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Effect of Changing Substrate Density and Water Application Method on Substrate Physical Properties and Container-Grown Seedling Growth

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Abstract: The quality of container-grown seedlings is influenced by the air and water properties of the substrate. These properties are closely tied to the amount and frequency of water supplied through sprinkler systems in nurseries, as well as the density of the substrate in the container cells. Throughout the entire growing season, this study examined how various parameters of Scots pine, Norway spruce, European beech, and pedunculate oak seedlings cultivated in HIKO V120SS and V265 containers were affected by two factors. Firstly, the study analyzed the impact of increased substrate density when filling the containers. Secondly, it explored the precise dosing of water applied by the sprinkler system, which was determined based on substrate sensors and meteorological conditions surrounding the seedlings. The results revealed that increased substrate compaction led to a long-term reduction in air capacity and an increase in water capacity within pine, spruce, and beech containers. However, oak seedlings were not affected by the increased substrate density. Additionally, the higher density of the compacted substrate positively influenced the growth parameters of pine seedlings but did not affect the other species. As a result, the current substrate compaction level used in the nursery where the measurements were taken appears to be optimal for spruce, beech, and oak seedlings. Furthermore, precise control over the amount of water applied during irrigation allowed for a reduction in water consumption by about 8%. This control also resulted in improved seedling sturdiness quotient and a more developed root system in the case of pine seedlings. However, no significant differences were observed for the other species.

Keywords: HIKO container; Pinus sylvestris; Picea abies; Fagus sylvatica; Quercus robur

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1. Introduction

The growth of seedlings in nursery containers is mainly influenced by the air and water properties of the substrate, as well as its chemical composition [1,2]. Various authors have provided recommended parameters for the commonly used peat–perlite substrate. According to Cabrera and Johnson [3], these parameters include a total porosity of 93% by vol., a water capacity of 73% by vol., an air capacity of 20% by vol., available water of 48% by vol., and a wet weight of 864 kg·m^{-3}. Meanwhile, De Boodt and Verdonck [4] and Fernandes and Cora [5] suggest a total porosity of85% by vol., air capacity ranging from 20 to 30% by vol., and plant-available water ranging from 24 to 40% by vol. Szabla and Pabian [6], on the other hand, propose porosity >70% by vol., air capacity between 20 and 25% by vol., and water content ranging from 800 to 1000% by weight. The wide range of cited values, coupled with inconsistent measurement methodologies, poses challenges in effectively monitoring the substrate during seedling culture [7–9].

In Poland, seedling production in containers uses high sphagnum peat, which offers favorable characteristics such as high porosity, water-holding capacity, sterility, and low mineral content. These properties facilitate easier regulation of fertilizer application rates [6]. However, modifying inadequate physical parameters of the substrate proves challenging, particularly with air capacity levels that are either too low or too high, which can be attributed to substrate compaction [10,11].

The degree of substrate compaction and settlement in container cells increases with thicker substrate components, varying volumetric densities of components, and more intense watering. Over time, fine substrate particles move from the upper level to the lower level of the container cell while organic matter undergoes decomposition. Root growth contributes to substrate compaction, but it also enhances permeability, enabling gas diffusion [7,10,12–15].

Another significant aspect is the volume and frequency of irrigation, which depend on the air and water capacity of the substrate and air temperatures [2,16,17]. A seedling within a nursery container can deplete all available water within 2 days, and after intense watering, the substrate becomes primarily saturated in the lower part, resulting in air gaps until the plant takes up water or it drains by gravity. Conversely, if the substrate is watered in small doses, the water may remain in the upper part while the lower part remains dry [3,18–20]. Moreover, water supplied to the substrate is also intercepted by leaves, leading to a reduced amount reaching the substrate [21]. When the substrate becomes dry, the salt concentration in the soil solution can rise to high levels, while crucial elements like nitrogen and potassium can leach out of the container, resulting in potential deficits if not replenished through fertilization [3].

In Polish container nurseries, irrigation is generally carried out on a fixed schedule, modified on an ongoing basis in the event of rainfall or high air temperature, and based on macroscopic observation of plant conditions and organoleptic observation of the substrate. Such control of sprinkler irrigation is subjective, depending on the knowledge and experience of the person who supervises seedlings growing [22]. Nowadays, information about the moisture content of the substrate in containers is easy to obtain using a measurement system consisting of substrate moisture and temperature sensors, as well as leaf-wetting and sunlight sensors. Knowing the climatic parameters of the environment in which the seedlings grow, it is possible to precisely control the amount of water supplied, taking into account their actual needs [23–26]. In the year preceding the experiment presented here, seasonal changes in the physical and mechanical parameters of peat–perlite substrate (95/5 vol.) in containers with Scots pine, Norway spruce, European beech, and pedunculate oak seedlings were measured. It was observed that certain periods deviated from the reported optimal ranges, with air volume ranging from 10 to 35% and water volume ranging from 50 to 80% [3,11,27,28]. As a result, an experiment was designed to investigate the effects of increasing substrate compaction on water capacity and air capacity. In addition, a system was implemented to precisely control the amount of water supplied through the irrigation system, utilizing information from sensors installed in the containers and the microclimate station [26]. This study aimed to analyze the effect of increasing substrate density in nursery containers and controlling the water supply method in the production field impact the changes in physical and mechanical parameters of the substrate as well as seedling growth throughout the growing season. The study focused on seedlings of Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* (L.) H. Karst), European beech (*Fagus sylvatica* L.), and pedunculate oak (*Quercus robur* L.). The study aimed to test the following hypotheses: a) any differences in substrate density introduced during container filling would diminish over the growing season, and b) there would be no significant variations in morphological parameters among seedlings grown in different substrate densities and variants of irrigation methods.

2. Materials and Methods

The experiment took place at a nursery farm located in Nędza, southwestern Poland (coordinates:50°10′04.8″ N 18°18′57.7″ E). Hiko V120SS containers were utilized for Scots pine and Norway spruce, while Hiko V265 containers were employed for European beech and pedunculate oak. Species-specific production procedures were followed, as outlined in Table 1. The containers were filled with peat–perlite substrate (95/5 vol.), with the high sphagnum peat exhibiting the following 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%. The maximum degree of decomposition was 15%, and the organic matter content exceeded 85%.

Table 1. Container parameters and seedling production procedure.

Species	Tray Type	Substrate Filling/Seeds Sowing	Procedure after Sowing	Fertilizers Doses ($dm^3 \cdot m^{-2}$)
Scots pine (Sp)	Hiko V120SS 10.9 × 35.2 × 21.6 cm (W × D × S), 40 cells, volume 120 cm^3	14 April/ 14 April (automatic seeder)	Vegetation hall (8 weeks) than open production field	Bioekor: 0.0085 × 1 Floralesad: 0.0085 × 1
Norway spruce (Ns)		18 April/ 18 April (automatic seeder)		Bioekor: 0.050 × 5 Floralesad: 0.11 × 14
European beech (Eb)	Hiko V265 15.0 × 35.2 × 21.6 cm (W × D × S), 28 cells, volume 265 cm^3	19 April/22 April (sown manually)	Open nursery bed (2 weeks), vegetation hall (6 weeks), then open nursery bed In July, oak seedlings were sorted by transferring the low ones to a new container	Bioekor: 0.072 × 5 Floralesad: 0.02 × 10
Pedunculate oak (Po)		14 April/15 April (sown manually)		Bioekor: 0.038 × 4 Floralesad: 0.073 × 8

