

# Anchorage and Asymmetry in the Root System of *Pinus peuce*

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**Mickovski, S.B & Ennos, A.R.** 2003. Anchorage and asymmetry in the root system of *Pinus peuce*. *Silva Fennica* 37(2): 161–173.

The relationship between the anchorage mechanics and root architecture of *Pinus peuce* was investigated by carrying out winching tests and examining excavated root systems of 20 mature trees. The root system was dominated by  $6.1 \pm 1.3$  lateral roots, more than 70% of the lateral root cross sectional area (CSA) being distributed in the uppermost 10 cm of soil. Anchorage strength was related to the size of the tree and CSA. The overturning moment of trees was proportional to the diameter at breast height (DBH) to the power of 1.6. The trees exhibited significant asymmetry in anchorage rigidity, but although there was clustering of lateral roots in a preferred direction the root asymmetry was not significantly correlated with the asymmetry in anchorage rigidity, suggesting that much of the anchorage is provided by tap and sinker roots, rather than the laterals. However, the major laterals showed dorsoventral eccentricity, the more eccentric ones being those that were distributed closer to the soil surface and which pointed perpendicular to the direction of greatest resistance. This suggests that this is a result of thigmomorphogenetic effects. These results are compared with those for the related *P. sylvestris* and suggest that the assimilation and anchorage characteristics of root systems are controlled independently of each other.

**Keywords** anchorage, asymmetry, eccentricity, *Pinus peuce*, *Pinus sylvestris*, clustering, root morphology

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**Received** 9 July 2002 **Accepted** 13 January 2003

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# 1 Introduction

Recent years have brought new methods of investigation of root systems which supplement the old method of visual inspection (see reviews in Smit et al. 2000). Despite all the difficulties of measuring roots covered by layers of soil, a step forward was made with introduction of more efficient methods for exploring the distribution and function of roots in the soil in connection to a tree's anchorage (Cou tts (1983, 1986), Mattheck et al. (1995), Crook and Ennos (1996), Crook and Ennos (1997), Stokes et al. (1997), Nicoll and Armstrong (1998), and Goodman and Ennos (1999)). Acknowledging that anchorage is one of the two main functions of the root system (Cou tts 1987), it was suggested (see Ennos 2000) that a more advanced knowledge of the root morphology and architecture of as many species as possible might provide further insight into the way in which the form is related to the function in root systems.

Root system asymmetry increases along with the variability of the root system as trees age (Sutton 1969) as a result of the variety of stimuli the tree experiences, and this might significantly reduce the overall stability of a tree (Cou tts et al. 1998). Tree stability may also be reduced in trees in which structural roots are poorly developed or even missing on one side (Cou tts 1983). Previous studies on root symmetry have produced variable results; Somerville (1979) investigating the root system of *Pinus radiata* in New Zealand, showed that the root distribution was very close to symmetrical, whereas more recent studies on Sitka spruce have shown that their root systems are often asymmetric, developing less in the direction of the plough furrows (Cou tts et al. 1990), or just unevenly (Nicoll et al. 1995). The investigation of Mickovski and Ennos (2002) on *Pinus sylvestris* also showed that there is a preferred orientation and clustering of roots in many suppressed crown trees.

Root asymmetry can result from the asymmetric origin and growth of primary roots (Cou tts et al. 1998). This in turn can be affected by a number of external factors, including environmental factors such as water and nutrient supply (Mickovski and Ennos 2002), and physical factors such as the soil shear strength which can impede root growth

(Taylor and Gardner 1963), but also provide better anchorage for the tree. The soil environment also affects the secondary growth of roots. It is known that buttress root formation is stimulated in trees parallel to the prevailing wind direction (Nicoll and Ray 1996), particularly on the leeward side, and that the shape of the roots becomes more oval in weaker soils, in some instances even resembling the 'I' beams common in engineering (Nicoll and Ray 1996).

Trees also differ in their relative rooting depths, both between species and with growth conditions, and this in turn affects the tree stability. Soil compaction, or even waterlogging (Cou tts 1983, 1986), might restrict deeper rooting of trees, which will restrict the stability of the tree. Root systems of trees grown in such conditions often have larger lateral spread with stronger laterals which help the tree from toppling under external loads.

Nutrient supply can also have an effect on the rooting depth and the vertical distribution of the root biomass of a tree. Considering the fact that assimilates are more readily available closer to the surface of the soil, trees usually have a large portion of their major lateral roots in the uppermost layers of the soil (Sutton 1969, Somerville 1979, Stokes and Guitard 1997). This kind of vertical distribution may also decrease the stability of the tree. It is also possible that the lateral roots in the uppermost soil horizons use the major portion of the nutrients available near the soil surface and thus occlude the growth of the deeper roots, sinkers and the tap roots (Sutton 1969, Wilson 1975).

In spite of their frequent designation as deep-rooted, windfirm species, pines can be very susceptible to windthrow on sites that restrict rooting (Sutton 1969). Problems with windthrow in the UK have focused the vast majority of the research on the anchorage of Sitka spruce as the most widespread plantation conifer. One of the aims of this study is to extend knowledge to another forestry species: Macedonian pine (*Pinus peuce* Gris.), endemic to the Balkans, and grown in completely different environmental conditions from those prevailing in the UK.

In order to reveal the anchorage mechanics of this species, this study investigated the anchorage strength of mature trees and related it to the size of the tree and the root cross sectional area (CSA).

The asymmetry of the overall root system as well as the vertical distribution of root biomass was also explored, especially in relation to possible thigmomorphogenetic effects and competition for nutrients. An attempt was made to relate the root asymmetry to the asymmetry in anchorage rigidity, and to relate the overall root morphology to the primary functions of the root system. By comparing these findings to those on other species, particularly to the related *P. sylvestris*, it was hoped to gain knowledge of the factors that determine root development and root biomass distribution both in depth and around the tree.

