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Root system development in two provenances of *Picea abies* at two different sites

Abstract: The paper examines the development of the root system (both skeletal and fine roots) in 19-year-old Norway spruce (*Picea abies* (L.) Karst.) of two provenances (from altitudes 320 m and 1100 m), growing on two plots (540 m a.s.l., lowland, modal Cambisol; 820 m a.s.l., slope, ranker podzol), by comparing 34 parameters. The results show that the root system emergence is not affected by provenance but rather by site, namely by soil type and terrain slope. At an altitude of 540 m, both provenances produced an anchoring root system of circular floor projection with a rooting depth of 80 cm, while at an altitude of 820 m they had an elliptical superficial root system with a rooting depth of 45 cm. At the higher-situated plot, the provenance from an altitude of 1100 m showed a higher biomass, vitality, and specific length of fine roots.

Additional key words: Norway spruce, root system architecture, skeletal roots, fine roots

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Introduction

Populations of the same species originating from different geographic conditions differ in physiological, biochemical and morphological characteristics. Physiological variations manifest themselves in growth and its periodicity, in the seasonal and daily course of photosynthesis, in light requirements, and in resistance to biotic and abiotic agents; they also determine morphological traits such as general habit, stem form, length and colour of needles, wood and bark properties (Schmidt-Vogt 1977; Boratyński and Bugała 1998). When assessing provenance trials, attention is usually paid to height and diameter growth, stem form, phenology, and resistance to pests and diseases. Being important in economic terms, these parameters are also easily measurable and detectable. The root system, another integral part of the tree, has been the least explored tree organ up to now. Each forest tree species has its own genetically determined

type of the root system, which is modified by soil environment conditions (moisture, mechanical obstacles, aeration, temperature, chemical and microbiological conditions) and thus exhibits wide variability (Köstler et al. 1968; Polomski and Kuhn 1998; Puhe 2003). Since there are provenance-dependent differences in the morphology of the above-ground part of trees (Schmidt-Vogt 1977; Persson and Persson 1997; Boratyński and Bugała 1998), it would be interesting to know whether some differences due to provenance can also occur in their underground organs.

Engler (1905 ex Köstler et al. 1968) observed provenance-determined differences in the rooting of 2-year-old plants of Norway spruce, finding out that the seedlings raised from the seed of alpine spruces had not only a higher percentage of roots but also a larger root system than comparable seedlings from lowlands. The author claimed that the plants kept the feature even when transplanted to lower elevations. By contrast, in a provenance trial with 24-year-old

spruce trees, Nägeli (1932 ex Köstler et al. 1968) reported that the root systems of older spruces from mountain elevations were smaller than those of coeval lowland trees. Vincent (1941) observed that the length of hypocotyl including radicle as related to the length of cotyledon was greater in seeds originating from higher elevations than in those from lower altitudes. Askoy (1965 ex Schmidt-Vogt 1977) compared the dry weight of above-ground part, the total length of roots, and the number of first-order roots in 1- to 3-year-old transplanted plants of spruce, pine and larch originating from different elevations, and did not record any essential differences in these parameters, only the percentage of roots was larger in spruce and larch trees from mountain locations (1300 m a.s.l.) than in plants from altitudes of 600–700 m. Studying young larches of different provenances, Leibundgut (1964 ex Köstler et al. 1968) found wider variations in the dry weight of roots than in that of above-ground parts. Also Korotaev (1997) noted differences in the length and dry weight of roots and in the number of first-order roots in 2-year old seedlings of two different ecotypes of spruce studied in progeny tests. In a provenance trial with pine aged 28 years, Biebelriether (1964) recorded differences in the formation of both the above-ground part and root systems among provenances. The provenance which excelled in stem straightness had a taproot and a distinct division of the root system into a horizontal and vertical part, with the depth at which the taproot was branching being greater than in the other provenance studied. The two provenances differed also in the depth reached by the roots.

