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The Effects of Soil Compaction on the Growth and Architecture of the Seedlings of Species Commonly Used for Afforestation in Iran

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Abstract: The aim of the present study was to elucidate the effects of soil compaction on the seedlings of two species of deciduous (*Acer velutinum* and *Alnus subcordata*) and evergreen trees (*Pinus eldarica* and *Pinus nigra*) in terms of above- and below-ground morphology in a greenhouse. Six soil compaction levels were applied: the lowest intensity (control), very low, low, moderate, heavy, and very heavy. The results showed that there were different effects according to the species. These effects were on lateral root length, stem diameter, leaf dry biomass, SSL (specific stem length), SRL (specific root length), LMR (leaf mass ratio), RMR (root mass ratio), SMR (stem mass ratio), and R/S (root-to-shoot ratio). The results showed that soil penetration resistance (SPR) had a significant effect on seedling variables such as lateral root length, stem diameter, leaf dry biomass, and SRL ($p < 0.05$). *A. velutinum* seedlings have the highest values of growth variables compared to three other species, followed by *A. subcordata* seedlings. The two evergreen species, *Pinus eldarica* and *Pinus nigra*, have the lowest values of these growth variables. It is worth noting that we found that deciduous species had enhanced growth up to a moderate compaction level (1.3 MPa), while the growth decreased at an SPR that was higher than this value.

Keywords: soil compaction; morphological response; biomass growth; architectural response; velvet maple; Caucasian alder; eldar pine; black pine

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1. Introduction

Soil plays a crucial role in forest ecosystems, and it is a mediator of nutrients, water, and energy flows that guarantee the productivity of the forest ecosystem and maintain biodiversity [1–4]. Logging operations are required to obtain wood for multiple purposes [5–7]. However, it is well known that logging operations can trigger substantial disturbance to the forest soil [3,8–13]. Forest soils after logging are, indeed, in most cases, prone to compaction. Soil compaction is commonly represented by soil bulk density (oven dry mass/volume) or penetration resistance as measured by a penetrometer [14–16]. Soil compaction can cause several changes in soil structure and hydrology, especially separation of soil aggregates, reduced soil porosity, destruction of pore continuity, an increment in shear strength, and a decrease in infiltration capacity [17–22]. Even a minor increment in soil compaction may lead to a change in the growth of young seedlings and inhibit the development of the root system [23]. A set of factors, including soil strength, water and nutrient availability, and aeration, regulate the effects of compaction on root growth [24,25]. If root growth is restrained due to soil compaction, roots have a lesser volume of soil to explore, causing a decrease in the amount of water available for the plant [26]. Previous findings have also shown that soil compaction can negatively affect shoot growth [19,24,25]. Shoot growth of both *Leptospermum scoparium* and *Cordyline australis* was reduced by augmenting soil strength [27]. In another study, the authors found that shoot diameter and root–shoot ratio were influenced by soil type and degree of compaction [28]. In the bulk of research, soil compaction leads to reduced aboveground biomass to a different degree [24–26,29]. Variables such as height and diameter of seedlings in various species are frequently of lower values due to an increase in soil density [26,27]. For instance, some parameters, including shoot dry weight, leaf area, and dry weight, may be reduced by augmenting soil strength or density [28,30]. The interactions between root and shoot of perennial woody plants in response to increased soil compaction are a complicated topic due to the architecture and growth allocation of woody plants [26,31]. Previous studies have indeed indicated that increased soil strength may alter the growth allocation between the above- and below-ground fractions of seedlings [27,32].

Severe compaction of soil not only shortens and thickens roots but also may alter their branching patterns [18,23,33]. However, the decline in root growth may not lead to a decrease in the total biomass of woody plants in all cases [34,35]. Hence, some factors regulate the plant response to soil compaction, such as soil type and texture, climate, light, water and nutrient availability, species, and the degree and extent of soil compaction [25,32,34]. In general, the growth of plants in compacted soils causes them to have more branched roots [27]. Weak root architecture can be expected due to an increase in soil bulk density, particularly in loamy sand soil, which, in turn, results in a decline in root branches' development and propagation, which consequently can have detrimental influences on water and nutrient uptake [24]. Also, the total length of primary and lateral roots reduces as soil bulk density increases [36]. Woody plant root elongation is generally prohibited at soil strength values higher than 2–2.5 MPa. However, it depends on the soil texture and plant species [37]. However, Skinner et al. (2009) [38] reported that any increase in soil strength may change the root growth of woody plants.

In the Hyrcanian forests in Iran, forest soils are heavily compacted due to logging operations with heavy machines and cattle grazing [39–43]. In this area, four main species have been used for afforestation and ecosystem restoration. These are velvet maple (*Acer velutinum* Boiss.), Caucasian alder (*Alnus subcordata* C.A.M.), *Pinus eldarica* Medw., and *Pinus nigra* Arn. Despite the extensive literature on the topic of the interaction between soil compaction and seedling growth, such information is scarce for these four species used for afforestation in Iran. Therefore, the aim of the present study was to fulfill this knowledge gap by evaluating the effects of soil compaction on the growth of two species of deciduous trees (*Acer velutinum* Boiss. and *Alnus subcordata* C.A.M) and evergreen trees (*Pinus eldarica* Medw. and *Pinus nigra*) in a greenhouse experiment.

In this study, we tried to shed light on the relationship between penetration resistance and various growth variables in deciduous and evergreen seedlings to test the following hypotheses: (1) all the above- and below-ground variables, including seedling sizes (morphology) and biomass (growth), reduced as soil strength increased; (2) soil compaction can cause significant changes in growth allocation patterns (architectural variables) to the above- and below-ground fractions of these deciduous and evergreen tree seedlings.