In the vegetation hall, irrigation and fertilization were conducted using a GB-T1 (Greenhouse Boom, Type 1) sprinkler, while in the open fields, a HAB-T1 (Holding Area Boom, Type 1) sprinkler was employed. The following experimental variants were established: V1 as the control group with standard irrigation and substrate compaction in containers and V2 and V3 with controlled water supply to the production field. In V3, increased substrate compaction in the containers was applied. The control of the water supply in V2 and V3 was facilitated by solenoid valves that regulated the water flow to the HAB-T1 sprinkler [29]. The operation of the solenoid valves was managed by the DAV-6544 DAVIS controller, which received information wirelessly from substrate moisture sensors randomly distributed across the production field. Current evaporation data from the active surface was obtained through a DAVIS Vantage PRO V2 weather station recorder, employing the model proposed by Snyder and Pruit [30] of the California Department of Water Resources. Radio relays were connected to 32 humidity sensors and 32 substrate temperature sensors placed within the nursery containers, as well as 16 leaf wetness sensors positioned directly above the plants. Additionally, 32 rain gauges were installed above the plant surface, and 32 collectors were placed beneath the containers. The weather station, located adjacent to the production field, measured parameters such as rainfall totals, wind speed and direction, and solar radiation intensity. The substrate moisture level, along with favorable water balance parameters, was monitored by the system, which would subsequently halt the water supply to the production field. Increased substrate compaction (V3) was achieved using the BCC AB line during the container-filling process. It was ensured that the applied substrate compaction did not result in an air capacity ac below 15% (optimal range: 25%–35%) or a water capacity (wc), exceeding 75% (optimal range: 55%–65%) [27]. The degree of substrate compaction was regulated by adjusting the penetration depth of the rolling pins on the active substrate compaction unit and controlling the speed of the container movement on the vibrating table, which determined the vibration time.

2.1. Preliminary Experiment

Before the seedling experiment, a pilot experiment was conducted to evaluate different parameters. The containers were filled at the standard speed of container travel on the vibrating table (StdSp—400 cassettes/h), as well as at a reduced speed of 30% (LowSp—300 cassettes/h). Additionally, the compaction pins were set at the standard penetration depth (StD) and increased by 15% (15D) and 30% (30D). The pilot measurements were performed on 36 containers, including two container types (V120SS; V265) × 2 speeds (StdSp; LowSp) × 3 compaction pin depths (StD; 15D; 30D) × 3 repetitions. In 10 randomly selected cells of the V120SS container and 7 cells of the V265 container, the following parameters were determined: total porosity (po), bulk density (bd), air volume (ac), and water volume (wc). In the remaining cells, the penetration resistance (pr)of the substrate was measured. The penetration resistance of the substrate (pr) (Pa) was determined using an Eijkelkamp penetrometer type IB, 0606, equipped with a cone having a base diameter of 0.78 cm [31,32]. Subsequently, the container was immersed in water for 12 h. After removing and draining the gravity-bound water, the level of cell filling with the substrate was measured from the top surface of the container with an accuracy of ±1 mm. This measurement was conducted to determine the volume unoccupied by the substrate (Ve) (cm^3) in each cell. The actual volume (Vr) occupied by the substrate was calculated by subtracting (Ve) from the theoretical volume (Vt), which was 120 cm^3 for V120SS containers and 265 cm^3 for V265 containers. The substrate was then extracted and weighed using a BTA2100D analytical balance with an accuracy of ±0.01 g to determine the weight of the wet substrate (ms) in grams. After drying the substrate for 24 h at 65 °C and an additional 24 h at 105 °C, it was weighed again to obtain the mass of the dry substrate (dms) in grams. Bulk density (bd) was calculated using the values of (dms) and (Vr). For four randomly selected samples from each variant, the solid phase density (ds) was measured. Based on (ds) and (bd), the total porosity of the substrate (po) (%) was calculated, followed by the water volume (wc) (%) and air volume (ac) (%) [33–35].

2.2. Seedling Experiment

After determining the optimal configuration of the compaction unit, a total of 140 containers (35 containers for each of the four species) were prepared in the control variant (V1) and variant V2, and an additional 140 containers were prepared in variant V3 with substrate compaction using the selected filling unit setting. The timing of filling the containers with nursery substrate, seed sowing, and production procedures varied depending on the species (see Table 1). The seedlings received foliar fertilization usingBioekor fertilizer (containing NO_3–N 1.0%, NH_2–N 7.5%, P_2O_5 3.0%, K_2O 4.4%, and micronutrients such as Fe, B, Cu, Mn, Mo, and Zn) and Floralesad fertilizer (containing NO_3–N 1.2%, NH_2–N 8.0%, P_2O_5 3.5%, K_2O 5.0%, MgO 0.5%, and micronutrients including S, Fe, B, Cu, Mn, Mo, and Zn). Osmocote fertilizer (2.5 kg·m^{-3}) was used as a starter for spruce. At regular intervals of every 14 days, from May to October, 12 containers of seedlings were sampled, consisting of four species (Scots pine, Norway spruce, European beech, and Pedunculate oak) × 3 variants (V1, V2, and V3). Due to different sowing dates, the first sampling date (T1) for pine and oak was 14 days after sowing (DAS), while the final sampling date (T14) was 196 DAS. For spruce and beech, the first sampling date (T1) was 10 DAS, and the last sampling date (T14) was 192 DAS. During each sampling, substrate parameters were measured in 10 randomly selected cells of the V120SS container and seven cells of the V265 container. The substrate was separated from the roots, and its volume (Vr) was determined using the hydrometric method by immersing it in a graduated cylinder of water after removing the seedling with the root ball. The actual volume of the substrate (Vr) was calculated based on the difference between the theoretical volume (Vt) and the unoccupied volume (Ve), while the volumetric density (bd) was calculated from the substrate mass (dms) and Vr [7,9,36,37]. In the remaining cells of the containers, the penetration resistance (pr) of the substratewas measured using a penetrometer with a cone diameter of 0.78 cm. For the seedlings, various measurements were taken, including the length of the main root (lr) and the shoot (ls) using a tape measure (with an accuracy of ±1 mm), the diameter at the root neck (rcd)using a caliper (with an accuracy of ±0.1 mm), the dry mass of the root system (dmr), the aboveground part (dms), the assimilation apparatus (dmaa), and the whole seedling (dmw) (±1 mg). The seedling sturdiness quotient (SQ) (–) was calculated as the ratio of ls to rcd. A total of 1428 seedlings and substrate samples were analyzed in this study.

2.3. Data Analysis

To determine the significance of differences in physico mechanical parameters of the substrate and seedling parameters at different dates, a one-way analysis of variance (ANOVA) was conducted. Tukey's test was then applied for the separation of homogeneous groups. Furthermore, correlation analysis was performed to examine the relationships between substrate and seedling parameters. Additionally, regression analysis was conducted to analyze the changes over time in the measured substrate and seedling parameters. All statistical analyses were carried out using Statistica 11 StatSoft Polska Sp. z o.o software [38].

3. Results

3.1. Preliminary Experiment

In the pilot experiment (Table 2), a lower speed of container movement on the vibrating table (LowSp) resulted in a decrease in the total porosity (po) and air volume (ac) of the substrate. Conversely, there was an increase in water volume (wc), volume density (bd), penetration resistance (pr), and dry mass of substrate (dms). When comparing the LowSp variant with an increase in the immersion depth of the compaction fingers from 15 (15D) to 30% (30D), the desired changes in ac and aw parameters did not occur. However, there was an increase in substrate consumption (dms). Based on these findings, in the actual culture experiment (V3), the containers were filled at a lower speed (LowSp) and with a 15% increase in the immersion depth of the compaction fingers (15D).

Table 2. Physical and mechanical parameters of substrates in the pilot experiment (mean ± SD).

