JOURNAL OF FOREST SCIENCE, *51*, 2005 (6): 268–275

Effects of pressure on the root systems of Norway spruce plants (*Picea abies* [L.] Karst.)

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ABSTRACT: Roots are stressed quire often under natural conditions, e.g. when considering sloping terrain, layers of fluvial deposits, huge layers of melting snow, load of heavy forest machinery during logging and hauling operations, recreational activities of people, high density of deer or cattle, etc. We focused our experiments on Norway spruce (*Picea abies* [L.] Karst.) seedlings grown in containers with glass walls under the permanent load of 5.1 kPa during the whole growing season. The applied pressure affected roots both directly and indirectly due to the occurrence of hypoxia. Root growth ceased under such conditions. Growth dynamics and capability to occupy available soil also changed. For example, the total root area of experimental plants decreased to 52% but the root area index (RAI) was higher by 33% when compared to the control. It indicates that the pressure applied to the soil surface caused the development of only smaller root systems but more compacted into smaller volumes of soil. Mean longitudinal growth of stressed roots decreased by about 50% when compared to the control. Growth of experimental roots was also delayed, which is a typical general response to stress. However, a tendency to create dense and small root systems is in contradiction with the typical strategy of tree root systems.

Keywords: root growth; stress; pressure; RAI; *Picea abies* (L.) Karst.

The functionality of a growth system is important for the health status of plants. From the aspect of research, however, smaller attention is paid to roots as compared with aboveground parts of plants, particularly due to lack of available data.

Roots can respond to compacted soils by increased requirements for photosynthates (Zaerr, Lavender 1974) necessary for exacting metabolism inevitable to overcome the increased resistance of soil during the elongation of roots. Subsequently, we can expect decreased development of mycorrhizas and increased turnover of fine roots (Kozlowski 1971). Physiological cost for the renewal of the function of fine roots can be as many as 70% of available carbon (Ågren et al. 1980).

Terminal and fine roots with predominating absorption functions are naturally subject to fast changes in soil chemistry (pH, O_2 content e.g. during sudden abundant precipitation) and also to immediate changes in their integrity due to an injury (activities of soil organisms, etc., Kolek, Kozinka 1988). The majority of thick roots dies together with the whole tree whereas the ratio of living to dead fine roots often changes continuously with the high rate of dead and regenerating roots (Persson 1979).

Fine roots are those the diameter of which ranges between < 1 and 10 mm (Vogt, Persson 1991). In the majority of cases, a functional substantiation for the selection of classes of particular diameters is missing. Nevertheless, for the majority of trees the distribution and classification of roots to < 1 and > 1 mm is based on morphology. Roots of the diameter of < 1 mm consist of mycorrhizal root tips which differ morphologically and functionally very much from the rest of the root system (Vogt, Persson 1991). Roots of the diameter of > 1 mm show a

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Supported by the Grant Agency of the Czech Republic, Grants No. 4140/1021/1GA0792 and No. 526/03/H036, and the Ministry of Education, Youth and Sports of the Czech Republic, Grant No. 6215648902.

tendency to a secondary structure, i.e. rhizodermis and primary bark were already separated and xylem was closed by phloem with the upper layer of endodermis and pericycle.

We can distinguish two groups of fine roots, viz long and short roots. From the aspect of anatomy, they are very different showing various rates of elongation (Hatch 1933). The function of long fine roots is to occupy a new space thus making the expansion of the root system possible; they represent a high potential for extensive growth (Orlov 1980) and show relatively considerable longevity. Long roots are characterized by secondary growth; they are diarchal up to polyarchal (in monocotyledonous plants) showing a root cap. Short roots are monoarchal (e.g. in spruce), grow slowly, ramify abundantly and do not increase their diameter. Short roots elongate more slowly than long roots although in some cases they can reach considerable length (Lyford, Wilson 1966). The rate of growth of short roots in Scots pine does not exceed 0.1–0.15 mm/day (Orlov 1980). Short-term longevity is typical of short roots.