2. Materials and Methods

2.1. Soil Strength Experiment

Seeds of deciduous (*Acer velutinum* Boiss. and *Alnus subcordata* C.A.M.) and evergreen (*Pinus eldarica* Medw. and *Pinus nigra*) trees were chosen from the seed center of Amol city (north of Iran), then transported to a seed laboratory situated in the Faculty of Natural Resources, Karaj, to investigate the quality and quantity of seeds. The deciduous *Acer velutinum* and *Alnus subcordata* are mainly distributed in the north of Iran in areas with temperate characteristics. The evergreen *Pinus eldarica* (Eldar pine) and *Pinus nigra* (Black pine) are mostly planted in arid and semi-arid areas of Iran.

Undisturbed soil from a depth ranging from 1 to 30 cm from Kheyrud Educational and Research Forest Station (located in the Nowshahr, north of Iran) was collected from the A_0 (litter), A_1, and A_2 horizons and transferred to the greenhouse with a temperature-controlled situation in the Faculty of Natural Resources in Karaj city. Dry air is needed to prevent seeds from decaying because they contain a high amount of moisture. Then, the seeds were preserved in the seed laboratory refrigerator at 4 °C. In February, four types of seeds were planted in loam or clay loam soils in plastic pots (20 × 15 cm) with a constant moisture regime, controllable temperature and humidity (between 18 °C and 24 °C, and a relative humidity level between 50% and 60%, depending on the type of seed) without adding fertilizer to avoid the possible confounding effects of different soil water regimes. Small seeds like *Alnus subcordata*, *Pinus eldarica*, and *Pinus nigra* were potted at a depth of 1–3 mm, and *Acer velutinum* was planted at a depth of 2–3 cm because its seeds are larger than the others. Pots were irrigated every day for 70 days in a greenhouse located in the Faculty of Natural Resources, Karaj.

After 70 days, seedlings began to sprout; thus, in late March, seedlings were transplanted into larger pots (20 × 30 cm) so as to avoid the limitation of space for root growth over the experiment period. Six soil compaction levels with three replicates—including C, the lowest intensity (no compaction or control); VL, very low; L, low; M, moderate; H, high; and VH, very high—were applied with a compaction hammer (4.736 kg weight) from the height of 45.7 cm by manually applying 1, 2, 4, 6, and 8 blows. Water was supplied consistently each day using a sprinkler irrigation system (20 min of irrigation day^{-1}), and greenhouse situations were uniformly adjusted for all seedlings for light, water, humidity, and temperature throughout the entire experiment by changing the pot locations in the greenhouse during the experiment period. Soil penetration resistance (SPR) was determined with a hand-held penetrometer (Eijkelkamp 06.01.SA penetrometer, Wilmington, NC, USA) by measuring every 10 cm along the soil profile. The six values were averaged for each pot. The total number of pots was 72 (4 deciduous and evergreen tree species × 6 levels of soil strength × 3 replicates).

2.2. Seedling Growth Measurements

The seedlings were extracted and harvested from pots after 130 days (starting in late March and ending in late September). After carefully harvesting each seedling from the pots, the roots were washed and lightly dried. Then, the measurements of the fresh weight of the leaves, stems, and roots of each seedling were carried out. Seedling morphology parameters such as collar diameter and seedling height were determined by digital Collis calipers (0.01 mm accuracy, E-Base, MC 02050282-I, Taiwan, China) and scaled rulers (with 0.1 cm accuracy), respectively. After drying all fractions of seedlings at 70 °C, the dry weight of all seedlings was obtained.

Finally, for each seedling, the following parameters were determined or counted: The seedling morphological (or size) variables are as follows: length and diameter of the stem, length of the main root, main root diameter, and lateral root length. The seedling growth or dry biomass variables are as follows: total, shoot, stem, leaf, total root, main root, and lateral root biomass. The seedling's architectural variables are as follows: lateral/main root length ratio; lateral/main root dry biomass ratio; SSL: specific stem length (stem length/stem dry biomass); SRL: specific root length (fine root length/fine root dry biomass); LMR: leaf mass ratio (leaf dry biomass/total dry biomass); RMR: root mass ratio (root dry biomass/total dry biomass); SMR: stem mass ratio (stem dry biomass/total dry biomass); R/S: root-to-shoot ratio (root/shoot dry biomass).

2.3. Statistical Analysis

After checking data normality and homoscedasticity with Kolmogorov–Smirnov and Levene tests, respectively, we selected the statistical model for the analysis. Considering the lack of any nesting structure in our data (date independence), we selected the two-way ANOVA with interaction. Specifically, we considered the effects on all the investigated variables of two fixed factors: species and experimental treatment (compaction level), as well as their interaction. The SPSS version 15.0 (IBM, New York, NY, USA) statistical package was applied to carry out all the statistical analyses.

3. Results

3.1. Compaction Level

The level of compaction in the pots significantly augmented the value of soil penetration resistance from 0.38 ± 0.03 MPa in the C treatment to 1.93 ± 0.13 MPa in the VH treatment ($p \leq 0.01$). Results showed that the values of soil bulk density were increased from 1.08 ± 0.03 g cm^{-3} in the C treatment to 1.38 ± 0.03 g cm^{-3} in the VH treatment ($p \leq 0.01$; Table 1). Also, the values of total porosity significantly declined from 54.04 ± 1.3% in the C treatment to 41.36 ± 1.2% in the VH treatment ($p \leq 0.01$).