## 2 Materials and Methods

### 2.1 Site Description and Experimental Layout

Twenty-two 19 to 23-year-old suppressed crown *Pinus peuce* trees were randomly selected from a 50 m × 100 m naturally regenerated tree stand in the Pelister National Park near Bitola, Macedonia, with the longer side of the site oriented in north-south direction. The trees were grown on a brown clay soil and the spacing between the trees varied from 1.5 to 1.9 m. The selection included as many trees as we were allowed to use from the outside tree belt (more exposed to the wind and external factors), while the majority of the sample consisted of trees grown inside the tree stand.

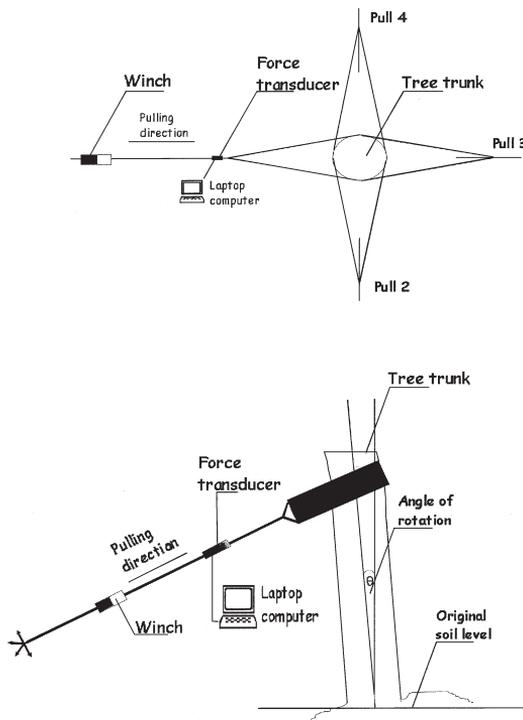
In the spring of 2001, 22 trees were marked as a part of the study sample. Seven trees from the outer belt of the stand were selected together with 15 from the inner part. The trees had an average diameter at breast height (DBH) of  $11.8 \pm 1.3$  cm (throughout this study '±' is followed by the standard deviation). The trees on the outer belt of the stand had average DBH of  $11.7 \pm 0.8$  cm, not significantly ( $p > 0.05$ ) different from the average DBH of inner trees  $11.8 \pm 1.4$  cm. No thinning of this particular stand had been done in recent years. Prevailing winds on this site come from the SouthEast.

During the investigations in May 2001, each tree was cut on average 1.75 m above the ground, and the upper part of the tree, together with the tree crown was carefully transported outside the tree stand.

### 2.2 Overturning Tests

In order to investigate the movements of the root systems of the trees when they are pulled over and the soil around them, preliminary qualitative overturning tests were first carried out in March 2001 on two test trees using the trenching technique developed by Coutts (1983) and Crook and Ennos (1996). The litter around the tree trunk was first cleared to reveal the orientation and location of the main lateral roots. A trench was then cut, 60 cm deep, 50 cm wide and extending approximately 80 cm from each side of the trunk, parallel to the direction in which the tree was going to be pulled over. Lateral roots growing out from the trunk on the side of the trench were cut away with an axe. This reveals a 'cross section' of the root/soil system which can be observed during overturning. Each tree was then winched over at a rate of about  $15^\circ \text{ min}^{-1}$  simultaneously recording the movements of the soil and roots and sounds of root breakage. After the tree had toppled, the root system was cleared from the soil and examined closely in search of broken roots or other signs of mechanical failure.

The trenching method revealed that like the root systems of Scots pine *P. sylvestris* (Mickovski and Ennos, 2002) both of the test trees had several strong horizontal lateral roots distributed around the stem but only a few sinker roots which originated from some of the laterals. Both trees had deep tap roots, oval in shape but far from the 'I' beam shaped roots recorded in some previous studies (Mattheck et al. 1995, Stokes et al. 1997). The pattern of failure was also strikingly similar to that in *P. sylvestris*. Both trees failed in their roots as they were pulled over. Soil failure was recorded first close under the stem, and cracks in the soil then spread towards the edges of the root-soil plate as the winching continued. There was significant movement in the roots, accompanied by the development of a complex network of cracks in the soil on the windward side and loud noise of root snapping after the trunk had been displaced by ca.  $20^\circ$  from the vertical. Both trees rotated about a point below the tree base, just on leeward side, and the leeward laterals were bent and pushed into the soil while the tap root was bent and pulled up a bit. Consequently, as the test proceeded, windward laterals were pulled up out



**Fig. 1.** a) plan and b) side view of the equipment and method used for testing the overturning resistance of *P. peuce* trees (after Mickovski and Ennos 2002).

of the surrounding soil. The tap root of one of the test trees snapped when the trunk had been displaced approximately  $45^\circ$  from the vertical.

The qualitative similarities to *P. sylvestris* justified the use of similar tests to those used in Mickovski and Ennos (2002) to quantitatively examine overall anchorage strength and asymmetry in anchorage rigidity. To do this the apparatus shown in Fig. 1 was used to sequentially pull each tree in four directions, all oriented approximately  $90^\circ$  from each other around the tree trunk. A further twenty trees ranging in DBH from 8.60 cm to 14.32 cm were pulled over during May, 2001 in this way. The needle litter from around the trunk was removed, and the lateral root system was revealed by careful removal of the few uppermost centimetres of soil. Trunks were then manipulated by to determine the direction in which the anchorage seemed most rigid. One end

of a winch (TIRFOR, T532) was connected via a force transducer (Defiant Weighing Ltd., Kent, England), and via a sling to the tree at an average height of 1.72 m. The other end of the winch was secured to the base of another tree in the stand using another sling. The force transducer, which was capable of measuring forces up to 20 kN, sent its output to a portable battery-powered data logger with a live display which showed a graph of force against time on a laptop computer using PICOLOG (Pico Technology Ltd., UK) software. As shown in Fig. 1 the winch was then used to pull the tree first at  $90^\circ$  to the most rigid direction, then at  $180^\circ$ ,  $270^\circ$ , and finally towards the most rigid direction. The last pull that determined the anchorage strength was therefore from the side where the maximum overturning resistance was expected.