Mechanical pressure is inherent during the growth of roots in soil. To be able to push its way through the soil environment the root has to generate such a force that can overcome the mechanical resistance of soil aggregates either by their translocation or deformation. The resistance of soil to the pressure of roots is called soil resistance being affected by many parameters such as soil texture and soil skeleton while other parameters such as soil specific density and water content are related to climate – particularly precipitation and temperature. The drier and the heavier the soil, the greater its “force” (Taylor, Ratliff 1969) or resistance.

The root growing in soil has to overcome axial and radial pressure and also friction forces (Greacen 1986). Although relationships of the components differ in relation to the soil texture, cohesion and adhesion properties of soils and also to a certain extent to the shape and diameter of roots, axial forces are a predominating factor (Abdalla et al. 1969; Richards, Greacen 1986; Bengough, Mullins 1990).

The exposure of roots to mechanical pressure induces a number of physiological changes which have been well described on a macroscopic level. For example, the elongation of roots decreases within a response time from minutes (Sarquis et al. 1991; Bengough, MacKenzie 1994) to hours (Eavis 1967; Croser et al. 1999). Generally, root caps become more rounded being even concave, root diameter increases and root meristem and the elongation zone become shorter (Eavis 1967; Atwell 1990; Croser et al. 2000). The observation of root thickening behind the root tip makes it possible to reveal a long-term mechanical pressure on root tips (Abdalla et al. 1969).

The threshold value of soil resistance which can result in significant physiological changes was investigated in several studies. Measurements carried out using penetrometers indicate that it refers to a value of about 2 MPa. Experiments where the cells of roots growing in soilless cultures were exposed to an increased pressure resulted in a conclusion that an external hydrostatic pressure of 0.01–0.02 MPa caused deformations of cell walls resulting in significant reductions of the growth of roots (Russell, Goss 1974; Goss 1977). In several studies only soil resistance to root penetration was measured directly (Eavis 1967; Stolzy, Barely 1968; Misra et al. 1986; Bengough, Mullins 1991; Clark, Barraclough 1999). It has been found that the values of maximum axial pressure affecting the growth of root tips when the root can develop range from 0.9 to 1.3 MPa and the pressure resulting in a significant reduction of the rate of root elongation ranges from 0.3 to 0.5 MPa. However, these values were found in the course of short-term experiments.

The present paper deals with problems concerning the effect of soil pressure on the growth and development of root systems of two-years-old plants of Norway spruce in the course of the growing season.

MATERIAL AND METHODS

For the determination of soil pressure on the growth of roots during the growing season of 2003, we selected the method of root containers (Waisel et al. 2002). We used an iron construction with lateral wooden walls and a front and rear panel of glass 5 mm thick. Roots could be monitored and photographed through the glass and documented in this way. The front part of root containers was oblique in order to achieve the growth of roots along the

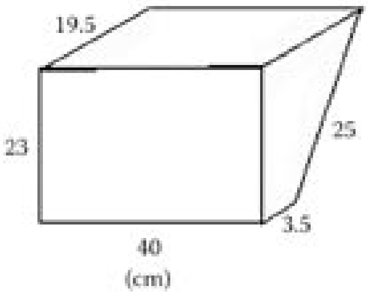

Fig. 1. The diagram of a root container

Table 1. Comparison of various parameters of root systems in control and stressed plants of Norway spruce (*Picea abies* [L.] Karst.), Brno 2003

