Fine root morphology of *Pinus pinaster* as affected by site fertility

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ABSTRACT

Fine roots are essential for nutrient uptake and the morphology of fine roots may adapt to variations in environmental conditions such as the availability of nutrients and water. Our objective was to investigate how fine root morphology of *Pinus pinaster* in the Landes of Gascony (France) was affected by site fertility. Our hypothesis was that site fertility differs between stands having different understory vegetation and that these differences would affect fine root morphology of *Pinus pinaster* fine roots. Data on specific root lengths (SRL) from top soil layers (litter, 0–15 and 15–30 cm mineral soil) were used as an evaluator of fine root morphology. Six treatments from a fertilisation trial were compared with data from 27 natural sites with contrasting understory. The results showed an overall range of SRL in litter and mineral soil of 11.8–34.6 in the fertilisation trial and of 4.8–32.6 m g^{-1} for the natural sites. The highest values occurred for increased levels of nutrients and or water (in the fertilisation experiment) as well as in a natural stand with *Ulex europeaus* (a nitrogen fixing species) as dominant understory and in a stand with mixed understory. The lowest values occurred consistently in *Calluna vulgaris* and *Erica cinerea* dominated stands. *Molinia* and *Pteridium* dominated stands show intermediate to high values. We conclude that differences in understory can be indicator of or contribute to differences in site fertility, which lead to morphological adaptations of the fine root system of overstory forest trees.
KEYWORDS: fine root morphology, *Pinus pinaster*, site fertility specific root length, understory

INTRODUCTION

Tree roots have diverse functions such as anchorage, storage and nutrient uptake (Fitter 2002, Jackson et al. 1997, Danjon et al. 2005) of which the latter is essentially fulfilled by the finest fraction. Fine roots and their symbiotic partners represent only a small proportion of total biomass (Brunner and Godbold 2007), but drain a much larger part of total NPP (Jackson et al. 1997). While fine roots and hyphae supply nutrients and water to the tree, in turn their respiration and turnover result in C fluxes to soils, as well as in belowground recycling of mineral nutrients (Brunner and Godbold 2007). Fine roots have been evaluated as indicators of environmental quality or change based on aspects such as fine root biomass, specific root length, the calcium to aluminium ratio, root electrolyte leakage, and ectomycorrhizal community composition (Godbold and Brunner 2007). Fine root systems may adapt to their environment in various ways: i) vertical niche differentiation in case of interspecies competition (Bolte and Villanueva 2006, Casper and Jackson 1997); ii) concentrated growth through root channels in case of physical or chemical barriers in the soil (van Noordwijk et al. 1991, Nambiar and Sands 1992); iii) physiological plasticity so that roots in optimal nutrient patches or layers can have a higher uptake rate per unit of root length (Göransson et al. 2006); or iv) morphological plasticity by adapting root morphology to local conditions and by directing growth into favourable micro-sites (Jackson et al. 1990, Robinson 1994, Hodge 2004). The optimum morphology and physiology of fine roots will depend on how a plant can best invest carbon to optimize benefits under given environmental conditions (Chapin et al. 1987, Eissenstat 1992, Ryser 2006). Roots of fast-growing species, constructed for fast growth into new soil areas, are suggested to possess a higher specific root length (SRL) compared to slower growing species (George et al. 1997, Comas et al. 2002). In a meta-analysis of different European tree species, SRL was also shown to vary with site and growth conditions, suggesting that this parameter could be a suitable indicator of environmental conditions (Ostonen et al. 2007). In the Landes of Gascony in southwest France maritime pine (*Pinus pinaster*) is intensively managed as mono specific forest stands. The species has a low leaf area index at any stage of stand rotation, so that understory species can develop and maintain themselves even after canopy closure. Soils are sandy podzols and poor in weatherable minerals (Augusto et al. 2006), so that mineral nutrient levels are poor and fertility is largely confined to organic top layers. Understory species contribute significantly to stand biomass and occur in patches as dominant species below overstory pines. We hypothesized that understory affects site fertility or indicates differences in inherent site fertility. Our objective was to investigate how fine root morphology of *Pinus pinaster* in this forest range varied with site fertility.