The trees in this experiment were pulled at a constant rate, deflecting the tree at the sling attachment by one pull of the winch, approximately 2 cm, every 4 seconds. The tree was winched in the first three directions only up to a displacement of approximately 14 cm (7 winch pulls) at the top of the stem, so as not to damage the anchorage system. This displaced the trunk by at most  $5^\circ$  from vertical, well below the angle at which roots would start to break, but high enough to calculate the slope of the graph of force versus stem displacement. These slopes were calculated by trigonometry for every pulling direction for each tree. While pulling from the fourth side, the winching was continued until the maximum resistance of the tree was mobilised and the tree failed. The test was terminated once the force registered on the display started to decline from its maximum. The maximum overturning moment was calculated for every tree by multiplying the maximum recorded pulling force by the perpendicular height of the sling from the stem base. Again, special attention was paid to the root and soil movements as well as to the sounds of breakage. The anchorage asymmetry ratio was defined as the ratio between the mean slopes of the force/displacement graphs parallel to the final pull and the mean slopes perpendicular to it.

### 2.3 Lateral Root Morphology and Distribution

To allow the root system to be examined and the distribution of cross sectional area (CSA) around the trunk to be measured, the trees were excavated completely following the anchorage tests and soil was cleared from the upper root system. Root system components were then measured with a technique similar to the one described by Nicoll and Ray (1996). Each structural root, defined as a root with diameter greater than 2.0 cm at a distance of 20 cm from the tree trunk, was investigated. The number of laterals was recorded, together with their horizontal and vertical diameters –  $d_h$  and  $d_v$  respectively – at the point 20 cm from the trunk, measured with callipers. These were used to calculate the CSA of each root using the equation  $CSA = (\pi d_h d_v) / 4$ . The orientation of the laterals was also measured using a compass, as well as the depth of their origin. The location of sinkers and eventual taproots was also noted and a sketch of the root system was produced for each tree.

To investigate the root distribution relative to the direction in which anchorage was strongest, roots were classified into four separate direction classes, depending on whether they were in the quadrants facing towards or away from the final pull, or in the two quadrants at right angles. The root asymmetry ratio was defined as the fraction of the CSA oriented in the direction parallel to the final pull divided by the CSA activated in direction perpendicular to it. The root asymmetry ratio was then plotted against the anchorage asymmetry ratio and subjected to correlation analysis to determine whether root system asymmetry and anchorage symmetry were related.

To investigate the overall degree of root system asymmetry, the centre of the root cross-sectional area was calculated for each tree using the method described in Nicoll and Ray (1996). The center of the CSA of a root system is the average position of structural roots relative to the center of the stem, using measured azimuth angles and weighted by their CSA.

The origin of the coordinate system is the center of the trunk and if the center of the CSA is also there it would indicate an even distribution of the root mass around the tree. In that aspect, the

center of the CSA of the root system of a tree has coordinates:

$$X = \Sigma X_i; Y = \Sigma Y_i$$

where the Cartesian coordinates of the  $i$ th root weighted by the CSA are:

$$X_i = D_i \sin \theta; Y_i = D_i \cos \theta$$

where  $\theta$  is the azimuth angle and

$$D_i = \frac{d_i}{\Sigma d_i}$$

where  $d_i = d_v d_h$  is the product of the horizontal and vertical diameters of the  $i$ th root. The distance between the center of the root CSA and the origin of the coordinate system is

$$R = (X^2 + Y^2)^{1/2}$$

while its orientation is:  $\theta = \tan^{-1}(X/Y)$ .

Large values of  $R$  indicate that roots tend to cluster together in a preferred direction  $\theta$ , whereas small values imply uniformity around the tree trunk (Mardia 1972).  $S_0 = 1 - R$  is the common variance of the independent variables  $X_i$  and  $Y_i$ , and the hypothesis of no clustering can be tested using the test statistic  $nR^2/S_0$ . Under the hypothesis of no clustering, this statistic has an F-distribution with 2,  $2(n-1)$  degrees of freedom, and the hypothesis is rejected whenever  $nR^2/S_0$  is greater than  $F(2, 2(n-1), \alpha)$  when testing at the  $\alpha\%$  significance level (Nicoll et al. 1995).

To investigate the root distribution with depth the underground part of the root system was divided into four depth horizons: 0 cm to 5 cm, 5 cm to 10 cm, 10 cm to 15 cm, and deeper than 15 cm; all of the major roots were categorised in one of the horizons according to the depth of their origin and the relative CSA in each depth horizon was calculated.

To investigate the shape of each of the major lateral roots their eccentricity and aspect ratio was also calculated. Each lateral roots was considered as an ellipse with  $d_h$  and  $d_v$  as its major and minor axes. The eccentricity,  $e$ , was calculated as:

$$e = (d_1^2 - d_2^2)^{1/2} d_1^{-1}$$

where  $d_1$  is the larger of two measured root diameters  $d_2$  is the smaller one. Values of  $e$  close to zero indicate that the shape of the root is close to circular, while eccentricity values closer to 1 indicate a flattened cross section.