Try Type	Control Parameters		Substrate Parameters (Diff. Sig. at $p < 0.05$)					
	Speed	Depth	bd	po	wc	Ac	dms	pr
V120SS	StdSp	StdD	0.083 ± 0.004 [a]	93.5 ± 0.3 [b]	55.5 ± 3.6 [b]	38.0 ± 3.9 [a]	9.5 ± 0.45	47.1 ± 10.8
		15D	0.089 ± 0.002 [ac]	93.0 ± 0.2 [bc]	63.9 ± 1.5 [a]	29.1 ± 1.6 [ab]	10.3 ± 0.23	60.8 ± 11.0
		30D	0.095 ± 0.005 [bc]	92.6 ± 0.4 [ac]	70.0 ± 2.7 [cd]	22.6 ± 3.1	10.3 ± 1.30	64.4 ± 10.1
	LowSp	StdD	0.087 ± 0.004 [a]	93.2 ± 0.3 [b]	59.2 ± 2.9 [ab]	34.0 ± 3.2 [c]	9.8 ± 0.49	48.2 ± 9.1
		15D	0.099 ± 0.003 [b]	92.3 ± 0.3 [a]	72.1 ± 2.5 [d]	20.2 ± 2.7 [a]	10.8 ± 0.39	85.8 ± 11.8
		30D	0.101 ± 0.002 [b]	92.1 ± 0.2 [a]	64.8 ± 2.4 [ac]	27.3 ± 2.5 [b]	11.2 ± 0.28	90.0 ± 12.2
V265	StdSp	StdD	0.087 ± 0.006 [a]	88.3 ± 0.4 [b]	54.6 ± 4.3 [a]	33.7 ± 4.6 [a]	21.3 ± 1.3	40.0 ± 10.1
		15D	0.097 ± 0.005 [b]	93.0 ± 0.4 [a]	59.1 ± 3.3 [b]	33.9 ± 3.0 [a]	22.1 ± 1.4	55.8 ± 10.4
		30D	0.096 ± 0.010 [b]	92.6 ± 0.8 [a]	58.8 ± 2.1 [b]	33.8 ± 2.3 [a]	22.6 ± 2.3	69.9 ± 10.9
	LowSp	StdD	0.095 ± 0.006 [a]	92.8 ± 0.5 [c]	55.2 ± 3.2 [a]	37.6 ± 3.2 [a]	22.0 ± 1.6	46.3 ± 14.9
		15D	0.099 ± 0.012 [b]	92.4 ± 0.8 [ab]	67.5 ± 1.9 [c]	24.9 ± 1.9 [c]	21.6 ± 2.1	57.3 ± 10.3
		30D	0.101 ± 0.011 [c]	92.2 ± 0.8 [ab]	61.9 ± 1.5 [b]	30.3 ± 1.2 [b]	22.8 ± 2.5	68.9 ± 16.1

Designations: bd, volume density (g·cm^{-3}); po, total porosity (% vol.); wc, water capacity (% vol.); ac, air capacity (% vol.); dms, dry mass of substrate in cassette cells (mg); pr penetration resistance (kPa); [abcd] denote homogeneous groups.

3.2. Seedling Experiment

By controlling the moisture content of the substrate in the containers and adjusting the parameters of the plant environment, water consumption during the seedling production season was reduced by 7.8% in variant V2 and 8.1% in variant V3 compared to the control variant V1. In the compacted and water-controlled variant V3, the average values of density (bd), dry mass (dms), and substrate penetration resistance (pr) for all species were higher compared to V1 and V2. However, for pine, spruce, and beech in V3, the air volume (ac) and porosity (po) were lower, while the water volume (wc) was higher compared to V1 and V2. No significant differences were observed for oak (Table 3).

Table 3. Average values of substrate parameters for the entire growing season (mean ± SD; denote homogeneous groups at $p < 0.05$).

Parameter	Variant V1	Variant V2	Variant V3	Variant V1	Variant V2	Variant V3
	Scots pine (Sp)			Norway spruce (Ns)		
po	93.4 ± 0.70 [a]	93.4 ± 0.89 [a]	93.0 ± 0.93 [b]	93.4 ± 0.87 [a]	93.4 ± 0.86 [a]	93.0 ± 0.76 [b]
wc	68.3 ± 9.0 [b]	69.2 ± 9.1 [b]	71.8 ± 7.7 [a]	68.3 ± 9.01 [b]	69.2 ± 9.12 [b]	71.8 ± 7.36 [a]
ac	25.1 ± 9.6b [a]	24.1 ± 9.8 [a]	21.1 ± 7.8 [b]	25.1 ± 9.63 [a]	24.1 ± 9.76 [a]	21.2 ± 7.82 [b]
bd	0.095 ± 0.013 [b]	0.096 ± 0.013 [b]	0.101 ± 0.012 [a]	0.095 ± 0.013 [b]	0.096 ± 0.013 [b]	0.101 ± 0.12 [a]
dms	9.7 ± 0.90 [b]	9.8 ± 0.89 [b]	10.5 ± 0.93 [a]	9.8 ± 0.92 [b]	9.8 ± 0.87 [b]	10.5 ± 0.74 [a]
pr	179.3 ± 60.1 [b]	179.7 ± 65.1 [b]	201.7 ± 51.3 [a]	179.3 ± 60.12 [b]	179.7 ± 65.10 [b]	201.7 ± 51.36 [a]
	European beech (Eb)			Pedunculate oak (Po)		
po	92.9 ± 0.66 [a]	92.9 ± 0.58 [a]	92.5 ± 0.68 [b]	92.5 ± 1.03	92.5 ± 1.02	92.1 ± 1.1
wc	66.3 ± 4.69 [b]	65.4 ± 4.47 [b]	68.9 ± 6.41 [a]	69.6 ± 5.16	68.5 ± 6.0	70.8 ± 3.7
ac	26.7 ± 4.93 [a]	27.5 ± 4.76 [a]	23.6 ± 6.71 [b]	21.9 ± 5.27	21.7 ± 3.87	23.8 ± 6.75
bd	0.102 ± 0.09 [b]	0.102 ± 0.008 [b]	0.108 ± 0.01 [a]	0.107 ± 2.35 [b]	0.108 ± 2.31 [b]	0.110 ± 2.33 [a]
dms	22.1 ± 1.4 [b]	21.9 ± 1.1 [b]	23.2 ± 1.35 [a]	21.8 ± 0.014 [b]	21.7 ± 0.015 [b]	23.0 ± 0.018 [a]
pr	178.5 ± 46.4 [b]	175.3 ± 62.9 [b]	201.6 ± 50.6 [a]	177.8 ± 60.4 [b]	175.6 ± 61.7 [b]	196.1 ± 49.9 [a]

Designations: bd, volume density ($g \cdot cm^{-3}$); po, total porosity (% vol.); wc, water capacity (% vol.); ac, air capacity (% vol.); dms, dry mass of substrate in cassette cells (mg); pr, penetration resistance (kPa); [ab] denote homogeneous groups.

In the compacted and water-control variant (V3), all seedlings exhibited larger diameters at the root neck (rcd) compared to V1 and V2. Additionally, for pine, spruce, and oak, there were larger values for root dry mass (dmr), and for spruce and oak, there were larger values for the dry mass of the assimilation apparatus (dmaa). However, most of the other parameters in V3 were lower compared to V1 and V2 (Table 4). When comparing substrate parameters at different dates (T) (Table 5), significant differences were observed for all parameters in containers with pine, spruce, and beech. For oak, differences were found in porosity (po), density (bd), substrate dry mass (dms), and penetration resistance (pr).

In terms of water quantity control (V1 vs. V2 and V3), significant differences in substrate parameters were observed for pine (with the exception of penetration resistance pr), spruce, and beech (with the exceptions of water volume (wc) and air volume (ac)). On the other hand, when comparing increased substrate density (V1 and V2 vs. V3), all substrate parameters were differentiated for pine, spruce, and beech, while for oak, the differences were only observed in density (bd) and penetration resistance (pr).

