We validated, by means of allometric relationships and root severing experiments, the modified earth impedance method developed for measuring absorbing root surfaces. For the allometric studies, a series of 350 small and large trees of six broadleaf and coniferous species in several experimental sites was examined. We found a good linear ln–ln fit between absorbing root surface area and basal area (or stem cross-sectional area at the root collar in seedlings) over a range of stem diameters from 0.5–55 cm. The absorbing root surface area also changed consistently with crown projected area and the root-accessed area (territory) of the tree. At the whole-tree level, absorbing root surface area reached about 70 times that of basal area and 40% of crown projected area, or roughly 1/3 of the root-accessed area in Norway spruce (in this species, the ratio was relatively larger in small trees and smaller in large trees). The absorbing root surfaces of mechanically severed parts of Norway spruce root systems changed in about the same proportions as the geometrically determined parts of the severed root systems. These results are promising and support field applications of the method in biological and ecological studies.

Keywords: broadleaf and conifer species, conductometry, instrumental measurement, whole tree root systems.

Introduction

The most frequently applied biometric parameters of large trees for forestry and ecological purposes are those that can be easily measured or calculated, such as diameter at breast height, basal area, crown projected area and leaf area (or leaf area index, LAI) (West et al. 1999, Eamus et al. 2000, Bond-Lamberty et al. 2002, Enquist 2003). Belowground biometric parameters are applied rarely, mostly as specific characteristics, e.g., root density in g m⁻² of stand area or g m⁻³ of soil volume (Berish 1982, Persson 1983, Van Noordwijk et al. 1996, Steele et al. 1997, Helmisaari and Hallbacken 1999, Vanninen and Mäkelä 1999, Lopez et al. 2001, Persson and Ahlstrom 2002, Danjon et al. 2005). However, in an analogy with aboveground parameters, it is possible to characterize, for example, root projected area and root surface area (Čermák et al. 2000, Čermák and Prax 2001). Although gentle excavation techniques (e.g., air spade: Rizzo and Gross 2000, Gross and Julene 2000, Nathenson and Jarabak 2001, Nadezhdina and Čermák 2003) can be used to expose even delicate roots, the ensuing difficulty of root quantification remains. Root surfaces can be measured, e.g., by digital photography followed by image analysis and sophisticated modeling (Stokes et al. 2002, Danjon et al. 2005) or by the classical, but laborious manual excavation and measurement of all the individual coarse and fine roots. Nevertheless, in contrast to foliage, which is almost entirely functional and cannot be confused with branches, it is difficult to distinguish between the absorbing and non-absorbing surfaces of fine roots (and mycorrhiza) and coarse roots, the latter being primarily engaged in the conduction of absorbed water (Kramer and Bullock 1966).

The study of root systems is especially complicated in adult trees because they are large, complex and include fine absorbing roots as well as presumably conducting coarse roots (e.g., Zygurovskaya 1958, Jeník and Sen 1964, Schuurman and Goedwaagen 1965, Kolesnikov 1972, Bohm 1979, Sutton and Tinus 1983, Steele et al. 1997, Coutts et al. 1999, Johnson et al. 2001). Coarse (skeleton) tree roots have been analyzed by manual excavation from the soil (Jeník 1957, 1978, Kutschera 1960, Kolesnikov 1972, Vyskot 1976, Mauer and Palátová 1996, 2003). Fine roots and coarse roots have been visualized by ground-penetrating radar (GPR; Hruška et al. 1999, Čermák et al. 2000, Šustek et al. 2002, Wielopolski et al. 2000, Stokes et al. 2002). Although this technique is useful for visualizing and qualitatively mapping whole-tree root systems (Barton and Montagu 2004), the 3D images obtained are difficult to quantify reliably in terms of surface area because of the relatively large measurement errors associated with small objects such as roots (Čermák et al. 2000).
Several methods have been used to estimate fine and thin root density. Indirect methods include surface adsorption of acid or basic organic dyes (Wilde and Voigt 1949, Dunham 1958, Carman 1982, Costa et al. 2001), gravimetrically estimated loss of concentrated salt solution (Carley and Watson 1966), absorption and desorption of nitrite (Ansari et al. 1995) and photoelectric measurements (Morrison and Ormsen 1968). Direct measurements of root surface area are based on, e.g., sequential soil core sampling techniques or the use of root-free in-growth cores and miniirizitonones (McQueen 1968, Persson 1983, Vogt et al. 1987, Persson et al. 1990, Steele et al. 1997, Helmisaari and Hallbacken 1999, Janssens et al. 1999, Johnson et al. 2001). Special software and image analysis is often applied, including fractal modeling and sophisticated allometric analysis (Coutts et al. 1999, Drexhage et al. 1999, West et al. 1999, Combes and Grubb 2000, Bond-Lamberty et al. 2002, Salas et al. 2004), but such techniques usually preclude studies of entire tree root systems. Several kinds of non-destructive methods (radioactive tracers, combining soil water content and sap flow) have been used to estimate the functional extent and depth of root systems of forest trees (Woods 1969, Čermák et al. 1980, Čermák and Kučera 1990a, 1990b, Nadezhdina and Čermák 2003). The limitation of these methods is that they provide little to no resolution of root structure and so are unsuitable for quantification of root absorbing surface areas. Absorbing root surfaces represent a compartment through which plants absorb soil water or, more precisely, diluted solutions of mineral elements. The magnitude and permeability of such species are crucial parameters for plant survival. Reliable data on absorbing root surface are needed for modeling root water transport and nutrient uptake (Smerthurst and Comerford 1993, Comerford et al. 1995, Steudle 1995, Eckhard and Horst 1996).