The root systems of 28-year-old spruces of various provenances were compared by Šika (1966) on two provenance plots situated on different sites. The parameters measured in two well-growing and two poorly-growing provenances were the type and morphology of the root system, rooting depth, and the vertical distribution of roots in the soil. In some provenances, a benchmark measurement was made of the length of roots at the start of their growth. The author found out that the character of the root systems of trees on both plots was affected by soil conditions. All transplants monitored on the unfavourable site possessed an identical type of the root system. On the favourable site, the Norwegian provenance differed from the others in that it had a more superficial root system. The author assumed that the differences observed in the vertical distribution of roots were caused by soil factors.

As follows from the above outline, the existing knowledge does not make it possible to formulate unambiguous conclusions about the impact of provenance on the formation of the root system in forest tree species. Therefore, the objective of the present study is to make a complex analysis of the root system

of spruce trees originating from different altitudes on two experimental plots differing in site conditions.

Material and methods

Basic methodological procedures

The survey was carried out on two standard provenance plots established in the Czech Republic in 1988.

The provenance plot in Křtiny (hereinafter referred to as 'the Křtiny plot'; 49°19'42" N, 16°45'15" E) is situated at an altitude of 540 m, in the area where the mean annual air temperature is 7.0°C and the mean annual precipitation amounts to 540 mm. It lies on the plain, the soil type is modal Cambisol, the site is fertile. The plot was established using bare-rooted planting stock.

The provenance plot in Ostravice (hereinafter referred to as 'the Ostravice plot'; 49°29'39" N, 18°23'50" E) lies at an altitude of 820 m, in the area where the mean annual air temperature is 5.6°C and the mean annual precipitation amounts to 1171 mm. It is situated on 20% slope, the soil type is ranker podzol, the site is acidic. The plot was established using containerised planting stock.

The provenances studied on both plots were No. 34 (originating from an altitude of 320 m, fertile site) and No. 45 (originating from an altitude of 1100 m, acidic site). In both cases, the reproductive material was taken from stands of superb quality: an autochthonous one for provenance No. 45 (established on the basis of historical records), and an allochthonous one for provenance No. 34.

The basic methodological procedure was as follows: each provenance plot was subjected to analyses and mutual comparison of the trees of identical height of both provenances, undamaged by abiotic or biotic agents. The analyses did not include marginal trees in the square of the provenance concerned.

Root system analyses were carried out according to the methodology developed by the Brno school of rhizology (Mauer 1989).

Analyses of the root system architecture and health condition

A total of 12 root systems of trees of identical height were lifted by hand and analysed on each provenance plot for each of the two provenances. Since the size and development of the root system is incomparably more affected by the height of the above-ground part than by the age or stem diameter of a tree, all trees on the two provenance plots were measured prior to analysing the root system (height and diameter differences of the two provenances being minimal).

Further details of the methodological procedures were as follows:

- Stem diameter was measured at a height of 1.3 m from the ground surface.
- Horizontal skeletal roots (in tables referred to as ‘HSR’), i.e. plagiotropic roots growing parallel to soil surface, which provide for the mechanical stability of the tree, were counted and characterised.
- The shape of horizontal skeletal roots was defined as a ratio of root height to root width, with the diameter of horizontal roots being the average of these values.
- The measurements were taken near the stem (10 cm from the stem perimeter) and 60 cm from the stem (60 cm from the stem perimeter) in order to find out how the parameters of horizontal skeletal roots change depending on their length.
- The measurements on the Ostravice plot were made separately in Semicircle 1 (180° of the sector above the contour line) and in Semicircle 2 (180° of the sector below the contour line).
- The length of horizontal roots was measured as a distance from the stem perimeter to the tip of the horizontal root.
- The right anchor was assumed to grow perpendicular to the ground surface (maximum deviation from vertical line being 45°).
- The aslant anchor was assumed to penetrate the soil at an angle of 45° from the ground surface.
- The diameter of anchors was measured at a distance of 5 cm from their setting.
- The number of branching roots on anchors was established by counting all roots shooting from the anchor.
- The rooting depth was defined as a perpendicular distance from the ground surface to the tip of the deepest reaching root.
- The maximum angle between horizontal skeletal roots, which characterises regularity of the distribution of these roots within the circular root pattern, was determined by measuring the angle between the two most distant roots.
- Index *p* (in tables referred to as ‘Ip’), used to assess the relation between the development of the root system and the development of the above-ground part of a tree, was calculated as a ratio of the cross-sectional area of all horizontal skeletal roots and anchoring roots at a gauging place (in mm²) to the tree length (in cm). The greater the *Ip* value, the larger the tree root system.
- All horizontal skeletal roots and anchors were longitudinally cut to visually examine the occurrence of rots or the root damage by biotic agents.
- All stems were cut into 1 m sections to visually examine the occurrence of rots or the infestation by biotic agents.

