

Variation in root morphology amongst tree species influences soil hydraulic conductivity and macroporosity

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- 1 Variation in root morphology amongst tree species influences soil hydraulic conductivity and
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10 Abstract

11 Natural approaches to flood risk management are gaining interest as sustainable flood mitigation 12 options. Targeted tree planting has the potential to reduce local flood risk, however attention is 13 generally focused on the hydrological impacts of catchment afforestation linked to generic tree 14 features, whilst the species-specific impacts of trees on soil hydrology remain poorly understood. This 15 study compared effects of different tree species on soil hydraulic properties. Monocultures of Alnus 16 glutinosa (common alder), Fraxinus excelsior (European ash), Fagus sylvatica (European beech), Betula 17 pendula (silver birch), Castanea sativa (sweet chestnut), Quercus robur (English oak) and Acer 18 pseudoplatanus (sycamore maple) were used to determine effects of tree species identity on soil 19 hydraulic properties (near-saturated K and soil water retention) in a sandy loam soil, North Wales, 20 United Kingdom. The interaction of F. excelsior root properties and soil class on hydraulic conductivity 21 was also examined in four different soils (Rendzic Leptosol, Haplic Luvisol, Dystric Fluvic Cambisol and 22 Dystric Gleysol) across England and Wales. Fine root biomass (FRB) and morphological characteristics were determined at three depths (0-0.1, 0.1-0.2 and 0.2-0.3 m) and complemented by in situ surface 23 measurement of soil hydraulic conductivity. Root morphological traits were closely associated with 24 25 species identity and pore-size distribution, and FRB was strongly correlated with soil hydraulic 26 conductivity (R²=0.64 for 0-0.1 m depth FRB; R²=0.69 for 0.1-0.2 m depth FRB). Fine root biomass of F.

27 *excelsior* was six-fold greater than *C. sativa* (p<0.001), and the frequency of 0.01 mm radius soil pores 28 under *F. excelsior* was twice that of *Q. robur*. Near-saturated hydraulic conductivity under *F. excelsior* 29 was 7.91 ± 1.23 cm day⁻¹, double the mean rate of the other species. Soil classification did not 30 significantly influence FRB (p = 0.056) or near-saturated hydraulic conductivity (p = 0.076) in the 0.0-31 0.1 m depth soil, but soil water retention varied with depth. Species-specific traits of trees should be 32 considered in landscape design to maximise the local hydrological benefits of trees.

Keywords: Land use; Infiltration;; Hymenoscyphus fraxineus; Hydrology; Soil porosity; Soil
 classification.

35 1. Introduction

Anthropogenic activities are driving an acceleration of climate change and, as a result, the occurrence and intensity of extreme weather events is predicted to increase (IPCC5 WGII, 2014). Precipitation in the United Kingdom (UK) over the past 250 years has increased during the winter and decreased during the summer (Dadson et al., 2017). Climate change has motivated greater attention to mitigating the impact of extreme events, such as flooding, with a policy focus on the role land use management can play (Mcintyre and Thorne, 2013).

42 Trees have the potential to influence soil hydrological processes by increasing water infiltration into 43 soil, evapotranspiration, interception and groundwater recharge (Dadson et al., 2017; Dixon et al., 44 2016; Lane, 2017; Wolton et al., 2014). Plot-scale research has notably found that even when young 45 (5-years-old), trees can increase infiltration rate by 67 times and reduce surface runoff by 78% 46 compared with grazed pasture (Marshall et al., 2013), but heterogeneity of effects on hydraulic 47 conductivity at plot scale is also evident (Chandler and Chappell, 2008). The interplay between soil and 48 vegetation shapes soil hydraulic functions, but the relative importance of these functions is context 49 specific. In arid zones, vegetation is highly influential in increasing hydraulic conductivity (Thompson 50 et al., 2010), whereas soil class dominates the process in humid tropical and temperate (Geris et al., 51 2015) ecosystems. In contrast, soil classification has generally been shown to have little effect on

infiltration capacity, with interactions between soil fauna (e.g., earthworms), roots, plant species
richness and soil structure of greater importance (Fischer et al., 2015; Jarvis et al., 2013).

54 The role of tree roots in shaping hydraulic response has often been overlooked (Chandler et al., 2018). 55 Understanding of inter- and intra-species variation in root morphology is largely based on the 56 questionable assumption that root architecture and hydrological function can be predicted from 57 above-ground morphological characteristics (Sinacore et al., 2017). Therefore, a more thorough 58 investigation of species-specific, below-ground hydrological function is required. Macropores within 59 soil can be associated with root channels developed through the process of root production and 60 turnover, and enable preferential flow (Ghestem et al., 2011). Bioturbation from soil flora and fauna 61 can also increase porosity and hydraulic function, the effects of which are influenced by landuse 62 intensity and antecedent soil conditions, such as pH (Spurgeon et al., 2013). Preferential flow in 63 wooded ecosystems has been shown to be related to tree species; Luo et al. (2019) reported that 64 coniferous forests dominated by Platycladus orientalis (L.) Franco (oriental arbo-vitae) exhibited 65 greater preferential flow than deciduous forests dominated by Quercus variabilis Blume (Chinese cork 66 oak). Separately, a positive relationship ($R^2 = 0.91$) was identified between macroporosity and tree roots of Pinus coulteri D.Don (Coulter pine), but total porosity (and near-saturated conductivity) was 67 68 greater under Quercus dumosa Nutt. (California scrub oak) and Adenostoma fasciculatum Hook. & Arn. 69 (chamise), where conditions were more conducive to macrofaunal (e.g., earthworm) activity (Johnson-70 Maynard et al., 2002). Luo et al. (2019) reported that whilst tree roots were strongly associated with 71 macropore development and preferential flow, the interaction between macroporosity, total porosity 72 and infiltration was less clear. Soil total porosity and infiltration rate can have a positive relationship 73 (Sun et al., 2018), however Bodner et al. (2014) attributed an increase in infiltration to an increase in 74 macroporosity in soil where total porosity remained unchanged. Inconsistent effects describing the 75 relationships between total porosity, macroporosity, preferential flow and tree species identity implies 76 that more research is required to understand these associations.

Preferential flow in the vadose zone mediates water infiltration and is associated with macropores,
including artificial drainage (Bathurst et al., 2018; Marshall et al., 2009), macrofaunal pathways
(Bargues Tobella et al., 2014), biomat flow (Gerke et al., 2015) and root channels (Zhang et al., 2015).
However, not all fine roots are conduits for preferential flow (Luo et al., 2019), suggesting that root
size distribution may be more important than root biomass. For example, root length density has been
shown to have a strong positive correlation with preferential flow (Zhang et al., 2015) but this
relationship is spatially variable (Luo et al., 2019).

84 The difference in fine root production across a spectrum of the broadleaved tree species that are 85 abundant in Europe, and the consequential effect on soil hydraulic conductivity, is largely unknown. 86 Fine root production is known to be plastic, with its spatial distribution being highly responsive to 87 antecedent moisture conditions (Fan et al., 2017), which is influenced by soil texture as well as by 88 climate. Differences in hydrological response have been shown between coniferous and deciduous 89 forest ecosystems, but the response was mitigated by spatially contrasting soil texture (Luo et al., 90 2019). The relative influence of tree species identity and soil classification on infiltration capacity 91 remains poorly understood. The aim of this study was to characterise the root morphology of seven 92 species of broadleaved, deciduous trees and investigate the relationship with near-saturated soil 93 hydraulic conductivity within one type of soil. The study then seeks to understand the effect of soil 94 classification on hydraulic conductivity in plantations of a single using tree species. The objectives 95 were to (i) investigate the variation in infiltration rate between seven tree species growing in the same 96 soil classification and (ii) compare the tree species' corresponding root morphological characteristics 97 to determine whether soil hydraulic function depends on species' root characteristics, then (iii) to 98 investigate the relative influence of tree roots and soil classification on soil hydraulic function. We 99 hypothesise that (i) tree species affect soil hydraulic conductivity; (ii) tree species' growing on the 100 same soil differ in their production of fine root biomass (FRB) and infiltration rate; and (iii) soil 101 classification affects the soil hydraulic function associated with the abundant European tree species 102 Fraxinus excelsior L (European ash).

