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BIOMASS ALLOCATION, LEAF AND FINE ROOT MORPHOLOGICAL ADAPTATIONS IN YOUNG BLACK ALDER (*Alnus glutinosa* (L.) Gaertn.), SILVER BIRCH (*Betula pendula* Roth.) AND SCOTS PINE (*Pinus sylvestris* L.) PLANTATIONS ON RECLAIMED OIL SHALE POST-MINING AREAS

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Abstract. *The biomass allocation, as well as leaf and short root morphological parameters in young (1–7-year-old) black alder (Alnus glutinosa (L.) Gaertn.), silver birch (Betula pendula Roth.) and Scots pine (Pinus sylvestris L.) plantations on the oil shale post-mining area were investigated with the aim to analyze morphological adaptations of studied parameters in relation to tree species and stand age. The adaptive strategies of tree species in young plantations on the reclaimed stony and alkaline mining area were different. Scots pine allocated more biomass into leaves and fine roots while black alder and silver birch into stems and coarse roots. The black alder leaves were heavier and with larger area, but thinner than those of silver birch. Different strategies of short root morphological adaptations were observed in coniferous and deciduous tree species on the oil shale post-mining area. Deciduous species were found to have higher short root specific root area and specific root length values, and lower short root tissue density and diameter values compared to coniferous species such as Scots pine. An extensive building of the fine root system was inherent to Scots pine, whereas deciduous trees improved mineral nutrition more by morphological adaptations of fine roots.*

Keywords: *post-mining reclamation, leaf and fine root characteristics, belowground biomass allocation, black alder, silver birch, Scots pine.*

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1. Introduction

Mining activities, especially opencast mining, create significant areas of degraded land that need restoration. The goal of restoration is usually to develop a long-term sustainable ecosystem native to the area where mining was carried out [1]. By the year 2006 the area damaged by oil shale opencast mining in Northeast Estonia was 13 098 ha, of which 10 347 ha had been afforested [2]. After opencast mining, the relief of the alkaline (ca 8) wasteland is rugged, the soil heterogeneous and extremely stony, and the N and organic content of oil shale mining spoil is low. Since the agricultural use of post-mining landscapes has been made difficult by the heterogeneity of the soil and poor moisture conditions, it will be more reasonable to afforest such lands [3, 4]. Afforestation is a sustainable option for reclamation of post-mining landscapes [4–7] to capture CO_2 and to create renewable energy sources. For a long time Estonian oil shale mining areas have been “research laboratories” where large-scale investigations have been conducted to find out the most suitable tree species for restoration [8]. Results of a previous research on restoration of post-mining areas in Estonia showed that new stands have higher growing stock than the stands that grew in those areas before mining [3]. Among coniferous trees, various introduced larch species (*Larix europaea*, *L. sibirica*, *L. kurilensis*) have shown the fastest growth, while native species of silver birch and black alder have proved to be the most productive deciduous trees [3, 9, 10]. Despite successful restoration, it should be noted that so far the share of Scots pine planted (86% of the afforested area) has been disproportionately high [3]. Moreover, the opencast mining in Northeast Estonia has been moving toward areas requiring deeper excavation [3, 11] and the quality of the substrate has deteriorated and its stoniness has increased due to the thickening overburden in new mining areas. These harsh growing conditions might limit the growth and survival of different tree species at different rates, hence the choice of tree species is a decisive factor for a successful reclamation of the mined land.

For successful forestation and stability of plantations, the proportion of deciduous trees in new stands should rise to 40–60%. Deciduous species have a number of advantages over conifer monocultures, such as increased N and P availability in the soil, faster growth at a young age, and higher resistance to pests, diseases and fires [3, 4, 12]. Black alder could be considered to be a “biological fertilizer”, which improves soil nitrogen status, fixing N_2 in symbiosis with *Frankia* in its root nodules, and increases phosphorus availability in soil by the activity of its roots and associated microbial communities [13, 14]. However, the potential of different tree species for the reclamation of exhausted opencast oil shale mines in relation to biomass production, as well as leaf and fine root adaptations has still been poorly investigated.