Analyses of fine roots

The analyses included roots of diameter below 1 mm. The following parameters were measured and assessed:

- Biomass of fine roots. There were 30 soil cores excavated for each provenance on both plots by using a soil sampler of 5 cm diameter. The soil cores were divided according to soil horizons and homogenised. All humus horizons (Humus) and the mineral layer 0–10 cm under the humus horizons (Mineral) were examined. A total of 6 samples (bulk volume 100 ml) were taken from the homogenates for analyses. The separation and manual cleaning of fine roots was followed by the measurement of their length and weight after drying.
- Specific length of fine roots (Clemensson-Lindell 1994) was calculated as a ratio of fine roots length to their weight (mm gdw⁻¹).
- Vitality and mycorrhizal colonisation of fine roots. In each stand, 5 soil cores (20 × 20 cm) were sampled from the humus horizons. Fine roots were separated by hand, cleaned and homogenised. To prevent impact on the vitality of roots, care was taken to complete the whole operation within 12 hours of the sampling of soil cores in the stand. The samples were transported to the laboratory in refrigerators.
- Vitality was determined by a method involving 2,3,5-triphenyltetrazolium chloride reduction, described by Joslin and Henderson (1984). The results were subjected to correlation analysis, and the percentage of vitality was calculated.
- Mycorrhizal colonisation was established quantitatively by chemical methods described by Plassard et al. (1982) and Vignon et al. (1986).

General notes

In the case of the occurrence of rots or damage to the root and stem, their cause was established by special analyses.

The results of the measurements were processed by common statistical methods. The significance of the results was determined by t-test at the significance level of 95%. In tables, the significance of variances between the provenances was marked with an asterisk.

Results

Křtiny plot (Tables 1, 2, Fig. 1)

On the Křtiny plot, both provenances produced identical and equally-sized anchoring root systems with a circular floor projection, and exhibited identical rooting depth. The provenances had the same layout of horizontal skeletal roots (HSR) in the circular

Table 1. Biometric parameters of above-ground part and root system architecture of two Norway spruce provenances at two different sites