Table 4. Average values of seedling parameters for the entire growing season (mean ± SD; denote homogeneous groups at $p < 0.05$).

Parameter	Variant			Variant		
	V1	V2	V3	V1	V2	V3
	Scots pine (Sp)			Norway spruce (Ns)		
ls	11.1 ± 1.85 [a]	9.7 ± 1.48 [b]	9.6 ± 1.57 [b]	16.9 ± 2.94 [a]	17.8 ± 3.22 [b]	18.1 ± 2.97 [b]
lr	11.9 ± 2.03	11.6 ± 1.66	11.6 ± 1.80	11.0 ± 1.54 [a]	11.0 ± 1.62 [a]	10.5 ± 1.71 [b]
rcd	1.5 ± 0.35 [b]	1.5 ± 0.29 [b]	1.6 ± 0.30 [a]	1.8 ± 0.25 [b]	1.8 ± 0.30 [b]	1.9 ± 0.30 [a]
SQ	71.9 ± 1.91 [a]	63.3 ± 1.25 [b]	58.9 ± 2.24 [c]	84.7 ± 15.2 [c]	88.4 ± 14.54 [b]	92.2 ± 18.36 [a]
dms	0.196 ± 0.080	0.159 ± 0.048	0.165 ± 0.048	0.361 ± 0.114	0.403 ± 0.123	0.404 ± 0.130
dmr	0.187 ± 0.0.74 [b]	0.187 ± 0.059 [b]	0.195 ± 0.058 [a]	0.207 ± 0.062 [b]	0.228 ± 0.078 [b]	0.254 ± 0.099 [a]
dmaa	0.364 ± 0.130	0.335 ± 0.094	0.346 ± 0.087	0.451 ± 0.126 [b]	0.480 ± 0.146 [b]	0.491 ± 0.149 [a]
dmw	0.749 ± 0.259	0.681 ± 0.173	0.705 ± 0.169	1.020 ± 0.256	1.111 ± 0.273	1.149 ± 0.299
	European beech (Eb)			Pedunculate oak (Po)		
ls	31.0 ± 8.8 [a]	29.4 ± 7.83 [b]	28.6 ± 9.18 [c]	22.8 ± 8.68	23.1 ± 8.97	22.5 ± 8.60
lr	14.9 ± 1.53	14.5 ± 1.54	14.3 ± 1.59	14.8 ± 1.43	14.8 ± 1.47	14.9 ± 1.43
rcd	3.4 ± 0.88 [b]	3.4 ± 0.79 [b]	3.5 ± 0.87 [a]	4.8 ± 1.31 [c]	4.9 ± 1.37 [b]	4.95 ± 1.26 [a]
SQ	87.2 ± 16.32	82.7 ± 15.87	79.5 ± 17.37	48.2 ± 15.05	47.2 ± 15.09	47.8 ± 16.10
dms	0.979 ± 0.663	0.966 ± 0.559	0.908 ± 0.585	1.039 ± 0.669	1.080 ± 0.705	1.142 ± 0.692
dmr	0. 528 ± 0.372	0.569 ± 0.334	0.559 ± 0.381	2.564 ± 1.338 [c]	2.615 ± 1.339 [b]	2.811 ± 1.423 [a]
dmaa	0. 485 ± 0.259	0.468 ± 0.247	0.461 ± 0.295	0.721 ± 0.431 [b]	0.713 ± 0.419 [b]	0.746 ± 0.443 [a]
dmw	1.549 ± 0.906	1.517 ± 0.783	1.448 ± 0.856	4.324 ± 2.351	4.408 ± 2.449	4.699 ± 2.511

Designations: ls—length of shoot (cm), lr—length of main root (cm), rcd—root collar diameter (mm), SQ—sturdiness quotient (-), dms—dry massof shoot (g), dmr—dry massof root system (g), dmaa—dry massof assimilation apparatus (g), dmw—dry massof total seedling (g), [abc] denote homogeneous groups.

Table 5. Effect of analyzed factors on physical and mechanical parameters of the substrate (* for $p < 0.05$; ns for $p > 0.05$).

Factor	Parameter Analyzed											
	po	wc	ac	bd	dms	pr	po	wc	ac	bd	dms	pr
	Scots pine (Sp)						Norway spruce (Ns)					
Timing (T)	*	*	*	*	*	*	*	*	*	*	*	*
(V1 vs. V2 and V3)	*	*	*	*	*	ns	*	ns	ns	*	*	*
(V1 and V2 vs. V3)	*	*	*	*	*	*	*	*	*	*	*	*
	European beech (Eb)						Pedunculate oak (Po)					
Timing (T)	*	*	*	*	*	*	*	ns	ns	*	*	*
(V1 vs. V2 and V3)	*	ns	ns	*	*	*	ns	ns	ns	ns	ns	ns
(V1 and V2 vs. V3)	*	*	*	*	*	*	ns	ns	ns	*	ns	*

Designations: po, total porosity (% vol.); wc, water capacity (% vol.); ac, air capacity (% vol.); bd, volume density ($g \cdot cm^{-3}$); dms, dry mass of substrate in cassette cells (mg); pr, penetration resistance (kPa).

Water control (V1 vs. V2 and V3) had an impact on shoot length (ls), sturdiness quotient (SQ), and shoot dry mass (dms) in pine (Table 6). On the other hand, increased substrate compaction (V1 and V2 vs. V3) influenced ls, diameter at the root neck (rcd), and SQ. In the case of spruce, both water control (V1 vs. V2 and V3) and substrate compaction (V1 and V2 vs. V3) resulted in variations in main root length (lr), (SQ), and root dry mass (dmr). For beech, water control (V1 vs. V2 and V3) affected main root lengths dmr and SQ, while increased substrate compaction (V1 and V2 vs. V3) ls, lr, and SQ. There were no significant differences in seedling parameters for oak due to water control (V1 vs. V2 and V3), and compaction (V1 and V2 vs. V3) only differentiated the dry mass of the root system (dmr).

Table 6. Effect of analyzed factors on seedling parameters (* for $p < 0.05$; ns for $p > 0.05$).

Factor	Parameter Analyzed															
	ls	**lr**	**rcd**	**SQ**	**dms**	**dmr**	**dmaa**	**dmw**	**ls**	**lr**	**rcd**	**SQ**	**dms**	**dmr**	**dmaa**	**dmw**
	Scots pine (Sp)								Norway spruce (Ns)							
(V1 vs. V2 and V3)	*	ns	ns	*	*	ns	ns	ns	ns	*	ns	*	ns	*	ns	ns
(V1 and V2 vs. V3)	*	ns	*	*	ns	ns	ns	ns	ns	*	ns	*	ns	*	ns	ns
	European beech (Eb)								Pedunculate oak (Po)							
(V1 vs. V2 and V3)	ns	*	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
(V1 and V2 vs. V3)	*	*	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns

Designations: ls—length of shoot (cm), lr—length of main root (cm), rcd—root collar diameter (mm), SQ—sturdiness quotient (-), dms—dry mass of shoot (g), dmr—dry mass of root system (g), dmaa—dry mass of assimilation apparatus (g), dmw—dry mass of total seedling (g).

