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Root system asymmetry of Mediterranean pines

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Abstract

Three groups of Mediterranean pines were examined to describe the development of root symmetry on sites characterized by shallow soils and low water availability. Sampling included: (1) 3-year-old planted seedlings of *Pinus halepensis* Mill. taken from Sithonia Halkidiki, northern Greece, (2) 5-year-old natural regenerated seedlings of *Pinus brutia* Ten. taken from Kedrinos Lofos, Thessaloniki and (3) 65-year-old trees of *Pinus brutia* taken from Kedrinos Lofos, Thessaloniki. Root system symmetry was examined by measuring the number, the diameter, the cross-sectional area (CSA), the root area index (RAI) and the length of the lateral roots of each root system, and by analyzing their distribution around the stem. Above-ground plant symmetry was also estimated. The findings of the study indicated that there was an asymmetric root system in all three groups that is characterized by the concentration of the main laterals along the contour lines instead of uphill or downhill; however, the asymmetry was much higher in the young plants. This asymmetry was not correlated with the above-ground plant growth form, which was found to be symmetric. The asymmetric development of root can be attributed to the shallow soil and the high mechanical resistance of the underground bedrock that stopped the taproot growth, restricted the root penetration in the deeper layers and obliged the roots to elongate towards the surface soil layers, where there is more available water.

Introduction

In situ investigations on root systems face many practical difficulties. However, the development of a root system, capable of anchoring the shoot and obtaining water and nutrients, is essential to the terrestrial plants' survival and growth (Bengough et al., 1997; Clark et al., 2003). Since the environment of root systems is highly heterogeneous both in time and space, it appears important that the root systems have the ability to react to that heterogeneity, even at a local level within the root (Stokes et al., 1998); in other words they possess phenotypic plasticity (Fitter, 1991).

Usually, shallow forest soils in combination with high soil consistency affect root architecture since root elongation is permitted only when the root pressure exceeds the soil mechanical impedance. Drought also increases penetration resistance of the soils (Moroni et al., 2003) as soil strength increases with decreasing soil water content (Clark et al., 2003). Pathways of lower mechanical impedance give rise to preferential root growth. As a consequence, the distribution of roots in a soil profile depends on soil depth and the mechanical resistance of the different soil layers. When the root-impeding layers are near the surface, they will slow the downward root growth that results in a shallower root system which finally will be restricted to the upper part

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of the soil profile (Bennie, 1991; Ehlers et al., 1983).

Root systems of forest trees are often markedly asymmetric, and there are many factors that affect asymmetry. However, most of the relevant work has been carried out on species with shallow root systems due to the problems of windthrow (Coutts et al., 1999; Mickovski and Ennos, 2002; Nicoll and Ray, 1996). These findings conclude that the root system of many plant species is often asymmetric. Root systems of trees growing under adverse site conditions such as shade or water stress may be less symmetrical than normal but there is no information on this (Coutts et al., 1999; Ganatsas and Tsakaldimi, 2003). Concerning trees growing on slopes the reported results are quite controversial; Nicoll et al. (1995) found most roots of Sitka spruce on down-slope side of trees, but, Nicoll and Ray (1996) found for the same species most root mass up-slope; it should be noticed that in both cases root mass was concentrated on the side away form the prevailing wind direction. However, Sundström and Keane (1999) reported that both numbers of roots and root area seemed to concentrate along the contour lines.

The Mediterranean pines *Pinus halepensis* Mill. and *Pinus brutia* Ten. are considered two important tree species for reforestation in the Mediterranean region because they are early successional species, they have a woody deep tap root with vigorous laterals and they are drought tolerant. In deep soils, the diameter of taproot reaches 15–20 cm at a depth of 1 m, while in shallow soils they form a shallow root system (Moulopoulos, 1962).

This research was an in situ study of the root architecture of *Pinus halepensis* and *Pinus brutia* grown on sites characterized by shallow soils and low water availability, with the aim of examining to what extent their root system is asymmetric, what the changes are with the tree age and if there is any relationship between root asymmetry and above-ground plant growth.