	Dry matter (DM) of roots (g)	Fresh weight of roots (g)	Specific volume density of roots [DM (g)/ volume (cm^3)]	Water content (%)	Area of root surface (cm^2)	Area of root projection (cm^2)	RAI
Control plants (C)							
Min.	3.81	21.36	0.20	79.7	208	87	2.4
Max.	7.15	37.91	0.26	82.9	518	142	3.7
Mean	6.18	33.01	0.23	81.3	378	116	3.2
Stressed plants (EX)							
Min.	2.16	10.81	0.19	80.0	132	34	2.6
Max.	5.34	31.87	0.25	83.6	312	91	6.8
Mean	3.85	21.24	0.21	81.6	236	61	4.3

glass. Glass parts of the containers were protected from solar radiation with a strong black foil overlaid by a rigid aluminium foil to increase albedo. For the purpose of an experiment, we manufactured 4 containers depicted in Fig. 1. Two containers were control ones, i.e. they were not stressed, and two were stressed by iron cylinders in the course of the whole experiment (wrapped in polythene to prevent the escape of iron compounds) thereby achieving a constant pressure of 5.1 kPa. The containers were planted with two-years-old plants of Norway spruce (*Picea abies* [L.] Karst.) on 20 April 2003. Control and trial containers were placed into a regularly irrigated hotbed in the Botanical Garden and Arboretum of Mendel University of Agriculture and Forestry Brno. After a three-week cultivation (i.e. on 15 May 2003), the first documentation with a digital camera was carried out and then on the following dates: 22. 5., 26. 5., 4. 6., 11. 6., 18. 6., 27. 6., 7. 7., 18. 7., 31. 7., 15. 8., 28. 8., 1. 9., 23. 9., 9. 10. and 29. 10. The data recording the growth of roots were evaluated by means of the computer-based image analysis program ImageTool. After the experiment terminated, control and experimental plants were taken out, separated and their root systems were cleaned carefully. After moderate drying, their green weight was measured and photographic documentation was carried out. In hanging root systems, a top view was recorded in order to measure the area of root projection. Further, in fresh root systems, their volume was measured using pycnometry. Finally, the whole root system was cut into pieces and disintegrated in such a way that the particular roots would not overlap and the area would not be biased by shadow. Roots were covered with a glass and photographed to find out the total area of roots (ImageTool program) which served for the determination of RAI (root area index). The measured root systems were put in marked bags which were subsequently dried to a constant weight at a temperature of 105°C and the dry weight of roots

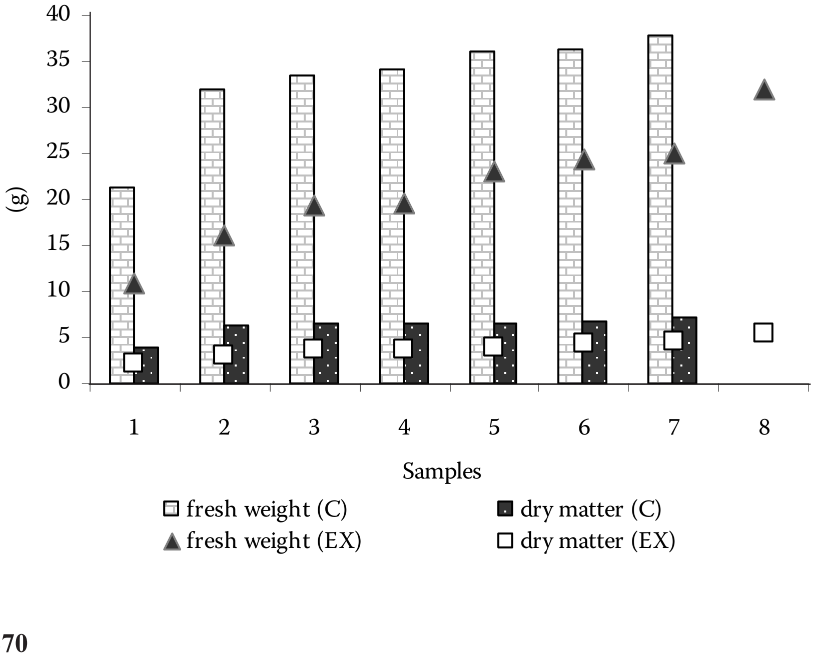

Fig. 2. Fresh weight and dry matter of root systems of Norway spruce plants from control containers (C) and containers stressed (EX) by 5.1 kPa. Particular plants are arranged in ascending order according to the size (growing season 2003, BZA Brno)