METHODS

Fine roots (diameter <2 mm) of *Pinus pinaster* were sampled in 2004–2006 and 2008 in 27 forest stands and 6 experimental treatments of a fertilisation trial (Table 1). Sampling depth was down to 120 cm (or more) in the 2004–2006 samplings and the following fine root parameters were assessed: fine root biomass (FRB), fine root length density (FRLD), fine root area desnity (FRAD), specific root length (SRL), root diameter and the number of ectomycorrhizal root tips per unit of root length (ECM-RL; Achat et al. 2008, Bakker et al. 2009). Based on this, and with the objective to study overstory–understory relationships, fine roots of Pinus and of understory species were sampled in summer 2008 down to 30 cm of soil depth. In the present work, we first present the general characteristics of fine roots of *Pinus pinaster*. Then we focus on the specific root lengths of Pinus from the 2004–2006 datasets and compare these with the values from the 2008 dataset. More in particular, specific root lengths in litter and 0-30 cm soil were evaluated with regards to dominating understory vegetation or applied fertilizers.

Table 1. Background of used datasets

Dataset	sampling	n° of sites	age (yr)	stand density[3]	treatment / understory
sustainable forestry[1]	2005-2006	8	26–56	150–584	different understory
fertilisation trial[2]	2005	6	13	680–914	Control, P, NPKCa, irrigation
understory project	2008	5	28–30	580–800	Erica cinerea
understory project	2008	5	12–37	267–1325*	Calluna vulgaris
understory project	2008	4	17–50	135–422	Pteridium aquilinum
understory project	2008	5	25–96	156–456	Molinia caerulea

[1] Achat et al. 2008 and unpublished; [2] Bakker et al. 2009; [3]only trees with diam ≥7 cm
* high stand density values related to high number of small understory pines

RESULTS AND DISCUSSIONS

The general characteristics of fine roots of *Pinus pinaster* based on the 2004–2006 datasets (8 natural stands and 6 stands from a fertilisation trial) are given in Table 2. This shows that the values of both datasets are in a comparable range, with somewhat lower FRB, FRLD, FRAD, root diameter and ECM-RL in the fertilisation trial relative to the other sites. In contrast, SRL values were slightly higher on average in the fertilisation trial. Highest values occurred for the two highest fertilisation levels, a site with *Ulex europeaus* (a nitrogen fixing species) as dominant understory and in a stand with mixed understory. In the fertilisation trial, compared with the control fine roots, increased nutrient supply resulted in a lower fine root biomass but the roots were finer. This agrees with the assumption that specific root lengths should be high at productive sites because fast growth requires fast and efficient acquisition of resources (Ryser 2006). The high specific root lengths in the fertilized treatments indicate that a larger proportion of the < 2 mm fraction commonly considered as fine roots fall in the finer root fraction (< 1 or < 0.5 mm diameter). This will have consequences on root uptake, respiration and turnover, because these processes differ among root diameter size fractions (Eissenstat and Yanai 1997, Pregitzer et al. 1998).

Table 2. Fine root (<2 mm diameter) averages for *Pinus pinaster* using soil cores

	FRB $g\ m^{-2}$		FRLD $cm\ cm^{-3}$		FRAD $cm^2\ cm^{-3}$	
layer	Fert_trial[1]	Sust_For[2]	Fert_trial[1]	Sust_For[2]	Fert_trial[1]	Sust_For[2]
litter	1–9	2–101	0.19–0.57	0.25–1.48	0.03–0.11	0.07–0.38
0-15 cm	42–121	19–178	0.33–0.86	0.34–2.64	0.06–0.15	0.05–0.39
15-30 cm	20–112	20–84	0.12–0.45	0.17–0.79	0.03–0.09	0.04–0.18
	SRL $m\ g^{-1}$		root diameter mm		ECM-RL tips m^{-1} root length	
layer	Fert_trial[1]	Sust_For[2]	Fert_trial[1]	Sust_For[2]	Fert_trial[1]	Sust_For[2]
litter	15.9–34.8	9.9–29.5	0.44–0.58	0.47–0.88	71–150	196–476
0-15 cm	10.5–19.7	8.5–17.1	0.55–0.61	0.46–0.89	174–242	203–406
15-30 cm	11.8–14.4	7.4–16.7	0.63–0.72	0.47–1.07	68–255	250–393