Materials and methods

Site description

The study was carried out in two areas, the reforestated area of Sithonia Chalkidiki and the artificial peri-urban forest of Thessaloniki. Both areas are characterized by adverse ecological conditions, namely, shallow soil, high mechanical resistance of the underground bedrock and low water availability (Ganatsas and Tsakaldimi, 2003; Tsitsoni, 2001). The altitude of both studied areas ranges from 100 to 200 m. According to data from the meteorological station of Saint Mamas and the University of Thessaloniki (for the two respective areas), the climate is Mediterranean, with a mean annual precipitation of 420 mm and 397 mm, respectively; the dry period lasts from April or from the middle of May to the end of September. The vegetation of the first area belongs to the *Oleo-lentiscetum* association while the second to the *Ostryo-Carpinion* alliance (Tsitsoni et al., 2004). Geologically, the Sithonia peninsula belongs to the Axios zone and Circum Phodope zone; the rock materials are mainly igneous (granites) and crystalline schists. The area of the peri-urban forest belongs to magmatic series of Chortiatis and consists mainly of green-schists. The soils of both areas are slightly acid up to neutral (pH 5–6.8), and they are characterized by weak structure, low porosity, and high percentage of stones and pebbles resulting from soil compaction due to repeated fires and overgrazing. The soil depth ranges from 20 to 30 cm in the first case and from 40 to 50 cm in the second case. Usually, the limiting factor for plant survival and growth in both areas is the low soil water availability during the long dry summer period (Ganatsas and Tsakaldimi, 2003; Radoglou, 1987; Tsitsoni, 2001).

Root sampling

Three groups of trees were sampled for above and below-ground measurements. These were: (1) 3-year-old planted containerized seedlings of *Pinus halepensis* taken from Sithonia Halkidiki, northern Greece (2) 5-year-old natural regenerated seedlings of *Pinus brutia* taken from Kedrinos Lofos, Thessaloniki and (3) 65-year-old trees of *Pinus brutia* taken from Kedrinos Lofos, Thessaloniki. The third group was selected in order to compare the results and to investigate the changes with age from the young individuals to an advanced (mature) stage.

For each of the first two cases twelve randomly selected seedlings or saplings were extracted for root sampling; root excavation was made manually giving special attention to avoid root damage. The third group consisted of 12 trees of *Pinus brutia* that were selected during the Thessaloniki ring-road construction; these trees were cut and their stumps were extracted after the excavation performed during the roadworks. The tree selection included trees with roots that had been least damaged.

The trees were prepared for measurements by removing the litter around the stem, and the root system was revealed by careful removal of the soil (Mickovski and Ennos, 2002). Then, for each single root system of the first two groups of sampling, the following parameters were measured *in situ*, in their original positions: the number of medium sized lateral roots ($d > 1$ mm), the depth of their origin at the tap root, their vertical angle, their orientation using a compass and their length; as it was difficult in many cases to define the end of roots, a minimum diameter limit of 0.2 mm was chosen as root ends. Each root system was divided in situ into four sectors of 90° that were based on the four directions of the slope; two directions of contour lines and uphill and downhill (Figure 1). The direction of maximum roots (the thickest and longest laterals) was then determined for each root system, according to the root field measurements. The diameter of each root was recorded at four distances from the stem centre (Figure 1), 0 (the edge of the stem), 30, 60 and 100 cm using callipers (Sundström and Keane, 1999). The root diameters were taken in two directions on every occasion to get the cross-sectional area (CSA) of the root. The numbers of all roots and their CSA were totaled for each distance separately and for the entire root system. Number of roots, CSA and total root length were summed up for each of the four sectors and for the entire root system. The root area index (RAI), an index of evenness of root distribution in the four sectors, was used to estimate the root asymmetry (Lindström and Rune, 1999). This index was calculated as the ratio between root area in the sector with the largest root area (maximum roots) and the total root area. For an evenly distributed root system the RAI is 0.25 while higher RAI indices indicate a more asymmetrical root system. However, in the third group only the coarse laterals ($d > 10$ mm) were measured since more detailed measurements were not feasible. For the same reason the CSA at the edge of the stump and the root length measurements were omitted.

