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The root system architecture of young Greek fir (*Abies cephalonica* Loudon) trees

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Abstract

The root system architecture of young Greek fir (*Abies cephalonica* Loudon) trees was studied in Evritania, Central Greece. A sample of naturally regenerated fir plants were uprooted and divided into three age groups of 5 (5–6 years), 10 (9–11 years) and 15 (15–16 years) years old. Root architectural data (e.g. root length and volume, topology, branching structure) were obtained with a 3D digitizer (3SPACE Fastrak, Polhemus). In all nine trees the largest vertical root originating from the stump was selected, measured and coded as a taproot. The topological and geometrical information from the data file was analysed by computing the characteristics of each root segment. The AMAPmod software was used, providing the user with various tools for encoding, exploring and modelling plants. The findings showed that the age of fir trees is an important parameter that affects root architecture. Topological analysis revealed that the root system of Greek fir have almost a typical herringbone pattern during the first 10 years of tree life, and then the root systems changes to a less herringbone pattern. The root system is expanded with the tree age; however, the total root length and the total number of roots seems to increase in a linear trend, while the root volume appears to increase in a geometric way.

Key words: *Root topology, root length, herringbone pattern, tree age*

Introduction

The root system architecture of trees is influenced by both tree species and environmental conditions. Nonetheless, the initial root systems of all seedlings develop along a single axis, the taproot, from which lateral roots grow to form an extensively branched system (Coutts 1989). In most species the dominance of the taproot diminishes very early in the development, and is replaced by secondary roots (Coutts 1987). However, root morphologies are usually more complex and their variability is poorly understood (Dupuy et al. 2007). For example, it was observed that under drought conditions, more biomass is accumulated in lateral roots than in the taproot (Chiatante et al. 2006). Furthermore, the morphology and topology of root systems change throughout the life of a tree, depending largely on soil conditions (Khuder et al. 2007).

Tree root studies have been restricted to a limited number of species, often of young age, and there is a scarcity of data for many forest tree species (Coutts 1989; Ganatsas & Tsakaldimi 2003). Greek fir (*Abies cephalonica* Loudon) is an important forest species widely distributed in Greece, but there are no published reports on its root architecture.

Together with the overall size of a root system (e.g. root length) and the geometry of orientation and morphology of individual roots, topology determines the in situ space-filling properties of a root system within the soil and thus is an important component of nutrient uptake capacity (Fitter et al. 1991; Fitter 2002; Berntson 1997). A large number of parameters on the location of root quantities can be computed from 3D digitizing data of whole root systems (Danjon et al. 1999, 2005; Tobin et al. 2007). An overview of the most important methods used for root architecture measurements have been given by Reubens et al. (2007).

However, knowledge of root growth and architecture of trees grown on slopes in the Mediterranean conditions, where soil depth and moisture is usually

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limited, is necessary for understanding root–soil interactions. Root growth patterns and dynamics throughout tree life are important for the estimation of soil holding capacity and water and nutrient uptake ability.

The aim of this study was to record the root system architecture of young Greek fir trees growing on steep slopes, as well as the root expansion and/or transformation during the early tree life.

Materials and methods

Description of study area

This study was carried out in Eyritania, a prefecture located in central Greece. Young Greek fir trees were removed from a natural uneven-aged forest on steep slopes (approximately 30% inclination) on the location ''Profitis Hlias'', 8 km northeast from Karpenisi city. In order to avoid the influence of any external factors, sampling was carried out in a small area (100 m^2) with no obvious soil variation. The altitude is approximately 1200 m a.s.l. The soils are mainly luvizols and acrisols developed on limestone and flysch; they are of medium depth (40–60 cm), relatively rich in organic matter in the surface horizons (5–8%) and slightly alkaline (pH 7.5). Greek fir dominates the vegetation in the area and creates extensive uneven-aged stands. The climate of Evritania region belongs to the continental-Mediterranean type, characterized by cold and moist winters and dry summers. The mean annual rainfall is 1100 mm, while the mean maximum air temperature is 12.3°C and mean minimum air temperature 8.6°C. The dry season lasts on an average 2.5 months from June up to the middle of August.