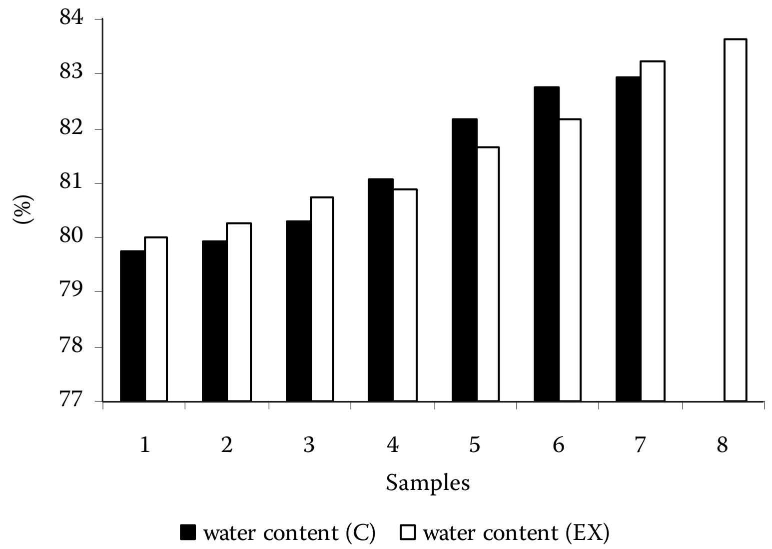

Fig. 3. Water content in % of green weight of root systems of Norway spruce plants from control containers (C) and containers stressed (EX) by 5.1 kPa. Particular plants are arranged in ascending order according to the size (growing season 2003, BZA Brno)

and water content were determined (thereinafter expressed in % fresh weight).

Information on fresh weight, dry matter (DM), water content, root system volume, RAI, rate and time of their growth served for the determination of relationships between variables and comparison of particular parameters of root systems developing under control (unstressed) and experimental (stressed, compacted) conditions of the soil environment.

RESULTS AND DISCUSSION

Values obtained by measurements of root systems are given in Table 1.

Mean DM weight of the root system in control plants was 6.18 g and values ranged from 3.81 to 7.15 g. In stressed root systems, mean DM weight was 3.85 g and values ranged from 2.16 to 5.34 g. Mean fresh weight of roots in the control variant was 33.01 g and values ranged from 21.36 to 37.91 g. In the stressed variant, mean fresh weight was 21.24 g and values ranged between 10.81 and 31.87 g.

Mean specific volume density of root systems (DM in g/root system volume in cm^3) in the control was 0.23 g/cm^3 ranging between 0.2 and 0.26 g/cm^3. In the stressed variant, specific volume density was 0.21 g/cm^3 and values ranged between 0.19 and 0.25 g/cm^3.

The mean content of water in roots ranged from 79.7 to 82.9% in control plants and that in stressed plants from 80 to 83.6% of green weight. The mean content of water in control plants was 81.3% and that in stressed plants 81.6% (Fig. 2).

The total area of roots ranged between 207.98 and 518.02 cm^2 in control plants and mean area was 377.7 cm^2. In stressed plants of spruce, the total area