Above ground measurements

The above-ground measurements were carried out in all sampled trees. Radial crown width and

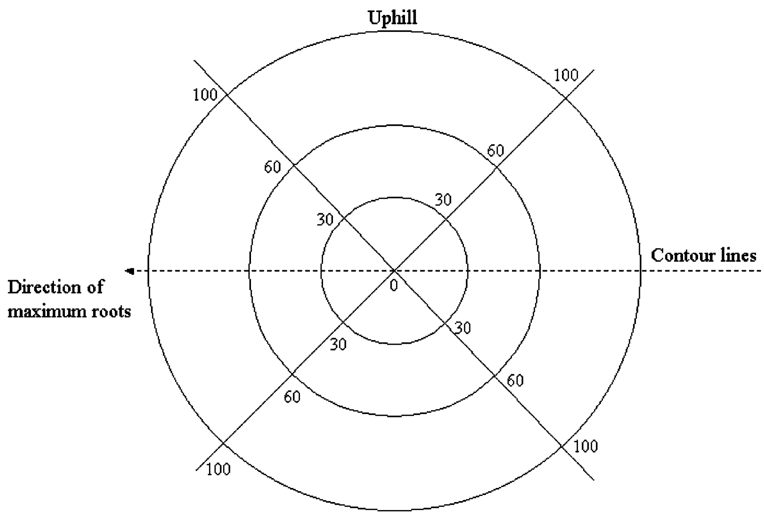

Figure 1. Details on the method of root sampling; the figure shows the distances from the center of root system (in cm) to where the CSA was measured and the separation of the four sectors of 90°. The direction of maximum roots was always found to be parallel to the contour lines regardless of the slope orientation.

diameter of three dominant branches were measured in two directions; the direction of the maximum roots and the opposite direction. Based on the branches' diameter, the cross-sectional area of the maximum branches was calculated. The stem diameter was measured in the direction of contour lines as well as in the direction perpendicular to them. Finally, the total plant height was measured.

Statistical analysis

The statistical analysis was accomplished by SPSS statistical program. The comparison of means between the four sectors was assessed by one-way ANOVA followed by Waller–Duncan test ($P < 0.05$, Norusis, 2002). Correlations between above and below-ground parameters were tested with Spearman' bivariate correlation coefficient.

Results

Root characteristics

The number of medium-sized roots was found to be very low in the case of 3-year-old *Pinus halepensis* seedlings; an average of 4.2 lateral roots per seedling were recorded (Table 1); the remaining roots were thinner and usually their development was restricted to within the space occupied by the growing medium. The number of roots was much greater in the case of 5-year-old naturally regenerated saplings of *Pinus brutia*; the average number of roots in this case was 19.5 laterals per individual. Mature trees exhibited an average number of 49.5 coarse roots ($d > 10$ mm) and a much greater number of medium and fine roots (Ganatsas and Tsakaldimi, 2003) that it was unfeasible to record.

The percentage of cross-sectional root area (CSA) of the medium-sized roots near the stem decreased with the age of the plants. It was on average 78% of the total root CSA in the case of 3-year-old *Pinus halepensis* seedlings (Figure 2a), as no roots were recorded further than 100 cm from the centre of the root system, and very few roots were found further than 60 cm from the centre. A lower percentage was found in 5-year-old *Pinus brutia* saplings (65%) as the contribution of the CSA recorded in the other distances increased (Figure 2b). In the case of 65-year-old trees of *Pinus brutia*, a lower decrease rate of the CSA of coarse roots with the distance was observed (Figure 2c). Thus, the main root volume in the first two cases was recorded within a distance of 30 cm around the centre of the stem while in the third case it was observed within the distance of 60 cm from the stump. Roots originating from the upper part of the root system were the thickest and the longest. In the case of young trees, these laterals originated from a depth of 5–15 cm while in the case of mature trees they originated from a depth of 10–30 cm. However, most of the roots originated from the taproot and they developed almost horizontally, parallel to the soil surface (their vertical angle was in almost all cases above 75°).

