Oil Shale, 2004, Vol. 21, No. 1
pp. 43-58

ISSN 0208-189X

https://doi.org/10.3176/oil.2004.1.05

PRODUCTIVITY OF BLACK ALDER (*ALNUS GLUTINOSA* (L.) GAERTN.) PLANTATIONS ON RECLAIMED OIL-SHALE MINING DETRITUS AND MINERAL SOILS IN RELATION TO RHIZOSPHERE CONDITIONS

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The present research was carried out in three black alder plantations in Estonia in 1998–2002. The above-ground productivity and the efficiency of nitrogen and phosphorus use in a plantation in reclaimed opencast oil-shale mining area in Sirgala were analyzed and compared with two plantations growing on fertile mineral soils. The activity and diversity of microbial communities in the soil–root interface and in bulk soil were investigated. The above-ground productivity of the plantations was comparable (14.3 to 17.2 t ha^{-1} yr^{-1}); nitrogen use efficiency (116.5 kg kg^{-1}) was highest in Sirgala. Although initial phosphorus content in oil-shale mining detritus is low, the availability of phosphorus was highest in Sirgala. Alders created a favorable environment for microbes at their soil–root interface in oil-shale mining detritus. A planting density from 2,000 to 2,500 trees per hectare is recommended for establishing plantations of black alder on exhausted oil-shale opencast mines.

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Introduction

Every year opencast oil-shale mining in Estonia creates substantial areas of wasteland that require recultivation. Since the use of the wasteland for agriculture is made difficult by the heterogeneity of the soil [1] and by poor moisture conditions [2], their afforestation is more suitable. On the 1st of January 2002, exhausted oil-shale mines covered 12,319 ha of land, and 9,246 ha of that had been forested [3]. Since 1960, when extensive afforestation of exhausted oil-shale opencast mines in Northeast Estonia was begun [4], a disproportionately large share of conifers has been planted (over 90% of the area). At the same time, deciduous species have a number of important advantages over conifers on exhausted oil-shale opencast mines. Deciduous trees grow faster than conifers and are less susceptible to insect damage and fungal diseases. The creation of deciduous plantations on wasteland also helps to improve the soil conditions and reduces air pollution and the threat of forest fire [5].

Black alder (*Alnus glutinosa* (L.) Gaertn.) is found naturally in most parts of Europe, as well as in Asia and North Africa [6], and has also been planted in North America [7, 8]. Black alder survives in very wet soil conditions during the dormant season, tolerates late spring and early autumn frosts, and produces stump sprouts after cutting. The species grows at a wide pH range, but optimum development is usually on soils ranging between pH 4.0 and 7.5 [9].

Owing to the ability to fix dinitrogen by the symbiosis of actinomycetes *Frankia* in alder root nodules, the soil under alders is enriching by nitrogen, mainly *via* above- and below-ground litter. Due to low nitrogen retranslocation from senescing leaves (from 2.5 to 14%), alder leaf litter is extremely rich in nitrogen and mineralizes easily [10–14]. Moreover, the leaf litter of alders can accelerate the decomposition of nitrogen-poor leaf litter from other tree species [15]. Thus, alders could be considered to be ‘biological fertilisers’ that improve soil nitrogen status. Macro- and micronutrients other than nitrogen should mainly be assimilated from the soil or retranslocated from senescing leaves. Alders increase phosphorus availability in soil by the activity of their roots and associated microbial communities [16, 17].

The majority of alder roots with primary structure are ectomycorrhizas. According to recent results, half of the soil respiration in a stand could be supported by forest trees *via* ectomycorrhizal hyphae [18]. Hence, plant roots can be considered to be ‘biological engineers’ in the soil, since they create and maintain their own milieu not only by their physical presence but also by actively transforming biotic and abiotic components of the system. Examples of such transformations include the maintenance of microbial communities [19] and increased weathering of minerals [20] due to processes such as exudation of organic acids and enzymes to the rhizosphere and to the soil–root interface. In spite of the small volume the rhizosphere occupies in the mineral soil [21], it plays a central role in the maintenance of the soil–plant system. Interactions between roots, microbial communities and the soil, under forest conditions, could involve feedback loops driven by photosynthates released by roots.