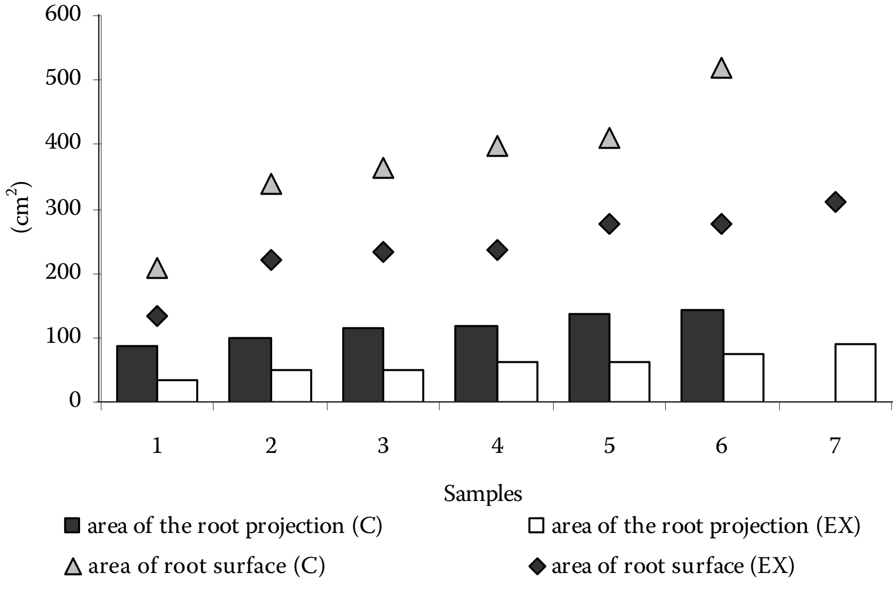

Fig. 4. Comparison of root systems of Norway spruce plants from control containers (C) and containers stressed (EX) by 5.1 kPa. Area of the projection of entire root systems and summary area of all roots of particular systems. Particular plants are arranged in ascending order according to the size (growing season 2003, BZA Brno)

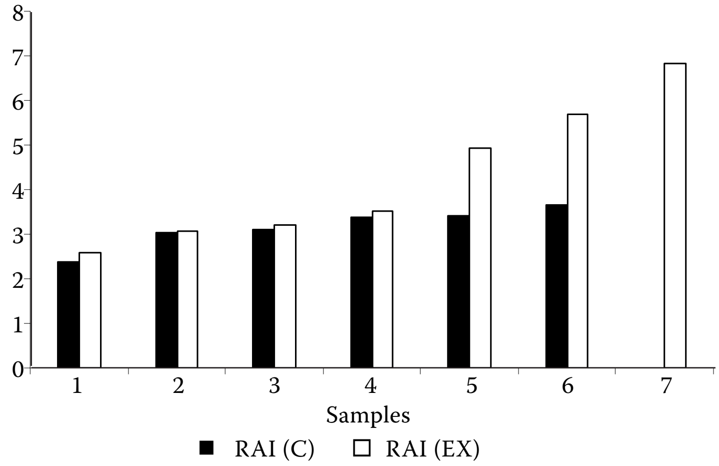

Fig. 5. RAI of root systems of Norway spruce plants from control containers (C) and containers stressed (EX) by 5.1 kPa. Particular plants are arranged in ascending order according to the size (growing season 2003, BZA Brno)

ranged from 132.2 to 312.1 cm^2 and mean area was 236.26 cm^2.

Area of root projection in control plants ranged between 86.91 and 141.67 cm^2 and mean area of the root projection was 116.18 cm^2. In stressed plants, area of root projection ranged from 34.4 to 90.72 cm^2 and mean area of the root projection was 60.63 cm^2.

RAI values in control plants ranged from 2.39 to 3.66 (mean value 3.16) and those in stressed plants from 2.58 to 6.84 (mean value 4.26) (Fig. 3).

In the course of the year, the growth of roots of control spruce plants increased from the value 0.09 cm/day to the value 0.23 cm/day until 15 August with the exception of deviations on 4 June and 18 July. Starting the day the growth of roots began to slow down to the final value 0.01 cm/day. During the whole growing season, mean growth of unstressed plants was 0.14 cm/day. We recorded the growth of 192 roots and the length of their total increment amounted to 308.9 cm in the period under study.

In stressed plants of spruce, the growth of roots increased until 28 August from the value 0.03 cm/day to the value 0.14 cm/day with the exception of two deviations on 7 July and 31 July and starting the day the growth of roots began to slow down to the value of 0.04 cm/day. From 26 May to 4 June, the increment of roots was not noticed. In the course of the year, mean growth was 0.07 cm/day.