Methods

In 2004, naturally regenerated young Greek fir trees were uprooted and measured with a 3D digitizer (3SPACE Fastrak, Polhemus, Long Ranger option, using low-frequency electromagnetic field sensing). Trees were randomly selected among those presumably estimated belonging to the target age classes of 5, 10 and 15 years. Trees were then divided into the three age groups: 5 years (actual tree age of 5–6 years), 10 years (actual tree age of 9, 10, 11 years) and 15 years (actual tree age of 15–16 years). However, the total uprooted trees were 12 but the age of the other three trees was not suited to the selected age class (their age differed more than two years from the mean class age). Uprooting was performed manually in order to minimize fine root loss. Root systems were then transported to the laboratory for architectural analysis. The largest vertical root originating from the stump was selected, measured and coded as a taproot. The stump was defined as the first 0.25 m of the first order root (Danjon et al. 2007). All roots with a diameter at the origin of greater than 1mm (Collet et al. 2006) were measured.

The topological and geometrical information from the data file was analysed by computing the characteristics of each root segment. Data were saved in files and exported to the software AMAPmod (Polhemus 1993; Godin et al. 1997), which handles topological structure at several scales and also provides 3D graphical reconstruction for data checking (Di Iorio et al. 2005). The AMAPmod software provides to the user various tools for encoding, exploring and modelling plants. Diameters and the branching structure (i.e. branching and location of the root ends) had entered by the operator, using the plant topology coding. During measurements the root systems were positioned upside down and fixed to the ground (Sinoquet et al. 1997). Finally, each scale was formally represented by a tree graph and the whole structure by a Multiscale Tree Graph (MTG).

Topology encompasses the non-metric aspects of branching structure. Topologically identical root systems can still take on very different appearances if they vary in metric aspects of their geometry, particularly the lengths of individual links. In a topological classification, links can be regarded as external (determining in a meristem) or internal, and external links (external–external, EE) are more usefully than those that joint with internal links (external–internal, EI). Root topological analysis was based on the branching pattern (Fitter 2002; Danjon et al. 2004) and determined the magnitude (μ) as the number of external links, the altitude (a) as the number of links in the longest individual path length, the total external path length (p_e) as the sum of the number of links in all paths from all external links to the base link, and finally the topological index as the slope of the regression of $\log_{10} p_e$ or $\log_{10} a$ on $\log_{10} \mu$ (Fitter 2002). This index is a figure between 0 and 1, which indicates that for a value 0 a root system has an extreme dichotomous pattern while for a value 1 an extreme herringbone pattern.

Statistical analysis

For analysis of directional data each root system was individually analysed (Fisher 1993) using the MATLAB program. Numbers of roots were grouped in 45° intervals giving k (= 8) intervals, and calculating a chi-squared test, tested the hypothesis of uniformity.

$$Y = (k/n) \sum_{i=1}^{k} n_i^2 - n,$$

where $n = n_i + \ldots + n_k$, the observed values in each interval. The hypothesis of uniformity will be rejected if Y is found to be too large (Fisher 1993). For root volume data means of all trees were compared between downslope and upslope side using a Mann–Whitney test (Zar 1999) and the SPSS program. Means were considered to be significantly different when the P-value was less than 0.05. The relation of the main root characteristics with the tree age was tested using linear and nonlinear models.

Results

The comparison of root characteristics indicated that the root architecture of Greek fir changed with tree age (Table I). All root parameters were higher in the older trees and there was a positive linear relationship between the number of roots and total root length with the tree age (Figures 1, 2, $R^2 = 0.88$ and $R^2 = 0.95$, respectively), while the root volume seems to increase in a geometric way with the tree age (Figure 3, $R^2 = 0.87$). Examples of root images at each tree age are shown in Figures 4–6.