We applied a new method for measuring absorption surfaces of root trees based on earth electrical impedance (Staněk 1997, Aubrecht et al. 2006). Briefly, if a plant root system is submersed in an aqueous solution (such as soil water) and connected to a simple electric circuit, the electric current from the external source (represented by ion flow) enters the plant through the electrically conducting (ion absorbing) root surfaces. Other root surfaces, irrespective of their size, do not conduct electric current, except lenticels and damaged areas. Based on differences in conductivity of tree tissues and soil, we can estimate the soil–root interface, which can be interpreted as the actual conducting or absorbing root surface. Our specific objective was to verify the technique in different woody species and trees of different sizes. Because no alternative method for direct measurement of absorbing root surfaces at the whole-tree level (especially large trees) is available for comparison, we compared the method with several indirect approaches based on allometric relationships and root severing experiments.

**Materials and methods**

**Experimental sites, soils and study species**

The modified earth conductometric (more precisely, earth impedance) method for root surface measurement was tested on a series of 350 small and large trees of six species at nine experimental sites in the Czech Republic, Italy and Sweden. The studies were made in various soil types at a range of soil water contents (25–45%vol) and air temperatures (10–15 °C), as summarized in Table 1.

**Method of root surface measurement**

The absorbing root surface was measured by the earth electrical conductometric method (Staněk 1997, Aubrecht et al. 2006). This method measures only the actual absorbing root surfaces and ignores non-absorbing root surfaces such as those covered by impermeable suberin. The method is based on the fact that water solution from the soil enters (or exits) the plant mostly through the permeable surfaces close to the root cap and partially along fine roots with some component entering through the non-suberized parts of coarse roots (Kramer and Bullock 1966, Clarkson and Robards 1975, Weatherley 1975). If a plant growing in the soil (or in a water solution) is connected to a simple serial electric circuit, then current flowing through this circuit from the external source enters (or exits) the plant entirely through the absorption zones (Figure 1). Other parts of the root surface are not considered because they do not conduct electric current to a significant extent. The resulting expression of the theory has the form:

\[ A_{\text{root}} = \rho I \frac{l}{U} \]  \hspace{1cm} (1)

where \( A_{\text{root}} \) is total actual root absorption surface, \( \rho \) is the resistivity of the water conducting tissue, \( l \) is distance from the stem, \( I \) is current flowing from an external supply through the woody stem, root system and soil to an auxiliary metal electrode (or system of electrodes), and \( U \) is the potential difference between the stem boundary and potential electrode.

Implementation of the method is based on Figure 1. Metal electrodes were gently hammered into the stem of the measured tree and connected to the circuit with generator GEN, ammeter \( I \) and one (or a series) of auxiliary current electrodes in the soil. The insertion depth of current and potential electrodes in the soil was 0.15–0.20 m. The electrodes were about 0.01 m in diameter to ensure a sufficient conducting surface (this does not apply to metal electrodes in stems where the insertion depth and contacting surface of electrodes were not critical). We used an alternating current with a frequency of several hundreds of Hz. The potential soil electrodes were located at a defined distance \( l \) (3–8 m) from the stem. The distances of the auxiliary current electrodes and of the potential soil electrode from the stem of the measured tree are determined by the course of the potential characteristic measured before the particular root measurements. Over a series of times, the potential electrode was hammered in the soil at locations from the stem up to the boundary of the plateau and hyperbolic parts of the potential characteristic.