The correlation analysis (Table 7) indicated that as the containers were sampled later (T), there was a decrease in substrate porosity po and air volume ac for pine and spruce, as well as a decrease in substrate dry mass (dms) for pine. Conversely, there was an increase in water volume (wc), density (bd), and penetration resistance (pr) for pine and spruce. Notably, strong negative correlations were found between the sampling date (T) and air volume (ac) (–0.725) as well as water volume (wc) (0.711) of substrates taken from under pine, and between penetration resistance (pr) (0.713) and the sampling date from under spruce. For the substrate taken from under beech, there was an increase in penetration resistance (pr) and a decrease in substrate dry mass (dms) over time, while for oak, there was an increase in density (bd) and penetration resistance (pr) and a decrease in porosity (po) and substrate dry mass (dms). All substrate parameters taken from under pine (Table 6) showed correlations with seedling parameters. Particularly strong negative correlations (generally $r > 0.5$) were observed with (po) and (ac), while there were high positive correlations with density (bd) and (wc) (r generally > 0.5) and weaker correlations with (dms) and (pr). In the case of spruce, there were strong positive correlations between the increase in pr and all seedling parameters. A similar, albeit weaker, relationship was observed with (wc) and an inverse relationship with air volume (ac). For beech, only substrate penetration resistance (pr) showed positive correlations with all seedling parameters, while for oak, there were fewer correlations between substrate and seedling parameters, and the highest positive correlations were observed with substrate penetration resistance (pr) and substrate density (bd).

In regression analysis, strong agreement with measured data ($R^2 > 0.8$) was observed for pine seedlings, particularly for shoot length (ls), diameter at the root neck (rcd), and (dms) (Figure 1a,b,e,f). Weaker agreement ($0.5 < R^2 < 0.7$) was found when analyzing changes in the (SQ) (Figure 1c,d). On the other hand, for spruce seedlings, there was very high agreement between the model and the measured data ($R^2 > 0.95$) for root system dry mass (dmr) (Figure 2e,f), but a lower agreement for sturdiness quotient (SQ) and main root length (lr) (Figure 2a–d). High model agreement ($R^2 > 0.9$) was observed for shoot length ls in beech seedlings (Figure 3e), while weaker agreement ($0.6 < R^2 < 0.8$) was found for main root length (lr) and SQ (Figure 3a–d). Regression analysis for oak showed highly consistent results ($R^2 > 0.94$) when mapping root dry mass (dmr) (Figure 3f).

The results for pine seedlings (Table 8) indicate that in the water control variant, there were lower values for shoot length (ls), sturdiness quotient (SQ) and shoot dry mass (dms), while higher values were observed for root system dry mass (dmr). Conversely, in the variant with increased substrate density, pine seedlings exhibited higher values for diameter at the root neck (rcd), dry mass of the root system dmr, assimilation apparatus (dmaa), total seedling dry mass (dmw), and a lower seedling sturdiness quotient (SQ). For spruce, water control resulted in a shorter main root length (lr), while increased substrate density led to higher values for root system dry mass (dmr) (Figure 2f) and lower main root length (lr). In the case of beech, water control was associated with a lower length of shoot (ls) and main root (lr), while increased density resulted in a lower length of shoot (ls), main root (lr), root collar diameter (rcd), and shoot dry mass (dms). Water control did not differentiate oak seedlings, but increased substrate density was associated with lower values for tap root length (lr), the diameter at the root neck (rcd) and dry mass of root (dmr) (Figure 3f) was lower, and the seedling sturdiness quotient (SQ) was higher (Table 8).

Table 7. Correlations of physical and mechanical parameters of substrate and seedlings (correlation coefficients are given for $p < 0.05$; ns for $p > 0.05$).

Feature	Parameter Analyzed											
	po	**wc**	**ac**	**bd**	**dms**	**pr**	**po**	**wc**	**ac**	**bd**	**dms**	**pr**
	Scots pine (Sp)						Norway spruce (Ns)					
T	−0.655	0.711	−0.725	0.694	−0.353	0.517	−0.117	0.406	−0.408	0.112	ns	0.713
po	1.000	−0.688	0.735	−0.996	−0.822	−0.418	1.000	−0.204	0.303	−0.899	−0.712	−0.107
wc		1.000	−0.998	0.705	0.423	0.455		1.000	−0.995	0.202	ns	0.348
ac			1.000	−0.751	−0.471	−0.463			1.000	−0.290	−0.120	−0.350
bd				1.000	0.812	0.430				1.000	0.838	ns
dms					1.000	0.268					1.000	ns
ls	−0.620	0.662	−0.676	0.656	0.300	0.488	ns	0.385	−0.382	ns	ns	0.639
lr	−0.322	0.462	−0.462	0.363	0.134	0.258	ns	0.280	−0.280	ns	ns	0.411
rdc	−0.547	0.603	−0.614	0.582	0.237	0.432	−0.116	0.367	−0.369	0.103	ns	0.590
SQ	−0.392	0.363	−0.375	0.412	0.261	0.271	ns	0.312	−0.307	ns	ns	0.538
sms	−0.603	0.610	−0.626	0.626	0.290	0.469	ns	0.372	−0.370	ns	ns	0.646
dmr	−0.605	0.600	−0.617	0.631	0.331	0.459	−0.134	0.340	−0.345	ns	ns	0.633
dmaa	−0.645	0.673	−0.688	0.679	0.338	0.468	ns	0.375	−0.373	ns	ns	0.636
dmw	−0.646	0.658	−0.674	0.675	0.335	0.483	ns	0.377	−0.377	ns	ns	0.658
	European beech (Eb)						Pedunculate oak (Po)					
T	ns	ns	ns	ns	−0.145	0.475	−0.534	ns	ns	0.587	−0.290	0.514
po	1.000	−0.538	0.613	−0.983	−0.683	ns	1.000	−0.203	0.391	−0.994	−0.836	−0.218
wc		1.000	−0.982	0.525	0.178	ns		1.000	−0.981	0.197	ns	−0.143
ac			1.000	−0.594	−0.235	ns			1.000	−0.385	ns	ns
bd				1.000	0.685	ns				1.000	0.819	0.242
dms					1.000	0.154					1.000	ns
ls	ns	ns	ns	−0.004	ns	0.407	−0.432	ns	ns	0.456	0.313	0.374
lr	−0.138	ns	ns	−0.092	ns	0.160	ns	ns	ns	ns	ns	ns
rdc	ns	ns	ns	0.040	0.148	0.397	−0.434	ns	ns	0.451	0.256	0.375
SQ	ns	ns	ns	−0.047	ns	0.196	ns	ns	ns	ns	ns	ns
sms	ns	ns	ns	0.111	0.205	0.369	−0.503	ns	ns	0.539	0.306	0.407
dmr	ns	ns	ns	0.132	0.223	0.349	−0.544	ns	ns	0.581	0.325	0.457
dmaa	ns	ns	ns	0.035	ns	0.205	−0.269	ns	ns	0.304	ns	0.358
dmw	ns	ns	ns	0.111	0.194	0.360	−0.518	ns	ns	0.556	0.306	0.452

Designations: po, total porosity (% vol.); wc, water capacity (% vol.); ac, air capacity (% vol.); bd, volume density ($g \cdot cm^{-3}$); dms, dry mass of substrate in cassette cells (mg); pr, penetration resistance (kPa); ls—length of shoot (cm), lr—length of main root (cm), rcd—root collar diameter (mm), SQ—sturdiness quotient (-), dms—dry mass of shoot (g), dmr—dry mass of root system (g), dmaa—dry mass of assimilation apparatus (g), dmw—dry mass of total seedling (g).