Fine root adaptations are among the key factors determining the growth rate and performance of species. The morphological plasticity of fine roots has been proposed as a mechanism by which plants respond to variation in soil nutrient supply [15–17]. Alterations in fine root morphological traits reflect exploitation of water and nutrients in the soil [18], as well as the cost/benefit ratio of the fine root system [19].

Trees exhibit plasticity in leaf morphology, allowing them to optimize photosynthetic efficiency as well as other ecophysiological functions [20]. Specific leaf area (SLA) describes the photosynthetic surface area that can be constructed from a unit dry mass of organic matter. SLA is a key trait in plant growth, and has been used as an indicator of the potential for light-resource utilization and hence plant photosynthetic capacity [20]. The morphology of roots and leaves affects their functions and changes with tree age. There must be coordination between the aboveground and belowground parts of trees with respect to the acquisition and allocation of limiting resources and adaptation to different stressors [21].

The ecological restoration of post-mining areas offers a rare opportunity to examine the development of ecosystems starting at “point zero” [22]. Soil formation and the development of the whole ecosystem in the levelled spoil of post-mining areas can be considered as a primary succession. The first years of stand development are most critical. The present study deals with above- and belowground biomass allocation, as well as with the leaf and root characteristics of young black alder, silver birch and Scots pine plantations on reclaimed oil shale mining areas. The species survival, as well as above-ground biomass production and nutrient accumulation in the same plantations have been considered in a previous study [23].

The working hypotheses of the present research were that root and leaf adaptation strategies differ between tree species and stand age affects tree structure, and leaf and root morphology. Also, based on the results of previous studies establishing that black alder had a higher survival, and better biomass and nutrient accumulation, the current work suggests this to be associated with more effective root and leaf adaptations in the reclaimed mining area, unlike silver birch and Scots pine. The main aim of the research was to assess the suitability of the studied species for the reclamation of oil shale post-mining areas. The specific aim of this investigation was to analyse the biomass allocation, as well as leaf and short root morphological adaptations in relation to tree species and stand age in young black alder, silver birch and Scots pine plantations on post-mining areas.

2. Material and methods

2.1. Study area

The study was carried out in experimental plantations established on the reclaimed Narva oil shale mining area, Northeast Estonia (59º15'N, 27º42'E). According to the data of Narva meteorological station, which is closest to the experimental area, the mean annual temperature in the region during the observed period was 5.8 °C, and mean annual precipitation was 747 mm.

The plantations had been established directly on the levelled quarry spoil, with no soil preparation being done before planting.

Black alder, silver birch and Scots pine plantations of different age (1-, 2-, 4- and 7-year-old) were investigated. The planting density was 1.5 × 1.5 m for Scots pine, and 2.0 × 2.0 m for black alder and silver birch. The experimental area of 0.56 ha was established in May 2005 by planting 1-year-old seedlings of the species to be studied in 25 × 25 m plots in three replications in the Latin square design. The measurement of trees and estimation of biomass were carried out in 1-, 2- and 4-year-old plantations respectively in August 2005, 2006 and 2008. The short root morphology was assessed in October 2005, 2006 and 2007. The measurements in 1-year-old plantations were made separately in each replication. Considering that there were not any significant differences between replications within a tree species [24], later measurements were performed per plantation. Also 7-year-old plantations (total area 3 ha), which had been established in 2002 by using 2-year-old seedlings, were investigated. In those plantations, fieldwork was carried out at the end of August 2008. A sample plot of 0.1 ha was established per each species plantation. The short root morphology in the plantations was assessed in October 2006. The growth parameters of plantations, aboveground biomass and biomass allocation, as well as soil and plant nutrient concentrations were published earlier [23]. In this paper, results of the research about belowground biomass allocation and morphological adaptations of leaf and fine roots in young plantations are presented. The initial pH of soil in the studied plantations was about 8 and N concentration about 0.030. Soil pH decreased 0.5 unit during the first 7 years and soil N concentration increased to 0.020 [23].

