



Unusual fine root distributions of two deciduous tree species in southern France: What consequences for modelling of tree root dynamics?

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Abstract

The spatial distribution of fine roots of two deciduous tree species was investigated in contrasting growing conditions in southern France. Hybrid walnut trees (*Juglans regia*×*nigra* cv. NG23) and hybrid poplars (*Populus euramericana* cv. I214) were both cultivated with or without annual winter intercrops for 10 years on deep alluvial soils. Soil samples for measuring the fine root distribution of both trees and crops were obtained by soil coring down to 3-m depth at several distances and orientations from the tree trunk. The distribution of live fine roots from walnut and poplar trees was patchy and sometimes unexpected. In the tree-only stands, fine root profiles followed the expected pattern, as fine root density decreased with increasing depth and distance from the tree trunk. However, many fine root profiles under intercropped trees were uniform with depth, and some inverse profiles were observed. These distributions may result from a high degree of plasticity of tree root systems to sense and adapt to fluctuating and heterogeneous soil conditions. The distortion of the tree root system was more pronounced for the walnut trees that only partially explored the soil volume: in the tree-only stand, the walnut rooting pattern was very superficial, but in the intercropped stand walnut trees developed a deep and dense fine root network below the crop rooting zone. The larger poplars explored the whole available soil volume, but the intercrop significantly displaced the root density from the topsoil to layers below 1 m depth. Most tree root growth models assume a decreasing fine root density with depth and distance from the tree stem. These models would not predict correctly tree–tree and tree–understorey competition for water and nutrients in 3D heterogeneous soil conditions that prevail under low-density tree stands. To account for the integrated response of tree root systems to such transient gradients in soils, we need a dynamic model that would allow for both genotypic plasticity and transient environmental local soil conditions.

Introduction

Many ecological, hydrological and biogeochemical processes are strongly dependent on fine root distribution (Fitter, 2002; Hutchings and John, 2003). Fine roots are the pathway for water and nutrient uptake by plants, but they are also a

prominent sink for carbon acquired by plant communities (Canadell et al., 1996). Root distribution is of special importance in the field of both modelling and applied research as it is either a predicted or a forcing variable of most ecological and hydrological models (Caldwell and Richards, 1986; De Willigen et al., 2002). Although fine root distribution data are essential model inputs, their availability is very limited (Hutchings and John, 2003; Huxley, 1999), especially

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for perennial plants such as trees with deep rooting patterns (Livesley et al., 2000; van Noordwijk et al., 1996). *In situ* root profile characterisation is laborious and time consuming, and sampling strategies should be optimised (Bengough et al., 2000). As a consequence, most fine root profiles characterisations are limited to the top layers of the soil, leaving root processes in deeper soil horizons undocumented. In mixed cropping systems, knowledge of the spatial distribution of the different root systems is required to understand the interaction between plant species (Gregory, 1996; van Noordwijk et al., 1996).

Models of root system growth often simulate separately the maximum root depth and the root length density, and incorporate controls by local soil conditions such as water content, nitrogen content, soil temperature, soil strength or aluminium toxicity on both processes (Pagès et al., 2000). Such models were essentially applied to annual plants, and usually predict a distribution of monotonic decrease of root density with soil depth. Distorted profiles may be obtained when the model incorporates controls of local soil conditions on root proliferation, but the trend of a declining root length density with depth and/or distance from the stem is usually maintained.

Dynamic tree root growth models are very scarce. Balandier et al. (2000) and Perttunen et al. (2001) proposed mechanistic models to simulate the growth of an individual tree but they did not consider below-ground processes. Most (if not all) forest growth models reviewed by Porté and Bartelink (2002) and carbon-based models of individual tree growth reviewed by Le Roux et al. (2001) also simulate only above-ground processes. Some detailed multi-layer dynamic soil chemistry models such as the SAFE model (Martinson et al., 2005) include a static description of the tree root profiles, but fail to include a dynamic of the fine roots over time linked to their activity. The only tree root growth models available are likely those included in the two biophysical agroforestry models HyPAR (Mobbs et al., 1999) and WaNuLCAS (van Noordwijk and Lusiana, 2000). Both models assume a negative exponential decrease of root distribution with lateral and vertical distance from the tree trunk. In these models, the size (total root length or mass) of the root system develops over time. However, the rooted soil volume and the distribution of both coarse and fine roots still

follow the assumed exponential decline. Some levels of controls by local soil conditions were however introduced in WaNuLCAS (van Noordwijk and Lusiana, 2000).