Parameter	Křtiny		Ostravice	
	Provenance 34	Provenance 45	Provenance 34	Provenance 45
Length of above-ground part (cm)	1054.1 ± 31.2	999.6 ± 50.7	907.2 ± 53.9	862.5 ± 31.3
Diameter of stem (mm)	111.3 ± 5.1	108.4 ± 6.2	113.0 ± 6.2	106.3 ± 4.3
Terminal increments (cm)				
2004	69.3 ± 13.4	62.3 ± 9.3	78.4 ± 12.1	72.5 ± 10.4
2005	77.5 ± 9.7	82.3 ± 9.5	79.3 ± 14.1	85.7 ± 12.2
2006	85.5 ± 13.8	79.0 ± 9.1	80.6 ± 9.7	78.5 ± 16.3
Type of root system	anchoring	anchoring	superficial	superficial
HSR shape (floor projection)	circular	circular	elliptical	elliptical
HSR count (pcs) – Semicircle 1				
near the stem	–	–	6.0 ± 2.7	6.3 ± 1.2
60 cm from the stem	–	–	9.4 ± 2.8	11.0 ± 2.1
HSR count (pcs) – Semicircle 2				
near the stem	–	–	4.0 ± 0.7	4.0 ± 1.2
60 cm from the stem	–	–	7.0 ± 1.2	5.5 ± 1.5
HSR count (pcs) – Total				
near the stem	9.1 ± 2.1	7.5 ± 1.8*	10.0 ± 3.0	10.3 ± 2.4
60 cm from the stem	15.7 ± 5.0	13.6 ± 3.1	16.4 ± 2.6	16.5 ± 1.9
HSR diameter (mm) – Semicircle 1				
near the stem	–	–	51.6 ± 11.9	51.8 ± 6.4
60 cm from the stem	–	–	17.2 ± 4.9	15.7 ± 3.7
HSR diameter (mm) – Semicircle 2				
near the stem	–	–	46.4 ± 10.1	40.8 ± 8.6
60 cm from the stem	–	–	17.6 ± 6.5	14.8 ± 6.7
HSR diameter (mm) – Total				
near the stem	50.1 ± 5.0	56.5 ± 7.7*	48.8 ± 3.7	47.8 ± 5.7
60 cm from the stem	21.3 ± 3.0	21.0 ± 2.2	17.4 ± 2.1	15.7 ± 3.7
HSR shape – Semicircle 1				
near the stem	–	–	1.49 ± 0.21	1.53 ± 0.14
60 cm from the stem	–	–	1.03 ± 0.04	1.03 ± 0.03
HSR shape – Semicircle 2				
near the stem	–	–	1.52 ± 0.27	1.34 ± 0.15
60 cm from the stem	–	–	1.01 ± 0.02	1.02 ± 0.03
HSR shape – Total				
near the stem	1.46 ± 0.09	1.50 ± 0.22	1.50 ± 0.19	1.46 ± 0.12
60 cm from the stem	1.05 ± 0.06	1.03 ± 0.04	1.03 ± 0.02	1.03 ± 0.08
Representation of trees with genuine anchors (%)	100	100	0	0
Representation of trees with aslant anchors (%)	50	67	100	100
Genuine anchors – Semicircle 1				
number (pcs)	–	–	0.0 ± 0.0	0.0 ± 0.0
Genuine anchors – Semicircle 2				
number (pcs)	–	–	0.0 ± 0.0	0.0 ± 0.0
Genuine anchors – Total				
number (pcs)	2.3 ± 0.8	3.5 ± 1.0*	0.0 ± 0.0	0.0 ± 0.0
diameter (mm)	45.5 ± 9.4	30.1 ± 5.4*	0.0 ± 0.0	0.0 ± 0.0
number of branching roots (pcs)	6.5 ± 1.0	5.7 ± 1.0	0.0 ± 0.0	0.0 ± 0.0
rooting depth (cm)	78.2 ± 8.2	71.7 ± 7.9	0.0 ± 0.0	0.0 ± 0.0