103 2. Methods

104 2.1 Site descriptions and experimental design

105 The BangorDiverse forest diversity and ecosystem function experiment, located at the Henfaes 106 Research Centre, Abegwyngregyn, UK (53°14'15"N, 4°1'4"W), was used to determine the effect of tree 107 species on soil hydraulic function. Monocultures of seven tree species were planted as 1.0 m tall 108 saplings in March 2004: Alnus glutinosa [L.] Gaertner (common alder), F. excelsior, Fagus sylvatica L. 109 (European beech), Betula pendula Roth. (silver birch), Castanea sativa Mill (sweet chestnut), Quercus 110 robur L (English oak) and Acer pseudoplatanus L. (sycamore maple) (Ahmed et al., 2016). Initial planting density was 10,000 stems ha⁻¹, but trees were thinned to 2,500 stems ha⁻¹ in 2012/2013 to facilitate 111 112 continued tree development. Randomised, replicate plots (0.1 ha) of each species (n=4) were blocked 113 across two adjacent fields (2.36 ha total area). The soil at BangorDiverse is a Dystric Fluvic Cambisol, developed from glaciofluvial deposits (Smith et al., 2013) with pH ranging from 5.4 (surface) to 6.3 (1-114 115 m depth) (Ahmed et al., 2016). Soil texture is a sandy loam/loam determined by laser diffraction 116 (Coulter LS particle size analyser) from soil in the 0-0.1 m depth. The site is hyperoceanic with mean 117 annual rainfall of approximately 950 mm and mean annual air temperature of 10.6 °C (Gunina et al., 118 2017).

119 Plots of *F. excelsior* planted in different sites across the UK with four contrasting soil classifications 120 (IUSS Working Group WRB, 2015) were used to investigate how interaction of a single tree species 121 with soil classification influences soil hydraulic function. Originally established as part of a provenance 122 trial in 1993 (Cundall et al., 2003), three sites, Gloucestershire (England), Hampshire (England) and 123 Gwynedd (Wales), were selected based on the soil classifications (Table 1) that best represented the 124 range of textural characteristics (sand, silt or clay) commonly occurring across the UK. Each 125 experimental site consisted of three fully replicated, randomised blocks of different provenances of F. 126 excelsior. Saplings (same age from seed) were planted at 2500 stems ha⁻¹ and had subsequently been 127 thinned to 50% density at the Gloucestershire site only. One plot from each block (n=3) comprised of *F. excelsior* trees of UK (Powys, Shropshire) or French (Normandy) provenance were selected for study.
Due to the presence of the fungal pathogen *Hymenoscyphus fraxineus* at the Hampshire site only,
plots were selected where only visibly healthy trees were found following condition assessment (SI 1).

To increase the diversity of soils used in this analysis (Table 1), an additional site with *F. excelsior* (provenance unknown) established in 1987 at Rothamsted Research, North Wyke, Devon (England) was selected. At North Wyke, three plots were randomly selected from two blocks, avoiding edge trees. All plots were planted with seedlings at 2500 stems ha⁻¹ and had not been thinned. No obvious signs of *H. fraxineus* were present at North Wyke.

136 *2.2 Root morphology*

137 Two soil cores of 0.08-m diameter were collected from three depths (0-0.1, 0.1-0.2, 0.2-0.3 m) 138 equidistant between two trees randomly selected near to the centre of each plot to mitigate against 139 edge effects (SI 2). Roots were collected to a depth of 0.3 m; in soil above this depth, in temperate 140 forest ecosystems, 65% of roots exist and there is a predominance of fine ephemeral roots involved in nutrient and water uptake (Jackson et al. 1996). To minimise canopy damage and variation 141 142 introduced by root growth during the sampling period, 168 samples were collected between January 143 and February, after leaf fall and during a period of dormancy in line with previous sampling campaigns 144 conducted at the site (Smith et al., 2013). Soil cores were placed into sealable polythene bags and 145 stored at 4 °C for a maximum of 4 days before processing.

Each core was washed with water in a sieve stack (1- and 2-mm mesh size) to remove soil adhered to roots and separate roots into two size classes, fine (<2 mm diameter (ϕ)) and coarse (>2 mm ϕ), the latter of which were discarded. Tree species identity of the roots was based on morphological characteristics, such as surface colour, structure and colour of the periderm and ramification pattern, outlined by Mrak and Gricar (2016) and necromass (dead fine roots) was identified based on black or dark brown colour and a decaying fragmented appearance (Eissenstat and Yanai, 1997; Leuschner et al., 2004 ; Smith et al., 2013). Fine roots were scanned using an Epson 4990 scanner at a resolution of
300 dots per inch (dpi) and images were analysed with WinRhizo (version 2005c, Regent Instruments
Inc., Quebec, Canada) to measure fine root length, surface area, surface volume, projected surface
area and number of root tips, divided into 20 (0.1 mm) diameter classes (0-2 mm). Necromass and the
biomass of fine and coarse roots were determined after drying at 80 °C until constant mass. Data from
the two soil cores collected per plot were averaged to avoid within-plot pseudoreplication.

158 2.3 Root characteristics

Root area index (RAI, m² m⁻²) was derived from the root surface area divided by the surface area of 159 the sampled core. Specific root area (SRA, m² kg⁻¹) was calculated from the surface area of fine root 160 161 divided by root dry mass (Lohmus et al., 1989). Specific root length (SRL, m g⁻¹) was determined from 162 the total length of fine roots divided by root dry mass (Ostonen et al., 2007). Root length density (RLD, 163 cm cm⁻³), which indicates the proportion of soil occupied by fine roots, was estimated from the ratio of root length to the volume of the sampled core. Root tip density (RTD) was calculated as thousands 164 of tips per m⁻². For each of the aforementioned root metrics an arithmetic mean was calculated from 165 166 data exported from WinRhizo output.

167 2.4 Soil hydraulic function

168 Minidisk infiltrometers (0.045 m ø) (Meter Group, Pullman, USA) were used to measure the rate of 169 infiltration of water into soil and to calculate near-(field)-saturated hydraulic conductivity (K_{fs}) within 170 each plot. Surface vegetation was carefully removed, and a thin layer of fine sand (~0.001 m) was 171 applied to the soil surface to ensure optimal contact between the infiltrometer disc and the soil. The tension was set at -0.02 m to eliminate water flow through the largest macropores (> 0.742 mm), to 172 173 provide a more representative estimation of water flow through the soil matrix and to achieve steady-174 state infiltration rate. Water level was recorded every minute until 20 cm³ of water had infiltrated the 175 soil. Three measurements were taken at each plot to give an average K_{fs}. Near-saturated hydraulic

176 conductivity for the respective soil water potential was calculated using the method of Zhang (1997)177 and van Genuchten soil classification tables (Meter Group Inc, 2018).

178 At each plot, a 250 cm³ soil core was collected from the 0-0.05 m and 0.1-0.15 m depths. Cores were 179 stored at 4 °C and then soaked for at least 24 hours in degassed, deionised water prior to analysis. Soil 180 water retention was measured using a HYPROP 2 (Meter group, Pullman, USA) (Schindler et al., 2010), 181 and then dry bulk density and porosity were determined for the cores (SI 3). To account for the 182 stoniness of the experimental plots, stones (>0.002 m Ø) were sieved out of the oven-dried soil and 183 weighed (SI 3). The vapour equilibration technique (Scanlon et al., 2002) was used to measure the dry-184 end matric potential on sub-samples taken from each core. Soil water retention curves (SWRC) were 185 modelled using the HypropFit (Schindler et al., 2010) (UMS, Munich, Germany) implementation of the 186 Fredlund-Xing water retention model (Fredlund and Xing, 1994), using the measured soil water retention, dry bulk density, K_{fs} (applied to cores from 0-0.05 m depth only) porosity, dry-end matric 187 188 potential, volumetric moisture content and stoniness data.