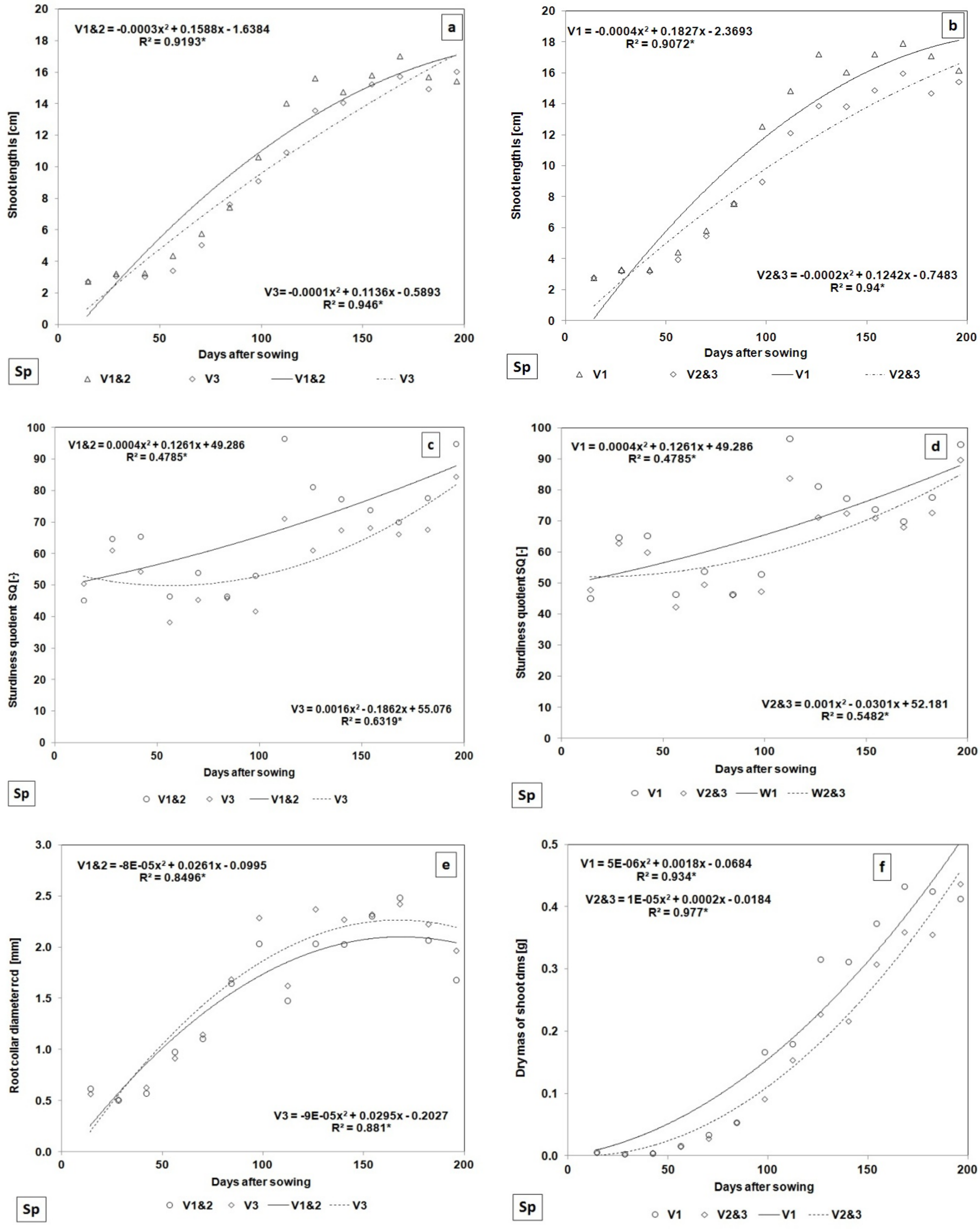

Figure 1. Change over time of pine seedling parameters depending on the variant of the experiment: shoot length (ls) for density change (**a**) and water control (**b**), sturdiness quotient (SQ) for density change (**c**) and water control (**d**), diameter at the root neck (rcd) for density change (**e**), shoot dry mass (dms) for water control (**f**) (* significant at $p < 0.05$).

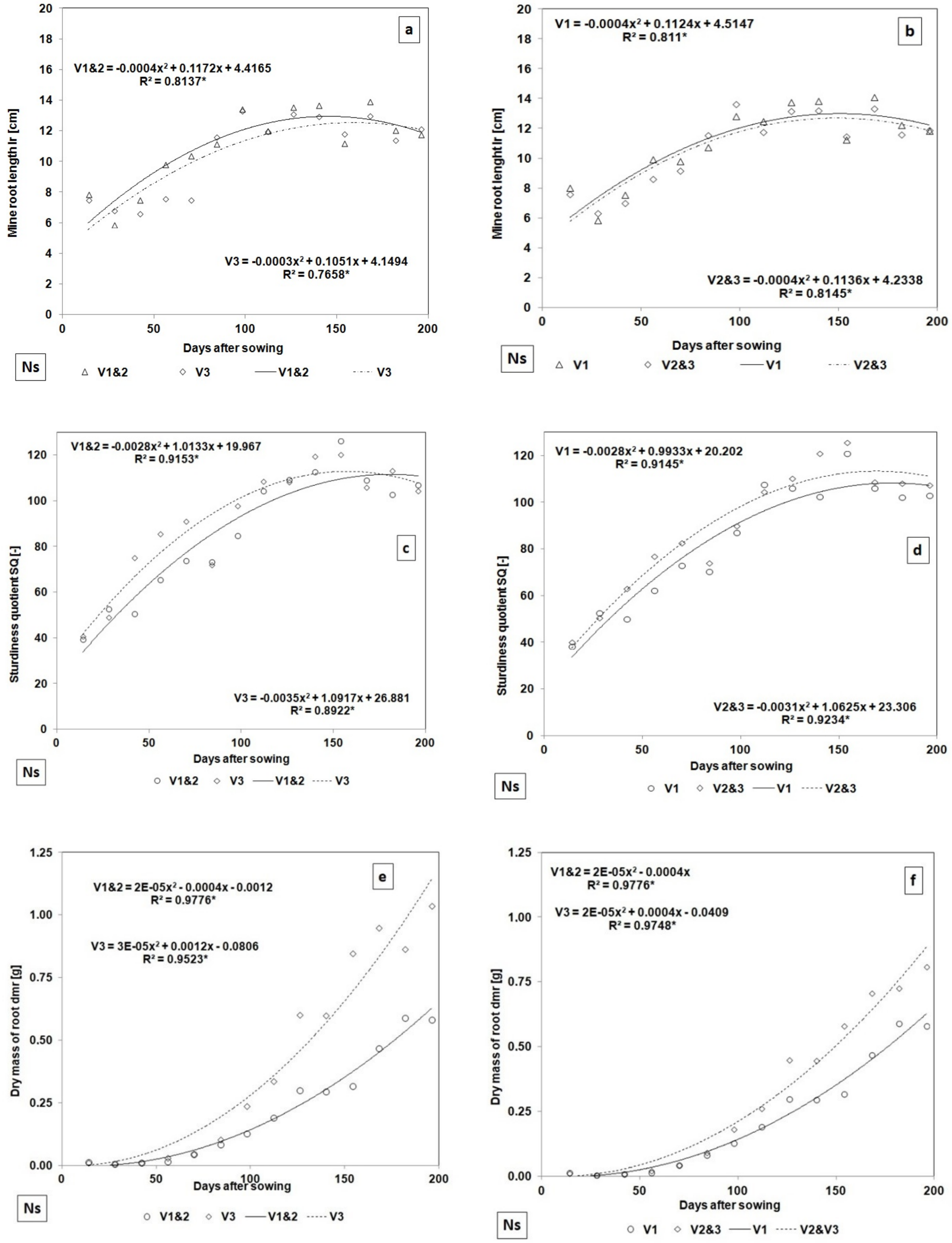

Figure 2. Change over time of spruce seedling parameters depending on the variant of the experiment: length of the main root (lr) for density change (**a**) and water control (**b**), dry mass of the root system (dmr) for density change (**c**), and water control (**d**), sturdiness quotient (SQ) for density change (**e**) and water control (**f**) (* significant at $p < 0.05$).