Table 1. Mean (±standard deviation) of soil compaction indexes (i.e., penetration resistance, bulk density, and total porosity) in each of the six levels of compaction treatments measured in this study.

Compaction Treatment	Penetration Resistance (MPa)	Bulk Density (g cm^{-3})	Total Porosity (%)
1 (C, control)	0.38 ± 0.03	1.08 ± 0.03	54.04 ± 1.28
2 (VL, very low)	0.65 ± 0.10	1.14 ± 0.02	51.35 ± 0.89
3 (L, low)	0.95 ± 0.11	1.21 ± 0.03	48.37 ± 1.07
4 (M, moderate)	1.27 ± 0.08	1.26 ± 0.06	46.38 ± 2.66
5 (H, high)	1.51 ± 0.14	1.34 ± 0.04	43.12 ± 1.61
6 (VH, very high)	1.93 ± 0.13	1.38 ± 0.03	41.36 ± 1.15

3.2. Species and Growth Variables

Results showed that the species was a significant variable that statistically affected the seedling variables such as lateral root length, stem diameter, leaf dry biomass, SRL, SSL, SMR, LMR, RMR, R/S, lateral/main root length, and lateral/main root dry biomass ($p < 0.05$) (Figure 1).

The degree of lateral root length statistically differed among species, with Velvet maple (41.93 cm) as the highest and Caucasian alder (29.24 cm) as the lowest lateral root length. The value of stem diameter was statistically significant among species, with Velvet maple (4.32 mm) as the highest and black pine (3.13 mm) as the lowest. Duncan's test showed that species had significant effects on leaf dry biomass, with Velvet maple (11.39 g) as the highest and black pine (1.49 g) as the lowest for leaf dry biomass. Duncan's test showed that species had significant effects on SRL (root length/root dry biomass), with Eldar pine and black pine (39.8 and 37.4 cm g^{-1}) having the highest values and Velvet maple and Caucasian alder (3.3 and 2.7 cm g^{-1}) having the lowest values of SRL.

The same was confirmed for SSL (stem length/stem dry biomass), with Eldar pine (15.54 cm g^{-1}) as the highest and Caucasian alder (1.83 cm g^{-1}) as the lowest SSL. Duncan's test showed that species had significant effects on SMR, with Caucasian alder (0.32) having the highest and Eldar pine (0.17) having the lowest SMR. Duncan's test also showed that species had a significant effect on LMR; for this variable, black pine (0.34) had the highest value, while Velvet maple (0.18) had the lowest. Duncan's test showed that species had significant effects on RMR, with Velvet maple (0.53) as the highest and black pine (0.45) as the lowest. Similar effects were detected for root–shoot ratio; indeed, Velvet maple (1.15) showed the highest value and black pine (0.87) the lowest root–shoot ratio. Duncan's test showed that species had significant effects on lateral/main root length, with Eldar pine (by 3.26) having the highest and Velvet maple (by 1.63) having the lowest. Finally, Duncan's test showed that species had a significant effect on lateral/main root dry biomass; specifically, black pine (1.69) showed the highest values and Caucasian alder (0.71) the lowest one.