189 Effective soil pore-size distribution was estimated using the method outlined by Blonquist et al. (2006). 190 Hydraulic capacity was estimated using data from the SWRC (modelled in HypropFit) to derive the 191 change in moisture over the change in hydraulic head $(d\theta_n/dh)$. Hydraulic capacity was plotted as a 192 function of pore radius. The scaled effective pore-size distribution associated with each tree species 193 was then derived by taking the inverse relationship between pressure (h) from the water retention 194 curve and log10 pore radius, resulting in a dimensionless, scaled, effective pore-size distribution. The 195 distribution is displayed as a function of effective pore radius f(r) proportional to the abundance of 196 each pore-size within a given volume of soil.

197 To give context, *in situ* soil moisture was measured using ML3 ThetaProbe Soil Moisture Sensors 198 (Delta-T Devices Ltd, Cambridge, UK) (n=9) in each plot at 10 cm depth. Particle-size distribution was 199 ascertained using an air-dried sub-sample from soil used for the HYPROP analysis, repeatedly quartered to mitigate selection bias (Lebron and Robinson, 2003) (Table 1). Particle-size distribution
was determined from a 0.5-0.8 g subsample of sieved (<2 mm) soil using a LS13 320 laser diffraction
particle-size analyser (Beckman Coulter Inc, Indianapolis, USA) (Table 1). Soil organic matter
concentration was determined by loss-on-ignition (LOI) analysis of 10 g of sieved (<2 mm) soil (Ball,
1964) (Table 1). For quality assurance, two standard soil and two replicate samples were included for
all LOI and particle size analyses.

206 2.5 Statistical analyses

207 Two statistical models were used to analyse the datasets: (i) for the data collected from BangorDiverse 208 (n=4), a two-factor ANOVA to test factors and interaction effects, with species and depth as factors, 209 and root biomass, root morphological characteristics and K_{fs} as dependant variables; (ii) for data 210 collected at the pan-UK F. excelsior provenance trial sites (n=4), a two-factor ANOVA with soil 211 classification and soil depth as factors and root biomass, root morphological characteristics and K_{fs} as 212 dependant variables. The Tukey Honest Significant Difference (HSD) post-hoc test was used to 213 determine within-factor significance for both statistical models. Relationships between dependent 214 variables were explored using ordinary linear regression. All data were tested for homogeneity of 215 variance using Levene's test and normality using the Shapiro-Wilk's test. Root biomass, root 216 morphological variables and K_{fs} data were log transformed to satisfy normality. To visualise the 217 relationships between variables, the dimensionality of the dataset was reduced from 44 parameters 218 that included root morphological metrics (e.g., SRL, RAI, SRA, RLD) within three soil layers (0-0.1 m, 219 0.1-0.2 m and 0.2-0.3 m), K_{fs} at the soil surface and soil porosity within two soil layers (0-0.05 m and 220 0.10-0.15 m) by conducting a principal component analysis (PCA). Stepwise multiple regression 221 (forward and backwards) was then used to determine the parameter that best predicted K_{fs} . All 222 statistical analyses were completed with SPSS v22.0 (IBM SPSS, Armonk, NY, USA) with p < 0.05 used as the limit for statistical significance. All figures were produced using SigmaPlot v13.0 (Systat 223 224 Software, San Jose, CA, USA).

225 **3. Results**

226 *3.1 Tree species' effects*

227 3.1.1 Hydraulic conductivity and root biomass

Mean surface K_{fs} ranged from 3.47 ± 0.56 standard error cm day⁻¹ for *A. pseudoplatanus* to 7.91 ± 1.23 cm day⁻¹ for *F. excelsior*, although the difference between the species did not reach the threshold of statistical significance (*p*=0.056) (Fig. 1a). However, a positive correlation (R253,254, = 0.64 (0-0.1 m depth) and R² = 0.69 (0.1-0.2 m depth)) was observed between tree species' FRB and K_{fs}, with a high degree of variation around mean K_{fs} within some species (e.g. *Q. robur*).

233 Fine root biomass was affected by both species and soil depth (p<0.001), but no interaction effect was 234 evident (Table 2). Fraxinus excelsior was the species producing highest FRB at every soil depth (Table 3), with the largest difference in FRB between *F. excelsior* and the other species at a depth of 0-0.1 235 236 m(p<0.001; Fig 1b). Fine root biomass of F. excelsior was between three-fold (B. pendula; p<0.001) 237 and six-fold (C. sativa; p < 0.001) greater than the other species. Deeper in the soil where the 238 proportion of total F. excelsior FRB was much less (24%, 0.1-0.2 m; 17%, 0.2-0.3 m), F. excelsior FRB 239 was greater than *F. sylvatica* FRB only (*p*=0.05, 0.1-0.2 m; *p*<0.01, 0.2-0.3 m). The biomass:necromass 240 (B:N) ratio of A. pseudoplatanus (37.19) was significantly (p<0.05) greater than A. glutinosa (4.21) and 241 C. sativa (5.56) within the 0-0.1 m soil layer and was significantly greater for A. pseudoplatanus (103.9) than A. glutinosa (3.27), C. sativa (1.05), F. sylvatica (6.60) and Q. robur (5.23) within the 0.1-0.2 m soil 242 243 layer (*p*<0.05).

Soil total porosity (0-0.05 m depth; Fig 1c) was similar between all species (p>0.05) at all soil depths. Despite the aforementioned positive correlation between K_{fs} and FRB, a similar relationship was not observed between FRB and total porosity. There is some evidence of a positive linear relationship between the mean K_{fs} and FRB of each species, although it reached the p<0.05 threshold of significance in the 0.1-0.2 m depth only. Fine root biomass explained 64, 69 and 25% of the variation in K_{fs} for the 0-0.1 m, 0.1-0.2 m and 0.2-0.3 m depths, respectively (Fig. 2a-c). **250** 3.1.2 Soil water retention and pore-size distribution

251 Saturated soil water content was highest for F. excelsior (57%) and lowest for F. sylvatica (52%) in the 252 0-0.05 m soil layer (Fig. 3a). As soil water potential decreased, the soil water content under F. excelsior decreased rapidly, becoming comparable to the other species. Continued decreases in soil water 253 254 potential caused F. excelsior to have the second lowest retention capacity. Conversely, Q. robur was 255 ranked 5th in species' retention capacity at saturation but retained the highest percentage of soil water content at mid-range potentials (i.e., between -100 and -1000 cm). Castanea sativa had consistently 256 257 low soil water content compared with the other species. Within the 0.10-0.15 m soil layer (Fig. 3b), Q. 258 robur had the highest water content (57%) at saturation, whereas F. excelsior had the second lowest 259 (50%), with *F. sylvatica* lowest (49%). All species had similar water content once pressure was applied 260 (< -10 cm), apart from C. sativa, which again had consistently lower soil water content than other 261 species.

Figures 3c and 3d show the scaled effective pore-size distribution. Soil developed under *F. excelsior* exhibited the greatest abundance (0.24) of macropores, followed by *B. pendula* (0.20), whilst the poresize distributions of soil under *Q. robur* and *C. sylvatica* are skewed towards smaller pore sizes. By contrast, the proportion of macropores deeper in the soil (0.1-0.15 m) were similar amongst species, with the exception of *Q. robur* and *A. pseudoplatanus* (Fig 3d).