Up to the fifth year, the root systems consisted of a taproot and the first-order lateral roots, and only very few second order laterals were formed (0.7 roots per tree). During the next five years, the numbers of both first- and second-order lateral roots increased and the first third-order lateral roots appeared. Thereafter, root systems expanded by increasing the number of roots of every order. However, this increase seems to follow a different pattern and the number of

Table I. Mean root architecture characteristics of all roots above 1 mm diameter of young Greek fir trees (5, 10 and 15 years old), based on analysis using AMAPmod, $n = 9$. Values are means and standard errors of means (in parenthesis).

	Average tree age (years)		
	5	10	15
Total number of roots	12.3(2.84)	22.3(4.10)	40.0(2.31)
Total root length (cm)	127.0(10.5)	257.0(50.7)	509.0(24.1)
Total volume of all roots and stump (cm^3)	3.33(0.88)	15.67(4.91)	42.67(9.68)
Number of first-order lateral roots	10.7(2.18)	16.3(0.67)	17.0(2.00)
Number of second-order lateral roots	0.7(*)	4.3(2.96)	15.3(0.33)
Number of third-order lateral roots	0.0	0.7(*)	6.7(1.45)
Total root volume without stump and taproot (cm^3)	0.33(0.16)	2.00(1.00)	10.33(3.38)
Total root volume without stump (cm^3)	1.00(0.33)	2.33(1.33)	14.33(6.88)
Total root length without stump (cm)	110.7(10.3)	218.0(60.1)	468.3(37.8)
Total root length without taproot (cm)	81.3(10.7)	205.7(55.8)	440.0(19.9)

*Inadequate data for statistical analysis; second- (or third-) order lateral roots existed only in one sample tree.

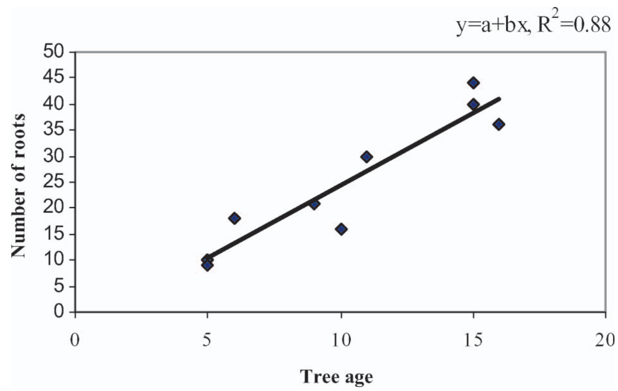

Figure 1. Relationship between the total number of roots of young Greek fir trees and tree age, based on the analysis using AMAPmod. The regression equation for the relationship between number of roots (y) and tree age (x) is: $y = -3.62 + 2.79x$.

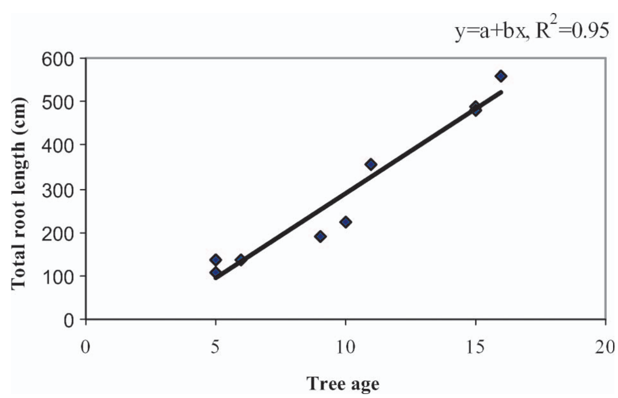

Figure 2. Relationship between the total root length (in cm) of young Greek fir trees and tree age, based on the analysis using AMAPmod. The regression equation for the relationship between total root length (y) and tree age (x) is: $y = -101.33 + 39.03x$.