Table 1. Number of roots recorded in the three groups of samples (3-year-old *Pinus halepensis* seedlings, 5-year-old *Pinus brutia* saplings and 65-year-old *Pinus brutia* trees) in the four sectors and totally

	Number of roots in the four sectors				Total number of roots
	Contour lines		Uphill	Downhill	
	Direction of maximum roots	Opposite direction			
3-year-old seedlings of *Pinus halepensis*	2.4 (0.14)a	1.8 (0.12)b	0	0	4.2 (0.28)
5-year-old saplings of *Pinus brutia*	5.8 (0.41)a	5.7 (0.40)a	4.4 (0.28)b	3.6 (0.37)b	19.5 (1.31)
65-year-old trees of *Pinus brutia**	15.8 (1.1)a	12.2 (0.8)b	11.5 (0.8)b	10.0 (0.9)c	49.5 (2.3)

*The values concern only the coarse roots (diameter > 10 mm).
Values are means and standard errors of mean (in parenthesis). Values in the same row followed by different letters are significantly different ($P < 0.05$, Waller–Duncan test).

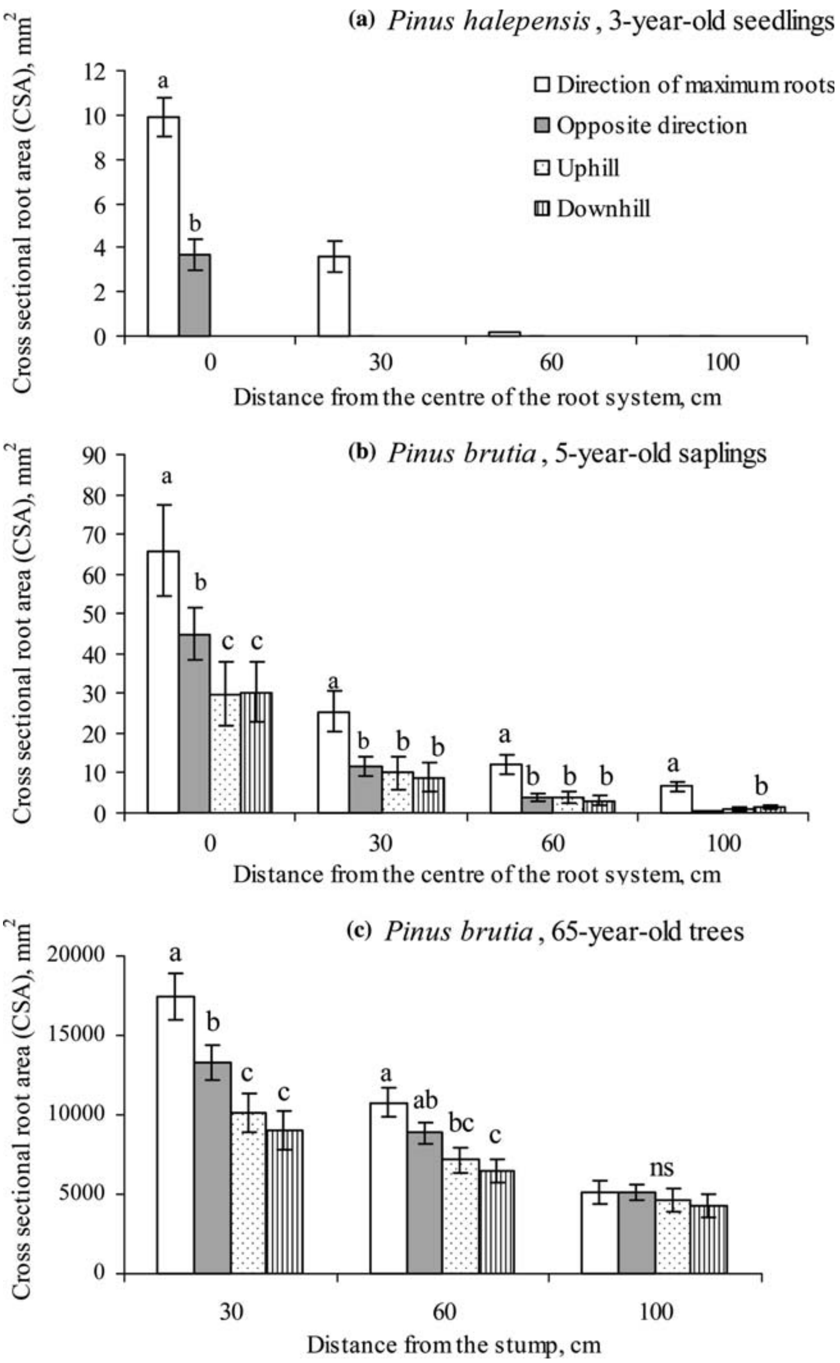

Figure 2. Mean CSA at the four distances from the center of root system and at the four sectors, for the 3-year-old *Pinus halepensis* seedlings (a), for the 5-year-old *Pinus brutia* saplings (b) and for the 65-year-old *Pinus brutia* trees (c). Vertical bars represent the standard error of mean (SE). Values for the same distance followed by different letters are significantly different ($P < 0.05$, Waller–Duncan test). ns = no significant differences.