2.2. Estimation of aboveground biomass and leaf parameters

The aboveground biomass of the stand was estimated in the month of August. The model tree method was used to estimate the aboveground biomass production [25, 26].

In 1- and 2-year-old plantations the trees were categorised into three height classes on the basis of height distribution in the stand. One model tree from each height class was randomly selected. In 1-year-old stands the model trees were selected per replication [24] and in 2-year-old stands per plantation. In 4- and 7-year-old stands the trees were divided into five height classes, and a model tree was selected randomly from each class. Additionally, for the purpose of study, a tree from two classes with the largest number of trees was felled. A total of seven model trees per plantation were sampled. Detailed information about the distribution of model trees by height class is presented in [23].

In 1- and 2-year-old stands the aboveground parts of model trees were divided into three compartments: leaves, shoots (current-year shoots and branches (older shoots, age > 1 year)) and stems. In 4- and 7-year-old stands the living crowns of model trees were divided into three equal sections of length. In each section, different compartments including leaves, current-year shoots and branches were separated. The plant material was dried at 70 °C until constant weight and weighed to 0.001 g. For estimation of leaf characteristics, 20–25 leaves with the petiole were randomly taken from each model tree of 1- and 2-year-old plantations and from each crown section of a model tree, and dried under pressure. Leaf area (including the petiole) was measured using the program WinFOLIA (Regent Instruments Inc., Canada). The measured leaves were dried at 70 °C until constant mass; each leaf was weighed to 0.1 mg, and specific leaf area (SLA, m^2 kg^{-1}) was calculated.

2.3. Estimation of belowground biomass and short root morphological parameters

Belowground biomass was estimated by the method of excavation of the root system of model trees. In the youngest plantations (1-, 2-year-old), the root systems of all model trees were excavated, and in 4- and 7-year-old plantations the root system of an average model tree was excavated and investigated. An earlier investigation [27] showed that in stands of deciduous trees of the same age the ratio of aboveground to belowground biomass was practically constant and the ratio found on the basis of one model tree can be used for the whole stand, affording quite an exact estimation of the belowground biomass of the stand. The excavated root systems were washed free of soil and separated into living and dead roots. Living fine roots were differentiated from dead roots by using visible criteria: resilience texture, colour of bark and xylem [28]. Their proportion being negligible, dead roots were not subjected to further analysis. To analyse belowground biomass allocation, root systems were divided into two diameter classes: $d < 2$ mm (fine roots) and $d \geq 2$ mm (coarse roots). In 4- and 7-year-old plantations only coarse roots were under observation. All fractions were dried at a temperature of up to 70 °C and weighed to 0.01 g.

In 1- and 2-year-old plantations the root ratio (RR, %; the proportion of the root system as part of total tree mass) and the ratio of fine roots (FR/R, %; the proportion of fine (< 2 mm in diameter) roots in the root system) were calculated. The foliage/fine root ratio (L/FR) [29] was calculated by dividing the mass of leaves by the mass of fine roots of a tree. In 4- and 7-year-old plantations the coarse root/(shoots + stem) ratio was calculated.

Short roots with living cortex [19] were used to analyse morphological adaptations of fine roots. Prior to measuring morphological parameters, the roots of 10 random root samples per stand were washed with tap water to remove the soil particles. Two random living short root subsamples (on average 15 short root tips) were taken per sample and root tips were counted under a microscope. Short roots were considered alive if the exposed stele was still shiny and resilient [28]. Short root length, projection area and mean diameter (D, mm) of the sample were measured using WinRHIZO^{TM} Pro 2003b (Regent Instruments Inc., Canada). After measuring, short root samples were dried at 70 °C for 2 h and weighed with an accuracy of

0.01 mg (W, mg). The method for determining short root morphological parameters – mean short root length (L, mm), specific root area (SRA, $m^2\ kg^{-1}$), specific root length (SRL, $m\ g^{-1}$) and tissue density (RTD, $kg\ m^{-3}$) is described in detail in [17, 19].