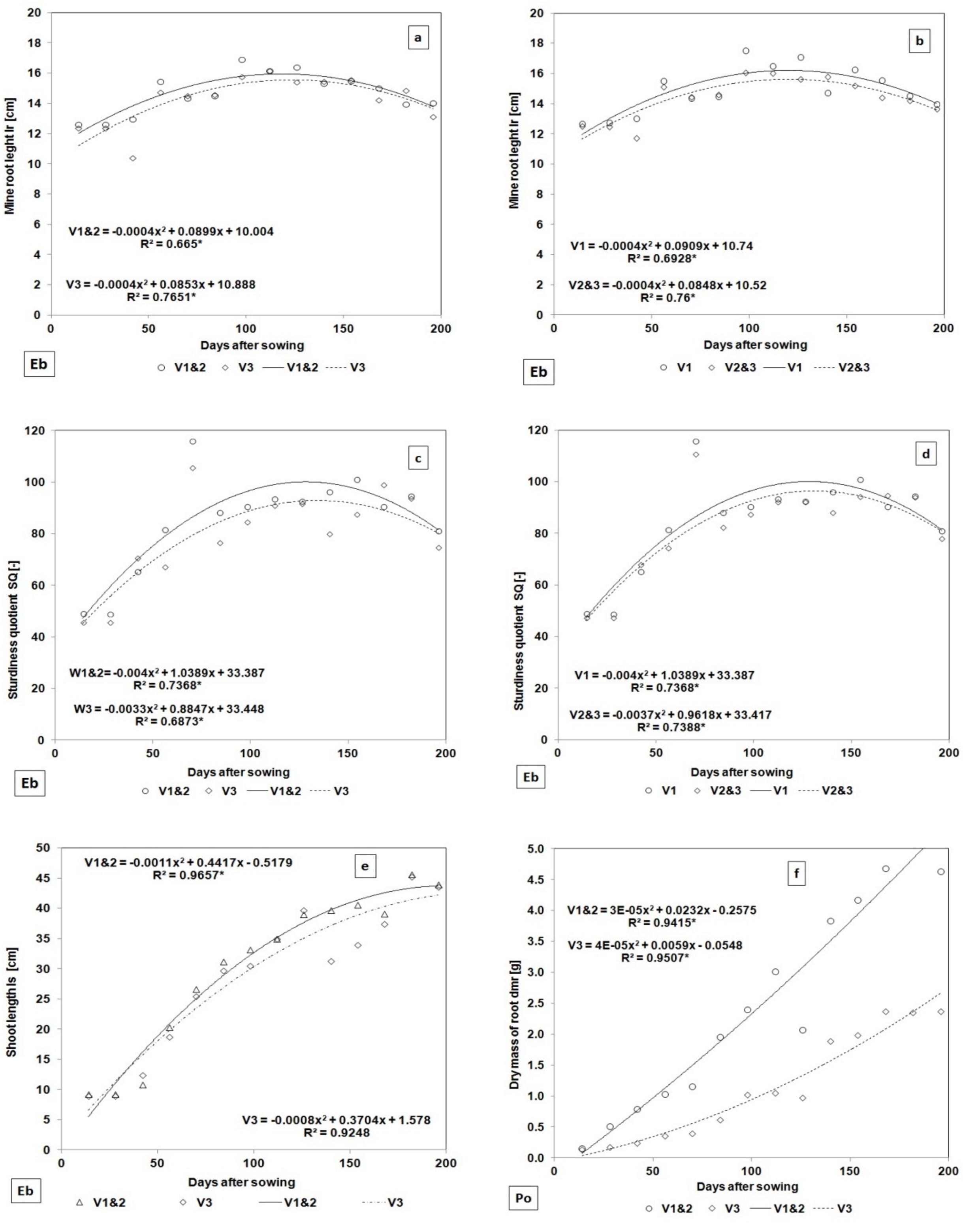

Figure 3. Change over time of beech seedlings parameters depending on the variant of the experiment: length of the main root (lr) for compaction change (**a**) and water control (**b**), sturdiness quotient (SQ) for compaction change (**c**) and water control (**d**), shoot length (ls) for compaction change (**e**), and dry mass of the oak root system (dmr) depending on the compaction variant (**f**) (* significant at $p < 0.05$).

Table 8. Seedling parameters at the end of the production season—last three terms (mean ± SD; denote homogeneous groups at $p < 0.05$).

Parameter	Water Control V1	Water Control V2 and 3	Increased Compaction V1 and 2	Increased Compaction V3	Water Control V1	Water Control V2 and 3	Increased Compaction V1 and 2	Increased Compaction V3
	Scots pine (Sp)				Norway spruce (Ns)			
ls	17.0 ± 2.4 [a]	15.4 ±2.5 [b]	16.1 ± 2.5	15.6 ± 2.6	27.2 ± 5.0	27.2 ± 6.1	27.6 ± 5.5	26.6 ± 6.3
lr	12.7 ± 1.4	12.5 ± 1.4	12.7 ± 1.4	12.4 ± 1.4	12.8 ± 1.3 [a]	12.2 ± 1.4 [b]	12.6 ± 1.4 [a]	12.1 ± 1.3[b]
rcd	2.1 ± 0.5	2.1 ± 0.5	2.1 ± 0.5 [b]	2.2 ±0.4 [a]	2.6 ± 0.3	2.6 ± 0.5	2.6 ± 0.4	2.6 ± 0.6
SQ	87.0 ± 19.6 [a]	74.2 ± 17.1 [b]	81.2 ± 18.8 [a]	73.1 ± 18.1 [b]	104.0 ± 19.1	107.1 ± 23.3	106.3 ± 19.5	105.9 ± 25.6
dms	0.424 ± 0.172[a]	0.385 ± 0.113 [b]	0.393 ± 0.146	0.410 ± 0.115	0.897 ± 0.309	0.905 ± 0.346	0.923 ± 0.318	0.871 ± 0.356
dmr	0.403 ± 0.152[a]	0.466 ± 0.155 [b]	0.426 ± 0.141 [b]	0.483 ± 0.180 [a]	0.544 ± 0.177	0.588 ± 0.185	0.546 ± 0.164 [b]	0.721 ± 0.203 [a]
dmaa	0.612 ± 0.212	0.628 ± 0.181	0.602 ± 0.196 [b]	0.665 ± 0.179 [a]	0.932 ± 0.267	0.946 ± 0.306	0.943 ± 0.283	0.940 ± 0.311
dmw	1.438 ± 0.482	1.479 ± 0.383	1.421 ± 0.417 [b]	1.558 ± 0.413 [a]	2.373 ± 0.598	2.439 ±0.698	2.412 ± 0.632	2.431 ± 0.725
	European beech (Eb)				Pedunculate oak (Po)			
ls	36.3 ± 14.1 [a]	32.6 ± 11.8 [b]	35.1 ± 12.5 [a]	31.3 ± 12.2 [b]	29.3 ± 11.3	27.7 ± 11.3	28.0 ± 11.5	28.3 ± 11.1
lr	13.6 ± 1.9 [a]	12.7 ± 1.7 [b]	13.2 ± 1.8 [a]	12.6 ± 1.6 [b]	14.4 ± 1.3	14.0 ± 1.5	14.4 ± 1.4 [a]	13.7 ± 1.4 [b]
rcd	3.9 ± 1.7	3.5 ± 1.6	3.8 ± 1.6 [a]	3.3 ± 1.5 [b]	6.0 ± 2.0	5.4 ± 2.3	5.8 ± 2.1 [a]	5.2 ± 2.3 [b]
SQ	96.1 ± 18.7	98.6 ± 25.8	96.4 ± 19.3 [a]	100.1 ± 27.9 [a]	50.5 ± 16.5	55.1 ± 22.5	49.0 ± 15.7 [b]	61.3 ± 25.6 [a]
dms	1.672 ± 1.536	1.451 ± 1.158	1.650 ± 1.360 [a]	1.313 ± 1.088 [b]	2.020 ± 1.268	1.961 ± 1.453	1.978 ± 1.346 [a]	1.977 ± 1.486 [a]
dmr	0.937 ± 0.834	0.938 ± 0.681	0.965 ± 0.753	0.904 ± 0.671	4.915 ± 2.320	4.581± 2.718	4.89 ± 2.438 [a]	3.346 ± 2.833 [b]
dmaa	0.600 ± 0.420	0.696 ± 0.456	0.640 ± 0.455	0.716 ± 0.440	1.015 ± 1.636	0.857 ± 0.568	0.925 ± 0.620	0.871 ± 0.552
dmw	2.555 ± 1.578	2.561 ± 1.139	2.610 ± 1.388	2.495 ± 1.056	7.507 ± 3.638	7.062 ± 4.149	7.368 ± 3.851	6.918 ± 4.238