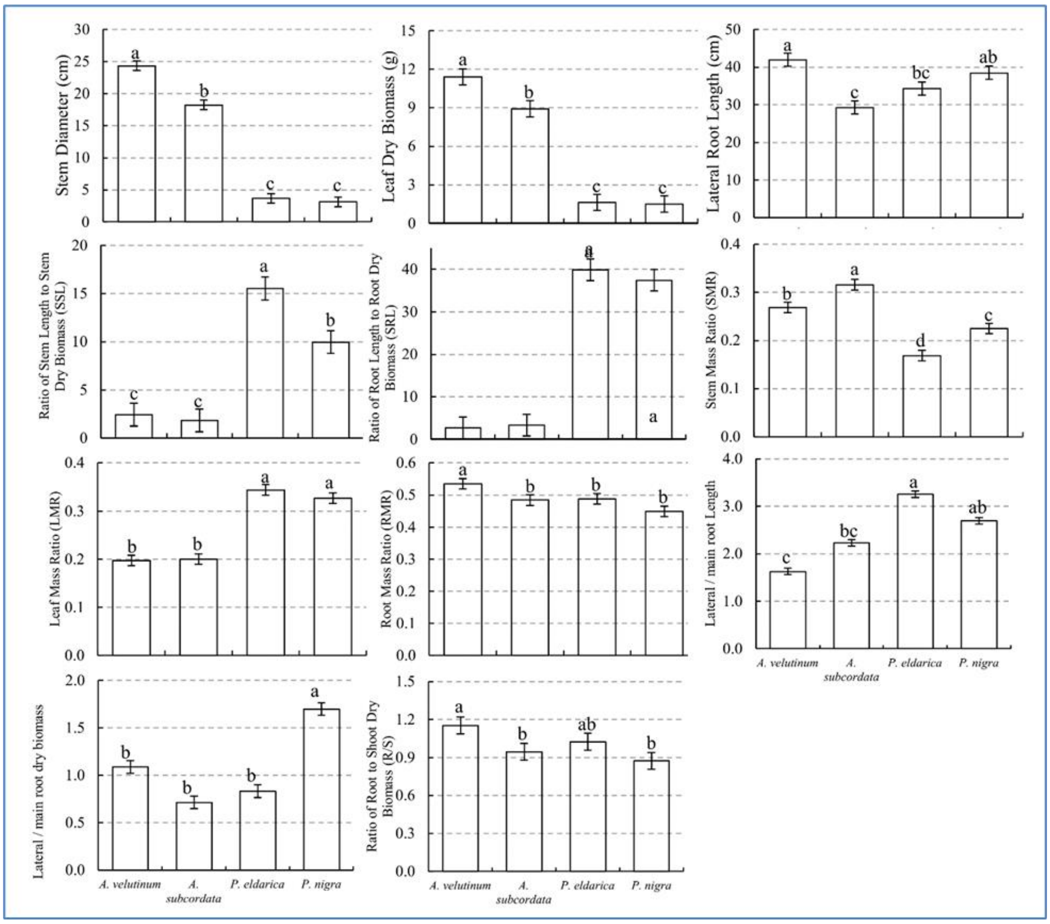

Figure 1. Mean (±standard deviation) of the species effect on seedling growth variables (different letters in a row indicate significant differences among intensities of soil compaction ($p < 0.05$) based on Duncan's tests).

3.3. Soil Penetration Resistance and Growth Variables

Results reported in Figure 2 showed that the experimental treatment was a significant driver of seedling growth, specifically for lateral root length, stem diameter, leaf dry biomass, and SRL ($p < 0.05$). In particular, lateral root length decreased with increasing soil compaction. Stem diameter decreased as well with increasing compaction, even if there were no significant differences in the stem diameter among the very low (VL), low (L) soil compaction, and C treatments. Leaf dry biomass and specific root length (SRL) followed a similar trend, with decreasing values with increasing soil compaction but no significant differences among C, VL, L, and M treatments.

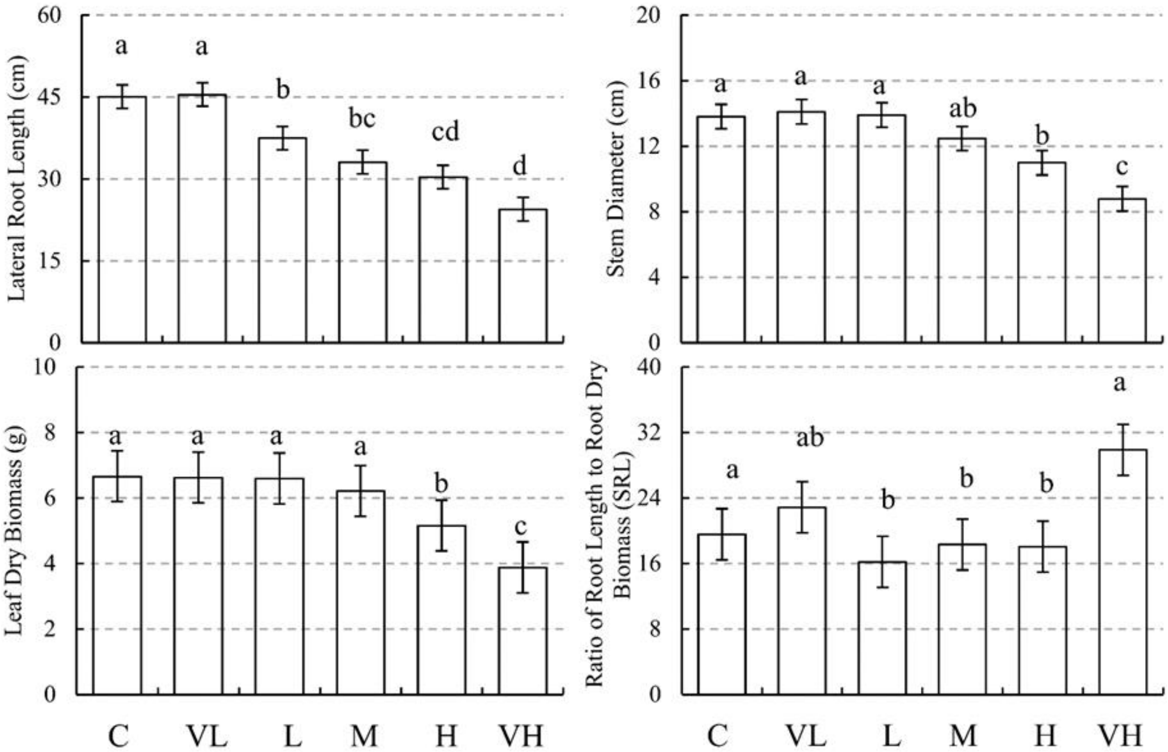

Figure 2. Mean (±standard deviation) of soil penetration resistance (SPR) effect on seedling growth variables (different letters in a row indicate significant differences among intensities of soil compaction ($p < 0.05$) based on Duncan's multiple range tests). Different levels of soil compaction include C: control, VL: very low, L: low, M: moderate, H: high, and VH: very high.

3.4. Interaction Effect between Species and Soil Compaction

Tables 2 and 3 show the analysis of the seedling growth variable data as affected by species and soil penetration resistance (SPR) for deciduous and evergreen species.

Results showed that the interaction effect between species (SP) × experimental treatment was significantly affecting seedling variables such as stem length, main root length, root diameter, dry biomass of total, shoot, root, stem, main root, and lateral root ($p < 0.05$). Contrarily, we did not detect any effect of the interaction between species and experimental treatment: lateral root length, stem diameter, leaf dry biomass, SRL, SSL, SMR, LMR, RMR, R/S, lateral/main root length, and lateral/main root dry biomass.