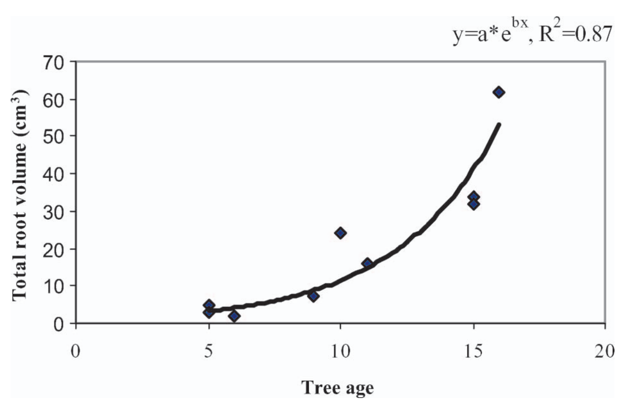

Figure 3. Relationship between the total root volume of young Greek fir trees and tree age, based on the analysis using AMAPmod. The regression equation for the relationship between total root volume (y) and tree age (x) is: $y = 0.885\ e^{0.256x}$.

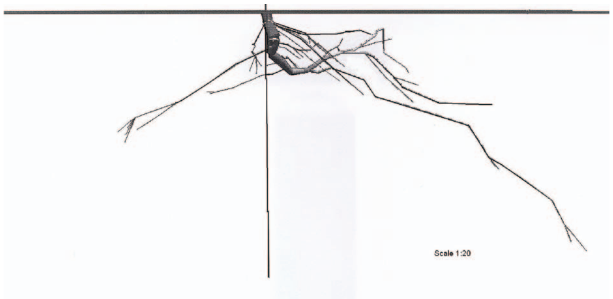

Figure 4. Root architecture of average 5 years old trees of Greek fir (digitized by 3D Fastrak/Polhemus).

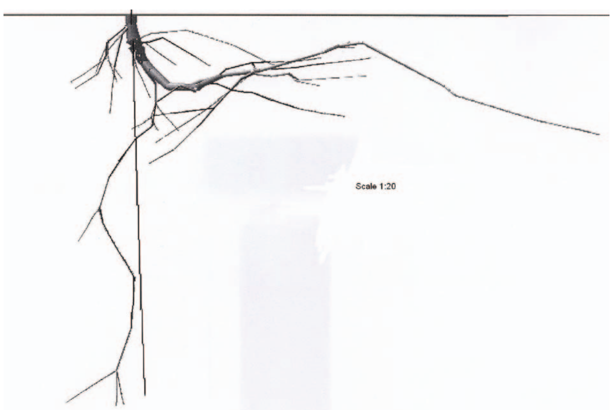

Figure 5. Root architecture of average 10 years old trees of Greek fir (digitized by 3D Fastrak/Polhemus).

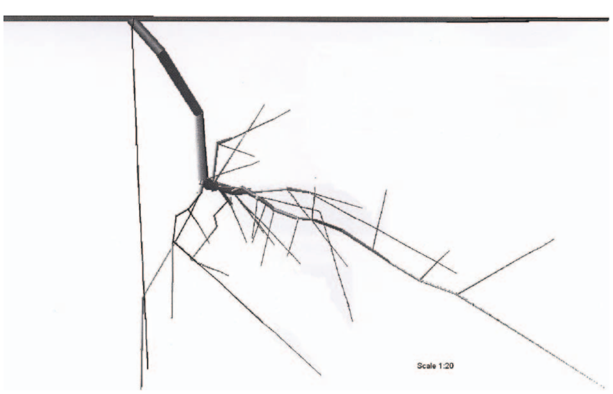

Figure 6. Root architecture of average 15 years old trees of Greek fir (digitized by 3D Fastrak/Polhemus).

second-order laterals was found over three-fold and the number of third-order was found ten-fold compared to the respective number at the age of 10 years, while the first order laterals increased only 4%.