Populations of microbes in the rhizosphere and the soil–root interface differ quantitatively and qualitatively from those in the bulk soil; their numbers are generally higher, and different populations are commonly represented. Unless rhizodeposition strongly affects the structure and activity of soil microbial communities and plant nutrition, few studies focus on root surface bacteria of forest trees. Interaction of roots and soil microbial communities is especially important in unfavourable site conditions, including reclaimed opencast oil-shale-mining areas. Our recent investigations of natural deciduous and coniferous stands in Estonia revealed significantly higher diversity and activity of microbial communities in the soil–root interface of grey alder (*Alnus incana* (L.) Moench.) than of other investigated tree species: silver birch (*Betula pendula* Roth.), Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) [22]. The diversity and activity of rhizosphere microbial communities were already approximately the same in a 6-year-old grey alder plantation on abandoned agricultural land [17], as they were in a riparian grey alder stand of high fertility in Porijõgi [22, 23]. It has been shown that in black alder the size of the total microbial population and the numbers of ammonifying and proteolytic microorganisms were higher in the plant rhizosphere and soil–root interface than in bulk soil, litter, and root-free soil under trees [24].

For economic reasons, the production of a considerable amount of biomass and high-quality timber makes black alder a preferred species in soil improvement activities (mining areas, sandy soils, etc.) in Europe as well as in North America [5, 25]. The potential of black alder for the recultivation of exhausted oil-shale opencast mines is still poorly understood.

The aims of the present study were (i) to analyze the above-ground productivity and the efficiency of nitrogen and phosphorus use in a black alder plantation on reclaimed oil-shale mining detritus in comparison with the plantations growing on mineral soils, (ii) to compare the activity and diversity of microbial communities in the soil–root interface and in the bulk soil, and (iii) to give recommendations on the suitability of black alder for recultivation of exhausted oil-shale opencast mines.

Material and Methods

Study Sites

The present study was carried out in three plantations of black alder established in 1978. Planted seedlings were one year old, with an average height of 30 cm [26]. The distance between planting rows varies from 2 to 3 m depending on the plantation.

Table 1. **Main Characteristics of the Studied Black Alder Plantations**

Stand Characteristics (Age 21 Years)

Plantation	Location	Site	Number of stems per ha	Mean overbark diameter at breast height (DBH), cm	Mean height *H*, m	Mean height of the beginning of the living crown *C*, m	Basal area BA, $m^2\ ha^{-1}$	Growing stock G, $m^3\ ha^{-1}$
Sirgala	59°17'N 27°44'E	Reclaimed oil shale mining detritus	2300	12.4 ± 0.2	13.4 ± 0.2	8.1 ± 0.2	27.9	189
Parapalu	58°20'N 27°24'E	Abandoned agricultural land	2788	10.4 ± 0.2	12.4 ± 0.2	8.2 ± 0.2	23.5	153
Songa	58°19'N 25°21'E	Forest land	1530	13.9 ± 0.3	15.1 ± 0.2	8.8 ± 0.2	23.2	172

Topsoil Properties

Plantation	Soil type FAO-UNESCO	Depth of horizon, cm	Bulk density BD, $g\ cm^{-3}$	Content of clay (<0.002 mm), %	Acidity pH_{KCl}	Total N, %	Available P, $mg\ kg^{-1}$	Available K, $mg\ kg^{-1}$	Organic matter, %
Sirgala	Oil shale mining detritus	0–10	n.e.[*]	11.8	7.9	0.29	60.4	88.3	8.5
Parapalu	Humic Gleysol	0–24	0.24	2.7	5.3	0.75	33.3	46.4	9.4
Songa	Mollic Gleysol	0–20	1.09	2.8	6.5	0.36	18.2	58.0	7.0

[*] n.e. – not estimated.