Resistivity of the water conducting tissue in roots was determined by the four-point Wenner method, as described previously (Staněk 1997, Aubrecht et al. 2006), using a correction
determined with a Megger apparatus on coarse roots near the stem at the soil surface. We thus obtained the conducting root surface area corresponding to one root segment. (A root segment is defined as any part of rooted space around a tree occurring within a selected angle, e.g., 60°). The minimum number of root segments that need to be measured to obtain a reliable measure of whole-tree root absorption surface area depends on the size of the given tree and on the symmetry of the root distribution patterns and the position of the main roots (Aubrecht et al. 2006). We usually measured six (4–8) root segments, and calculated $A_{\text{root}}$ as the sum of the areas of absorption zones of the individual segments ($A_{\text{root},i}$):

$$A_{\text{root}} = \sum_{i=1}^{n} A_{\text{root},i}$$

(2)

where $n$ is number of measured segments.

Verification of the magnitude of root absorbing surfaces

Because no alternative direct method of measuring root absorbing surface at the whole-tree level is available for comparison with the conductometric method, we attempted to validate the method indirectly on the basis of allometric relationships and root severing experiments.

Allometric relationships

Several tree parameters are easily measured in the field and are suitable for allometric studies. For this study we chose basal area ($A_{\text{bas}}$, i.e., stem cross-sectional area at breast height, 1.3 m) (Philip 1994), projected crown area ($A_{\text{crown}}$) and the root-accessed area (or territory) ($A_{\text{acs}}$, taken as part of the stand area associated with a particular sample tree according to its size and the magnitude of the available surrounding space). We calculated $A_{\text{acs}}$ from the mean distance ($L_{\text{acs}}$) of the particular sample tree to its neighbors, weighted by the ratio of their basal areas ($\bar{e}$ermák 1990):

$$L_{\text{acs}} = \frac{1}{n} \sum_{i=1}^{n} L_i \left( \frac{A_{\text{bas},i}}{A_{\text{bas},i} + A_{\text{bas},\text{Neighb}}} \right)$$

(3)

where $L_i$ is distance to each neighboring tree, and $A_{\text{bas},i}$ and $A_{\text{bas},\text{Neighb}}$ are basal areas of the sample and a particular neighboring tree (Figure 2).

Comparison of root parts of the same tree

The Jedovnice site, which has a high ground water table, limiting the rooting depth to a maximum of 30 cm, was selected for this experiment. The whole-tree root surfaces of seven large Norway spruce trees were measured and then part of the root system (almost 50%) on one side of the stem was mechanically severed by an excavator as close to the stem as possible. The two parts of what remained of the root system were then remeasured—the undisturbed intact part on one side of the stem and the part of the root system remaining on the other side of the stem after roots on that side of the stem had been severed (Figure 3).
The three values for each of the seven sample trees, each measured by both methods, were compared.

Results

Examples of particular measurements

Fine roots usually create a network that is especially dense in nutrient-rich surface soil layers. The applied conductometric method does not measure individual roots, but the total absorbing root surface of a given tree. As an example of the procedure, we describe the measurement of the root system of a small oak tree (*Quercus petraea*) that was growing in a forested area near Brno. The tree had a diameter of 43 mm, a height of 0.7 m and was well foliated. We determined the distance of the auxiliary potential soil electrode from the stem as \( l = 75 \text{ cm} \) from the potential characteristic (consisting of two unequal nonlinear hyperbolic sections near the stem and auxiliary current electrode). We then specified a linear part with a small slope (Figure 4). Also, the location (i.e., the radius of the sphere) of the soil current electrodes can be specified, such as \( R > l \). The number of current electrodes in the stem is determined by the magnitude of the saturated current; the same condition also applies to the number of auxiliary electrodes in the soil. Resistivity determined by the method of the long cylinder was \( \rho = 85.3 \, \Omega \text{m} \). The applied power supply was of 35 V, 500 Hz with a maximum current of 300 mA, the resulting voltage was \( U = 0.46 \text{ V} \) and current \( I = 2.47 \text{ mA} \). The absorbing root surface \( A_{\text{root}} \) calculated according to Equation 1 was:

\[
A_{\text{root}} = \rho \frac{l}{U} I = 0.3435 \, \text{m}^2
\]