To investigate whether the lateral roots had larger vertical or horizontal diameter, i.e. to explore the average direction of biomass allocation in the CSA of lateral roots, the aspect ratio was calculated for each major lateral root as:

$$AR = \frac{d_v}{d_h}$$

The distribution of roots whose vertical diameter is larger than their horizontal diameter ( $AR > 1.0$ ), labelled 'vertically eccentric' roots, were of particular interest in this study as this shape will aid the overall stability of the tree since it maximises the resistance to bending in the vertical plane. The distribution of these roots around the tree trunk, as well as in depth, was further investigated in order to determine whether there is an association between root eccentricity and anchorage strength or rooting depth.

## 2.4 Soil Measurements

Soil resistance to penetration was measured around every tree with a Proctor field penetrometer (Wille Geotechnik, Germany). It consisted of a special spring dynamometer with a calibrated scale on the stem of the handle, where a sliding ring indicated the maximum applied load. A special needle with a cross-sectional area of 19.63 cm<sup>2</sup> was mounted on the measuring end of the penetrometer.

The soil was cleaned from the litter and the surface from which the reading was taken was flat, so the needle could adhere better to the soil. The penetrometer was held in a vertical position and pressure was applied at the same time controlling the rate of penetration by steadying the arms against the front of the legs. The usual rate of penetration was around 13 mm sec<sup>-1</sup> for a depth of no less than a 76 mm. Three tests in each soil horizon (5 cm, 10 cm, and 15 cm) were carried out in each of the pulling directions, and special care was taken that the individual penetrations were

not interfering with each other. The resistance of the soil was then calculated by dividing the average penetrometer reading by the cross-sectional area of the needle.

## 2.5 Statistical Methods

All the data were put in the SPSS computer package, and several statistic methods, such as one- and two-way ANOVA, regression and correlation, were used to compute the parameters presented in this study. ANCOVA and the multiple regression tests were also carried out in a DOS application written by Dr Robert Callow, University of Manchester.

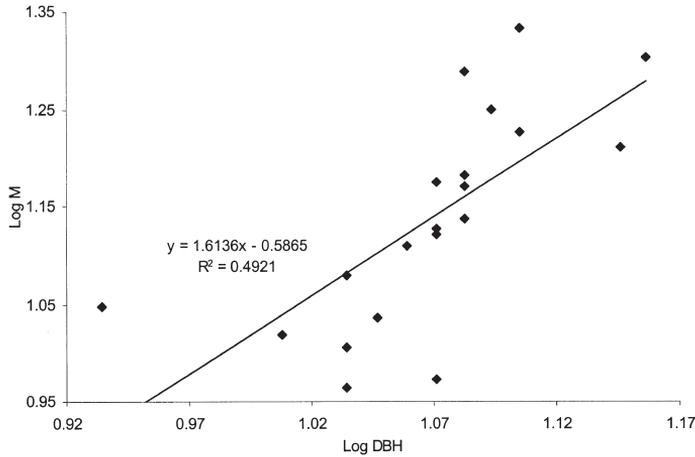
# 3 Results

## 3.1 Overturning Tests

As overturning proceeded, the overturning moment,  $M$ , increased linearly at first with displacement before starting to level off at angles over 7°, reaching a maximum and falling once there was a root breakage (recorded in 18 out of 20 investigated trees), or a stem breakage (recorded in 2 out of the 20 investigated trees). A similar pattern was recorded in the shape of the overturning force vs. time graph for both inner and outer belt trees.

Overturning moments ranged from 9.2 kNm at an angle of 12.3° to 21.5 kNm at an angle of 29.5°, or  $14.2 \pm 3.6$  kNm on average at an angle of 21.8° for the whole population. The average overturning moment for the inner trees was  $13.9 \pm 3.5$  kNm, which was lower but not significantly ( $p=0.559$ ) different from the average overturning moment for the outer trees:  $14.8 \pm 4.2$  kNm.

The overturning moment increased with the increase of DBH for the trees studied. The regression line from the LogDBH vs. Log  $M$  graph ( $r^2=0.492$ , Fig. 2.) show that the overturning moment increased according to the equation:  $M=0.259 (DBH)^{1.613}$ . ANCOVA showed that the slopes of the overturning moment with the DBH for the inner and the outer trees in the stand were not significantly different ( $F_{1,19}=0.401$ ).



**Fig. 2.** Regression lines between Log DBH and log M for the *P. peuce* trees from the inner and outer part of the stand in the Pelister National Park, Macedonia.

**Table 1.** Mean anchorage rigidity and distribution of the major lateral root CSA in four different quadrants in the investigated *P. peuce* trees (means ± SD).

	90°	180°	270°	Parallel to the most rigid direction
Mean anchorage rigidity (kNm deg <sup>-1</sup> )	0.73 ± 0.37	0.94 ± 0.35	0.87 ± 0.43	3.02 ± 1.33
Root CSA (%)	17.3 ± 16.7	32.2 ± 25.1	22.9 ± 20.0	27.6 ± 25.7

### 3.2 Anchorage Rigidity

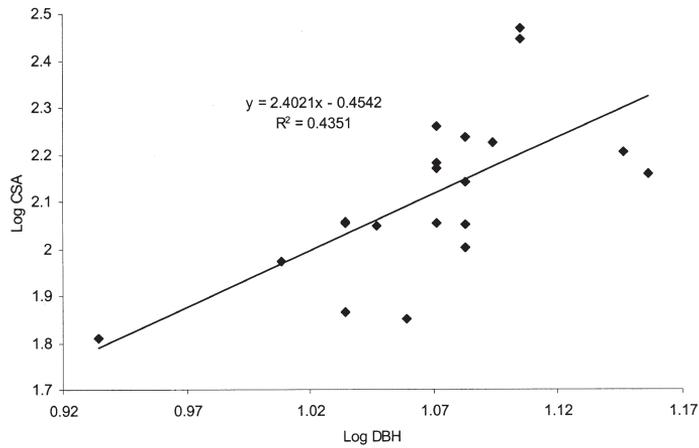
The rigidities of the root systems in the four different directions are given in Table 1. One-way ANOVA showed that the mean slope of the overturning resistance of outer belt trees was not significantly ( $p=0.714$ ) different from the slope of the inner trees. Furthermore, there was no significant ( $p=0.890$ ) difference between the rigidity of the trees that failed in their roots and those ones that failed in their stems.