Parameter	Křtiny		Ostravice	
	Provenance 34	Provenance 45	Provenance 34	Provenance 45
Aslant anchors – Semicircle 1				
number (pcs)	–	–	2.6 ± 1.1	2.5 ± 0.8
diameter (mm)	–	–	25.6 ± 5.4	24.3 ± 3.5
number of branching roots (pcs)	–	–	4.1 ± 1.2	3.7 ± 0.8
rooting depth (cm)	–	–	44.8 ± 6.5	47.7 ± 7.6
Aslant anchors – Semicircle 2				
number (pcs)	–	–	2.4 ± 0.5	1.7 ± 0.4
diameter (mm)	–	–	23.6 ± 8.1	22.2 ± 4.8
number of branching roots (pcs)	–	–	4.8 ± 1.9	3.7 ± 0.8
rooting depth (cm)	–	–	41.6 ± 6.8	41.3 ± 8.5
Aslant anchors – Total				
number (pcs)	1.3 ± 0.5	2.7 ± 0.9*	5.0 ± 1.0	4.2 ± 0.4
diameter (mm)	32.7 ± 4.1	24.0 ± 6.1*	24.4 ± 5.8	23.5 ± 5.7
number of branching roots (pcs)	4.3 ± 1.5	5.5 ± 1.3	4.6 ± 1.3	3.7 ± 0.8
rooting depth (cm)	42.3 ± 4.1	44.2 ± 6.4	43.4 ± 4.6	45.3 ± 7.4
Maximum angle between HSR (degr.)	106.6 ± 29.4	90.0 ± 8.9	56.0 ± 13.4	65.0 ± 24.2
Ip value	24.3 ± 3.4	24.8 ± 2.8	27.3 ± 2.8	27.2 ± 2.2
share of all HSR in Ip (%)	83.2	86.3	88.7	90.9
share of all anchors in Ip (%)	16.8	13.7	11.3	9.1
share of HSR in Semicircle 2 in Ip (%)	–	–	56.2	65.1
share of HSR in Semicircle 2 in Ip (%)	–	–	32.5	25.8
Maximum HSR length (cm)				
Semicircle 1	214 ± 47	224 ± 38	–	–
Semicircle 2	–	–	172 ± 19	157 ± 24
Semicircle 2	–	–	357 ± 38	321 ± 41
HSR branching	monopodial	monopodial	monopodial	monopodial
HSR ending	tufts	tufts	–	–
Semicircle 1	–	–	tufts, bend	tufts, bend
Semicircle 2	–	–	tufts	tufts
Ending of anchors	brush	brush	brush	brush

pattern, and the same length and share of HSR and anchors in the Ip values. The only significant differences were as follows: provenance No. 45 had a smaller number of larger-diameter HSR (60 cm from the stem, the differences disappeared), and a greater number of small-diameter genuine and aslant anchors.

Ostravice plot (Tables 1, 2, Fig. 2)

On the Ostravice plot, both provenances produced identical and equally sized superficial root systems with an elliptical floor projection and an eccentric position of the stem base. Both provenances had the same distribution of horizontal skeletal roots in the circular patterns, as well as the same length and share of HSR and anchors in the Ip values. Significant differences were found in nearly all parameters of fine roots. Although the two provenances exhibited an identical vertical distribution of fine roots, provenance No. 34 had lower biomass, specific length, mycorrhizal colonisation, and particularly the vitality

of fine roots. Provenance No. 34 showed the occurrence of honey fungus (*Armillaria ostoye* (Romagn.) Herink), which induced rots to horizontal skeletal roots and anchors in all the trees studied.

Discussion

Up to now, little attention has been devoted to monitoring the root systems of forest trees of various provenances. Differences in the formation of the root systems of spruce of various ecotypes were found by such authors as for example Engler (1905 ex Köster et al. 1968) and Korotaev (1997) in the material at a juvenile stage of development. Because the development of a root system is markedly affected by soil conditions, differences are not already evident at an older age (Šika 1966). Our team did not succeed in demonstrating the effects of provenance on the formation of the root system, either. As shown by our analyses, no significant differences existed in the architecture of the root system of spruce aged 19 years coming from