2.4. Statistical analyses

Normality of variables was checked by Lilliefors and Shapiro-Wilk tests. When necessary, log and root transformations were used to normalise the data. The data were subjected to analysis of variance (ANOVA, two-factor cross-factored unreplicated model). The Tukey test was used for a multiple comparison of means. Throughout the study, the means are presented with the standard error of the mean (± SE). Statistical analyses were carried out with the software Statistica 7.0 and the level of significance $\alpha = 0.05$ was accepted in all cases.

3. Results

3.1. Biomass allocation

Statistical results showed that FR/R and L/FR greatly depended on tree species ($F_{[2,2]} = 360.1$ and 9.9 for FR/R and L/FR, respectively; $p < 0.05$) and stand age ($F_{[1,2]} = 34.6$ and 20.1 for the respective ratios; $p < 0.05$). After the first growing season RR was similar in all species (Fig. 1).

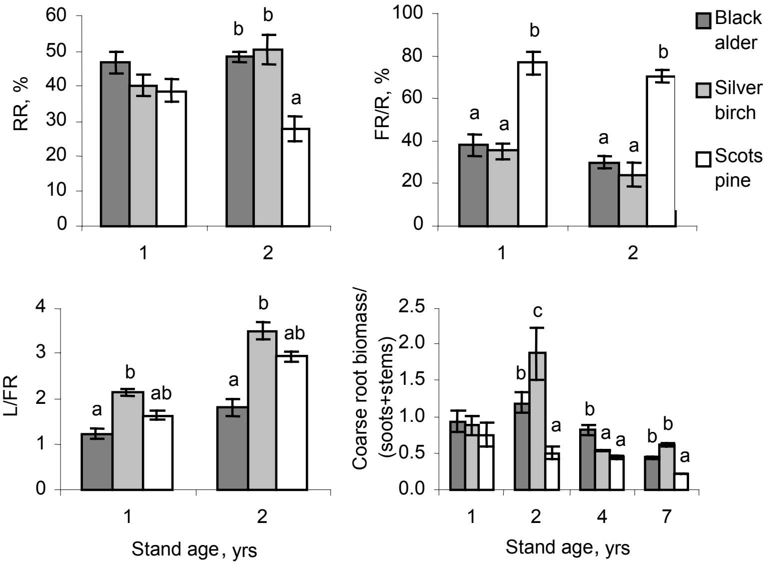

Fig. 1. Root (RR, %), fine root (FRR, %), foliage to fine root (L/FR) and coarse root biomass/(shoots + stem) ratios in the studied plantations (letters indicate differences between tree species in the Tukey test at $p < 0.05$; bars signify standard errors).

After the second growing season RR was similar for deciduous species, but significantly smaller for Scots pine. The FR/R for Scots pine was twice as high as for black alder or silver birch in both growing seasons (Fig. 1). The L/FR ratio was the highest for silver birch and the smallest for black alder (Fig. 1). The coarse root biomass/aboveground woody biomass ratio exhibited a decreasing trend with stand age for Scots pine and black alder (Fig. 1).

3.2. Leaf characteristics

The single leaf mass and leaf area of black alder were significantly larger than those of silver birch in young (1–7-year old) plantations. However, SLA was significantly larger for silver birch (Tukey test, $p < 0.05$; Fig. 2). Although stand age ($F_{[3,3]} = 9.5$, 8.6 and 8.8 for leaf mass, leaf area and SLA, respectively; $p < 0.05$) and tree species ($F_{[1,3]} = 27.8$, 21.1 and 18.7 for the respective parameters, $p < 0.05$) greatly influenced all leaf characteristics, no significant relationship between stand age and any particular leaf characteristic was observed.