Importantly, however, the rigidity during the fourth and final pull was significantly ( $F_{1,79}=6.125$ ,  $p=0.019$ ) higher than the other pulls and this was so for every tree investigated. This was always followed by the rigidity during the second pull, in which the tree was pulled in the opposite direction from the final pull. These

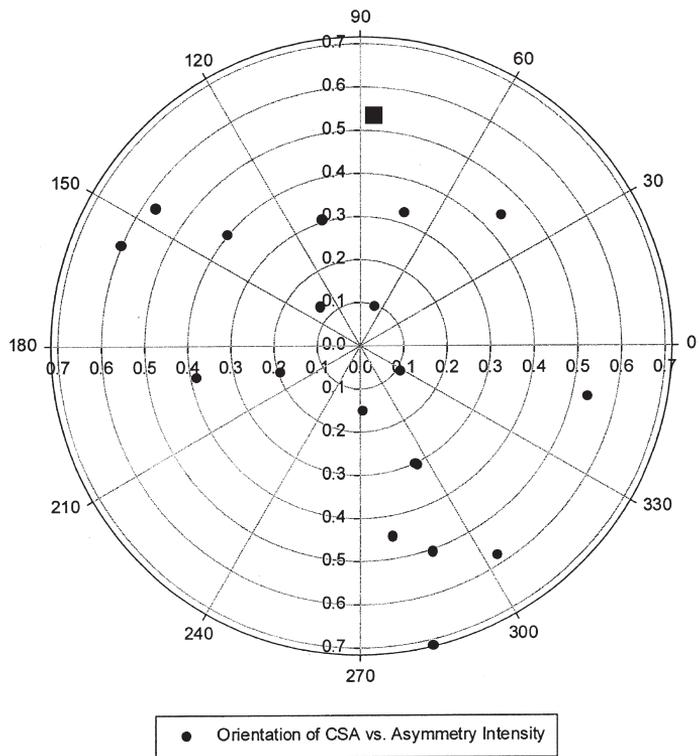
results justified the chosen direction of pulling as the strongest and most resistant. For the outer belt trees, the most rigid direction was always oriented towards the inside of the stand.

### 3.3 Root System Architecture

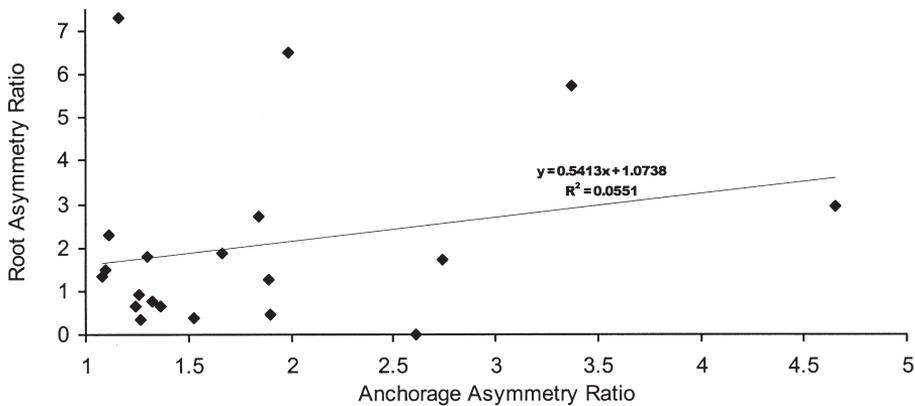
Trees had a mean of  $6.1 \pm 1.3$  lateral roots, significantly fewer ( $F_{1,38}=7.23$ ,  $p=0.011$ ) than the  $7.3 \pm 1.4$  found in *P. sylvestris* (Mickovski and Ennos 2002). The total cross sectional area (CSA) of major roots varied from 64 to 295 cm<sup>2</sup>, or  $130 \pm 51$  cm<sup>2</sup> on average for the population. The trees from inside the stand had mean CSA of  $137 \pm 56$  cm<sup>2</sup>, slightly but not significantly ( $p=0.985$ ) lower than the average CSA of the outer trees:  $114 \pm 35$  cm<sup>2</sup>. The vertical distribution



**Fig. 3.** Regression lines between Log DBH and Log CSA for the *P. peuce* trees from the inner and outer belt of the stand in the Pelister National Park, Macedonia.



**Fig. 4.** Average orientation of the centre of the root CSA (circular direction) plotted against the magnitude of asymmetry (radial direction) for the *P. peuce* trees investigated.



**Fig. 5.** Regression between root asymmetry ratio and the anchorage asymmetry ratio in investigated *P. peuce* trees.

of the CSA, showed that  $41 \pm 23.01$  % of it was distributed between 0 and 5 cm depth,  $30 \pm 18.2$  % between 5 and 10 cm depth,  $25 \pm 7.52$  % between 10 and 15 cm depth, and  $4 \pm 1.83$  % lower than 15 cm. Only 2 of the 20 trees had major lateral roots originating deeper than 15 cm, and 4 trees had all their major roots in the first 10cm depth.