In total, we recorded 72 roots and the length of their total increment amounted to 65.37 cm during the period under study. The highest rate of growth in stressed plants (0.14 cm/day) was recorded on 28 August, i.e. 14 days later than in control plants. Relationships between the growth of roots in control and stressed conditions showed that as for the time dynamics the highest differences occurred in the period from the end of May to the end of July when root systems stagnated under the impact of pressure (Fig. 4).

The obtained results are corroborated by findings of other authors. They help to elucidate the decline of trees along forest roads or of trees forming the edge of

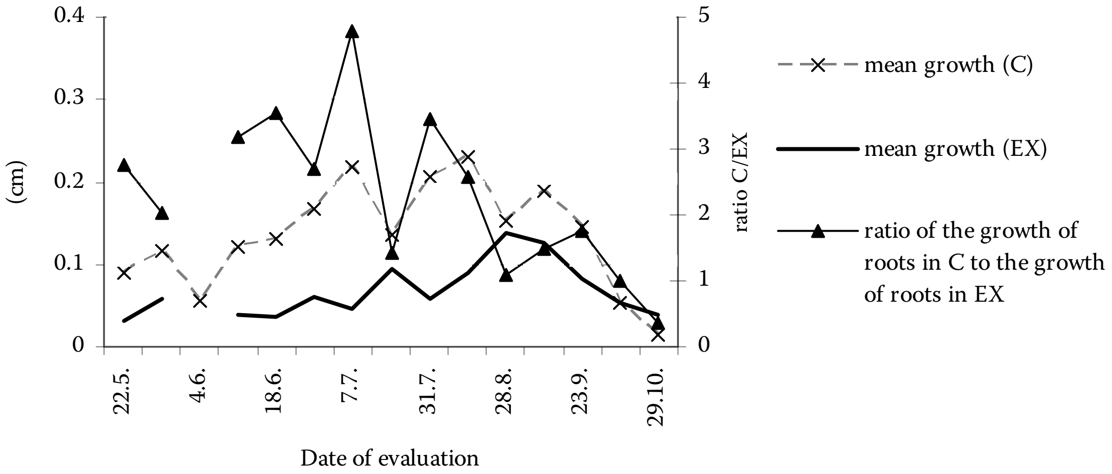

Fig. 6. Comparison of the rate and dynamics of the growth of root systems of Norway spruce plants in control containers (C) and containers stressed by 5.1 kPa (EX). Mean increment of roots for time intervals during the growing season 2003 (BZA Brno)

a stand. In roads treated with deicing salts it is possible to express an assumption that negative consequences of soil compaction can be increased by decreased soil water potential and lack of mycorrhizas.

CONCLUSION

Based on the results it is evident that root systems in the control variant accumulated on average 38% more dry biomass and also their specific volume density was about 7% higher as compared with the stressed variant. It follows that the root system of control plants of spruce was heavier than that in trial plants which also obviously showed changed inner architecture.

The total area of root systems of stressed plants was 38% lower than that of control plants, however, RAI values were 33% higher in stressed plants. It means that under conditions of pressure on the soil surface, plants created not only smaller root systems but also crowded into a smaller soil space.

The average elongation growth of roots in stressed plants reached only 50% of that in control plants. It is also of great importance that stressed plants delayed the growth of roots, which is a typical general response to stress.

It is possible to conclude that root systems of spruce are much more sensitive to pressure than the other plant species. Already a pressure of 5.1 kPa acting for a long time can be the reason for a decreased rate and changed time dynamics of root growth, reduced ability to occupy the soil space and, therefore, to create dense and intensive root systems. This fact is in contradiction with the typical strategy of tree root systems. Another phenomenon is evidently the changed inner architecture of roots which will be further studied. From the methodical aspect, for similar experiments with root growth monitoring it would be suitable to cover transparent walls of root containers with a grid net.