One of the plantations (Sirgala) was established on oil-shale mining detritus, the second (Parapalu) on abandoned agricultural land (periodically flooded meadow), and the third (Songa) on a patch of forest land (clearing at *Aegopodium-Dryopteris* site type).

One sample plot (0.1 ha) was established in each plantation in 1998. Overbark diameter at breast height, the height, and the height of the beginning of the living crown were measured for all alders growing on sample plots. In Songa and Parapalu one soil pit (down to 1.0 m depth) was made, and soil type was determined according to the FAO-UNESCO classification. As a result of opencast oil-shale mining, the relief in Sirgala is rugged, and the soil extremely stony. Uneven distribution of limestone rubble and fine earth causes heterogeneous soil. The stone content varies from 15 to 100% in oil-shale mining areas [1, 2]. Main characteristics of the alder plantations are presented in Table 1.

Productivity and Nutrient Estimation

Dimension analysis techniques [27] were used to estimate the total above-ground biomass and biomass production in 21-year-old plantations of black alder. All alders growing on sample plots were categorized into five diameter classes. In early August 1998 one tree from each diameter class was felled. The estimation of biomass and nitrogen, as well as phosphorus, pools in the above-ground parts of the plantations was described by Vares [28]. Total above-ground biomass production consists of the annual increment of leaves, branches and stems. Foliar biomass and production are equal; the production of branches consists of primary growth (current year shoots without leaves) and secondary growth. The later part was estimated by dividing branch overbark (wood + bark) mass (without current year shoots) by branch age.

To estimate stem production, each bole was divided into 1-m sections; discs from the base of each section were taken, and the overbark diameter and the fresh mass of each section were determined. Bark thickness, the widths of the last 3–5 annual rings, and the number of annual rings were measured, and the annual increments were calculated using WINDENDRO (Regent Instruments, Inc.) software. The relative increments of the wood and bark of stems were assumed to be equal. For estimation of the biomass and biomass production of alders' above-ground compartments, the allometric equation was used:

$$\ln y = \mathrm{a} + b \ln x \tag{1}$$

where y is the biomass, kg, or biomass production, kg yr^{-1}, of a compartment;
x is the overbark diameter at breast height, cm.

As foliar parameters on leaf area basis (single leaf area, leaf weight per area (LWA), specific leaf area (SLA) and leaf area index (LAI)) are important for tree and stand functioning, leaf measurements were made. To measure foliar parameters, 60–75 leaves per crown were herbarized, and the area and the oven-dry mass of each leaf were determined. All leaf measurements were made in early August when leaf mass was the largest. In all, 882 single leaves were measured using WINFOLIA (Regent Instruments, Inc.) software.

Chemical Analysis

The plant samples were analyzed for total Kjeldahl nitrogen (Tecator AN 300) and phosphorus (Tecator ASTN 133/94). The total nitrogen in soil samples was determined by the Kjeldahl procedure. To analyze available (ammonium lactate extractable) phosphorus and potassium in soil samples, flame photometry was used. Soil organic matter content was determined by ashing at 360 ºC. All samples were analyzed in the Laboratories of the Estonian Agricultural University.

Microbiological methods

Samples for microbiological analysis were collected in black alder plantations from 10 random points (20×20 cm^2) from a depth of up to 10 cm in October 2002. The samples were bulked and the fractions of bulk soil, rhizosphere and soil–root interface were separated according to Gobran and Clegg [21]. All roots were carefully removed by hand from the field-moist mineral soil, which was then passed through a 2-mm mesh sieve, to give the bulk fraction (Bulk). The coarse roots ≥ 2 mm in diameter were separated, the remaining fine roots ($d < 2$ mm) and soil were gently shaken for 1 min in a plastic container to separate the soil aggregates from the roots to give the rhizosphere fraction. The remaining fine roots with adhered soil gives the soil–root interface fraction (SRI).

Community-level physiological profiles of microbial samples (CLPP). BIOLOG EcoPlates (Biolog, Inc.) were used to determine community-level physiological profiles of Bulk and SRI microbial samples. A 150-µl aliquot of a 10^{-4} dilution of the soil sample was added to each of the 96 wells in the microplate. Plates were incubated at 25 ºC and color development was measured every 24 h for 120 h as absorbance at 590 nm, with optical density plate reader Multiscan 340C.