[1] dataset of Fertilisation trial: range for 6 treatment averages (each average based on n=16 values)
[2] dataset of sustainable forestry project: range from 8 stands (each average based on n=8–16 values)

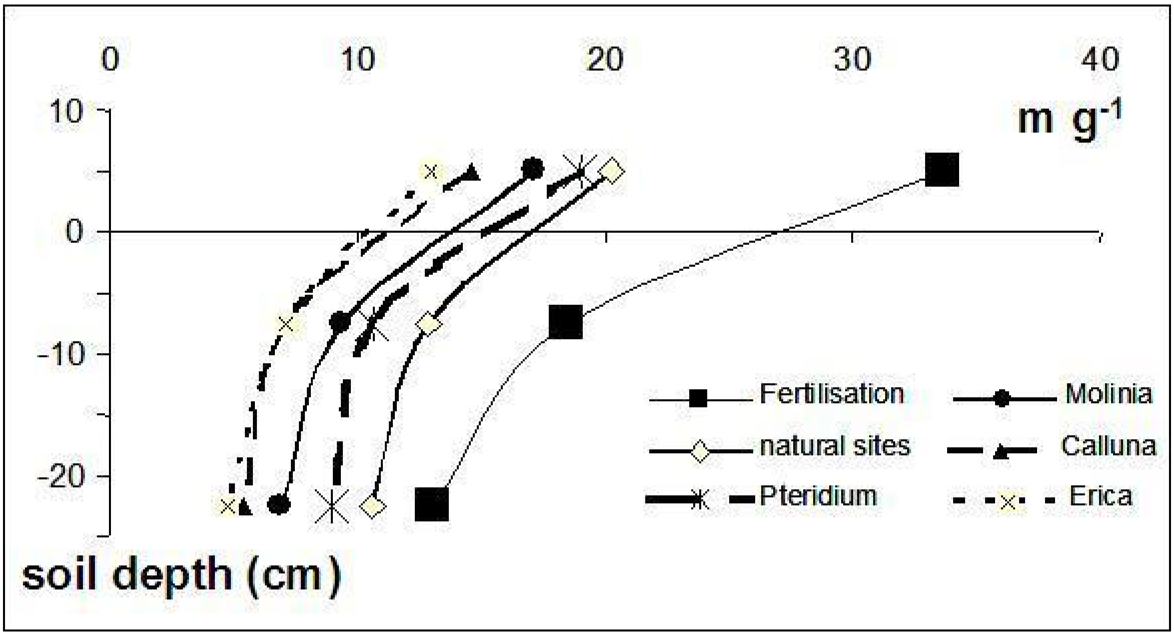

Figure 1. Specific root length of Pinus pinaster for litter and top soil

In Figure 1 the SRL data from the sustainable forestry dataset (natural sites; mean of 8 stand averages) are compared with the average of the highest fertilisation levels (mean of 2 treatment averages) and the averages for pine stands with four different understories (mean of 4 or 5 stand averages; n=19 stands). This shows that the high fertilizer treatments resulted in the highest SRL. Control values were similar to the average of the sustainable forestry dataset (data not shown).

The figure further indicates that under ericaceous understory (i.e dominated by *Erica cinerea* or *Calluna vulgaris*) *Pinus pinaster* has finer roots than under understory dominated by *Molinia caerulea* or *Pteridium aquilinum*. This finding could be related to the fact that ericaceous species produce organic matter which is exceptionally rich in phenolic compounds, many of which are highly fungi toxic and are known to inhibit the microbial decomposition of litter (Read et al. 2004). In contrast, litter of Molinia and Pteridium might be easier to decompose. Indeed, root densities on trench walls were lower in Erica dominated understories in the case of *Pinus pinaster* whereas Pinus roots were densely colonizing stools of *Molinia* (Achat et al. 2008). Overall, our results suggest that the sites differ in fertility (either due to understory or leading to differences in understory). Further work is warranted to explicitely investigate such relationships and to clarify whether this has consequences for nutrient uptake, root turnover and carbon balance.