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Received for publication February 14, 2005
Accepted after corrections April 12, 2005

Vliv tlaku na kořenové systémy sazenic smrku ztepilého (*Picea abies* [L.] Karst.)

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ABSTRAKT: Tlak na kořeny se vyskytuje poměrně často – ať již na svažitých terénech, pod nánosy naplavenin, při jarním tání vysoké sněhové pokrývky nebo činností člověka při pojezdu těžkých mechanismů v lesních porostech, při rekreačních aktivitách, při vysokých stavech zvěře a pastvě hospodářských zvířat v lesích aj. Byly provedeny experimenty se sazenicemi smrku ztepilého (*Picea abies* [L.] Karst.), které byly pěstovány v kontejnerech s prosklenými stěnami pod zátěží 5,1 kPa během celého vegetačního období. Za podmínek tohoto tlaku a neměřených podmínek hypoxie se prokázala snížená rychlost, změněná časová dynamika růstu kořenů a snížená schopnost obsazovat půdní prostor. Konkrétně např. celková plocha kořenových systémů experimentálních sazenic byla o 52 % nižší, avšak hodnota RAI (root area index) byla u zatížených kořenů o 33 % vyšší proti kontrolním sazenicím. To znamená, že tlakem na půdní povrch vytvořily sazenice kořenový systém nejen menší, ale i nahloučený do menšího půdního prostoru. Také průměrný délkový růst kořenů byl u experimentálních sazenic proti kontrolním o 50 % nižší. Významným výsledkem bylo, že u experimentálních sazenic byl růst kořenů časově zpožděný, což je typická obecná reakce na stres. Tendence vytvářet pod zvýšeným půdním tlakem kořenový systém hustý a intenzivní je v rozporu s typickou strategií kořenových systémů stromů.

Klíčová slova: růst kořenů; stres; tlak; RAI; *Picea abies* (L.) Karst.

Studie se zabývá vlivem tlaku na kořeny, problémem, který v literatuře citelně chybí, přestože se tento stresor vyskytuje poměrně často – ať již na svažitých terénech, pod nánosy naplavenin, při jarním tání vysoké sněhové pokrývky nebo činností člověka při pojezdu těžkých mechanismů v lesních porostech.

Pro zjištění vlivu tlaku půdy na růst kořenů jsme zvolili metodu kořenových kontejnerů (Waisel 2002). Použili jsme železnou konstrukci s bočními dřevěnými stěnami a s předním a zadním panelem ze skla o tloušťce 5 mm. Dva kontejnery byly kontrolní, tj. nebyly zatížené, a dva byly v průběhu celého měření zatíženy železnými válci, čímž jsme dosáhli stálého tlaku 5,1 kPa. Kontejnery byly osázeny dvouletými nenarašenými sazenicemi smrku ztepilého (*Picea abies* [L.] Karst.). Kontrolní i pokusné kontejnery jsme umístili do pravidelně zavlažovaného pařeniště v botanické zahradě a arboretu Mendelovy zemědělské a lesnické univerzity v Brně. Po třítýdenní kultivaci (tj. 15. 5. 2003) proběhla první dokumentace digitální kamerou, dále se pokračovalo v termínech: 22. 5., 26. 5., 4. 6., 11. 6., 18. 6., 27. 6., 7. 7., 18. 7., 31. 7., 15. 8., 28. 8., 1. 9., 23. 9., 9. 10. a 29. 10. Získaná data zachycující růst kořenů byla vyhodnocena pomocí programu na analýzu obrazu ImageTool.