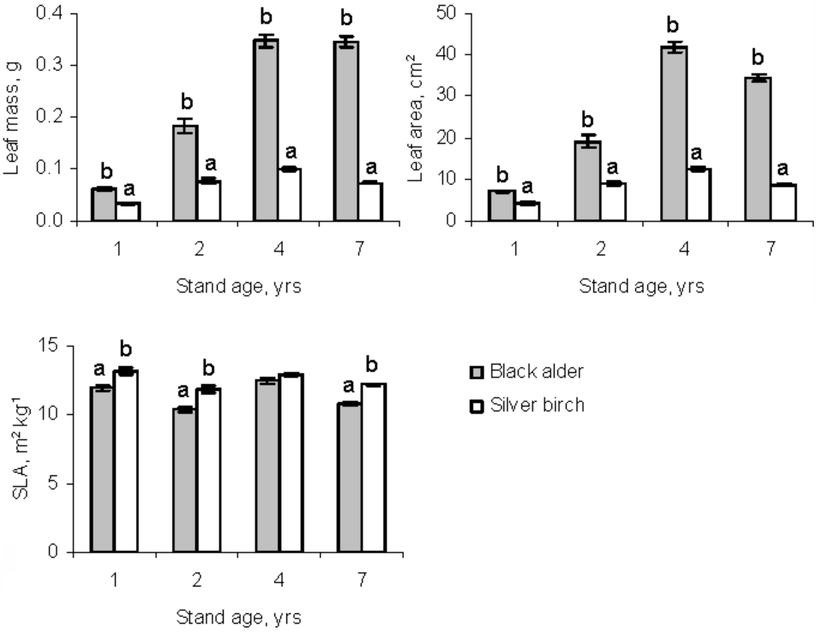

Fig. 2. The dynamics of leaf mass, area and specific leaf area (SLA) in black alder and silver birch stands on reclaimed post-mining area (letters indicate differences between tree species in the Tukey test at $p < 0.05$, bars signify standard errors).

3.3. Root characteristics

The correlation between tree species and short root parameters was considerable ($F_{[2,6]}$ = 6.5, 9.3, 12.6, 73.8, 19.1 and 20.4 for SRA, SRL, RTD, D, W and L, respectively; $p < 0.05$), contrary to that between stand age and short root parameters. Deciduous species were found to have higher specific root area (SRA) and specific root length (SRL) values of short roots and lower short root tissue density (RTD) and diameter (D) values than Scots pine (Tukey test, $p < 0.05$; Fig. 3). The mean short root mass (W) was the smallest for silver birch, while black alder had the highest short root length (L) values (Tukey test, $p < 0.05$; Fig. 3).

A tendency towards decreasing mean short root SRA and SRL and increasing mean short root RTD with increasing stand age was observed for all the studied tree species; however, correlations were not statistically significant.