267 3.1.3 Root morphological traits

Tree species and separately soil depth affected all root traits (both p<0.001) except soil depth for SRA 268 269 (p>0.05), but there were no species × depth interactions (Table 4). In the 0-1.0 m soil layer, F. excelsior 270 had greater RLD (6.56 ± 0.65 cm cm⁻³, p<0.05) and RAI (6.02 ± 0.86 m² m⁻², p<0.01) than all other 271 species, more than 11 times greater than lowest ranked C. sativa (RLD 0.57 \pm 0.07 cm cm⁻³, RAI 0.51 \pm 272 0.51 m² m⁻²). Root tip density (RTD) was also greatest in *F. excelsior* (1275.01 \pm 199.3 \times 10²m⁻²), significantly more than A. glutinosa (242.89 ± 45.28 × 10² m⁻²; p<0.001), C. sativa (174.35 ± 17.17 × 10² 273 274 m^{-2} ; p<0.001) and Q. robur (p<0.01) (Table 5). The lowest RTD, associated with C. sativa, was more 275 than seven-fold less than *F. excelsior. Fraxinus excelsior* had the greatest RLD, RAI and RTD in the 0.1276 0.2 m soil layer (p<0.01) and in the 0.2-0.3 m soil layer; RLD and RAI of *Fraxinus excelsior* (1.55 ± 0.47 277 cm cm⁻³ RLD; 1.78 ± 0.57 m² m⁻² RAI) were three- to eight-fold and four- to seven-fold greater 278 respectively than all other species (p<0.05) except *A. pseudoplatanus* (p>0.05; Table 5).

279 Ordination analysis was used to examine the relationship between tree root morphological traits and 280 soil physical properties developed under the different tree species. The dimensionality of the data was 281 reduced to three principal components (PC) that explained 95% of the variation. Principal component 282 1 explained 63%, PC2 18% and PC3 14% of the variation (Fig. 4). Tree species were tightly grouped 283 together along the dominant PC1 with the exception of *F. excelsior*, which was strongly separated and associated most strongly with FRB, RAI, RTD, RLD and root projected surface area. Necromass was 284 285 weakly separated from other root traits along PC2 and associated with A. glutinosa and F. excelsior 286 (Fig 4a). Soil porosity in the 0-0.05 m depth and K_{fs} were associated with each other along PC1 and 287 weakly associated with F. excelsior and A. glutinosa along PC2 compared with the other five species, 288 whereas, deeper in the soil (0.1-0.15 m), total porosity related more strongly to the other five species 289 than F. excelsior and A. glutinosa. Fine root biomass and other morphological traits (i.e., root projected 290 surface area, RAI, RTD and RLD) were all closely associated with each other along PC1, and with F. 291 excelsior. Stepwise multiple regression analysis (forward and backward) showed that root necromass 292 was the best single predictor of K_{fs} ($R^2 = 0.224$; p < 0.05) with all other variables excluded during the 293 analysis.

294 3.2 Fraxinus excelsior across soil classifications

Fine root biomass of *F. excelsior* differed significantly amongst soil depths and only between soil class where the fungal pathogen *Hymenoscyphus fraxineus*, which causes ash dieback disease on *F. excelsior* affected tree growth (i.e., Rendzic Leptosol). No interaction effect was evident between soil class and depth (Table 6). Fine root biomass was lowest in the Rendzic Leptosol through the whole profile (0-0.3 m), with a B:N ratio of 1.16, compared with the Haplic Luvisol (3.17), Dystric Fluvic Cambisol (6.62) and Dystric Gleysol (2.04) soils (SI 4). The relationship between FRB and hydraulic conductivity previously observed across all tree species was reproduced when the relationship between *F. excelsior* FRB and hydraulic conductivity was examined across the four soils; the R² was 0.49 for the two soil
 layers 0-0.1 and 0.1-0.2 m and 0.43 for the 0.2-0.3 m layer.

304 Soil water retention curves were similar under F. excelsior across all four soil classifications in the 305 surface layer (Fig 5a). At saturation, the soil water content at 0.0-0.05 m depth did not vary 306 significantly and ranged between 61% and 57% for all soil classes. The shapes of the retention curves 307 were also similar throughout the range of water potentials. Conversely, SWRC from deeper in the soil 308 profile (0.1-0.15 m) differed substantially (Fig 5b). While the SWRC of the Dystric Gleysol from Devon 309 retained the same form as the surface soils, all other soils had decreased water retention at saturation 310 with depth. The two silty clay loam soils, Haplic Luvisol and Rendzic Leptosol, had the greatest change 311 in soil water content at saturation, both reducing from ~58% at the surface to ~48 and ~42% 312 respectively with depth. The silt loam, Haplic Luvisol, soil had a unimodal pore-size distribution, but 313 the other soils all had a bimodal distribution (Fig 5c&d). For all four soils macro- and meso-size pores 314 were clearly evident in the surface layer, but decreased with depth, particularly the mesopores, with 315 small pores becoming more prevalent with depth especially in the Dystric Gleysol and Haplic Luvisol 316 soils.

Compared with reference soils in the Rosetta database (Schaap et al., 2001), soils from the present study retained a greater volume of water at saturation, regardless of soil classification (Fig. 6). The modelled soil water retention, based on physical soil characteristics of agricultural soils, was-15-50% less at saturation than those measured in the forested soils of the present study. Increasing soil water potential (-cm) rapidly reduced the volumetric water content of measured SWRCs to become comparable with the predicted reference soils by -100 cm.

323 4. Discussion

324 4.1 Tree root morphology and hydrology

325 This study showed that FRB production is tree species-specific, broadly agreeing with Chandler et al. 326 (2018). Notably, F. excelsior, a ubiquitous species across much of Europe, establishes fine roots far 327 more extensively, up to six-fold greater biomass, than the other common European broadleaved 328 species assessed. Across species, total soil porosity remained consistent, but variation in FRB changed 329 soil macroporosity and soil water retention. The results indicated that, although variation in species' 330 FRB roughly mirrors that of K_{fs}, there was no relationship between FRB and total soil porosity. Soil 331 under F. excelsior had the greatest water retention capacity at saturation (soil water potential = -1 332 cm), but the negligible variation between species indicated comparable total porosity. As soil water 333 potential decreased the soil water content generated from soil collected under F. excelsior decreased 334 rapidly, signifying the low bulk density and larger pore sizes (Radcliffe and Simunek, 2010) associated 335 with F. excelsior.

336 Differences in pore-size distribution, rather than total porosity, linked to tree species-specific 337 differences in fine root morphology are likely to be driving the relationship between tree species and 338 hydraulic conductivity, but is moderated by fine root necromass. Fraxinus excelsior had the largest K_{fs}, 339 root biomass and number of macropores, but the overall total porosity did not differ significantly from 340 the soils under the other six tree species. The high FRB of *F. excelsior* might suggest adventitious root 341 development and a greater RTD leading to the creation of macropores surrounding the root (Ghestem 342 et al., 2011). However, it is apparent that FRB, projected root surface area and RTD are not as strongly 343 related to porosity as are other root traits (Fig. 4). Despite the high FRB and hydraulic conductivity 344 associated with *F. excelsior*, a correspondingly high RTD was not identified, suggesting that RLD, rather 345 than RTD, is an important factor in the creation of macropore channels.

Despite nuanced relationships between live root morphological variables, macroporosity and K_{fs}, root necromass was the best predictor of K_{fs} suggesting that root turnover has an important role in soil hydraulic function. Fine root longevity in trees is complex, ranging from days to years (Bengough, 2012) and is dependent on root diameter, root density, nitrogen concentration, colonisation of mycorrhizal fungi and phenolic compound accumulation mediated by interaction with soil fauna (Eissenstat et al., 2000). During root development, exuded organic compounds contribute to the stability of the root channel, but following root death dehydration initially occurs, allowing gradual decomposition that creates progressively larger channels within the soil matrix available for preferential flow, and subsequently sub-surface sediment transfer causes channels to collapse or fill over time (Bengough, 2012; Ghestem et al., 2011). Variation in root turnover rates should have a large influence on the size and longevity of root-derived macropores (Wang et al., 2020).