Po ukončení pokusu byly kontrolní a experimentální rostliny vyjmuty, separovány od sebe a jejich kořenové systémy byly jemně vyčištěny. Po mírném osušení byla zjištěna jejich čerstvá hmotnost a provedena fotografická dokumentace. Při závěsu kořenových systémů byl zachycen pohled shora pro změření plochy půdorysu kořenů (tj. plochy průmětu kořenů na základnu). Dále byl u čerstvých kořenových systémů pyknometricky zjištěn jejich objem. Nakonec byl celý kořenový systém rozstříhán a rozložen tak, aby se jednotlivé kořeny nepřekrývaly a nedošlo ke zkreslení plochy např. vrženými stíny. Kořeny byly přikryty sklem a nafotografovány s cílem zjistit celkovou plochu kořenů (program ImageTool), která nám posloužila pro stanovení RAI. Změřené kořenové systémy byly vloženy do označených sáčků, které byly následně vysušeny do konstantní hmotnosti při 105 °C; byla zjištěna hmotnost sušiny kořenů a obsah vody (dále je vyjadřován v procentech čerstvé hmotnosti).

Zjištěné informace o čerstvé hmotnosti, sušině, obsahu vody, objemu kořenových systémů, RAI, rychlosti a době jejich růstu nám posloužily ke stanovení vztahů mezi veličinami a ke vzájemnému porovnání jednotlivých parametrů kořenových systémů vyvíjejících se v kontrolních (nezatížených) a experimentálních (zatížených, zhutněných) podmínkách půdního prostředí.

Hodnoty získané měřením kořenových soustav jsou přehledně uspořádány v tab. 1.

V průběhu roku se růst kontrolních kořenů sazenic smrku zvyšoval z hodnoty 0,09 cm/den až na hodnotu 0,23 cm/den do 15. 8. kromě dvou výkyvů 4. 6. a 18. 7., a od tohoto dne se růst kořenů začal zpomalovat až na konečnou hodnotu 0,01 cm/den. Průměrný růst v průběhu celého vegetačního období byl u nezhutněných sazenic 0,14 cm/den.

U zatížených sazenic smrku se růst kořenů zvyšoval až do 28. 8. z hodnoty 0,03 cm/den na hodnotu 0,14 cm/den kromě dvou výkyvů 7. 7. a 31. 7., a od tohoto dne se růst kořenů začal zpomalovat na hodnotu 0,04 cm/den. V průběhu roku byl průměrný růst 0,07 cm/den. Nerychlejší růst u zatížených sazenic (0,14 cm/den) byl zaznamenán 28. 8., a to je o 14 dní později než u kontrolních sazenic. Poměr růstu kořenů v kontrolních a zatížených podmínkách ukázal, že v časové dynamice byly největší rozdíly v období od konce května do konce července, kdy kořenové systémy pod vlivem tlaku stagnovaly.

Z dosažených výsledků je zřejmé, že kořenový systém u kontroly akumuloval v průměru 38 % více suché biomasy a také jeho měrná objemová hustota byla asi o 7 % vyšší, než tomu bylo u zatížené varianty. Z toho plyne, že kořenový systém kontrolních sazenic smrku byl těžší než u pokusných sazenic, které měly navíc zřejmě pozměněnou i vnitřní architekturu.

Celková plocha kořenových systémů zatížených sazenic byla o 38 % nižší než u kontrolních sazenic, avšak hodnota RAI (root area index) byla u zatížených kořenů o 33 % vyšší. To znamená, že pod tlakem na půdní povrch vytvořily sazenice kořenový systém nejen menší, ale i nahloučený do menšího půdního prostoru.

Průměrný délkový růst kořenů dosahoval u zatížených sazenic pouze 50 % proti kontrolním sazenicím. Významným výsledkem bylo také zjištění, že zatížené sazenice růst kořenů časově zpozdily, což je typická obecná reakce na stres.

Lze konstatovat, že kořenové systémy smrku jsou vůči tlaku mnohem citlivější, než je tomu u jiných rostlinných druhů. Již tlak 5,1 kPa vyvíjený dlouhodoběji může být příčinou snížené rychlosti a změněné časové dynamiky růstu kořenů, snížené schopnosti obsazovat půdní prostor, a proto vytvářet kořenový systém hustý, intenzivní.

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