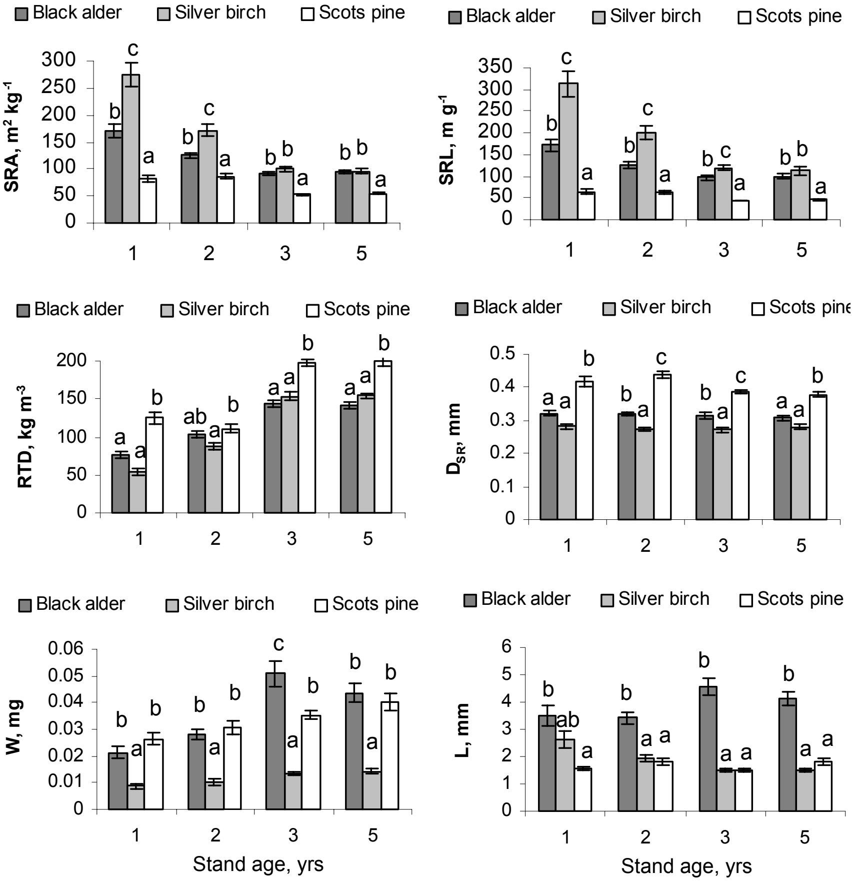

Fig. 3. Mean short root characteristics in the studied stands (1, 2, 3, 5 – age of stand in years) (letters indicate differences between tree species in the Tukey test at $p < 0.05$; bars signify standard errors).

4. Discussion

The current study demonstrated that biomass allocation, both above- and belowground, was tree species specific. Comparison of the shares of different compartments in the biomass of stands did not reveal significant differences between deciduous species, but in Scots pine more biomass was allocated to needles and less to roots than in the case of deciduous trees. At low nitrogen supply, the fast-growing species invest relatively more biomass in their roots than do slow-growing ones [30]. In this study, a tendency towards higher RR for alder and birch than for Scots pine was observed. However, Scots pines had about twice as high a share of fine roots in the root system as the deciduous trees. One possible reason for this is the size of trees and their root systems: both were the smallest in pine. Also, black alder and silver birch need more coarse roots due to their greater aboveground biomass and to ensure the stability of the tree [31]. In harsh soil conditions it is important first to invest more in fine roots to secure survival. Silver birch, black alder and Scots pine differed in L/FR ratio. Black alder had the lowest L/FR ratio and the greatest first-year survival [23, 24]; silver birch had the highest L/FR ratio and the lowest survival. The ratio of coarse roots/(shoots + stem) in black alder and Scots pine stands showed a decreasing trend with stand age. These results are in accordance with those of Helmisaari et al. [32] who found that in Scots pine stands on *Vaccinium* site type the ratios of belowground/aboveground biomass and fine root/needle biomass decreased with stand age. Also, some other investigators observed changes in biomass allocation with increasing age and size of trees [33–36].

SLA is related to the photosynthesizing capacity of the tree and to leaf nutrient concentration [37]. The estimated SLA of a 7-year-old silver birch (12.2 m^2 kg^{-1}) is in good accordance with the results obtained by Uri et al. [27] (15.0 m^2 kg^{-1}) on abandoned agricultural land, and with the data found by Rosenvald [38] in natural forest stand of *Oxalis* site type (14.8 m^2 kg^{-1}). The mean SLA (10.8 m^2 kg^{-1}) of a 7-year-old black alder is comparable to the 12.3 m^2 kg^{-1} found by Johansson [39] for young alders growing on abandoned farmland and the 13.3 m^2 kg^{-1} calculated for a 20-year-old black alder growing on the reclaimed oil shale mining area [12]. In the current study, stands of different age were found to differ in leaf characteristics, but no remarkable relationship between any specific leaf characteristic and stand age was established. For example, Uri et al. [40] did not observe any effect of stand age on the leaf characteristics of grey alder on abandoned agricultural land either. However, some authors have found that SLA decreases with increasing tree age [38, 41]. Morphological parameters of short roots are the best indicators of different root adaptation strategies because the functional compartment of the fine root system, which contains the primary structure and commonly has the highest rate of EcM colonization, assimilates most nutrients [19, 28]. Many studies have examined short root morphology in relation to species and soil conditions [4, 10, 16, 19, 42]. The results of this work showed that short root morphological parameters of the studied species growing on reclaimed mine sites were affected by both tree species and stand age. It is known that trees adapt to nutrient-poor soils by increasing either the mass and length of fine roots (extensive adaptation) or the nutrient uptake efficiency of fine roots or associated microorganisms, or both (intensive adaptation) [4]. The current results indicate different strategies of short root morphological adaptations in coniferous (Scots pine) and deciduous (black alder and silver birch) tree species on oil shale post-mining areas. Both SRA, which affects the uptake rate of nutrients, and SRL, suggesting an intensive exploitation of soil by short roots per root mass unit, were higher for deciduous species, being the highest for silver birch. Scots pine had higher RTD and D. Analogously, Ostonen et al. [19, 42] reported that the SRL and SRA of short roots were greater for silver birch than for Norway spruce and Scots pine. In addition, when comparing 1-year-old seedlings, Comas et al. [43] showed that fast-growing deciduous species have thinner short roots with greater SRL than Scots pine. Curt and Prevosto [44] reported that Scots pine has a relatively coarse fine root system, whereas silver birch has thin and densely branched roots that provide an efficient foraging system. Conifers use a more extensive strategy (increasing the mass and length of short roots) for nutrient acquisition [19, 42]. In the case of Scots pine, an extensive strategy, which leads to an expansion of the short root system, was also verified by the allocation of biomass in 1- and 2-year-old stands. The proportion of short roots in the root system of Scots pine was approximately twice as high as in the deciduous species. The higher SRL and SRA of deciduous species indicate that they use an intensive strategy in the uptake of nutrients: the species form a large assimilating area per mass unit of short roots. The highest SRL and SRA of short roots of silver birch imply a lower short root cost.