where \( \rho_{\text{long column}} (\Omega \text{m})^*l/R_{\text{megger}} (\Omega) \). The root-accessed area \( A_{\text{acs}} \) of the tree (which approximated the crown projected area of the given tree) was 1.9 m\(^2\) (thus, \( A_{\text{root}} \) was 18\% of \( A_{\text{acs}} \)) and coarse root surface \( A_{\text{root_coarse}} \) was 0.65 m\(^2\) (thus \( A_{\text{root_coarse}} \) reached 34\% of \( A_{\text{acs}} \) and \( A_{\text{root}} \) was 53\% of \( A_{\text{root_coarse}} \)).

The distribution of tree roots of different diameters is usually log-normal relative to the total root surface, although variable according to local site conditions and species. This is demonstrated in an example of a pine seedling growing on sandy soil (Figure 5, one of the series of sample trees measured there and included in Figure 6). Total root length, surface and volume in this particular seedling with diameter at the root collar of 9.8 mm reached 4106 cm, 1795 cm\(^2\) and 83 cm\(^3\), respect-
tively, and the actual absorbing root surface of 153 cm² (i.e., 8.5% total). (The roots were exposed manually with a brush over several days, resulting in a hole over 3 m in diameter). However, some fine roots of 0.5 mm in diameter and over 2 m long (runners) cannot be extracted this way in the field, so the root surface area was underestimated. Because it is impossible to expose whole root systems of large trees and measure them as seedling root systems are measured, we used indirect methods to verify the earth conductometric method in the case of the large trees.

Verification of the magnitude of root absorbing surfaces

Allometric relationships Basal area, which is the most precisely measurable of many forest inventory parameters, was used to estimate allometric relationships with root absorbing surface. Logarithmic plots over a wide range of tree sizes (stem diameters 0.5–55 cm) showed a good linear relationship ($r^2 = 0.90$; Figure 6). Although the relationship between basal area and projected crown area was variable ($r^2 = 0.76$, $P = 0.05$; Figure 7), the relationships between basal area and root absorbing surface ($r^2 = 0.88$, $P = 0.01$) and root-accessed area ($r^2 = 0.92$, $P = 0.01$) had similar comparative values. Generally, the actual absorbing root surface of the mean tree represented about 40% of the projected crown area (over the whole range of studied tree sizes studied, but with high variation) and about 33% of the root-accessed area. However, tree size was important: $A_{\text{root}}$ rep-

Figure 3. Illustration of root severing experiment with large Norway spruce trees. The hatched circle represents the total root area of an intact tree, the hatched semicircle represents half of the total root area of an entire tree after root severing and the cross-hatched section represents the root area remaining after roots on that side of the tree had been severed with an excavator.

Figure 4. Schematic of the potential characteristics, measured in one direction. Oak (Quercus petraea (Mattusch.) Liebl), crown diameter 1.5 m and stem diameter 4.3 cm. Potential characteristics consisted of two unequal nonlinear (hyperbolic) parts (I and III) near the stem and auxiliary current electrode and a linear part (II) with a small slope (plateau). Abbreviation: $I =$ current; and $U =$ voltage.

Figure 5. Relationship between root diameter and total root surface area in a pine (Pinus sylvestris) seedling growing on sandy soil.

Figure 6. Relationship between root absorbing surface and basal area in six coniferous and broadleaf species (altogether 350 trees) differing in tree size (stem diameter ranging from about 0.5 to 55 cm): $\log(A_{\text{root}}) = 0.88\log(A_{\text{bas}}) - 2$, $r^2 = 0.90$ (statistically significant at $P < 0.001$) and SE = 0.33.
represented a larger percentage of the root-accessed area in small trees (i.e., trees with DBH < 20 cm, $A_{\text{root}}$ reached about 90% of $A_{\text{acs}}$) than in large trees (down to 20–25% of $A_{\text{acs}}$ in the largest sample trees with DBH around 30 cm). In the smallest trees, the tree crown was umbrella shaped, which is why $A_{\text{crown}}$ decreased from over 200% to around 70% of $A_{\text{acs}}$. The $A_{\text{root}}$ was about 70 times larger than $A_{\text{bas}}$, whereas $A_{\text{crown}}$ and $A_{\text{acs}}$ were around 200 times larger than $A_{\text{bas}}$.