Substrate induced respiration (SIR) and basal respiration. Active microbial biomass was determined as described by Schinner and others [29], using the method of substrate-induced respiration (SIR). Microbial respiration activity (BAS) was measured by trapping the evolved carbon dioxide in sodium hydroxide. The carbon availability index, which relates the respiration rate without (sufficient readily available) substrate, BAS, and with the addition of sufficient readily available substrate, SIR, was also calculated.

Statistical Analysis

Normality of variables was checked by the Lilliefors and Shapiro-Wilk tests; single leaf area and mass were normalized. Data were analyzed by regression analysis and multifactor analysis of variance (MANOVA) using STATISTICA 6.0 software. Assumptions of MANOVA were fulfilled in all cases. The measure of the fit of Equation (1) was based on coefficient of determination (R^2), standard error of estimate (S.E.E.), and level of probability (p). Means are presented together with standard error of the mean (±S.E.). In all cases, level of significance $\alpha = 0.05$ was accepted. Biolog profiles were summarized as AWCD (average well color development) and by Shannon diversity index. Raw optical density values, as well as data normalised by AWCD, were processed by Principal Component Analysis.

Results and Discussion

Productivity and Foliar Characteristics

Several authors have found strong allometrical relationships between alder dimensions and dry mass [27, 30, 31]. Allometrical relationships were strong also in this study, as all equations had considerably high determination coefficients (from 0.866 to 0.996) and low probability levels (<0.01) (Table 2). Parameter estimates of the regression Equation (1) for estimation of the above-ground biomass were published previously [28].

Table 2. **Parameter Estimates of the Regression Equation (1) for Estimation of the Above-Ground Biomass Production (kg yr^{-1}) of Black Alder Trees**

Fraction	a	b	R^2	S.E.E.	p
Sirgala					
Stems	–4.468	2.365	0.943	0.26	<0.006
Branches	–7.017	2.719	0.866	0.41	<0.007
Leaves	–6.096	2.480	0.901	0.36	<0.009
Total	–4.233	2.437	0.913	0.29	<0.003
Parapalu					
Stems	–4.982	2.674	0.978	0.24	<0.002
Branches	–4.920	2.123	0.982	0.18	<0.001
Leaves	–4.792	2.191	0.981	0.19	<0.001
Total	–3.830	2.400	0.987	0.17	<0.001
Songa					
Stems	–3.559	1.967	0.982	0.12	<0.002
Branches	–5.536	2.268	0.996	0.06	<0.001
Leaves	–7.397	3.130	0.938	0.35	<0.007
Total	–3.769	2.278	0.983	0.12	<0.001

Despite different site conditions and planting density, the main growth parameters (mean H and DBH) (see Table 1) and productivity of the plantations were comparable. The total above-ground biomass of the plantations ranged from 88.8 to 100.6 t ha^{-1} and biomass production from

14.3 to 17.1 t ha^{-1} yr^{-1} (Table 3). In Sweden, Johansson [32] calculated the above-ground mean total biomass for 21- to 91-year-old black alder stands to be 152.3 ± 7.7 t ha^{-1}. In the Netherlands, the amount of living biomass in 30-year-old black alder stands ranged from 107.1 to 146.0 t ha^{-1} [33]. The largest amount of biomass per hectare was estimated at Sirgala. Thus, black alder is a very fast-growing and productive deciduous tree on reclaimed oil-shale mining detritus and is suitable for recultivation of exhausted oil-shale opencast mines. Moreover, black alder surpasses remarkably the growth of conifers on reclaimed oil-shale mining areas [34]. The author calculated mean height for 19-year-old black alder and Scots pine plantations as 12.0 and 5.3 m, respectively.