357 Tree root morphological traits in this study better explained K_{fs} variations near the soil surface (0-0.2 358 m) than deeper in the soil (0.2-0.3 m depth). Root length density was greatest near the soil surface 359 facilitating connectivity of root-induced macropores and greater opportunity for infiltration. A similar 360 strong relationship between macroporosity near the soil surface and preferential flow in three tree 361 species (Styphnolobium japonicum (L.) Schott, Platycladus orientalis (L.) Franco, and Quercus dentata 362 Thunb.), which diminished with depth, has also been reported (Zhang et al., 2015). A comparison with 363 pedotransfer functions, largely used for agricultural soils, indicated that, by excluding sub-surface flow 364 through macropores, hydraulic functions quickly converge with those predicted by the pedotransfer 365 functions for the given soil texture in the 0-0.1 m soil layer. However, deeper in the profile (0.1-0.3 m) 366 where the density of fine roots is lower, soil texture had a greater influence on soil hydraulic 367 conductivity. Results of the present study, combined with the apparent lack of accountability for 368 macropores generated by trees in pedotransfer functions, suggests that improvement could be made 369 to the parameterisation of hydrological models based on the below-ground characteristics of 370 vegetation.

371 4.2 Soil classification and hydrology

Our study explored whether variation due to soil textural properties would temper the influence of afforestation with a single tree species (*F. excelsior*) on water retention capacity. Data from the forested plots were compared to agricultural soils with the same textural properties (loam, silty clay loam and clay loam) in the Rosetta database to obtain comparable values of hydraulic response. Modification of soil structure by the presence of trees enabled greater water retention capacity at saturation (Fig. 6). As water potential increased, which effectively excludes the influence of macropores, the forest SWRCs migrate closer to the Rosetta predictions. Therefore, landcover, specifically the presence of trees, appears to mediate the influence of soil textural properties on hydraulic response, regardless of soil classification, although within landcovers impacts, such as tillage, may regulate the response.

382 Using F. excelsior as an example, this study showed that soil texture, a considerable influence on 383 ambient soil moisture, does not influence fine root growth near the soil surface. Furthermore, in the 384 0-0.1 m depth, fine tree roots modified pore-size distribution, negating the effect of soil class on 385 hydrological function. At 0-0.1 m depth, where 50-58% of total FRB of *F. excelsior* was present, little 386 variation in soil water retention was observed between sites differing in soil classification. Deeper in 387 the soil, soil water retention was more divergent amongst sites as the influence of fine roots decreased 388 and soil class started to dominate the hydraulic response. Hydraulic conductivity, therefore, is 389 influenced by the combination of root morphology and soil classification, which varied with depth. 390 Indeed, within-species variation in root morphology and rooting extent throughout the soil profile has 391 been shown to be contingent on ambient hydrological soil conditions, oxygen availability and access 392 to groundwater resources (Feng et al., 2017).

During very dry conditions, such as those recently preceding the study period (mean volumetric soil water content of 16%), soil class had a nuanced effect on rooting morphology and macroporosity. The sandy silt loam and clay loam textures of the Dystric Fluvic Cambisol and Dystric Gleysol exhibited similar pore-size distributions. By contrast, the silty clay texture of the Haplic Luvisol was associated with a lower FRB. There was a lack of organic matter, or limestone, in the Haplic Luvisol that could disaggregate the clay compared with the other clay-containing soils (i.e., Dystric Gleysol and Rendzic Leptosol). The high clay content resulted in a substantially hardened soil that reduced plasticity and 400 was likely to be related to the observed lower abundance of macropores. Root dieback, however, 401 caused by tree disease may have a greater, though time limited, impact on soil hydraulic function than 402 soil classification. Root dieback is positively associated with crown reduction due to infection from 403 Hymenoscyphus fraxineus (Bakys et al., 2011). Where H. fraxineus was observed at a moderate -404 advanced stage (assessment methods described in SI) (i.e., Hampshire; Rendzic Leptosol), necromass 405 accounted for half of the total fine root mass (B:N = 0.98) in the 0-0.1 m depth, substantially more 406 than in the other clay-dominant soils (Haplic Luvisol, 2.49; Dystric Gleysol, 2.05). Once necromass has 407 fully decomposed, the residual root channels will be vulnerable to collapse, potentially reducing 408 hydraulic conductivity in the longer-term.

409 *4.3 Implications for land managers*

410 Fraxinus excelsior had the greatest potential to improve surface water infiltration regardless of soil 411 class. A ubiquitous species in much of Europe, F. excelsior is likely to have a disproportionately larger 412 influence on landscape hydraulic function than the other tree species assessed here due to its root 413 morphology and influence on macroporosity.. Therefore, loss of F. excelsior in the landscape due to 414 the fungal pathogen H. fraxineus could have serious implications for local soil hydrological function 415 throughout Europe. Consideration of hydraulic function should be a major component in the selection 416 of alternative tree species to replace F. excelsior, and tree species' root morphological traits and 417 influence on soil hydrology should be used as a criterion to select tree species in the future to 418 maximise the potential benefits of establishing new woodlands. However, whilst results of the present 419 study showed that tree species-specific root morphological traits have a role in altering soil hydraulic 420 function at the plot scale, the complex interactions that influence catchment hydrology (e.g., field 421 boundaries, land use and drainage) suggest that caution should be exercised before extrapolating such 422 plot-scale results to the landscape scale.

423 5. Conclusion

Species-specific variation in fine root morphological characteristics of seven common European broadleaved tree species were shown to alter soil macroporosity and hydraulic function. Fine root length density and necromass were correlated with an increased abundance of macropores within the soil, facilitating greater hydraulic conductivity, despite little change in total porosity. Notably, *F. excelsior* had up to a six-fold greater FRB than the other tree species studied, however RLD rather than FRB was shown to be the strongest driver of the observed changes in macroporosity.

Soil water retention curves and porosity data indicated that tree roots influence soil structural characteristics in the 0-0.1 m layer of the soil, where more than 50% of the FRB was present, maximising macroporosity regardless of soil texture. Species with the greatest RLD exhibited correspondingly greater macropore abundance and higher hydraulic conductivity when soils were at or close to saturation.

The species-specific influence of trees on hydraulic function and the associated impact of tree diseases, such as the fungal pathogen *Hymenoscyphus fraxineus* which causes ash dieback disease on *F. excelsior*, suggests that changes to the composition of tree species present in the landscape could have implications for hydrological hydraulic regulation. Further work is necessary to determine if hydrological models can be improved by the incorporation of below-ground tree trait data.

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- biomass on soil preferential flow in forest ecosystems. For. Syst. 24, 1–11.
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- 615 Tables

616 **Table 1.** Location of *Fraxinus excelsior* provenance trial experimental plots by World Reference Base (WRB) soil classification (WRB for soil resources, 2006),

617 UK county, mean particle size distribution of the mineral soil to 0.015 m soil depth and soil texture based on measured soil particle size distribution (Soil

618 Classification for England and Wales) (Avery, 1980).

WRB classification soil group	Site (UK county)	Latitude Longitude		n soil par istributio		Soil texture	Mean soil organic matter content (%)		
			Sand	Silt	Clay				
Dystric Fluvic Cambisol	Gwynedd	53° 14′ 19.38″ N 4° 01′ 05.91″ W	40	44	16	Sandy silt loam	6.4		
Haplic Luvisol	Gloucestershire	51° 54′ 24.93″ N 2° 18′ 39.68″ W	20	59	21	Silty clay loam	6.5		
Rendzic Leptosol	Hampshire	51° 12′ 02.02″ N 1° 31′ 39.48″ W	16	57	26	Silty clay loam - limestone rich	- 7.0		
Dystric Gleysol	Devon	50° 46′ 12.14″ N 3° 54′ 08.79″ W	25	51	23	Clay loam	11.5		

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620

621 Table 2. Main effects of seven tree species' (Alnus glutinosa, Fraxinus excelsior, Fagus sylvatica, Betula pendula, Castanea sativa, Quercus robur and Acer

622 *pseudoplatanus)* fine root biomass in three soil depths (0-0.1, 0.1-0.2, 0.2-0.3 m).