The architectural plasticity of a plant root system is defined as its ability to adjust to a dynamically heterogeneous soil environment (Huxley, 1999). Root systems are continuously adapting to modifications of their environment (Doussan et al., 2003; Robinson et al., 2003). Although root distribution patterns (such as deep/shallow or narrow/wide types) are valid at a species or genotype level, the actual root pattern is obviously the result of genotype \times environment interactions (van Noordwijk et al., 1996). The heterogeneity of the soil environment may be both vertical (usually as the consequence of the edaphic structure) and horizontal (usually as the consequence of the activity of competing plants).

In this paper, we present the fine root distribution of two temperate deciduous tree species (hybrid walnuts and hybrid poplars) grown on deep alluvial soils in southern France either in pure stands (forestry), or in mixture with an annual crop (agroforestry). Both tree species grew in heterogeneous soil conditions as the result of both vertical variability in soil texture and horizontal variability due to crop competition. Soil samples for measuring the fine root distribution were obtained by soil coring down to 3 m soil depth at several distances and orientations from the tree trunk using a homemade corer. The two following hypotheses were assessed in this paper: trees grown in association with annual winter crops in a Mediterranean climate develop a different rooting pattern as compared to trees grown in pure forestry stands; the modification of the rooting profiles is not limited to the mechanically disturbed top soil layers.

Material and method

Site and plot description

The experimental walnut plantation is located at the Restinclières farm, 15 km North of Montpellier city, France (Longitude 4°1' E, Latitude 43°43' N, elevation 54 m a.s.l.). The climate is sub-humid Mediterranean with an average

temperature of 14.5° C and an average annual rainfall of 951 mm (years 1996–2003). It features a typical Mediterranean low rainfall total during the tree growing months. Potential Evapotranspiration (PET) is higher than rainfall during 6 months (from March to August), and during the main growing season of the trees from May to August, the average rainfall is 183 mm while the average PET is 587 mm. The soil is a silty deep alluvial fluvisol (25% clay and 60% silt) (Dupraz et al., 1999).

The 12.5 ha hybrid walnut plantation includes two forestry control plots without intercropping (walnut trees at 7 m × 7 m spacing), and three agroforestry alley-cropping plots (13 m × 4 m spacing). All walnut trees were planted in February 1995 and intercropped since then with the following crop rotation: durum wheat for two or three years and a break crop that was rapeseed in 1998 and 2001. Soil tillage comprises a summer superficial stubble ploughing after the crop harvest, and a soil preparation by ploughing (20 cm depth) or disking (10 cm depth) before sowing in November. Ploughing was preferred during the first years, but was replaced by disking when the farmers realised that ploughing was not convenient in the alleys (deep furrow on one side that prevented to prepare a flat soil for seedling next to the trees). During the first 5 years, the farmers applied also a summer sub-soiling to 30 cm depth to favour water infiltration. Sub-soiling during the first years and soil ploughing each year act as tree root 'pruning' in the top 20–30 cm of soil in the alleys. This root study was performed in two adjacent blocks (forestry and agroforestry) with North–South tree rows.

The experimental poplar site is located in the Vézénobres township (Longitude 4°9' E, Latitude 44°2' N, elevation 138 m a.s.l.) 70 km North-East of Montpellier, France. The soil is a sandy alluvial fluvisol with 8% clay, 42% silt, and 50% sand, but pure sand and gravel layers occur at different depths in the profile (at about 1.1–1.3 m and 2.5–2.9 m soil depth). The climate is sub-humid Mediterranean with an average temperature of 14.8 °C and an average annual rainfall of 1172 mm (year 1996–2003). PET is higher than rainfall during 5 months (from April to August), and during the main growing season of the trees from May to August, the average rainfall is 267 mm while the average PET is 580 mm.

The 4.3 ha poplar plantation was planted in year 1996 with the I-214 clone, and is divided in two blocks with three plots: an agroforestry, a forestry and a pure crop plot. The crop is durum wheat with fallow every 3 or 4 years. Simplified soil preparation is done by disking to 10 cm depth to prepare the seed bed for the intercrop. All the poplars were pruned up to 6 m. The root study was performed in both the forestry and agroforestry plots.