In the deciduous species, results showed an increase in biomass with increased soil compaction until moderate levels (M treatment—about 1.3 MPa), while at higher compaction values, these variables were reduced. Evergreen species showed decreased growth with increasing compaction.

Table 2. Means of seedling morphology (size), growth (biomass), and architecture (allocation ratios) variables of *Acer velutinum* and *Alnus subcordata* seedlings at different intensities of soil compaction. Different letters in each species column indicate significant differences among intensities of soil compaction ($p < 0.01$) based on Duncan's tests.

		Seedling Morphology (Size)					Seedling Growth (Dry Biomass)							Seedling Architecture (Allocation Ratios)							
Species	**Compaction Intensity**	**Stem Length (cm)**	**Stem Diameter (mm)**	**Main Root Length (cm)**	**Main Root Diameter (mm)**	**Lateral Root Length (cm)**	**Total (g)**	**Shoot (g)**	**Stem (g)**	**Leaf (g)**	**Main Root (g)**	**Lateral Root (g)**	**Total Root (g)**	**Lateral/Main Root Length**	**Lateral/Main Root Dry Biomass**	**SSL (cmg^{-1})**	**SRL (cmg^{-1})**	**SMR**	**LMR**	**RMR**	**R/S**
Acer velutinum	control	38.67 ^{a}	26.93 ^{a}	28.5 ^{ab}	18.7 ^{ab}	46.6 ^{a}	64.79 ^{a}	30.43 ^{a}	17.81 ^{a}	12.63 ^{a}	16.5 ^{ab}	17.17 ^{a}	34.36 ^{a}	1.64 ^{a}	1.08 ^{a}	2.17 ^{a}	2.61 ^{a}	0.27 ^{a}	0.19 ^{a}	0.53 ^{a}	1.13 ^{a}
	very low	44.1 ^{a}	28.07 ^{a}	31.2 ^{a}	19.4 ^{ab}	46.7 ^{a}	65.86 ^{a}	29.89 ^{a}	17.58 ^{a}	12.31 ^{a}	18.01 ^{a}	14.71 ^{a}	35.97 ^{a}	1.52 ^{a}	1.0 ^{a}	2.53 ^{a}	2.61 ^{a}	0.27 ^{a}	0.19 ^{a}	0.55 ^{a}	1.21 ^{a}
	low	41.73 ^{a}	27.07 ^{a}	31.6 ^{a}	20.6 ^{a}	43.5 ^{ab}	67.54 ^{a}	32.02 ^{a}	19.44 ^{a}	12.58 ^{a}	16.6 ^{ab}	12.04 ^{a}	35.52 ^{a}	1.39 ^{a}	1.16 ^{a}	2.15 ^{a}	2.29 ^{a}	0.29 ^{a}	0.19 ^{a}	0.53 ^{a}	1.11 ^{a}
	medium	44.1 ^{ab}	24.5 ^{ab}	27.0 ^{ab}	20.9 ^{a}	43.6 ^{ab}	64.87 ^{a}	29.38 ^{a}	16.6 ^{a}	12.78 ^{a}	16.87 ^{a}	10.78 ^{a}	35.49 ^{a}	1.61 ^{a}	1.12 ^{a}	2.67 ^{a}	2.35 ^{a}	0.26 ^{a}	0.2 ^{a}	0.55 ^{a}	1.21 ^{a}
	high	29.6 ^{bc}	21.3 ^{ab}	22.8 ^{bc}	15.7 ^{bc}	37.8 ^{ab}	50.98 ^{b}	22.62 ^{b}	12.27 ^{b}	10.36 ^{a}	13.21 ^{b}	8.62 ^{b}	28.36 ^{b}	1.67 ^{a}	1.15 ^{a}	2.57 ^{a}	2.55 ^{a}	0.24 ^{a}	0.21 ^{a}	0.56 ^{a}	1.25 ^{a}
	very high	26.27 ^{c}	18.03 ^{b}	18.1 ^{c}	12.2 ^{c}	33.2 ^{b}	36.22 ^{c}	18.12 ^{b}	10.39 ^{b}	7.73 ^{b}	9.08 ^{c}	5.88 ^{c}	18.1 ^{c}	1.92 ^{a}	1.0 ^{a}	2.48 ^{a}	3.65 ^{b}	0.29 ^{a}	0.21 ^{a}	0.5 ^{a}	1.01 ^{a}
Alnus subcordata	control	29.13 ^{a}	18.9 ^{ab}	15 ^{a}	13.3 ^{ab}	30.4 ^{a}	46.76 ^{a}	24.31 ^{a}	14.81 ^{a}	9.49 ^{a}	13.46 ^{a}	17.86 ^{a}	22.46 ^{a}	2.05 ^{a}	0.68 ^{a}	1.96 ^{a}	3.39 ^{a}	0.32 ^{a}	0.2 ^{a}	0.48 ^{a}	0.94 ^{a}
	very low	29.03 ^{a}	19.33 ^{ab}	13.4 ^{ab}	14.5 ^{a}	34.5 ^{ab}	49.21 ^{a}	24.89 ^{a}	15.14 ^{a}	9.75 ^{a}	13.92 ^{a}	17.96 ^{a}	24.32 ^{a}	2.61 ^{a}	0.75 ^{a}	1.98 ^{a}	3.33 ^{a}	0.31 ^{a}	0.2 ^{a}	0.49 ^{a}	0.97 ^{a}
	low	27.1 ^{a}	21.33 ^{a}	15.4 ^{a}	15.1 ^{a}	33.3 ^{a}	50.92 ^{a}	26.98 ^{a}	16.7 ^{a}	10.28 ^{a}	14.49 ^{a}	18.95 ^{a}	23.94 ^{a}	2.2 ^{a}	0.65 ^{a}	1.62 ^{a}	3.55 ^{a}	0.33 ^{a}	0.2 ^{a}	0.47 ^{a}	0.88 ^{a}
	medium	28.4 ^{a}	19.43 ^{ab}	13.1 ^{ab}	13.1 ^{ab}	30.4 ^{ab}	48.0 ^{a}	24.31 ^{a}	15.02 ^{a}	9.3 ^{a}	13.81 ^{a}	18.62 ^{a}	23.68 ^{a}	2.37 ^{a}	0.74 ^{a}	1.91 ^{a}	3.18 ^{a}	0.31 ^{a}	0.19 ^{a}	0.49 ^{a}	0.98 ^{a}
	high	23.0 ^{ab}	17.0 ^{ab}	12.9 ^{ab}	10.1 ^{ab}	27.5 ^{ab}	45.37 ^{a}	23.3 ^{a}	14.96 ^{a}	8.34 ^{ab}	12.9 ^{a}	15.15 ^{a}	22.07 ^{a}	2.22 ^{a}	0.71 ^{a}	1.54 ^{a}	3.11 ^{a}	0.33 ^{a}	0.19 ^{a}	0.48 ^{a}	0.95 ^{a}
	very high	17.27 ^{b}	13.4 ^{b}	10.2 ^{b}	8.3 ^{b}	19.2 ^{b}	29.37 ^{b}	15.11 ^{b}	8.76 ^{b}	6.35 ^{b}	8.17 ^{b}	9.02 ^{b}	14.26 ^{b}	1.93 ^{a}	0.76 ^{a}	1.96 ^{a}	3.25 ^{a}	0.3 ^{a}	0.22 ^{a}	0.48 ^{a}	0.94 ^{a}