REFERENCES

Achat DL, Bakker MR and P Trichet (2008) Rooting patterns and fine root biomass of *Pinus pinaster* assessed by trench wall and core methods. J For Res 13:165–175.

Augusto L, Badeau V, Arrouays D, Trichet P, Flot J L, Jolivet C and D Merzeau (2006) Caractérisation physico-chimique des sols à l'échelle d'une région naturelle à partir d'une compilation de données. Etude et Gestion des Sols 13:7–22.

Bakker MR, Jolicoeur E, Trichet P, Augusto L, Plassard C, Guinberteau J and D Loustau (2009). Adaptation of fine roots to annual fertilization and irrigation in a 13-year-old *Pinus pinaster* stand. Tree Physiol 29:229–238.

Brunner I and DL Godbold (2007) Roots in a changing world. J For Res 12:78–82.

Chapin FS, Bloom AJ, Field CB and RH Waring (1987) Plant responses to multiple environmental factors. BioScience 37:49–57.

Comas LH, Bouma TJ and DM Eissenstat DM (2002) Linking root traits to potential growth rate in six temperate tree species. Oecologia 132:34–43.

Danjon F, Fourcaud T and D Bert (2005) Root architecture and wind-firmness of mature *Pinus pinaster*. New Phytol 168: 387–400.

Eissenstat DM (1992) Costs and benefits of constructing roots of small diameter. J. Plant Nutr 15:763–782.

Eissenstat DM and RD Yanai (1997) The ecology of root lifespan. Adv Ecol Res 27:1–63.

Fitter AH (2002) Characteristics and functions of root systems. In: Weisel Y, Eshel A, Kafkafi U (eds) Plant roots: the hidden half. 3rd edn. Marcel Dekker, New York, pp 15–32.

George E, Seith B, Schaeffer C and H Marschner (1997) Responses of *Picea*, *Pinus* and *Pseudotsuga* roots to heterogeneous nutrient distribution in soil. Tree Physiol 17:39–45.

Godbold DL and I Brunner (2007) The platform for European root science, COST action E38: An introduction and overview. Plant Biosyst 141:390–393.

Göransson H, Wallander H, Ingerslev M and U Rosengren (2006) Estimating potential nutrient uptake from different soil depths of *Quercus robur*, *Fagus sylvatica*, and *Picea abies*. Plant Soil 286:87–97.

Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. New Phytol 162:9–24.

Jackson RB, Manwaring JH and MM Caldwell (1990) Rapid physiological adjustment of roots to localized soil enrichment. Nature 344:58–60.

Jackson RB, Mooney HA and ED Schulze (1997) A global budget for fine root biomass, surface area, and nutrient contents. Proc Natl Acad Sci USA 94:7362–7366.

Nambiar EKS and R Sands R (1992) Effects of compaction and simulated root channels in the subsoil on root development, water uptake and growth of radiata pine. Tree Physiol 10:297–306.

van Noordwijk M, Widianto, Heinen M and K Hairiah (1991) Old tree root channels in acid soils in the humid tropics: important for crop root penetration, water infiltration and nitrogen management. Plant Soil 134:37–44

Ostonen I, Püttsepp Ü, Biel C, Alberton O, Bakker MR, Lõhmus K, Majdi H, Metcalfe D, Olsthoorn AFM, Pronk A, Vanguelova E, Weih M and I Brunner (2007). Specific root length as an indicator of environmental change. Plant Biosyst 141:424–442.

Pregitzer KS, Laskowski MJ, Burton AJ, Lessard VC and DR Zak (1998) Variations in sugar maple root respiration with root diameter and soil depth. Tree Physiol 18:665–670.

Read DJ, Leake JR, Perez-Moreno J (2004) Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. Can J Bot 82:1243–1263

Robinson DA (1994) The response of plants to non-uniform supplies of nutrients. New Phytol 127:635–674

Ryser P (2006) The mysterious root length. Plant Soil 286:1–6.