Table 3. **Above-Ground Biomass (B) and Biomass Production (ΔB), Nitrogen and Phosphorus (N, P) Content and Annual Use (ΔN, ΔP) in the Plantations**

Fraction	B, t ha^{-1}	ΔB, t ha^{-1} yr^{-1}	N	P	ΔN	ΔP
			kg ha^{-1}		kg ha^{-1} yr^{-1}	
Sirgala						
Stems	90.7	10.8	296.9	84.9	35.3	10.2
Branches	7.0	2.1	57.2	10.8	19.4	3.4
Leaves	2.9	2.9	88.5	6.5	88.5	6.5
Total	100.6	15.8	442.6	102.2	143.2	20.1
Parapalu						
Stems	76.9	10.2	309.6	20.3	41.2	2.7
Branches	7.9	2.9	63.5	3.7	27.5	1.7
Leaves	4.0	4.0	125.6	4.6	125.6	4.6
Total	88.8	17.1	498.7	28.6	194.3	9.0
Songa						
Stems	80.2	7.7	287.2	80.6	28.1	7.8
Branches	9.6	2.4	94.4	13.5	27.5	3.8
Leaves	4.2	4.2	119.3	8.9	119.3	8.9
Total	94.0	14.3	500.9	103.0	174.9	20.5

Based on our results, stems (wood + bark) form the biggest share, at 85.3 to 90.2%, in the studied plantations. The proportion of branches (wood + bark) in the total above-ground biomass varied from 7.1 to 10.3%, and that of leaves from 2.9 to 4.5%. Similarly to biomass, stems formed the largest share, from 53.8 to 68.4%, of total above-ground biomass production. The proportions of branches and leaves in total above-ground biomass production were 13.3 to 17.0% and 18.4 to 29.4%, respectively.

The biomass accumulation ratio (biomass/net production) is used in categorizing the production conditions of forest communities [35]. Biomass accumulation ratio was higher in Sirgala and Songa compared to that in Parapalu (Table 4).

Table 4. **Mean Productivity and Foliage Characteristics, Nitrogen (N) and Phosphorus (P) Use Efficiency in the Plantations of Black Alder**[*]

Characteristic	Sirgala	Parapalu	Songa
Biomass accumulation ratio	6.8 ± 0.4^{b}	5.1 ± 0.1^{a}	6.6 ± 0.2^{b}
Foliar assimilation efficiency, t t^{-1} leaf $year^{-1}$	5.6 ± 0.4^{a}	4.3 ± 0.4^{a}	4.9 ± 0.6^{a}
N use efficiency, kg kg^{-1}	116.5 ± 3.6^{b}	88.5 ± 9.8^{a}	95.0 ± 14.4^{ab}
P use efficiency, kg kg^{-1}	804.1 ± 12.5^{a}	1941.1 ± 225.2^{b}	736.9 ± 32.0^{a}
Leaf area index, m^2 m^{-2}	3.8	5.1	4.0
Single leaf area, cm^2	27.3 ± 0.9^{a}	31.9 ± 0.6^{b}	33.1 ± 0.9^{b}
Single leaf mass, mg	217 ± 5^{a}	230 ± 9^{a}	316 ± 11^{b}
Leaf weight per area, g m^{-2}	78.6 ± 0.8^{b}	70.1 ± 1.1^{a}	91.1 ± 1.0^{c}
Specific leaf area, m^2 kg^{-1}	13.1 ± 0.1^{b}	15.5 ± 0.3^{c}	11.5 ± 0.1^{a}

[*] Different letters denote a statistically significant difference.

Differences in biomass accumulation ratio may be caused by the differences in site and stand characteristics. In Parapalu, periodical flooding occurs, usually from October to June, and it may essentially affect stand growth.