Soil core sampling

We used the soil coring method (van Noordwijk et al., 2000) with an 8.5 cm diameter and 1-m long auger (Eijkelkamp, Giesbeek, NL). Soil coring activities were performed in several occasions during the year 2002–2004. For the first 2 years, we used an electrically powered percussion hammer (Makita HM 1800, Eijkelkamp) to drive the auger into the soil to a depth of 2 m. However, this was difficult as the system was designed to work down to only 1 m. In 2004, we used a micro caterpillar driller and we successfully cored down to 3 m depth. We built a new auger more resistant and with a non-removable cutting shoe, as recollecting the cutting shoe at the bottom of the pit was a serious difficulty. Soil coring was difficult in summer especially at Restinclières, as dry silty soils are extremely hard to core; as a consequence, no measurements were obtained for walnuts in summer. During the 3-year period, 10 walnut trees (8 in agroforestry, 2 in forestry) and fourteen poplar trees (9 in agroforestry, 5 in forestry) were sampled (Table 1). The average height of the trees was 7 and 20 m in 2003 for the walnuts and poplars respectively, and the sampled trees were representative of the mean size distribution.

For each tree, soil coring was performed at different positions on two transects: on the tree plantation row, and on the tree–crop interface (Figure 1). In 2002, the sampling was very intensive (16 positions per tree). The results showed that we could reduce the sampling intensity, and in 2003 and 2004, we cored only four positions per tree. The sampling scheme is basically the same for walnut trees and poplars. The distances are slightly different to take into account the differences in distances between tree rows (13 m for walnuts, and 16 m for poplars) and the width of

Table 1. Description of the experimental plots indicating the season and year of soil core sampling and the dimensions of the selected trees

Plot	Area (ha)	Tree-tree distance in tree row (m)	Distance between tree rows (m)	Season and year of soil coring	Number of trees	Average tree height (m)	Depth of soil coring (m)
<i>Walnut</i>							
Agroforestry	2.3	4	13	Spring 2002	2	5.98	2
				Spring 2003	3	7.98	2
				Autumn 2004	3	7.68	3
				Autumn 2004	2	6.31	3
Forestry	1.85	7	7	Autumn 2004	2	6.31	3
<i>Poplar</i>							
Agroforestry	2.56	4	16	Summer 2003	1	21.2	2
				Spring 2004	2	19.3	3
				Summer 2004	4	20.3	3
				Autumn 2004	2	19.5	3
				Spring 2004	1	21.2	3
				Summer 2004	2	19.6	3
				Autumn 2004	2	19.4	3
				Autumn 2004	2	19.4	3
Forestry	0.94	7	7	Spring 2004	1	21.2	3
				Summer 2004	2	19.6	3
				Autumn 2004	2	19.4	3

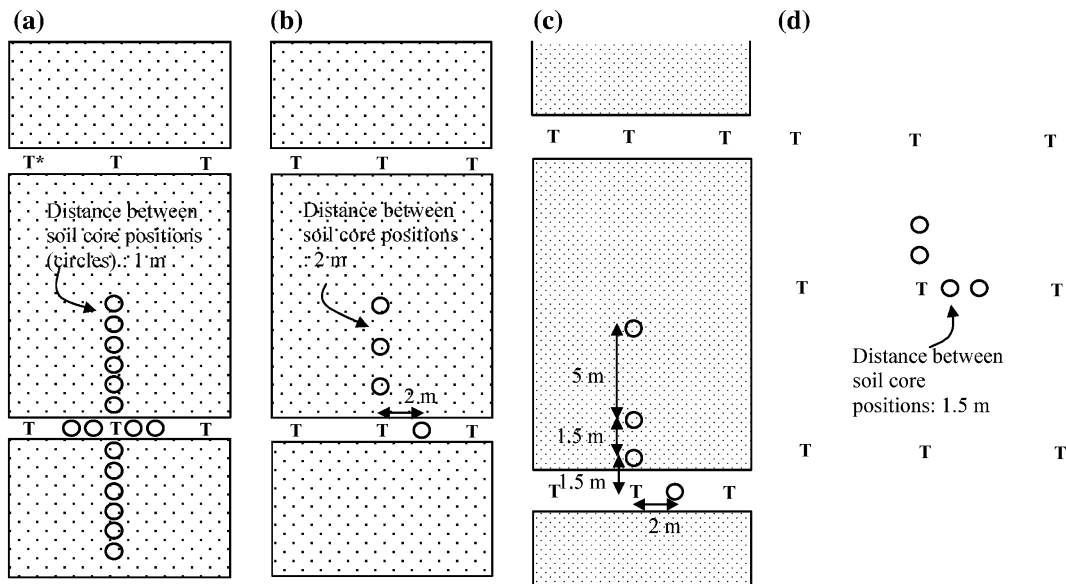


Figure 1. Soil coring positions in the different agroforestry and forestry plots: (a) walnut agroforestry plot in 2002; (b) walnut agroforestry plot in 2003 and 2004. (c) Poplar agroforestry plots in 2003 and 2004. (d) Forestry plots of both tree species in 2004.

the cropped alley. The tree-crop transect included three positions: one next to the tree under the tree canopy, one at the middle of the cropped alley, and one in between the two positions, close to the border of the canopy projection in 2003. The distances from the tree trunk were 2, 4 and 6 m from the tree trunk in the walnut plot, and 1.5, 3 and 8 m in the poplar plots.