The percentage of the lateral root CSA in each quadrant ( $180^\circ$ ,  $90^\circ$ ,  $270^\circ$ , and parallel to the direction of maximum rigidity) is shown in the Table 1. Percentages of roots was higher in the directions oriented towards and away from the direction of maximum rigidity, but because of the great variability ANOVA showed no significant differences between quadrants. However, the percentage of roots parallel to the direction of maximum rigidity was higher than that perpendicular to it ( $F_{1,38} = 8.61$ ,  $p = 0.006$ ) and the mean root asymmetry ratio was  $2.55 \pm 2.69$ , showing significant clustering of roots parallel to the direction of maximum rigidity. However, though there was positive correlation between the root asymmetry ratio and the anchorage asymmetry ratio ( $R = 0.235$ , Fig. 5) this was not significant ( $p = 0.319$ ). Therefore asymmetry in the lateral root system did not appear to cause the asymmetry in the anchorage rigidity.

The centre of root CSA, calculated with the statistical method explained in the methods section, showed significant ( $p < 0.05$ ) clustering of root direction in 4 out of the 20 trees studied. All

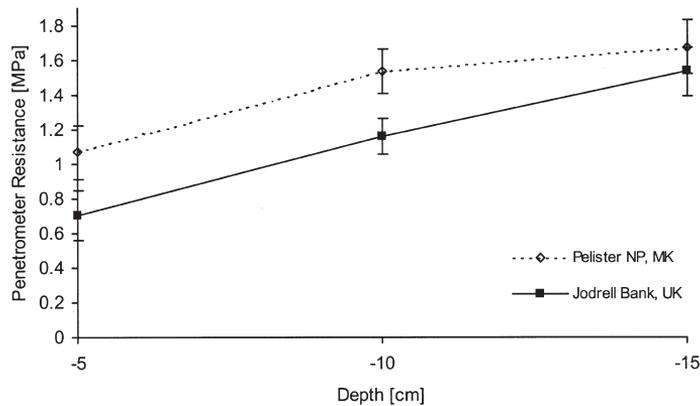
four of them were outer belt trees. For all 20 trees together as shown in Fig. 4, the mean centre of the root CSA pointed toward  $289^\circ$  from north, or to the side of the stand which was open to the wind. The mean  $R$ -value of 0.386 indicated significant ( $p = 0.029$ ) asymmetry.

Regression analysis showed that the trees with larger DBH have major roots with larger CSA ( $\text{LogCSA} = 2.402 \text{ LogDBH} + 0.454$ ,  $r^2 = 0.435$ , Fig. 3). Visual observation also suggested that the inner trees had more sinker roots and tap roots, though this observation was not quantified.

Multi-factorial (two factor) regression analysis showed that together root CSA and the trunk DBH had a significant ( $p = 0.001$ ,  $r^2 = 0.515$ ) effect on the overturning moment, though CSA itself had a non-significant ( $p = 0.192$ ) effect on the resistance of the whole tree.

### 3.4 Eccentricity and Aspect Ratio of Lateral Roots

The average lateral root eccentricity in the studied Macedonian pine trees was  $0.410 \pm 0.016$ , indicating that the major lateral roots had adopted elliptic form, i.e. one of the diameters was greater than the other. The mean aspect ratio of the major lateral roots was  $1.081 \pm 0.170$ , which was significantly ( $t = 5.291$ ,  $p < 0.001$ ) different from 1. In fact, in 76 % of the lateral roots in the investigated



**Fig. 6.** Penetrometer resistance of the soil in Pelister National Park, Macedonia, compared to the one in the Jodrell Bank Arboretum, UK. Error bars indicate  $\pm$ SD.

trees the major vertical diameter  $d_v$  was larger the major horizontal diameter  $d_h$ .

70% of roots with larger vertical major diameter were distributed in the direction perpendicular to the direction of greatest overturning resistance. Further investigations showed that the lateral roots with larger CSA were more eccentric. The eccentricity of the vertically eccentric roots was highly significantly correlated ( $r=0.461$ ,  $p<0.001$ ) to the CSA of the root. Furthermore, lateral root eccentricity was significantly correlated ( $r=-0.217$ ,  $p=0.038$ ) to the depth of origin of the root, more eccentric roots tending to be closer to the soil surface.

### 3.5 Soil Penetrometer Resistance

Soil penetrometer resistance as a marker of soil resistance to root expansion was not significantly ( $p=0.483$ ) different for the inner and outer trees. However, the soil penetrometer resistance increased with depth (Fig. 6), and it was on average  $1.066\pm 0.331$  MPa at 5 cm depth,  $1.535\pm 0.375$  MPa at 10 cm depth, and  $1.670\pm 0.294$  at 15 cm depth. According to the BS 8004: 1986 standard for soils, the soil in the uppermost soil horizon is classified as firm, and the soil in the lower two horizons as stiff.

## 4 Discussion

The methods developed and used in this study worked well and revealed the root system morphology and architecture, as well as the anchorage properties in the *P. peuce* trees investigated. The results of this study revealed many similarities but also some differences between *P. peuce* and the related *P. sylvestris* (Mickovski and Ennos 2002).

The similarities between these two species lie in their respective mechanisms of anchorage. The anchorage of the investigated *P. peuce* trees proved to be firm, with values in the overturning tests approximately 55% higher than those recorded for Scots pine trees which had a 25% greater DBH (Mickovski and Ennos 2002). Our results also showed that the trees with larger trunk DBH were better anchored than the trees with smaller trunk DBH, as in *P. sylvestris* (Mickovski and Ennos 2002), though anchorage only increased with DBH to the power of 1.6 compared with values of 2.1 for both *P. sylvestris* (Mickovski and Ennos 2002) and the tropical tree *Malotus wrayi* (Crook and Ennos 1997).

The morphology of the root system was also similar to other conifers studied (Rowe 1964, Sutton 1969, Coutts et al. 1998), most of the root biomass being concentrated in several large woody lateral roots.