The mean foliar assimilation efficiency of model trees (net production/unit weight of leaf) ranged from 4.3 to 5.6 t^{-1}t leaf $year^{-1}$. Although the differences between stands were statistically insignificant, in Sirgala the alders' foliage seemed to be the most efficient (see Table 4). We suppose that in Sirgala, the planting density of 2,300 stems per hectare provides near optimal photosynthetic conditions and results in the high productivity of black alder. Therefore, we recommend the planting of 2,000 to 2,500 alders per hectare on exhausted oil-shale opencast mines. Our results are in accordance with foliar assimilation efficiencies reported for other alder species. In 5-year-old red alder (*Alnus rubra* Bong.) plantations, at different planting densities the foliar assimilation efficiency ranged from 4.9 to 5.6 t t^{-1} leaf $year^{-1}$ [27]; in 10- to 50-years-old plantations of Himalayan alder (*Alnus nepalensis* D. Don), the parameter varied between 2.4 to 5.3 t t^{-} leaf $year^{-1}$ [36].

Leaf area index (LAI) ranged from 3.8 to 5.1 m^2 m^{-2} in our plantations. In Estonia, Tullus and others [37] reported LAI for a natural 18-year-old grey alder stand to be 3.8 m^2 m^{-2}. The highest values of mean single leaf area and mass were found in Songa. A significantly higher value of leaf weight per area (LWA) was also determined in Songa, where planting density was lowest. The mean LWA in this study was comparable to the 77.4 ± 5.6 g m^{-2} calculated for black alder in Estonia by Niinemets and Kull [38]. In Sweden, Johansson [32] reported the mean specific leaf area for black alder to be 13.3 ± 0.3 m^2 kg^{-1}. Besides, we observed a statistically significant variation in LWA in the vertical plane of the alders' crowns: the leaves at the top of the trees had higher LWA values. In North America, analogous vertical variation of LWA was found in red alder stands [31].

Nutrient Content and Annual Use

Productivity of forest ecosystems is closely related to the availability and demand of nitrogen (N) and phosphorus (P). Multifactor analysis of variance revealed that the concentration of N and P varied significantly between different compartments of model trees. In the studied plantations, N and P concentrations in tree compartments increased as follows:

for N:
stemwood < branches(wood + bark) ≤ stembark ≤ current year shoots < leaves
for P:
stemwood < branches(wood + bark), stembark < current year shoots ≤ leaves.

The leaves (2.84 to 3.14%) of black alder contained over three times more N than the branches and over twelve times more N than stemwood. The concentration of P in the leaves ranged from 0.114 to 0.223% and it was over two times higher than in stemwood. According to Mikola [10], the N concentration in alder leaves is 2–3 times higher than in the leaves of other European deciduous trees. The concentration of N in tree compartments did not vary significantly between plantations. Based on our results, we conclude that black alder is self-supporting regarding N in oil-shale mining areas, since the initial N content of oil-shale mining detritus is extremely low [5]. The P concentration of model trees also varied significantly among plantations, being the highest in Sirgala. Alders have a high requirement for P [16], and this is usually the most limiting nutrient for them.

The total above-ground N content was quite similar in all plantations (see Table 3). It can be concluded that black alder is able to assimilate large amounts of N, irrespective of different growing conditions. In all plantations, the largest content of nitrogen (57.3 to 67.1%) was found in stems. The total above-ground P content was similar in Songa and Sirgala, but more than three times smaller in Parapalu (see Table 3). Similarly to N, the largest content of P was found in stems (71.1 to 83.0%). Since estimation of N pools in above-ground compartments does not yield information about the origin of N, this question requires further investigation. It has been shown that grey alder can cover a major part of its N demand *via* biological fixation [39–42]. Annual rates of biological N fixation from 32 to 185 kg ha^{-1} have been measured in 14- to 30-year-old grey alder stands [14, 43, 44].