Table 3. Means of seedling morphology (size), growth (biomass), and architecture (allocation ratios) variables of *Pinus eldarica* and *Pinus nigra* seedlings at different intensities of soil compaction. Different letters in each species column indicate significant differences among intensities of soil compaction ($p < 0.01$) based on Duncan's tests.

		Seedling Morphology (Size)					Seedling Growth (Dry Biomass)							Seedling Architecture (Allocation Ratios)							
Species	**Compaction Intensity**	**Stem Length (cm)**	**Stem Diameter (mm)**	**Main Root Length (cm)**	**Main Root Diameter (mm)**	**Lateral Root Length (cm)**	**Total (g)**	**Shoot (g)**	**Stem (g)**	**Leaf (g)**	**Main Root (g)**	**Lateral Root (g)**	**Total Root (g)**	**Lateral/Main Root Length**	**Lateral/Main Root Dry Biomass**	**SSL (cmg^{-1})**	**SRL (cmg^{-1})**	**SMR**	**LMR**	**RMR**	**R/S**
Pinus eldarica	control	12.67 ^{a}	5.24 ^{a}	13.6 ^{a}	3.9 ^{a}	45.4 ^{a}	7.18 ^{a}	3.9 ^{a}	1.37 ^{a}	2.53 ^{a}	1.74 ^{a}	9.0 ^{a}	3.28 ^{a}	3.35 ^{a}	0.91 ^{ab}	9.65 ^{a}	30.0 ^{a}	0.19 ^{a}	0.35 ^{a}	0.46 ^{a}	0.86 ^{a}
	very low	12.06 ^{a}	4.55 ^{ab}	15.0 ^{a}	3.4 ^{ab}	48.3 ^{a}	6.16 ^{ab}	3.66 ^{ab}	1.1 ^{ab}	2.56 ^{a}	1.37 ^{ab}	10.4 ^{ab}	2.5 ^{abc}	3.26 ^{a}	0.85 ^{ab}	12.1 ^{a}	44.2 ^{a}	0.18 ^{a}	0.41 ^{a}	0.42 ^{a}	0.77 ^{a}
	low	12.23 ^{a}	4.02 ^{abc}	11.6 ^{ab}	3.1 ^{abc}	39.4 ^{ab}	5.08 ^{bc}	2.44 ^{bc}	0.79 ^{bc}	1.65 ^{ab}	1.37 ^{ab}	9.45 ^{ab}	2.64 ^{ab}	3.52 ^{a}	0.91 ^{ab}	18.9 ^{a}	35.1 ^{a}	0.15 ^{a}	0.33 ^{a}	0.51 ^{a}	1.09 ^{a}
	medium	8.21 ^{b}	3.27 ^{bcd}	9.03 ^{bc}	2.9 ^{bc}	28.0 ^{bc}	3.74 ^{cd}	2.13 ^{cd}	0.71 ^{bc}	1.42 ^{ab}	0.77 ^{c}	9.88 ^{bc}	1.62 ^{cd}	3.11 ^{a}	1.14 ^{a}	13.1 ^{a}	34.6 ^{a}	0.19 ^{a}	0.37 ^{a}	0.44 ^{a}	0.84 ^{a}
	high	8.45 ^{b}	2.83 ^{cd}	9.2 ^{bc}	2.2 ^{c}	25.1 ^{bc}	3.11 ^{d}	1.34 ^{cd}	0.47 ^{c}	0.87 ^{c}	1.02 ^{bc}	9.15 ^{bc}	1.76 ^{bcd}	3.26 ^{a}	0.73 ^{ab}	19.7 ^{a}	40.5 ^{a}	0.15 ^{a}	0.28 ^{a}	0.57 ^{a}	1.48 ^{a}
	very high	5.54 ^{b}	2.13 ^{d}	6.8 ^{c}	2.4 ^{bc}	19.2 ^{c}	2.12 ^{d}	1.0 ^{d}	0.33 ^{c}	0.68 ^{c}	0.78 ^{c}	6.09 ^{c}	1.12 ^{d}	3.04 ^{a}	0.44 ^{b}	19.7 ^{a}	55.0 ^{a}	0.15 ^{a}	0.32 ^{a}	0.52 ^{a}	1.1 ^{a}
Pinus nigra	control	12.49 ^{a}	4.13 ^{a}	24.1 ^{a}	3.7 ^{a}	57.6 ^{a}	6.18 ^{a}	3.41 ^{a}	1.41 ^{a}	2.0 ^{a}	1.38 ^{a}	1.55 ^{a}	2.77 ^{a}	2.47 ^{a}	1.0 ^{a}	9.49 ^{a}	42.3 ^{ab}	0.23 ^{a}	0.32 ^{a}	0.45 ^{a}	0.82 ^{a}
	very low	10.21 ^{ab}	4.44 ^{ab}	20.5 ^{ab}	2.8 ^{ab}	52.3 ^{ab}	5.55 ^{ab}	3.16 ^{a}	1.28 ^{a}	1.89 ^{ab}	1.06 ^{ab}	1.13 ^{a}	2.39 ^{ab}	2.56 ^{a}	1.39 ^{a}	8.92 ^{a}	41.4 ^{ab}	0.22 ^{a}	0.34 ^{a}	0.44 ^{a}	0.84 ^{a}