Designations: ls—length of shoot (cm), lr—length of main root (cm), rcd—root collar diameter (mm), SQ—sturdiness quotient (–), dms—dry mass of shoot (g), dmr—dry mass of root system (g), dmaa—dry mass of assimilation apparatus (g), dmw—dry mass of total seedling (g); [ab] denote homogeneous groups.

4. Discussion

Introduced during the container preparation stage, increased compaction of the substrate in pine, spruce, and beech containers led to a reduction in air capacity and an increase in water capacity. This effect remained consistent throughout the seedling growing season, as supported by the analysis of variance. However, in oak seedlings, the differences were observed only in certain substrate parameters. This dissimilarity could be attributed to the sorting process and the subsequent change in density across the container space, which oak seedlings undergo in July (after 95 DAS) (Table 1). Sorting involves removing taller seedlings from a container and transferring them to another container to ensure even spacing [39]. This process results in faster growth of smaller seedlings that were previously overshadowed by taller ones. During the transfer of seedlings, changes in the structure of the substrate lump, which is not yet well-established with roots, may occur due to the removal or siphoning off of parts of the substrate, lump deformation, loosening, or thickening when placed in a new cell. Analysis of the morphological traits of the seedlings revealed differences consistent with species characteristics, such as significantly higher total dry mass, root system volume, and tap root length in deciduous species [40]. The increased substrate compaction, which led to higher water capacity and reduced air capacity, also affected seedling parameters. This relationship may be associated with water and nutrient availability [41], microbial activity [42,43], and nutrient levels in the substrate [44,45]. Air capacity showed positive correlations with tap root length (pine and spruce), shoot length (pine), diameter at the root neck, and volume of the root system (oak). On the other hand, water capacity correlated positively with shoot length and diameter at the root neck (spruce). Volumetric density, however, exhibited a negative relationship with taproot length, shoot length (pine), diameter at the root neck (spruce), total dry mass (beech), and diameter at the root neck (oak). These findings differ slightly from previous studies, which generally reported a reduction in root system length and an increase in height and thickness at the root neck in response to soil compaction in various species [32,46–53]. The shortening of the root system length in response to increased soil compaction has been demonstrated in studies on *Quercus petraea* (Matt.) Liebl. seedlings [54] (density ranging from 0.81 to 1.32 $g{\cdot}cm^{-3}$), Tworkoski et al. [55] for *Quercus alba* L. (1.0–1.5 $g{\cdot}cm^{-3}$), Zisa et al. [56] for *Pinus nigra* Arn. (1.4–1.6 $g{\cdot}cm^{-3}$), Misra and Goibbons [57] for *Eucalyptus* L'Hér., or Mosena and Dillenburg [58] for *Araucaria angustifolia*. Researchers investigating this issue have indicated that increased compaction raises volumetric density and decreases soil pore diameter, resulting in decreased permeability, water flow, and, consequently, air capacity [50,59–61].

The appropriate level of substrate density can be utilized to regulate its retention properties, as demonstrated by the strong correlation between bulk density and water content in the cultivation of Lespedeza cyrtobotrya Miq. seedlings using various nursery substrate compositions [62]. The results of this study revealed a negative correlation between total porosity and shoot length, diameter at the root neck (for pine and oak), and tap root length (for beech). Similar results were obtained for pine seedlings growing in soil in a ground nursery by Kormanek et al. [49]. In contrast, a positive relationship was observed between penetration resistance and shoot length, diameter at the root neck, and total dry mass (for all species), as well as tap root length (for pine, spruce, and beech). Thus, penetration resistance can serve as a readily measurable indicator related to the growth conditions of seedlings for each species, given its total porosity, water capacity for V120SS containers, and dry mass of the substrate for pine (V120SS) and beech (V265) seedlings [11,63,64]. No significant correlations were found between total seedling dry mass, water capacity, and air capacity for beech and oak. A similar lack of correlation was reported by Allaire-Leung et al. [65] in an experiment involving *Prunus* × *cistena* sp. The patterns of changes in root system volume were comparable to those observed by Cannava et al. [36] in a study on Impatiens hawkeri, which employed a similar methodology to measure changes in root system volume. In contrast, the dry mass of shoots, roots, and whole seedlings exhibited positive correlations with substrate density (excluding spruce) and penetration resistance. Similarly, in an experiment with *Pinus sylvestris*, the dry mass of needles, shoots, and roots increased with higher substrate density [66], while in the case of Abies alba Mill., the dry mass of shoots showed a similar trend [67]. Zahreddine et al. [68] also reported an increase in the dry mass of Pinus nigra Arn. seedlings with an increase in substrate density from 0.71 to 1.01 $g \cdot cm^{-3}$. Evaluation of seedlings during the last three analysis dates, which represent the growth effect at the end of the season, revealed that both controlling the amount of water supplied to the production field and selecting the appropriate substrate density are factors that can influence seedling growth. However, the impact of these factors on individual seedling parameters appears to be species-dependent. An increase in substrate density within the accepted range led to improvements in pine seedling parameters, including an increase in root collar diameter, dry mass of the root system and assimilation apparatus, total seedling mass, and a decrease in sturdiness quotient. Conversely, for spruce, beech, and oak, these parameters deteriorated. Pine seedlings displayed a larger root collar diameter and a more developed root system, which facilitates their growth in the crop. Recent research suggests that the higher density of the nursery substrate benefits pine and oak seedlings due to the accumulation of elements [44,45].

5. Conclusions

- The increased compaction of the substrate during container filling was maintained throughout the growth period of pine, spruce, and beech seedlings, as evidenced by the differences in the physical–mechanical parameters of the substrate in the compacted and uncompacted variants.
- The increased compaction of the substrate led to an increase in the dry mass of the substrate, resulting in the desired effect of increasing water capacity and decreasing air capacity for pine, spruce, and beech seedlings. However, this effect was not observed in oak seedlings, which could be attributed to the sorting practices implemented for this species at a later stage. Furthermore, the increased substrate compaction had a positive impact on important seedling parameters, but only in pine seedlings at the end of the growth period. These improvements included an increase in diameter at the root neck, dry mass of the root system, leaf area, and total seedling mass, as well as a lower (improved) sturdiness quotient.
- The increase in substrate consumption justified the need for denser filling of containers only for pine seedlings. However, for the other species, increasing substrate

compaction would result in a waste of substrate. Therefore, the current level of substrate compaction used in HIKO nursery containers appears to be optimal for the overall growth of the seedlings.

- The implementation of precise water dosing during irrigation, based on a systematic water balance analysis, resulted in a reduction in water consumption of approximately 8.0%. This approach also led to a noticeable improvement in the sturdiness quotient of pine seedlings and the development of a more robust root system. However, no significant differences were observed for spruce, beech, and oak seedlings.

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