The distribution of the major lateral roots around the tree stem was, as the displacement of the centre of the root CSA showed, asymmetrical. The asymmetry in *P. peuce* is approximately of the same magnitude as in *P. sylvestris* (Mickovski and Ennos 2002). Judging by the value of the displacement of the root CSA, it might be deduced that roots with similar diameters are arranged approximately evenly around the stem in three directions, while the fourth direction is either lacking roots, or has roots with considerably smaller diameters. This kind of lateral root distribution was, in fact, recorded for 8 of the investigated 20 trees.

One reason for the asymmetrical distribution of lateral roots around the tree trunk might be nutrient acquisition. The preferred clustering direction would be the one where there are more assimilates and less competition. This was the case with the outer belt *P. peuce* trees which clustered their lateral roots on the side outside the tree stand, where their lateral spread was less impeded and where root competition would be lower. Another reason for clustering the lateral roots in a preferred direction might be connected with a tree's stability requirements. A larger number of stronger lateral roots would be needed on the windward side to prevailing winds in order to keep the tree from toppling under the lateral wind loads. This proved to be the case of our *P. peuce* trees since the general orientation of the lateral roots of the investigated trees coincided with the prevailing wind direction.

The fact that the trees had more root CSA distributed parallel to the direction of maximum anchorage rigidity than at right angles suggested that the laterals might be responsible for much of the root anchorage. However, just as in *P. sylvestris* (Mickovski and Ennos 2002) by no means all the tree had more root area parallel to this direction (in fact only 13 out of 20 trees) and there was no significant correlation between the anchorage asymmetry ratio and the root asymmetry ratio. This casts doubt on them being the most important element in the anchorage.

What was the cause of the firm anchorage if not the major lateral roots? It is known that in upright plants at least one rigid element is required to resist rotational moments transmitted by the stem: either a stiff tap root or a plate of horizontal roots

with sinkers with geotropic characteristics (Ennos 1993). Being a naturally regenerated stock, our *P. peuce* trees showed a tendency to develop large-diameter straight-grained tap roots, and had the tap roots and the sinkers as a major root component in larger depth horizons. Since sinker roots were recorded in only a few instances in the investigated trees, it is clear that, similarly to *P. pinaster* (Stokes and Guitard 1997) and *P. sylvestris* (Mickovski and Ennos 2002), the tap roots might be accounted as the major component of the root anchorage in *P. peuce*.

Alongside the similarities, there were several differences between the investigated *P. peuce* and related *P. sylvestris* trees. Although both stands were of suppressed crown trees and thus expected to have less proliferated root systems (Wilson 1975), the root system of *P. peuce* was even less proliferated and branched than the root system of *P. sylvestris* (Mickovski and Ennos 2002). This difference in root system morphology might be a result of the differences in the environmental conditions in which the species is grown, or it might be a part of the tree's strategy of adaptation to the soil conditions. In providing stability for the tree, the larger lateral roots in *P. peuce* would provide greater bending resistance in resisting external forces, since rigidity is proportional to the fourth power of the radius of the root, while the branched roots recorded in *P. sylvestris* would provide more rapid transfer of tensile forces into soil (Stokes and Guitard 1997), at the same time having a reinforcing effect on the soil. Furthermore, knowing that extension growth and branching are alternative strategies for exploration of soil volumes (Sutton 1969, Harper et al. 1991), it is clear that *P. peuce* benefits from its larger linear roots which are good in exploration for new nutrients while *P. sylvestris* grows branched roots which are more efficient in exploitation.

Another difference between the two related species, closely connected to the root system morphology, lies in the fact that *P. peuce* was more deeply rooted than the *P. sylvestris* (Mickovski and Ennos 2002), having only 70 % of the major lateral roots in the first 10 cm depth compared to the 80 % of the total lateral root CSA in the same depth recorded for *P. sylvestris*.

The difference in vertical root distribution may be related to differences between these related

species in the eccentricity of the lateral root; the lateral roots of *P. peuce* were on average 25 % less eccentric than the laterals of *P. sylvestris* which have an eccentricity of  $0.52 \pm 0.15$  (Mickovski and Ennos 2002). Being more shallowly rooted and in a weaker soil, the roots of *P. sylvestris* would be subjected to bending more than the roots of *P. peuce* and this could have led to greater adaptive changes in root cross sectional shape (Fayle 1968, Wilson 1975). Being more highly stressed at their tops and bottoms when the tree swayed in the wind the roots would have laid down more wood in these areas by a typical thigmomorphogenetic response and so become more elliptical in shape (Mattheck, 1991) and better at resisting bending in the dorsoventral plane. Furthermore, the aspect ratio calculations showed that vertical root diameter was larger than the horizontal diameter in the majority of major lateral roots, but the mean lateral root aspect ratio of  $1.08 \pm 0.17$  was significantly ( $t=3.209$ ,  $p=0.002$ ) different, in fact 8% lower, than the value of  $1.16 \pm 0.23$  calculated for *P. sylvestris* (Mickovski and Ennos 2002). This is also in accordance with the results of Nicoll and Ray (1996) who expected that vertically eccentric roots are less common in deeply rooted trees where strong anchorage is provided by roots held by a thick matrix of soil.

The adaptive secondary root growth of lateral roots caused by external forces in both species might also compensate to an extent for the asymmetrical arrangement of major lateral roots around the trunk (Coutts et al. 1998). 70 % of the vertically eccentric roots of *P. peuce* were distributed in quadrants in which the trees showed lower resistance to overturning. This distribution was similar to the one recorded in *P. sylvestris* (Mickovski and Ennos 2002), in which approximately 60 % of the vertically eccentric lateral roots were distributed in the 'weaker' direction. Although the eccentricity and the aspect ratio of the roots in *P. peuce* were far less extreme than that shown by roots with an 'I' or 'T' beam shape reported in previous investigations (Fayle 1968, Hintikka 1972, Wilson 1975, Mattheck et al. 1995, Stokes et al. 1997), it would still increase bending rigidity and move the hinge point away from the tree, increasing the length of the lever arm and the resistance to overturning (Nicoll and Ray 1996).