	low	9.12 ^{ab}	3.18 ^{abc}	14.8 ^{bc}	2.5 ^{b}	33.6 ^{bc}	5.6 ^{ab}	3.27 ^{a}	1.38 ^{a}	1.89 ^{ab}	0.89 ^{ab}	1.27 ^{a}	2.33 ^{ab}	2.42 ^{a}	1.79 ^{a}	6.82 ^{a}	23.9 ^{b}	0.25 ^{a}	0.34 ^{a}	0.41 ^{a}	0.71 ^{a}
	medium	7.2 ^{bc}	2.65 ^{bc}	13.6 ^{bc}	2.3 ^{bc}	30.2 ^{a}	4.46 ^{bc}	2.74 ^{ab}	1.38 ^{a}	1.37 ^{abc}	0.6 ^{bc}	0.85 ^{a}	1.72 ^{b}	2.23 ^{a}	2.59 ^{a}	6.41 ^{a}	33.3 ^{ab}	0.31 ^{a}	0.31 ^{a}	0.39 ^{a}	0.63 ^{a}
	high	6.78 ^{bc}	2.81 ^{abc}	9.8 ^{c}	1.6 ^{bc}	30.9 ^{c}	3.76 ^{c}	1.79 ^{bc}	0.72 ^{ab}	1.07 ^{bc}	0.75 ^{bc}	0.74 ^{a}	1.97 ^{b}	3.21 ^{a}	1.68 ^{a}	13.1 ^{a}	26.0 ^{ab}	0.18 ^{a}	0.28 ^{a}	0.54 ^{a}	1.29 ^{a}
	very high	4.22 ^{c}	1.57 ^{c}	9.6 ^{c}	1.2 ^{c}	26.0 ^{c}	1.93 ^{d}	1.08 ^{c}	0.31 ^{b}	0.77 ^{c}	0.35 ^{c}	0.34 ^{b}	0.85 ^{c}	3.29 ^{a}	1.73 ^{a}	15.0 ^{a}	57.7 ^{a}	0.16 ^{a}	0.37 ^{a}	0.47 ^{a}	0.95 ^{a}

4. Discussion

Augmenting soil strength vigorously influenced the morphological and growth parameters of four deciduous and evergreen seedlings in the present study and supported the current study's hypotheses that increasing the soil mechanical hindrance could cause decreased seedling growth. All of the morphological and biomass responses in maple and alder seedlings augmented slowly to the moderate (M) treatment (up to 1.3 MPa), then, with further increasing compaction, to the VH treatment, reduced quickly. Concerning the response to soil compaction of the evergreen species *Pinus eldarica* and *Pinus nigra*, all of the size and biomass variables in all these seedlings statistically decreased from the control treatment to the very high treatment with increasing compaction. The alterations in the morphological variables of the root system, such as the lateral root length and the main and lateral root dry biomass, were specifically conspicuous. Smaller primary and lateral roots reported in compaction-induced soils are in agreement with the former literature concluding that increased soil strength leads to a decrease in the growth rate of roots [25,27] and support the statement that increased soil penetration resistance is a crucial element that can unfavorably influence the initial progress of woody species seedling establishment and growth [18].

The reduction in the penetration of plant roots may hamper the approach to and absorption of nutrients and water [34]. This will then lead to insufficient water in the leaf, a reduction in the photosynthetic rate, a decrease in the size and growth of the stem and the total biomass of the seedling, and restricted seedling durability in drought conditions [32].