Based on the topological analysis, the root altitude of the young Greek fir trees, increased with the tree age from 11.0 at the age of 5 years to 17.3 at the age of 10 years while then, appears to remain almost stable (18.0) probably due to the gradual root system transformation to a less herringbone pattern (Table II). Greater increase was observed in root magnitude, from 12.3 to 22.3 (10 years) and to 40.0 (15 years), and in the external path length, which increased from 86.7 at the age of 5 years to 376.3 at the age of 15 years. According to the topological index the root system of Greek fir appears to have almost a typical herringbone pattern (topological index close to 0) during the first ten years of tree life. The root system of older trees seems to not follow this pattern and the dichotomy pattern appears.

Table II. Mean topological parameters of the root system of young Greek fir trees (5, 10 and 15 years old), based on analysis using AMAPmod, $n = 9$. Values are means and standard errors of means (in parenthesis).

	Average tree age (years)		
	5	10	15
Altitude	11.0(2.19)	17.3(0.69)	18.0(2.00)
Magnitude	12.3(2.84)	22.3(4.10)	40.0(2.31)
External path length	86.7(11.0)	210.3(56.0)	376.3(19.8)
Topological index	0.96(0.03)	0.93(0.06)	0.78(0.08)

Statistical analysis of root distribution around the stumps showed that the root system of all trees was not-uniformly distributed around the stump; the criterion *Y* was found to be too large in all cases ($Y > 40$), much higher than the upper 100a% value of the X^2_{k-1} distribution (Appendix A2 in Fisher 1993). The root systems developed on the downslope side, especially during the first 10 years of the trees. During this period all the root volume was found on the downslope side, indicating that the root mass was significantly clustered. Afterwards, the root systems expanded more uniformly, in all directions, and resulted in a root volume distributed 84.1% downwards and 15.6% upwards.

Discussion

The findings of the study show that the root architecture of young Greek fir trees are affected by age. During the early tree life, the root system of Greek fir consists of a taproot and the first-order lateral roots; then some second-order laterals are formed and later a few third-order laterals. The root system expands in space with tree age; however, the total root length and the total number of roots appears to increase in a linear trend, while the root volume appears to increase in a geometric way.

Topological analysis showed that the root system of Greek fir appears to have almost a typical herringbone pattern (topological index close to 1) during the first 10 years of tree life. This would provide an advantage for the tree, as herringbone pattern root systems are more efficient than other patterns in terms of nutrients uptake per unit carbon invested (Fitter et al. 1991; Bouma et al. 2001; Fitter

2002). Then, as trees become larger and the competition for nutrients increases, the root system seems to grow towards the dichotomy pattern (the topological index decreases to 0.78). The root magnitude and external path length of the root systems increase with tree age, while the root altitude appears to increase until the age of 10 years and then remain almost stable, probably due to the gradual root system transformation to a less herringbone pattern after this age.

The root systems had found to be non-uniformly distributed around the stumps. The root mass was found concentrated on the downslope side, especially during the first 10 years of tree life. This root asymmetry of the young Greek fir trees confirms that roots show plasticity in their development and respond to environmental conditions as they grow (Fitter 2002). Similar results were reported for papaya (*Canica papaya* L.) plants growing on a slope of 30° and around 70% of roots had formed on the downslope side (Marler & Discekici 1997). Clear root asymmetry on trees growing on slopes and a reduction in root asymmetry with age was reported for the Mediterranean pines *Pinus halepensis* and *P. brutia* (Ganatsas & Spanos 2005). However, it must be noted that the small number of studies on the asymmetry of root development on steep slopes has provided inconsistent results (Nicoll et al. 2006).

Root system architecture has a fundamental influence on root productivity, determining water and nutrient uptake efficiency, belowground competition and interactions between roots, soil and microorganisms (Fitter et al. 1991; Lynch 1995) and resistance to uprooting and stem straightness (Mason 1985; Stokes et al. 1996). Studies of plant root system branching patterns, aside from contributing to an integrated view of architecture, can provide valuable insights into developmental processes which produce root systems (Berntson 1997). More research is needed on the architecture root systems, in order to improve our understanding of how roots develop in relation to the soil environment as tree ages.

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