The total root length was on average 128.7 cm per seedling in the case of 3-year-old *Pinus halepensis* seedlings, while it was found to be much higher (1452.5 cm) in the case of 5-year-old saplings of *Pinus brutia* (Table 2).

Table 2. Sum of root length recorded in the two groups of samples (3-year-old *Pinus halepensis* seedlings and 5-year-old *Pinus brutia* saplings) in the four sectors and totally

	Sum of root length in the four sectors, in cm				Total root length in cm
	Contour lines		Uphill	Downhill	
	Direction of maximum roots	Opposite direction			
3-year-old seedlings of *Pinus halepensis*	93.7 (7.1)a	35.0 (2.2)b	0	0	128.7 (8.1)
5-year-old saplings of *Pinus brutia*	517.8 (53.6)a	406.0 (32.3)ab	280.3 (32.7)bc	248.4 (38.9)c	1452.5 (112.7)

Values are means and standard errors of mean (in parenthesis). Values in the same row followed by different letters are significantly different ($P < 0.05$, Waller–Duncan test).

Root asymmetry

The general trend observed in both pine species was that almost all the sampled plants developed their main lateral roots concentrated along the contour lines or with small deviation downwards on the slope, instead of uphill or downhill (Table 1); this resulted in an asymmetrical root development in all cases. The direction of maximum roots was always found to be at one of the two sectors along the contour lines, regardless of the slope orientation. The number of roots (Table 1), the CSA (Figure 2a–c) and the sum of root length (Table 2) were asymmetrically distributed around the stems. The RAI index was very high (0.79) in the case of 3-year-old *Pinus halepensis* seedlings, and lower (0.42 and 0.33) in 5-year-old *Pinus brutia* saplings and mature *Pinus brutia* trees, respectively (Table 3). The root growth pattern in the case of the planted *Pinus halepensis* seedlings was very characteristic; during the first year after outplanting almost all the roots grew within the space occupied by the growing medium; there were only few main laterals per seedling that elongated to the physical soil, in the same direction parallel to the soil surface, reaching a length of 50–70 cm. The same pattern seems to be followed by the 5-year-old naturally regenerated saplings of *Pinus brutia*, where the number of main laterals was higher and some of them were found in the opposite direction.

Relation of above and below ground plant dimensions

The average above-ground dimensions of the sampled pines are shown in Table 3. In contrast to the observed root asymmetry, the above-ground plant development was symmetric in all cases. Using either the fractions of crown width or the fractions of the CSA of the maximum branches and the stem diameter ratio, the tree crown and stem were found to be symmetric in all three groups of pines. No significant correlation was found between crown asymmetry fractions and below-ground parameters ($P > 0.05$).

Discussion

According to the analysis of all the three groups of samples, root system asymmetry was common in the studied Mediterranean pines. Both species (*Pinus halepensis* and *Pinus brutia*) as young seedlings and mature trees, planted or natural regenerated, developed their root system asymmetrically, which means that the tree root system is very susceptible to site stress factors during the whole plant life. This root asymmetry confirms that roots react to environmental modifications and show the plasticity of root systems (Fitter, 1991). Both, number of roots and root area, were mostly concentrated along the contour lines instead of uphill or downhill. This pattern of root system seems to allow for efficient water and nutrient uptake from the soil layers. Similar root orientation pattern was observed by Sundström and Keane (1999) for 10-year-old Douglas-fir trees. However, as only a few medium-sized roots were found in the case of 3-year-old *Pinus halepensis* seedlings this can be attributed to the great difficulties that the seedlings face during the first year after outplanting (a crucial period for seedling survival and growth (Tsakaldimi, 2001),