Soil core analysis and root length determination

The soil cores were analysed with the core-break method (Baldwin et al., 1971; Drew and Saker, 1980; van Noordwijk et al., 2000). During summer, the sandy soil of the poplar trial was occasionally too dry to allow breaking of the cores, as such all the roots on the sample were collected.

For the core-break method, each 1-m soil core was divided in five 20 cm long sub-cores with a knife. Each sub-core was then broken by hand into two parts, next to the middle, and the number of fine (diameter < 2 mm) and coarse roots (diameter ≥ 2 mm) on both horizontal surfaces was recorded. Branched roots were counted as one as the core break method predicts fine root density from the number of root intersections with a soil plan (van Noordwijk et al., 2000). For the trees, only the number of live fine roots was later used in the analysis. Dead (brittle or rotten) roots were not included in the counts. Tree roots were distinguished from other plant roots by their morphology and colour. Walnut roots have a black cork and a yellow cylinder, while poplar roots have a light brown cork and a white cylinder. The counting process was less easy for the poplars than for the walnuts: the roots of durum wheat and weeds (mainly *Bromus* sp., *Lolium rigidum*, and *Avena fatua* L.) are white in colour and have a different morphology. Differentiating roots of trees from roots of wheat and weeds was easier when all the roots were collected.

The measurement of durum wheat roots was conducted in March and April 2002 (150 days after sowing, heading stage, Grazzia variety) at Restinclières and in April 2004 (130 days after sowing, heading stage, Allure variety) at Vézénobres. At the other coring dates, the wheat was not measured, as it had been harvested.

We calibrated the core-break method with 18, 19, and 9 samples for walnut, poplar, and wheat, respectively. Samples representing the full range of root counts were selected from different soil depths. For the durum wheat crop, we assumed that the same calibration could be used for the two different varieties. The required number of samples was less because the roots of wheat were very regularly distributed in the soil, resulting in a good relationship between counts and densities. Two sieves with 2×2 mm and 1×1 mm mesh sizes were used in the washing process to avoid losing roots. Total root length per sample was measured with an image analysis software (OPTIMAS Corporation, Washington, USA). The relationship between the number of root intersection per square meter of a horizontal plane (N_{root} , m^{-2}) and the length of root per soil volume (L_{rv} , km m^{-3}) is usually $L_{\text{rv}} = 0.002 \cdot X \cdot N_{\text{root}}$, where the calibration factor X differs from 1 for preferentially

oriented roots (van Noordwijk et al., 2000). For the soil cores with all roots collected (i.e. for poplars in summer), the dry fine root biomass was converted into root length using a specific root length (SRL, m g^{-1}) obtained on 59 samples collected in spring (19 samples) and summer (40 samples) at different soil depths (0–2.5 m). The measured SRL value was 18.5 m g^{-1} ($\pm 2.5 \text{ m g}^{-1}$) without significant difference between the two seasons (18.1 m g^{-1} and 18.8 m g^{-1} in spring and summer, respectively). Our estimates refer to fine roots with a diameter in the range 0–2 mm. Coleman et al. (2000) reported a SRL value of 56.6 m g^{-1} for hybrid poplar (*Populus tristis* × *P. balsamifera* cv 'Tristis no. 1') but the fine roots collected were limited to the 0–0.5 mm range.

