagęszczenia substratu (ryc. 4).

Ze względu na optymalną zawartość analizowanych pierwiastków w aparacie asymilacyjnym sosny oraz wybrane cechy biometryczne aktualna gęstość objętościowa w zakresie od 0,258 $g \cdot cm^{-3}$ do 0,292 $g \cdot cm^{-3}$ (0,103-1,110 $g \cdot cm^{-3}$ gęstość objętościowa sucha) jest rekomendowanym przedziałem zagęszczenia do produkcji sosny pospolitej w kontenerach o objętości celi 120 cm^3.