Factor	df	F	<i>p</i> -value
Depth	2	16.156	<0.001
Species	6	11.677	<0.001
Depth*Species	12	0.831	0.618

624	Table 3. Mean fine root biomass and rank order of seven tree species (Alnus glutinosa, Fraxinus
625	excelsior, Fagus sylvatica, Betula pendula, Castanea sativa, Quercus robur and Acer pseudoplatanus)
626	at 0.1 m depth intervals and for the whole sampled profile (0-0.3 m). Mean fine root biomass at each
627	depth is given as a proportion of the whole profile (0-0.3 m) fine root biomass (%), B:N describes the
628	biomass:necromass ratio. SE = ±1 standard error. Superscript letters denote Tukey post hoc
629	comparison ($p < 0.05$) between species within each soil depth.

				Proporti on of total fine root				
		biomass	Rank	biomass	Necro			
		m⁻²)	order	(%)		m⁻²)	B:N	ratio
0–0.1 m	Mean	SE			Mean	SE	Mean	SE
Alnus glutinosa	0.84 ^b	± 0.15	4	60.31	0.25	± 0.05	4.21 ^b	± 1.53
Fraxinus excelsior	3.05ª	± 0.40	1	59.01	0.36	± 0.14	12.17 ^{ab}	± 3.69
Fagus sylvatica	0.55 ^b	± 0.12	6	51.36	0.03	± 0.01	16.85 ^{ab}	± 3.69
Betula pendula	1.12 ^b	± 0.13	2	48.71	0.14	± 0.05	10.08 ^{ab}	± 2.13
Castanea sativa	0.45 ^b	± 0.09	7	36.91	0.07	± 0.04	5.56 ^b	± 2.81
Quercus robur	0.62 ^b	± 0.29	5	49.10	0.12	± 0.07	7.30 ^{ab}	± 2.51
Acer								
pseudplatanus	0.87 ^b	± 0.28	3	42.88	0.08	± 0.06	37.19ª	± 16.73
0.1–0.2 m								
Alnus glutinosa	0.26	± 0.07	7	19.04	0.15	± 0.05	3.27 ^b	± 1.92
Fraxinus excelsior	1.22	±0.31	1	23.56	0.11	± 0.03	15.16 ^{ab}	± 4.73
Fagus sylvatica	0.35	± 0.11	6	32.45	0.05	± 0.02	6.60 ^b	± 3.76
Betula pendula	0.74	± 0.08	2	31.99	0.06	± 0.02	14.05 ^{ab}	± 2.42
Castanea sativa	0.41	± 0.10	4	33.62	0.17	± 0.06	1.05 ^b	± 0.40
Quercus robur	0.38	± 0.10	5	30.29	0.08	± 0.03	5.23 ^b	± 1.23
Acer								
pseudoplatanus	0.52	± 0.11	3	25.51	0.03	± 0.02	103.9ª	± 54.77
0.2–0.3 m								
Alnus glutinosa	0.29 ^{ab}	± 0.05	5	20.66	0.11	± 0.03	3.82	± 1.95
Fraxinus excelsior	0.90ª	± 0.32	1	17.43	0.11	± 0.06	10.67	± 2.73
Fagus sylvatica	0.17 ^b	± 0.04	7	16.18	0.02	± 0.00	8.96	± 2.80
Betula pendula	0.44 ^{ab}	± 0.06	3	19.30	0.08	± 0.01	6.95	± 1.86
Castanea sativa	0.36 ^{ab}	± 0.13	4	29.47	0.05	± 0.02	2.57	± 1.05

Quercus robur Acer	0.26 ^{ab}	± 0.04	6	20.61	0.09	± 0.03	3.78	± 1.05
pseudoplatanus	0.64ª	± 0.19	2	31.61	0.12	± 0.05	12.61	± 6.33
0–0.3 m								
Alnus glutinosa	1.39 ^b	± 0.26	4	N/A	0.51	± 0.11	3.43	± 1.20
Fraxinus excelsior	5.16ª	± 0.71	1	N/A	0.58	± 0.17	12.01	± 3.83
Fagus sylvatica	1.07 ^b	± 0.26	7	N/A	0.11	± 0.03	10.68	± 2.84
Betula pendula	2.30 ^{ab}	± 0.12	2	N/A	0.27	± 0.05	9.30	± 1.78
Castanea sativa	1.21 ^b	± 0.24	6	N/A	0.29	± 0.10	1.97	± 0.73
Quercus robur	1.26 ^b	± 0.34	5	N/A	0.30	± 0.09	4.57	±0.81
Acer								
pseudoplatanus	2.04 ^{ab}	± 0.56	3	N/A	0.23	± 0.07	14.82	± 6.65

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Table 4 Between-subject effects of species and depth on fine root traits including specific root length

632 (m g⁻¹), root area index (m² m⁻²), specific root surface area (m² kg⁻¹), root length density (cm cm⁻³) and

633 root tip density (× 10^3 m^{-2}).

		df	F-statistic	p
Species	Specific root length (m g ⁻¹)	6	21.825	<0.001
	Root area index (m ² m ⁻²)	6	22.757	<0.001
	Specific root surface area (m ² kg ⁻¹)	6	19.549	<0.001
	Root length density (cm cm ⁻³)	6	29.519	<0.001
	Root tip density (x 10 ² m ⁻²)	6	25.816	<0.001
Depth	Specific root length (m g ⁻¹)	2	76.572	<0.001
	Root area index (m ² m ⁻²)	2	22.994	<0.001
	Specific root surface area (m ² kg ⁻¹)	2	0.591	0.557
	Root length density (cm cm ⁻³)	2	39.089	<0.001
	Root tip density (x 10 ² m ⁻²)	2	57.046	<0.001
Species×Depth	Specific root length (m g ⁻¹)	12	0.395	0.961
	Root area index (m ² m ⁻²)	12	0.826	0.623
	Specific root surface area (m ² kg ⁻¹)	12	0.392	0.962
	Root length density (cm cm ⁻³)	12	0.852	0.598
	Root tip density (x 10 ² m ⁻²)	12	1.108	0.370

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635 **Table 5.** Fine root metrics (specific root length (m g⁻¹), root area index (m² m⁻²), specific root surface

area (m² kg⁻¹), root length density (cm cm⁻³) and root tip density (x 10^2 m⁻²) of seven tree species (*Alnus*

637 glutinosa, Fraxinus excelsior, Fagus sylvatica, Betula pendula, Castanea sativa, Quercus robur and Acer

pseudoplatanus) at three soil depths (0-0.1, 0.1-0.2, 0.2-0.3 m). SE = ±1 standard error. Superscript letters denote Tukey post hoc comparisons (*p* < 0.05) of

639 root traits within each soil depth.