The total annual above-ground N use was highest in Parapalu (194.3 kg ha^{-1} yr^{-1}) and lowest in Sirgala (143.2 kg ha^{-1} yr^{-1}), the leaves accounted for the greatest part (61.8 to 68.2%) of the total annual above-ground N use. The annual P use in Sirgala and Songa had similar values, but in Parapalu the total annual P use was two times lower than in the other plantations (Table 3). Our results show that 32.3 to 51.1% of the total annual P uptake accumulated in the leaves and 30.0 to 50.7% in the stems. Mean N use efficiency (mass of production per mass of annual N use) ranged in the plantations from 88.5 to 116.5 kg kg^{-1}. The highest value was calculated for the Sirgala plantation, probably due to suboptimality of the foliage characteristics. When comparing the N-fixing alders to non-fixing tree species, alders have lower N use efficiency [45]. Mean P use efficiency ranged in the plantations from 736.9 to 1941.1 kg kg^{-1} (see Table 4). The highest value was calculated for Parapalu and the lowest one for Songa. Sharma [46] reported N and P use efficiencies of an age series (7 to 56 years) of Himalayan alder plantations to be 48 to 70 kg kg^{-1} and 1,534 to 3,578 kg kg^{-1}, respectively.

Considering the fact that the largest share of the annual N uptake accumulates in the leaves and that the autumnal N retranslocation from black alder leaves is relatively low [13], at least half of the total annual above-ground N use returns to the soil through the leaf litter. In Sirgala, the analysis of topsoil nutrients showed a remarkable increase in total N and available P under the canopy of the black alder plantation, compared to the neighbouring Scots pine stand of the same age. Vares [34] found a more than two times higher topsoil total N and available P content in an alder plantation, compared to a pine stand.

Microbiological Characteristics in SRI and Bulk Soil

Soil microbial biomass was highest at the Sirgala, and lowest at the Songa site (Table 5). When soil microbial biomass was normalized by soil organic carbon content, the Songa and Sirgala sites also exhibited highest values.

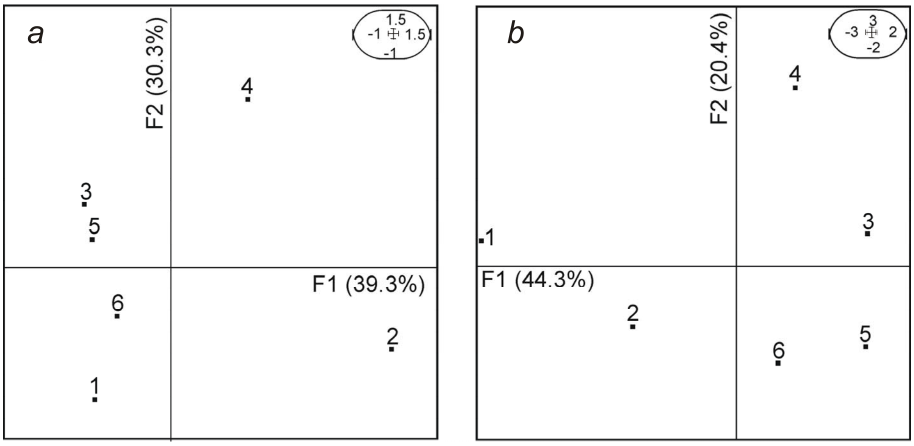
Table 5. **Microbiological Parameters of Soil and Rison Samples from Plantations**

Sample	SIR, mgC g^{-1}	SIR-C, mgC gC^{-1}	Respiration, mgCO$_2$ g^{-1} 24h^{-1}	CAI	Diversity	AWCD, OD 48h^{-1}	SRI/Bulk ratio of AWCD
Sirgala							
Bulk	2.89	34.0	0.35	0.12	4.34	0.54	1.81
SRI					4.59	0.98	
Parapalu							
Bulk	1.76	18.4	0.38	0.21	4.25	0.46	2.4
SRI					4.35	1.11	
Songa							
Bulk	0.70	10.0	0.11	0.16	4.27	0.47	1.49
SRI					4.44	0.70	

Legend: SIR – substrate induced respiration,
CAI – carbon availability index,
AWCD – average well color development,
SRI/Bulk ratio of AWCD – ratio of AWCD values for soil–root interface (SRI) and bulk soil.

Soil respiration measured from bulk soil represents the respiration of the humus-degrading microorganisms present in the bulk soil. The values for soil respiration were comparable at the Sirgala and Parapalu sites, and three times lower at the Songa site. The comparison of the carbon availability indices shows that at the Songa and Sirgala sites, the highly active microbial biomass depletes the readily available C sources (or easily degradable organic matter) regularly and starves.