Table 3. Plant above-ground dimensions (height, diameter), crown asymmetric fractions (values recorded in the direction of maximum roots divided by the respective values of the opposite side) and RAI in the sampled individuals

	Plant height (m)	Stem diameter (cm)	Stem diameter ratio[a]	Crown asymmetry fractions		Root area index
				Radial crown width	Cross sectional area of the maximum branches	RAI[b]
3-year-old seedlings of *Pinus halepensis*	0.33 (0.01)	0.68 (0.03)	1.00	0.98	1.00	0.79
5-year-old saplings of *Pinus brutia*	0.65 (0.02)	2.02 (0.08)	1.00	1.00	1.01	0.42
65-year-old trees of *Pinus brutia*	11.80 (0.29)	29.20 (1.01)	1.02	0.97	1.02	0.33

[a]The value is the fraction of the diameter values recorded in the direction of contour lines divided by the values recorded in the vertical to it axis.
[b]The ratio between the root area in the sectors with the largest root area and total root area. Higher values imply a more asymmetrical root system.
Values are means and standard errors of mean (in parenthesis where appropriate).

combined with the high soil compaction of the area (Tsitsoni, 2001). Number of roots and total root length were found much higher in 5-year-old naturally regenerated seedlings of *Pinus brutia*; this may show a greater adaptability of the naturally regenerated seedlings compared to the planting ones (Lindström and Rune, 1999). Also, the site conditions were better in the second case; the soil depth was much greater, 40–50 cm vs. 20–30 cm in the previous case.

The main laterals were observed to originate from the upper part of the taproot, as perhaps they have an advantage over deeper roots because they are the first to receive assimilates from the shoots (Coutts et al., 1999), while roots that originated from the lower part were smaller. Analyzing the changes of root asymmetry with age, it seems that the size of the main laterals increased with the age, while a clear typical taproot system was absent in all cases. However, the asymmetry was much higher in the young seedlings; as the trees grow, the symmetry of the structural root system maybe increasingly influenced by adaptive secondary growth related either to wind sway (Coutts et al., 1999) or to the exploration of microsites for more available water. Thus, young planted seedlings of *Pinus halepensis* had a more asymmetric root development (higher RAI index) than the 5-year-old naturally regenerated saplings of *Pinus brutia* while the mature trees generally showed a better and more uniform root distribution. The finding that root distribution is improved by trees age has also been reported earlier (Lindström and Rune, 1999).

The observed root asymmetry was not correlated with the above-ground tree form which was found to be symmetric in all cases. This crown symmetry indicates that wind has a minor effect on tree growth, including probably root-system growth. Furthermore, according to the local meteorological data there is no great risk from wind in the studied areas; the winds are seldom intensive enough to cause problems to tree stands. Taking into account that the risk from wind is very low during the early stages of tree life we concluded that the decisive factor for root development in our case, which results in root asymmetry, is the shallow soil that stopped the growth of the taproot in combination with the soil water scarcity; these probably have a more serious effect on distribution of the roots, than any climatic factor. In contrast to that, many studies reported that the root asymmetry of several tree species, mainly with shallow root systems, is attributed to the requirement for the tree to withstand winds (Coutts et al., 1999; Mickovski and Ennos, 2002, 2003; Nicoll and Ray, 1996). However, Konstandinidou (1998), in Kassandra peninsula North Greece, found that *Pinus halepensis* trees grown on deep soils on marls have a tap root system at the ages of 23 and 48 years and a heart-shaped root system at the ages of 70 and 100 years.

The results obtained from this work suggest that the existence of shallow soil and the mechanical resistance of the underground bedrock in combination with low soil water availability caused a modification of the typical tap rooted pine root system. The taproot growth has stopped, the root penetration in the deeper soil layers was restricted and the laterals were obliged to elongate towards the surface soil layers probably in the direction of the existence of preferential pathways for water infiltration in the surface soil; this growth pattern results in a root asymmetry. However, this root asymmetry decreases with age and it was not correlated with the above-ground tree form.

Finally, the authors believe that considerations of root system modification of Mediterranean pines could contribute to a better management of stands. It is suggested that more space be provided for each tree along the contour lines rather than perpendicular to them, by thinning methods and planting spacing. However, more studies are needed to improve the knowledge on the tree root modifications under Mediterranean conditions.

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