Root trait	Depth	Alnus gl	lutiı	nosa	Fraxinus	s ex	celsior	Fagus	sylv	atica	Betulo	ı pe	endula	Castane	a si	ativa	Quercu	ıs ro	obur	Acer pseu	doj	olatanus
Specific	0-0.1	8.27 ^b	±	1.94	22.23ª	±	3.62	26.38ª	±	3.22	14.88 ^{ab}	±	1.58	13.43 ^{ab}	±	1.22	20.20 ^a	±	3.04	22.43ª	±	3.57
root	0.1-0.2	4.13 ^c	±	0.41	10.09 ^{ab}	±	0.45	13.45ª	±	3.85	6.36 ^{abc}	±	0.29	5.79 ^{bc}	±	0.83	9.88 ^{ab}	±	2.50	9.42 ^{ab}	±	0.38
length (m g⁻¹)	0.2-0.3	3.37 ^c	±	0.45	8.98 ^{ab}	±	0.73	11.78ª	±	1.66	5.35 ^{bc}	±	0.57	5.53 ^{bc}	±	0.95	9.31 ^{ab}	±	1.06	6.52 ^{ab}	±	1.12
Root area	0-0.1	0.88 ^b	±	0.27	6.02ª	±	0.86	0.96 ^b	±	0.26	1.27 ^b	±	0.19	0.51 ^b	±	0.09	0.78 ^b	±	0.26	1.25 ^b	±	0.32
index (m ²	0.1-0.2	0.28 ^b	±	0.07	2.59ª	±	0.64	0.50 ^b	±	0.16	0.76 ^{ab}	±	0.11	0.47 ^b	±	0.10	0.45 ^b	±	0.09	0.70 ^b	±	0.17
m⁻²)	0.2-0.3	0.29 ^b	±	0.05	1.78ª	±	0.57	0.26 ^b	±	0.05	0.42 ^b	±	0.06	0.39 ^b	±	0.12	0.37 ^b	±	0.05	0.74 ^{ab}	±	0.20
Specific	0-0.1	10.29 ^c	±	1.87	19.40 ^a	±	0.41	16.97 ^{ab}	±	1.73	11.14 ^{bc}	±	0.78	11.58 ^{bc}	±	0.60	14.32 ^{abc}	±	1.36	14.90 ^{abc}	±	1.47
root	0.1-0.2	10.80 ^b	±	0.68	21.13ª	±	0.89	15.60 ^{ab}	±	1.96	10.17 ^b	±	0.36	11.59 ^b	±	1.28	13.74 ^b	±	2.74	13.17 ^b	±	0.66
surface area (m² kg⁻¹)	0.2-0.3	9.95 ^{cd}	±	0.70	20.15ª	±	1.30	15.92 ^{ab}	±	1.69	9.50 ^d	±	0.60	11.68 ^{bcd}	±	0.94	14.15 ^{abc}	±	0.85	11.92 ^{bcd}	±	1.27
Root	0-0.1	0.70 ^b	±	0.24	6.56ª	±	0.65	1.51 ^b	±	0.42	1.70 ^b	±	0.33	0.57 ^b	±	0.07	1.03 ^b	±	0.27	1.82 ^b	±	0.43
length	0.1-0.2	0.21 ^c	±	0.05	2.42ª	±	0.60	0.72 ^b	±	0.19	0.94 ^{ab}	±	0.15	0.43 ^{bc}	±	0.07	0.61 ^b	±	0.10	0.96 ^{ab}	±	0.20
density (cm cm ⁻³)	0.2-0.3	0.19 ^c	±	0.04	1.55ª	±	0.47	0.37 ^{bc}	±	0.06	0.46 ^{bc}	±	0.05	0.33 ^{bc}	±	0.07	0.48 ^{bc}	±	0.09	0.77 ^{ab}	±	0.19
Root tip density (x	0-0.1	242.89 ^{bc}	±	45.28	1275.01ª	±	199.30	515.07 ^{ab} c	±	127.84	625.53 ab	±	150.04	174.35 ^c	±	17.17	348.08 ^{bc}	±	88.43	528.29 ^{ab}	±	116.41
10 ² m ⁻²)	0.1-0.2	63.31 ^c	±	11.36	512.43ª	±	132.38	260.47 ^{ab}	±	64.56	307.72 ª	±	23.23	104.35 ^{bc}	±	14.62	205.66 ^{ab}	±	39.54	246.19 ^{ab}	±	36.84
	0.2-0.3	59.83°	±	9.99	314.58ª	±	84.47	130.93 ^{ab} c	±	17.09	137.32 ab	±	12.12	85.35 ^{bc}	±	16.00	157.04 ^{ab}	±	25.09	205.31ª	±	38.81

- 642 **Table 6.** Main effects of four contrasting soil textures' (Rendzic Leptosol, silty-clay loam limestone
- rich; Haplic Luvisol, silty-clay loam; Dystric Fluvic Cambisol, sandy silt loam; Dystric Gleysol, clay loam)
- 644 fine root biomass in three soil depths (0-0.1, 0.1-0.2, 0.2-0.3 m).

Factor	df	F	<i>p</i> -value
Depth	2	24.107	0.000
Soil class	3	6.394	0.002
Depth*Class	6	1.185	0.347

645 Figure legends

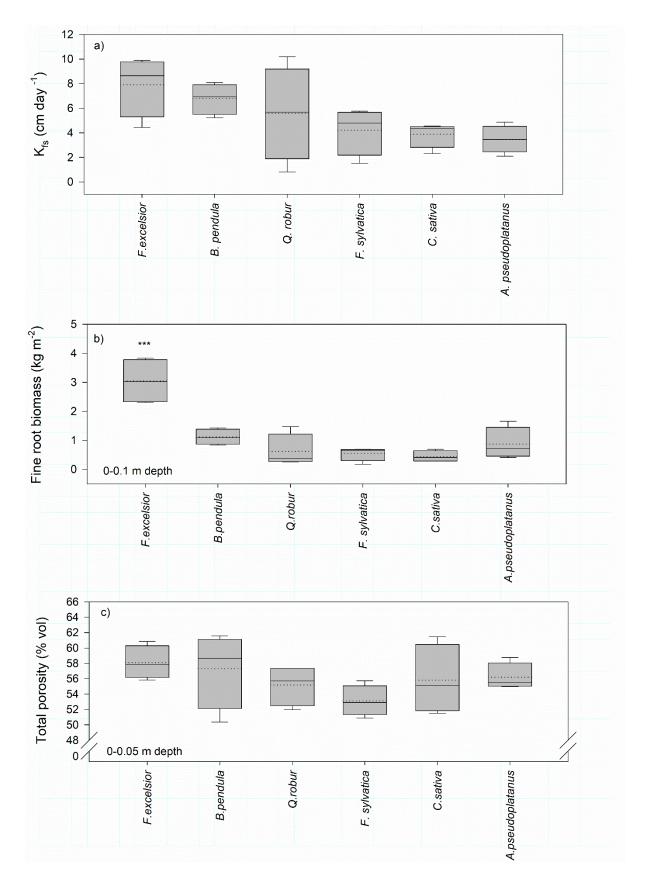


Fig. 1. Variation in soil and fine root properties amongst plots (n=4) of six tree species: (a) Surface field saturated hydraulic conductivity (K_{fs} ; cm day⁻¹), (b) fine root biomass (kg m⁻²) in the 0-0.1 m depth, (c)

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total soil porosity (% volume) calculated from cores (excluding stone fraction) taken from the 0-0.05 m depth. Data shown are mean (dashed horizontal line) and median (solid horizontal line). The boxes define quartiles and whiskers \pm one standard error. For fine root biomass, there was a species main effect p < 0.001. No statistically significant differences were found in K_{fs} or total porosity amongst species (p > 0.05). *Alnus glutinosa* is excluded from biomass analysis because the stand was in poor health, demonstrated by a large fraction of necromass amongst the fine roots.

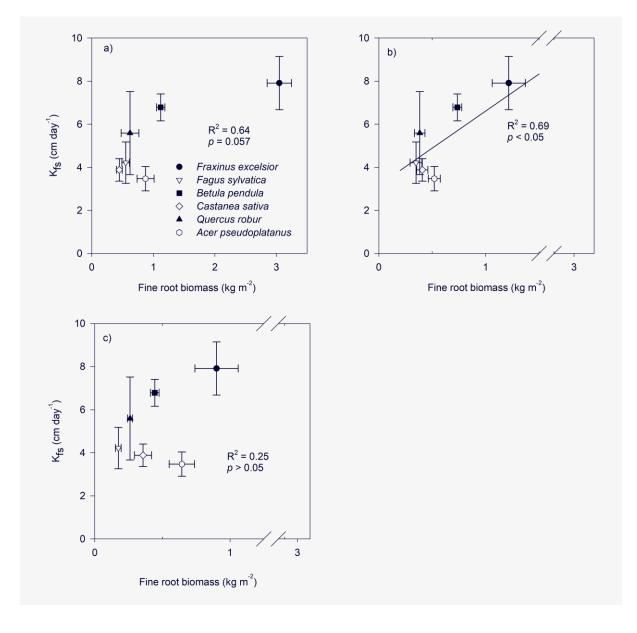




Fig. 2. Relationship between mean plot (n=4) surface field-saturated hydraulic conductivity (K_{fs} ; cm day⁻¹) and fine root biomass (kg m⁻²) for six species, *F. excelsior, F. sylvatica, B. pendula, C. sativa, Q.*

robur and *A. pseudoplatanus*, in the (a) 0-0.1 m, (b) 0.1-0.2 m and (c) 0.2-0.3 m soil depths. Data shown
are mean ± one standard error for each species. *Alnus glutinosa* is excluded from biomass analysis
because the stand was in poor health, demonstrated by a large fraction of necromass amongst the
fine roots.