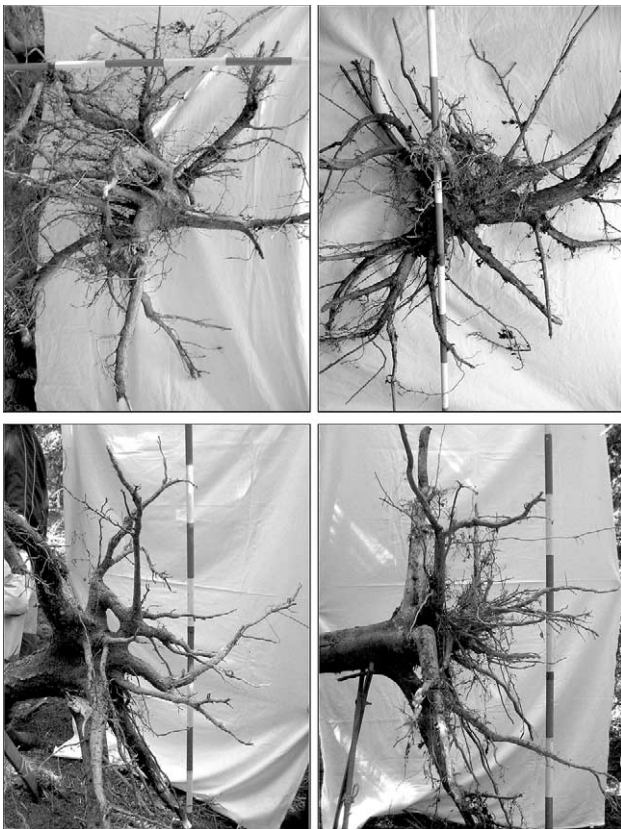


Fig. 1. Provenance plot in Křtiny. Left: root system of provenance No. 34. Right: root system of provenance No. 45 (photos taken by the authors)

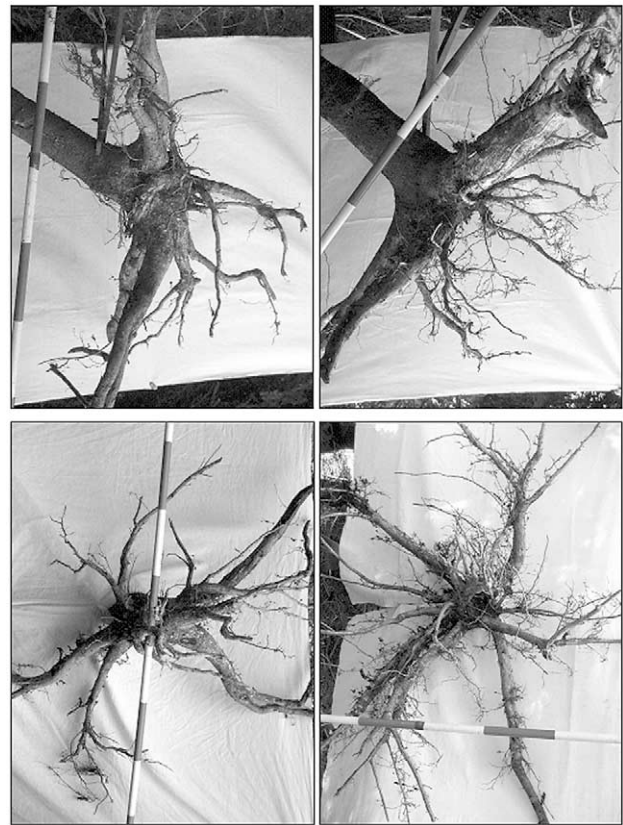


Fig. 2. Provenance plot in Ostravice. Left: root system of provenance No. 34. Right: root system of provenance No. 45 (photos taken by the authors)

altitudes of 320 and 1100 m. On the Křtiny plot, no differences were found between the two provenances in the root system size (magnitude of I_p values) or in the share of horizontal skeletal roots and anchors in

the I_p value. However, the alpine provenance No. 45 had a significantly smaller number of horizontal roots and a larger number of anchors (prerequisite for the creation of a strong anchoring root system). Never-

Table 2. Characteristics of fine roots, mycorrhiza, and root rots of two Norway spruce provenances at two different sites

Parameters and traits	Křtiny		Ostravice	
	Provenance 34	Provenance 45	Provenance 34	Provenance 45
Biomass of fine roots ($\text{g } 100 \text{ ml}^{-1}$)				
humus	0.357 ± 0.006	0.352 ± 0.005	0.445 ± 0.027	$0.516 \pm 0.026^*$
mineral	0.104 ± 0.004	0.097 ± 0.007	0.189 ± 0.009	$0.216 \pm 0.010^*$
total	0.461 ± 0.017	0.449 ± 0.016	0.634 ± 0.030	$0.732 \pm 0.033^*$
Vertical distribution of fine roots (%)				
humus	77.3	78.5	70.1	70.5
mineral	22.7	21.5	29.9	29.5
total	100.0	100.0	100.0	100.0
Specific length of fine roots (mm g^{-1})	11.2 ± 1.6	10.4 ± 0.9	9.2 ± 0.6	$11.0 \pm 0.7^*$
Mycorrhizal colonisation of fine roots ($\mu\text{g glucosamine mg}^{-1}$)	9.1 ± 0.3	8.7 ± 0.3	8.4 ± 0.4	$10.3 \pm 0.3^*$
Vitality of fine roots (%)**	100	90	38	82
Root rots				
% of trees with rots	0	0	100	0*
HSR with rots (pcs)	0	0	3.1 ± 0.9	$0.0 \pm 0.0^*$
anchors with rots (pcs)	0	0	1.2 ± 0.2	$0.0 \pm 0.0^*$