It is evident from the results of this study that many factors can shape root architecture: genetics, thigmomorphogenesis, competition for assimilates, as well as environmental factors such as the soil and the climate. However, the results of this investigation suggest that at least to an extent the assimilation and anchorage characteristics of root systems is controlled independently.

## Acknowledgements

We would like to thank the management and the staff of the Pelister National Park in Bitola, Macedonia for their help and support.

## References

- Coutts, M.P. 1983. Development of the structural root system of Sitka spruce. *Forestry* 56: 1–16.
- 1986. Components of tree stability in Sitka spruce on peaty gley soil. *Forestry* 59: 173–197.
- 1987. Developmental processes in the tree root systems. *Canadian Journal of Forest Research* 17: 761–767.
- , Walker, C. & Burnard, A.C. 1990. Effects of establishment method on root form of lodgepole pine and Sitka spruce and on the production of adventitious roots. *Forestry* 63: 143–159.
- , Nielsen, C.C.N. & Nicoll, B.C. 1998. The development of symmetry, rigidity and anchorage in the structural root systems of conifers. In: Stokes, A. (ed.). *The supporting roots of trees and woody plants: form, function and physiology*. Kluwer Academic, Dordrecht, Holland.
- Crook, M.J. & Ennos, A.R. 1996. The anchorage mechanics of deep rooted larch, *Larix europea* x *L. japonica*. *Journal of Experimental Botany* 47: 1509–1517.
- & Ennos, A.R. 1997. Scaling of anchorage in the tap-rooted tree *Mallotus wrayi*. In: *Plant Biomechanics: Conference Proceedings*. University of Reading, Reading.
- Ennos, A.R. 1993. The scaling of root anchorage. *Journal of Theoretical Biology* 161: 61–75.
- 2000. The mechanics of root anchorage. *Advances in Botanical Research* 33: 133–157.

- Fayle, D.C.F. 1968. Radial growth in tree roots. Technical Report 9, Faculty of Forestry, Univ. of Toronto. Toronto, Ont.
- Goodman, A.M. & Ennos, A.R. 1999. The effects of soil bulk density on the morphology and anchorage mechanics of the root systems of sunflower and maize. *Annals of Botany* 83: 293–302.
- Harper, J.L., Jones, M., Sackville Hamilton, N.R. 1991. The evolution of roots and the problems of analysing their behaviour. In: Atkinson, D. (ed.). *Plant root growth – an ecological perspective*. Blackwell Scientific Publications, Oxford. p. 3–22.
- Hintikka, V. 1972. Wind-induced root movements in forest trees. *Communications Instituti Forestalis Fenniae* 76(2). 56 p.
- Mardia, K.V. 1972. *Statistics of directional data*. Academic Press, London.
- Mattheck, C. 1991. *Trees: the mechanical design*. Springer Verlag, Berlin.
- , Bethge, K. & Albrecht, W. 1995. Failure modes of trees and related failure criteria. In: Coutts, M.P. & Grace, J. (eds.). *Wind and trees*. Cambridge University Press, Cambridge UK. p. 195–203.
- Mickovski, S.B. & Ennos, A.R. 2002. A morphological and mechanical study of the root systems of suppressed crown Scots pine *Pinus sylvestris*. *Trees* 16: 274–280.
- Nicoll, B.C. & Armstrong, A. 1998. Development of *Prunus* root systems in a city street: pavement damage and root architecture. *Arboreal Journal* 22: 259–270.
- & Ray, D. 1996. Adaptive growth of tree root systems in response to wind action and soil conditions. *Tree Physiology* 16: 891–898.
- , Easton, E.P., Milner, A.D., Walker, C. & Coutts, M.P. 1995. Wind stability factors in tree selection: distribution of biomass within root systems of Sitka spruce clones. In: Coutts, M.P. & Grace, J. (eds.). *Wind and trees*. Cambridge University Press, Cambridge UK. p. 276–292.
- Rowe, J.S. 1964. Studies in rooting of White spruce. Project H-131, 2nd progress report. Mimeo Dep. For. Can. No. 64-H-13: 23.
- Smit, A.L., Bengough, A.G., Engels, C., van Noordwijk, M., Pellerin, S. & van de Geijn, S.C. (eds.). 2000 *Root methods: a handbook*. Springer, Berlin.
- Somerville, A. 1979. Root anchorage and root morphology of *Pinus Radiata* on a range of ripping treatments. *New Zealand Journal of Forestry Science* 9: 294–315.
- Stokes, A. & Guitard, D. 1997. Tree root response to mechanical stress. In: Altman, A. & Waisel, Y. (eds.). *Biology of root formation and development*. Plenum Press, New York. p. 227–236.
- Stokes, A., Nicoll, B.C., Coutts, M.P. & Fitter, A.M. 1997. Responses of young Sitka spruce clones to mechanical perturbation and nutrition: effects on biomass allocation, root development, and resistance to bending. *Canadian Journal of Forest Research* 27: 1049–1057.
- Sutton, R.F. 1969. Form and development of conifer root systems. Technical Communication 7, Commonwealth Forestry Bureaux, Oxford.
- Taylor, H.M. & Gardner, H.R. 1963. Penetration of cotton seedling tap roots as influenced by bulk density, moisture content and strength of soil. *Soil Science* 96: 153–156.
- Wilson, B.F. 1975. Distribution of secondary thickening in tree root systems. In: Torrey, J.G. & Clarkson, D.T. (eds.). *The development and function of roots*. Academic Press, London.

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