The analysis of substrate utilization patterns of SRI and bulk soil microbial communities estimated using BIOLOG EcoPlates data show distinctive differences between SRI and bulk soil microbial communities. Microbial community activity and diversity measured with BIOLOG microplates was highest at the Sirgala site, and similar at the Songa and Parapalu sites. The maximum values for both parameters were found in SRI samples. The ratio of SRI and bulk soil microbial activity was highest at Parapalu, indicating a big difference between the metabolic activity of SRI and bulk soil microbial communities, probably due to poorer soil quality.



Principal component analysis (PCA) plots of substrate utilization patterns of SRI and bulk soil microbial communities estimated using BIOLOG EcoPlates data:

a) PCA based on covariance matrix of Biolog untransformed data. The first and second principal components describe 69.6% of the overall data variation.

b) PCA based on covariance matrix of Biolog data adjusted for average well color development (AWCD) values. The first and second principal components describe 64.7% of the overall data variation.

Legend: *1* – Parapalu bulk soil; *2* – Parapalu SRI; *3* – Sirgala bulk soil; *4* – Sirgala SRI; *5* – Songa bulk soil; *6* – Songa SRI

Figure,*a* shows the results of ordination of soil samples based on non-standardized BIOLOG data. In such a case, the main gradient (F1 axis) in the data set is related to differences in microbial community activity and abundance. While bulk soil samples have practically similar microbial abundances, the SRI microbial communities from Sirgala and Songa exhibit bigger differences in density values. The effect of microbial community density is removed from Biolog data when initial values are adjusted for average well color development (AWCD). This transformation yielded ordination of microbial communities, which shows grouping of samples by plantation (Figure,*b*). The structure of the microbial communities of bulk soil and SRI samples shows rather big variation among the three plantations. This suggests that these plantations have distinctive microbial communities, and that formation of SRI microbial community structure is mostly dependent on soil characteristics.

Alder plants spent a substantial part of their assimilated energy for the adjustment to environmental conditions, presumably mainly in order to establish the most appropriate beneficial rhizosphere [47]. Energy supplied to the rhizosphere supports the growth of microorganisms, which in turn enables the alder trees to utilize physically limited nutrient sources in the soil. Differences in soil microbial biomass in the studied plantations could not be explained by differences in above-ground biomass and biomass production, and thus the key factor in soil microbial processes at these locations should be rhizodeposition. The build-up of microbial biomass seems also to be linked to soil phosphorus content, as shown by analysis of the soil microbial community and chemical parameters (see Soil Properties in Table 1) of Sirgala plantation.

Conclusions

The above-ground productivity in the 21-year-old black alder plantation on reclaimed oil-shale mining detritus in Sirgala was comparable with the value for the stands of the same age growing on fertile mineral soils. Biomass accumulation ratio, foliar assimilation efficiency, and N use efficiency were highest in Sirgala plantation. In Sirgala, the planting density ensured near optimal photosynthetic conditions, and we recommend the planting of 2,000 to 2,500 black alders per hectare on exhausted oil-shale opencast mines. Black alder as an actinorhizal tree is self-supporting with N in oil-shale mining areas. Although initial phosphorus content in oil-shale mining detritus is low, the availability of phosphorus was highest in Sirgala. Comparing black alder and pine plantations of the same age in Sirgala, N and P pools in the soil and the mean height of trees were approximately two times higher for black alder. Our results indicate that even on oil-shale mining detritus, black alders create a favorable environment for microbes in their soil–root interface. The formation of active microbial biomass in the plantations was strongly affected by rhizodeposition. Hence, black alder is a very promising tree species for the recultivation of exhausted oil-shale opencast mines.

Acknowledgements

This study was supported by grants No. 4821 and 4895 from the Estonian Science Foundation. We would like to thank Mr. Ilmar Part for linguistic revision of the manuscript.

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Presented by J. Kann
Received May 20, 2003