Contrary to the commonly accepted notion that soil compaction has a negative impact on tree species accomplishment, the results that we obtained in studying deciduous species showed that total dry biomass increased by augmenting soil compaction to M treatment (up to 1.3 MPa). Similarly, Tracy et al. (2012) [33] demonstrated that plants developed on soil with clay loam texture commonly achieved higher growth at the greatest value of soil BD by 1.5–1.6 Mg m^{-3}, whereas plants developed on soil with loamy sand texture reached the greatest growth at the BD of 1.3 Mg m^{-3}. Similarly, Alameda and Villar (2009) [24] concluded that just 53% of the 17 studied woody species (nine from seventeen) revealed a greater total biomass after a slight increase in soil BD, which can be explained by a higher root–soil connection. Additionally, Mosena and Dillenburg (2004) [44] illustrated that the shoot expansion growth and total plant biomass enhanced by a higher degree of soil compaction could be explained by the observation of a closer contact in the root–soil matrix.

According to the results, we can conclude that restraint for seedling growth for the investigated species occurs at values that are lower than the commonly reported threshold of 2.0–2.5 MPa [35,45]. Although the above-mentioned limit may be further pertinent for woody species seedlings being to survive rather than grow [31], the value of SPR < 2.5 MPa found to be effective in reducing the growth variables of *Pinus radiata* [46], even the value of SPR < 0.6 MPa can impede the establishment of seedlings of the cabbage tree (*Cordyline australis*) [27]. Also, Alameda et al. (2012) [47] concluded that the increasing values of soil BD until 1.4 Mg m^{-3} boosted growth variables, but at BD values > 1.4 Mg m^{-3}, the growth variables reduced. Therefore, we can conclude that the species usually used for afforestation in the Hyrcanian forests in Iran are very sensitive to soil compaction, showing decreased growth at values lower than those generally reported as thresholds in the literature. Thus, we strongly recommend the application during the establishment of the skid trails of all those best management practices to decrease soil compaction, such as placing mats or mulches on the skid trails [48–50].

Our hypothesis states that increased soil mechanical hindrance would cause changes in the growth allocation patterns in the various seedling portions, leading to architectural alterations to the woody species seedlings. It is supported by the obtained results. According to the concept of a 'functional equilibrium' for the allocation of seedling biomass, woody species seedlings will devote somewhat greater biomass to the root portions if the restrictive parameter for the growth is below ground (e.g., nutrients and water). Conversely, plants will devote relatively higher biomass to shoots if the restrictive parameter is above ground (e.g., light and CO_2) [51]. It can, therefore, be said that the woody seedling devotes greater biomass to the organ that is in a situation of restricted resources and, therefore, compensates to obtain the most [51]. Our results revealed higher allocation to roots by enhancing soil strength to moderate treatment (up to 1.3 MPa) in deciduous species, both *A. velutinum* and *A. subcordata*. However, the two deciduous species selected in this study were fast-growing. A high allocation to root mass is typically associated with situations where soil resources, namely water and nutrients, are low [44]. Then, fast-growing tree species have, to some extent, greater LMR [52,53]. Contrarily, decreased architectural features were observed in evergreen species with increasing compaction.

The results revealed that the growth variables showed two trends: first, in deciduous species, the results showed that with enhancing SPR to moderate treatment (up to 1.3 MPa), total dry biomass improved. Second, following augmenting SPR from M to VH treatment, the total dry biomass diminished. In evergreen species, results showed that total dry biomass gradually decreased by enhancing soil compaction levels. However, there was a higher difference in total dry biomass between deciduous and evergreen species, with deciduous species up to 5 times higher in the moderate compaction level and up to 2 times higher in the very high compaction level than evergreen species. These results were consistent with Alameda and Villar (2009) [24], who found that total dry biomass follows two types of answers. Species type I are those in which increased SPR initially fosters higher growth, while further increasing SPR causes a growth decrease.

It is worth highlighting that there may be a study limitation. The results obtained in the greenhouse may be somewhat higher than those obtained in a natural context. This is due to the fact that the pots exert a force on the plant roots due to the rigid structure of the pot. This condition is very different from soil, where a root will move through cracks and fragile parts of the soil [34]. The soil texture was not changed in this study. However, the effects of soil texture on root growth could be primarily interpreted according to the differences in air, water, and strength of soil between textures [46,54–61]. In this study, the seedling pots were irrigated regularly daily and did not experience any water deficit.

For future studies, multivariate statistics can be applied to compare the growth and architecture variables of seedlings in different species and different soil conditions. Also, the functional characteristics of plants, such as the total surface of the roots, the absorption of elements on the roots and the rate of their uptake to the roots, the oxygen content under conditions of soil compaction, and root respiration, can be considered as basic variables.

5. Conclusions

We examined the alterations in seedling morphology, growth, and architecture of four species (two deciduous and two evergreen) usually used for afforestation in the Hyrcanian forests in Iran following experimentally set soil compaction levels in a greenhouse. Augmenting soil compaction heavily impacted the morphological and growth variables of four deciduous and evergreen seedlings and revealed that enhancing soil penetration resistance (SPR) would lead to a reduction in all variables of above- and below-ground seedling sizes and biomass of the total seedling. On the one hand, our results demonstrated that the features of deciduous species even improved with compaction levels up to 1.3 MPa. Above this threshold, the seedling features started to decline quickly. On the other hand, we found that the features of evergreen species decreased with increasing soil compaction in a uniform trend. However, the threshold value of 1.3 MPa is much lower than those reported in the literature for other species, so it is possible to state that the species used for afforestation in the Hyrcanian forests of Iran are very sensitive to soil compaction, and therefore, the application of reduced-impact logging and of best management practices to decrease soil disturbance are particularly recommended. However, extensive studies should be conducted on the sensitivity of selected tree species for afforestation in Hyrcanian forests to soil compaction so that species with less sensitivity to soil compaction may be selected for the restoration program of the Hyrcanian forest in northern Iran.

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