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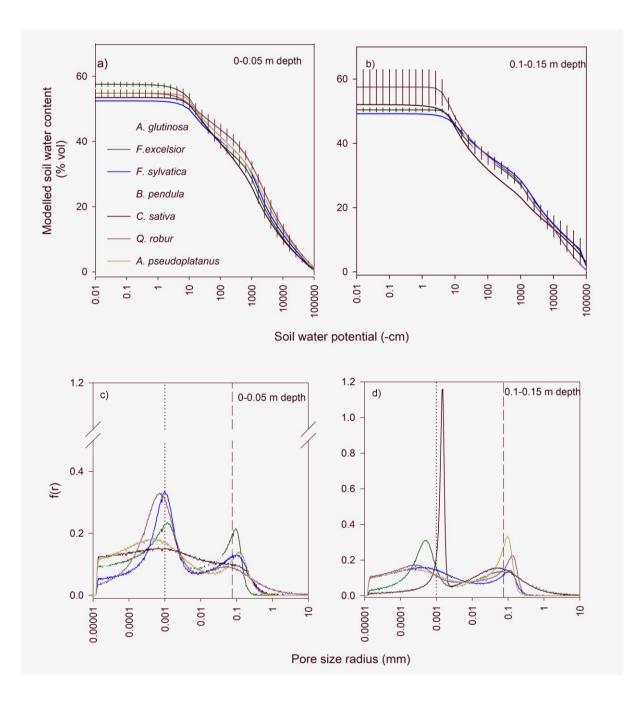
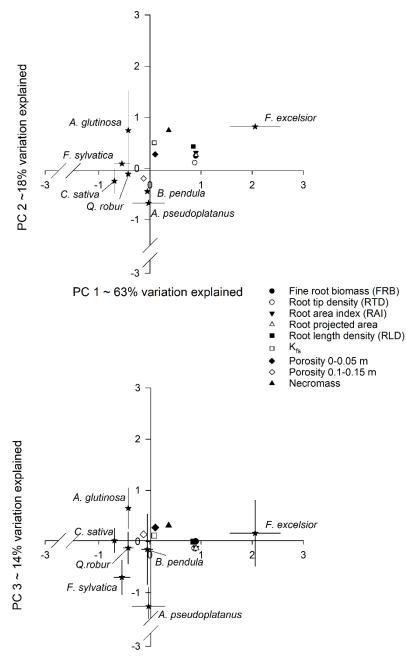


Fig. 3. Mean soil water retention curves for plots (n=4) of seven tree species in the (a) 0-0.05 m and
(b) 0.01-0.15 m depths. The data are modelled using the bimodal Fredlund-Xing PDI model using

666 measured soil water content and potential (HYPROP) data. Modelled effective pore-size radius 667 distribution (Blonquist et al., 2006), displayed on a common log scale, of the seven species in the (c) 668 0-0.05 m and (d) 0.1-0.15 m depths. The pore-size distribution (f(r)) represents the proportional 669 volume of the combined effective pore size radii. Values to the right of the dotted vertical line indicate 670 pore radius sizes where capillary forces dominate water movement (Kosugi et al., 2002). Values to the 671 right of the dashed vertical line indicate macropore radius sizes > 0.075 mm.



PC 1 ~ 63% variation explained

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Fig. 4. Principal component analysis examining the relationships between field saturated hydraulic
conductivity (K_{fs}), tree species (*A. glutinosa, F. excelsior, B. pendula, F. sylvatica, C. sativa, Q. robur* and *A. pseudoplatanus*), fine root morphological variables (root biomass, root tip number, root area index,
root projected area, root length density and necromass) and soil porosity (% volume) at two soil
depths (0-0.05 and 0.1-0.15 m). Error bars represent ± one standard error.

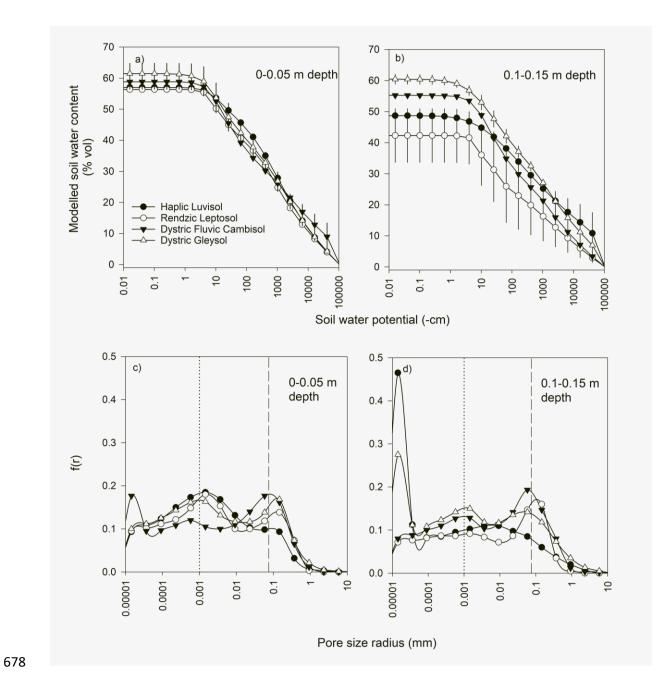
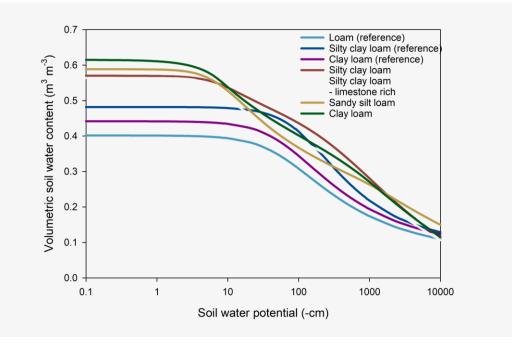


Fig. 5. Mean soil water retention curves for four sites with contrasting soil classes: Haplic Luvisol (silty clay loam); Rendzic Leptosol (silty clay loam - limestone rich); Dystric Fluvic Cambisol (sandy silt loam); and Dystric Gleysol (clay loam), at (a) 0-0.05 m and (b) 0.01-0.15 m depths. The data are modelled using the bimodal Fredlund-Xing PDI model (Fredlund and Xing, 1994) using measured soil water content (HYPROP) data. Modelled pore-size distribution (Blonquist et al., 2006) displayed on a common log scale from contrasting soil classes at (c) 0-0.05 m and (d) 0.1-0.15 m depths. The poresize distribution (f(r)) represents the proportional volume of the combined effective pore size radii.

- 686 Values to the right of the dotted vertical line indicate pore sizes where capillary forces dominate water
- 687 movement (Kosugi et al., 2002). Values to the right of the dashed vertical line indicate macropore pore
- 688 sizes > 0.075 mm. Values between the vertical lines indicate mesopores.

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Fig. 6. Soil water retention curves (SWRC) for the four soil textures used in our study: Haplic Luvisol (silty clay loam); Rendzic Leptosol (silty clay loam - limestone rich); Dystric Fluvic Cambisol (sandy silt loam); and Dystric Gleysol (clay loam), and modelled SWRC for three reference soil textures (loam, silty clay loam and clay loam) from the Rosetta modelling framework for pedotransfer functions (Schaap et al., 2001). pF, the decimal log of soil water potential (cm), describes the amount of force or suction required to extract water from the soil.