However, one cannot rule out the possibility that the lowest survival of silver birch is due to its too thin roots and the high ramification of roots decreasing water conductivity [45] and causing a shortage of assimilates. In this work, the stand age-morphological parameters correlation was detected. The decreasing trend of short root SRA and SRL and increasing trend of RTD with stand age for all the species under study were observed. The results of the current research about changes in root morphological parameters under similar growth conditions are in accordance with findings of other investigations [10, 46]. The results obtained differ from those of the study carried out in a chronosequence of 10-, 30-, 60- and 120-year-old Norway spruce stands where no effect of age on the SRL of fine roots was observed [47]; however, younger spruce stands were not included in the study. Borja et al. [47] concluded that functional changes in fine roots occur in response to quantitative change in biomass (production of more or longer roots) rather than as a result of morphological adaptations. However, silver birch is oriented more towards fine root adaptations than increasing fine root biomass compared to coniferous tree species [48]. Also, Lõhmus et al. [10]

found that unlike black alder, birch is oriented more towards fine root adaptations than support of rhizosphere communities.

The short root SRA of a 5-year-old silver birch in the reclaimed oil shale mining area was significantly higher than that of young birches growing in fertile *Oxalis* forest site type [38] and on agricultural land [49]. However, the short root SRL of silver birch found in this study was higher than that of young birches in forest [38]. Higher root SRL leads to better exploitation of soil by roots, facilitating nutrient uptake [50]. As reported by Rosenvald et al. [49], high SRL and SRA could be root nutrition stress indicators for silver birch.

5. Conclusions

Afforestation of alkaline mining spoil with fast-growing trees is the best means to accelerate the development of new forest ecosystems. The effect of tree species and stand age on biomass allocation, as well as root and leaf morphological adaptations was established. Scots pine allocated more biomass into leaves and fine roots while black alder and silver birch into stems and coarse roots. The leaves of black alder were heavier and with larger area, but with smaller SLA compared to those of silver birch. At the same time, no stand age-leaf characteristics relationship was observed. Strategies of short root morphological adaptations in coniferous and deciduous tree species on the oil shale post-mining area were found to differ. Deciduous species had higher short root SRA and SRL values, and lower RTD and D values compared to Scots pine. An extensive building of the fine root system was inherent to Scots pine, whereas deciduous trees improved mineral nutrition more by morphological adaptations of fine roots. The tendency towards decreasing mean short root SRA and SRL, and increasing mean short root RTD with growing stand age was noticed. The present investigation is primarily aimed at estimation of early ecosystem development on the reclaimed post-mining area. The suitability of tree species for reclamation of post-mining landscapes, their growth dynamics, as well as tree species- and stand age-related changes in it will need further study.

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