Comparison of root parts of the same large spruce trees
Excavation of the outer part of the root system resulted in a marked decrease in the magnitude of absorbing root surface. The proportions of absorbing areas of the different parts of root systems following the severing treatment corresponded to their geometrically measured areas (Figure 8). (Differences in root surface estimates were mostly characterized by a slightly different positioning of electrodes in the soil; therefore, we took slightly different segments in the replicate experiments). The relationships between basal area and absorbing root surface of the whole root system, its intact half and the remaining part of the root system on the treated side, indicated that the root surface increased rapidly with tree size up to $A_{\text{bas}}$ about 600 cm$^2$ (i.e., DBH = 28 cm) and appeared to reach a plateau in larger trees (Figure 9).

Discussion
Roots are generally distinguished according to their size and morphology (Jeník and Sen 1964, Kolesnikov 1972, Sutton and Tinus 1983). The absorbing root area density has usually been reported to be largely uniform in the area around each tree (Persson 1983). However, the classification of roots based on diameters only is not always clear cut. For example, some authors define fine roots as those with diameters of < 1 mm (Persson et al. 1995, Persson and Ahlstrom 2002), whereas other authors include roots with larger diameters, e.g., < 2 mm or even < 5 mm (Pregitzer et al. 1998, Vanninen and Mäkelä 1999, Ostonen et al. 1999). Furthermore, field studies of roots have rarely distinguished roots on the basis of their actual absorbing ability. Historically, only fine roots were considered to absorb water from the soil; however, Kramer and Bullock (1966) demonstrated the importance of skeleton coarse roots in the absorption of solutes. Therefore, we need a better basis for specifying what the measured root surface represents, whether it includes only fine roots or also the conducting parts of skeleton roots and the role of mycorrhiza.

The tree is a system that must be well balanced in order to work properly (Cruiziat et al. 2002, McCulloh et al. 2003), which is why allometric relationships can be used to investigate the absorbing root area of the whole tree (e.g., Marchand
1984, Bancalari et al. 1987, Carlson and Harrington 1987, Ter-Mikaelian and Korzukhin 1997, Drexhage and Gruber 1999, Drexhange et al. 1999, Komiyama et al. 2000, Niklas and Enquist 2002, Bond-Lamberty et al. 2002, Enquist 2002, Richardson and Dohna 2003, Ritson and Sochacki 2003). Basal area is the most precisely measurable of all simple biometric parameters; however, because it is much smaller (i.e., 0.01 to 0.15 m² in large trees) than the predicted root absorbing area (units up to tens of m²), it is less useful as an estimator of root absorbing area than parameters of equivalent magnitude, such as $A_{crown}$ and $A_{acs}$, even though they cannot be measured as accurately as $A_{bas}$.

The results from several hundred trees showed consistent and reasonable relationships between root absorbing surface area and $A_{bas}$, $A_{crown}$, and $A_{acs}$, thereby supporting the usefulness and robustness of the earth impedance method. Although the number of trees used for the root-severing experiment was large, the results obtained provided further verification of the modified earth conductometric method. For the allometric relationships, the ln–ln function indicated a scaling invariance, i.e., self-similarity at different scales. The rather high variation in the ln–ln plot is probably associated with the soil properties and the tree’s state of health. In grasses, the biometrically estimated root surface area is almost always larger than leaf area (Jackson et al. 1996, 1997). However, the situation is less clear in woody species because in most studies on fine roots the data have been expressed on a biomass basis and rarely in terms of root surfaces. As predicted, the values of the root absorbing surfaces measured in this study were lower than the maximum limits estimated for fine root surfaces, e.g., in large maple trees (Čermák et al. 2000) and the areas of oak root systems used in water balance studies (Krejzar et al. 1997, Čermák and Prax 2001).

In conclusion, at the individual-tree level, root absorbing (conducting) surface area can be measured in the field by the electrical conductometric technique (such as the earth impedance method). Although it remains unclear whether the actual measured area represents only fine roots or their parts, or includes additional components such as mycorrhiza and certain parts of skeleton coarse roots, the measured area changed consistently with crown projected area and with tree area. There was also a good linear ln–ln relationship between root absorbing surface area and stem cross-sectional area ($A_{bas}$) in six coniferous and broadleaf species over a range in tree size of two orders of magnitude. In Norway spruce, whole-tree root absorbing area reached about 70 times that of basal area and 40% of crown projected area, or roughly 1/3 of the root-accessed area of the tree (in this species, the ratio was relatively larger in small trees and smaller in large trees).

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