**100% = vitality of fine roots in provenance No. 34 in Křtiny

theless, no such pattern was recorded on the Ostravice plot.

Since the provenances studied on either plot did not conform to the current rules about the transfer of forest reproductive material in the Czech Republic, investigations into the root system architecture were conducted on spruce trees of identical height, coming from local provenances in the immediate vicinity of the two provenance plots. The root system architecture of the latter was identical with that of the two provenances concerned.

Although we monitored only two provenances, the same results were obtained on two different sites at altitudes of 540 and 820 m, on various soil types unaffected by water. We thus assume that at an age of 19 years, the development of the root system is influenced more by soil conditions than by genetic factors. However, we cannot rightfully claim that the root system architecture is not genetically determined. The reasons are specified below.

First, the seeds of provenance No. 34 came from an allochthonous stand of unknown origin. Due to the fact that the reproductive material to be transferred had not been checked thoroughly, the altitude of the original source might have been different from that of the stand which provided seeds for the establishment of the provenance plot.

Second, the architecture of the root system of a tree changes in the course of ontogenetic development. As the development of the root system in Norway spruce is rather periodical (stage 1 – after planting, stage 2 – at about 30 years, stage 3 – at about 70 years), and the production of new adventitious roots depends mainly on the size of the above-ground part of the tree, the possibility of further changes in the root system architecture of the provenances cannot be entirely excluded.

All differences found in the fine roots of spruces on the Ostravice plot were induced by the infection of the root system of the lowland provenance No. 34 with honey fungus. Although the provenance does not currently show any visual signs of decline, it can be expected that the negative impact of this aggressive parasitic fungus will be further intensifying. The predisposing factors include transfer of the reproductive material from an altitude of 320 to 820 m and deformations of the root system caused by the use of inappropriate containerised planting stock. More than a third of other root systems lifted could not have been included in the measurements due to severe malformations demonstrably resulting from the unsuitable technique of planting. In our experience, the most serious deformations of the root system induced by incorrect planting methods, that affect or will affect the development of trees but are not taken into account in the assessment of growth parameters in our experiment, occur also on other provenance plots.

Conclusions

Complex analyses of the root systems of trees, performed on two provenances of Norway spruce growing at two different sites, revealed that the root system at the age of 19 years is more influenced by the soil conditions of the site than by the altitude of the place of seed origin. Both in Křtiny and in Ostravice, the two provenances produced nearly uniform root systems of identical size: an anchoring root system of circular floor projection with the rooting depth of 80 cm on the Křtiny plot, and a rather superficial root system of elliptical floor projection with the rooting depth of 45 cm on the Ostravice plot. The two provenances exhibited also an identical type of ending of the horizontal roots and anchors on both plots.

As to the fine roots, no differences in the measured parameters were detected on the Křtiny plot. By contrast, on the Ostravice plot significant differences to the disadvantage of provenance No. 34 were noted in all the parameters assessed (except the vertical distribution of fine roots). The cause lies in the infestation of the root systems of this provenance with honey fungus (*Armillaria ostoye*) due to the inappropriate transfer of the reproductive material.

Acknowledgments

The work is a part of the Research Programme MSM 6215648902 and has received support from the Grant Agency for Agricultural Research of the Czech Republic (Grant No. QG 60060).

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