Data analysis and presentation

For walnut agroforestry trees, data sets obtained in 2002 and 2003 were limited to the first 2 m. Data sets obtained in 2004 included the first 3 m. We analysed separately the full 3 m root profiles and the partial 2 m root profiles. For poplars, few soil cores were taken in summer 2003 and most soil cores were obtained in 2004 (Table 1). In some cases, the depth reached by the soil corer was less than 3 m from the soil surface because of difficulties to penetrate the deep gravel layers. Among the 52 profiles sampled during the year 2004, only 18 (i.e. 34%) were complete down to 3 m soil depth. In many cases, the core sampling was stopped at 2–2.4 m depth (17 profiles, 33%) or at 2.4–2.8 m depth (17 profiles, 33%) to avoid serious damage to the auger. The depth of the gravel horizon was generally observed below 2.5 m soil depth. We hardly found any roots in the deep gravel layers of the complete profiles, and we therefore assumed that there were no roots in the missing core segments in the gravel or below the deep gravel layer. We obtained a similar number of complete profiles in agroforestry (10 from 32 sampled profiles) and forestry plots (8 from 20 sampled profiles). To analyse statistically the vertical root distribution patterns of the trees, the depth of 50% and 90% cumulative root length (d_{50} and d_{90}) were calculated by fitting the logistic-type equation (Silva and Rego, 2003) to the observed cumulative root fractions (Y_r):

$$Y_r = \frac{1}{1 + \left(\frac{\text{MaxD}-D}{a^b D}\right)^b}$$

where a and b are the model parameters, D is soil depth (cm), and MaxD is the maximum depth of the studied profile (200 or 300 cm). The depths corresponding to 50% and 90% of the cumulative root fraction ($Y_r=0.5$ and $Y_r=0.9$) are given by:

$$d_{50} = \frac{\text{MaxD}}{1 + a}$$

$$d_{90} = \frac{\text{MaxD}}{1 + a^*(0.11)^{\frac{1}{b}}}$$

The model was able to explain between 95 and 99% of the variance of the observed cumulated distributions. The d_{50} and d_{90} values could be considered independent as we always sampled different trees when repeating the sampling at different seasons or years. We deliberately never applied sequential coring on the same tree, to avoid any bias due to the disturbance induced by the previous coring at the sampling positions. We compared the averages of both d_{50} and d_{90} values between systems (forestry vs. agroforestry) and between zones (tree row vs. crop zone) with two-tailed t -tests. For these comparisons, the effect of distance from the tree trunk and season were confounded. A Kolmogorov–Smirnov test was used to check the normality of the distributions of d_{50} and d_{90} values for each level of the classification factors. The null hypothesis (the samples follow a normal distribution) was never rejected. For poplars, we had more replications and we could perform an additional analysis of variance to test the effect of the distance from the tree row and of the season of the year. The interaction between the two factors was not estimated due to the low number of replications for each distance in each season (for some combinations, the number of sampled profiles was less than five). The significant differences between the levels of each factor were checked with the Duncan's test. The two-tailed t -test was also used for the between-species comparison both for forestry and agroforestry plots, after a Levene's test was used to check the homogeneity of variance between species both for d_{50} and d_{90} values. The homogeneity of variance was however

rejected for d_{50} values ($P < 0.05$), imposing to carry the t -test with the log-transformed values. The sample number was in most cases low so the statistical results should be viewed with caution. The figures of root distribution profiles display average L_{rv} values with standard errors. However, to compare rooting patterns with different total rooting lengths, the use of relative L_{rv} values was preferred. Each L_{rv} value was normalised by a scaling factor that was the total L_{rv} of the profile. The standard error of relative values is obtained by dividing the standard error of absolute values by the scaling factor (Papoulis, 1984). Using relative L_{rv} is an unbiased approach for averaging root profiles obtained at different phenological stages, as long as we are interested in root distributions (patterns of root density inside the rooted volume). The parameter optimisation of the logistic-type model and the statistical analyses were performed with the STATISTICA software (StatSoft Inc., Maison-Alfort, France).

Results

Calibration equation to estimate root length density

The intercepts of the two-parameters calibration equations ($L_{rv} = C + 0.002 * X * N_{root}$) were not significantly different from zero (two-tailed t -test with $\alpha = 0.05$). We therefore used the calibration equations without intercept. The r^2 values were 0.56 ($X = 0.61$), 0.32 ($X = 0.46$), and 0.74 ($X = 1.11$) for walnut, poplar and wheat, respectively, and no systematic pattern of prediction errors was observed (Figure 2). The three values of X were statistically different from zero (two-tailed t -test, $P < 0.001$). They were statistically different from 1.0 for the two tree species, but not for durum wheat ($\alpha = 0.05$). X values for walnut and poplar were found to be statistically different ($P = 0.03$), and we therefore used two different calibration equations to estimate the root length densities of the two tree species.

Walnut and poplar root distribution in agroforestry and forestry plot

Average 3 m deep root profiles for the two tree species were obtained by using all measures

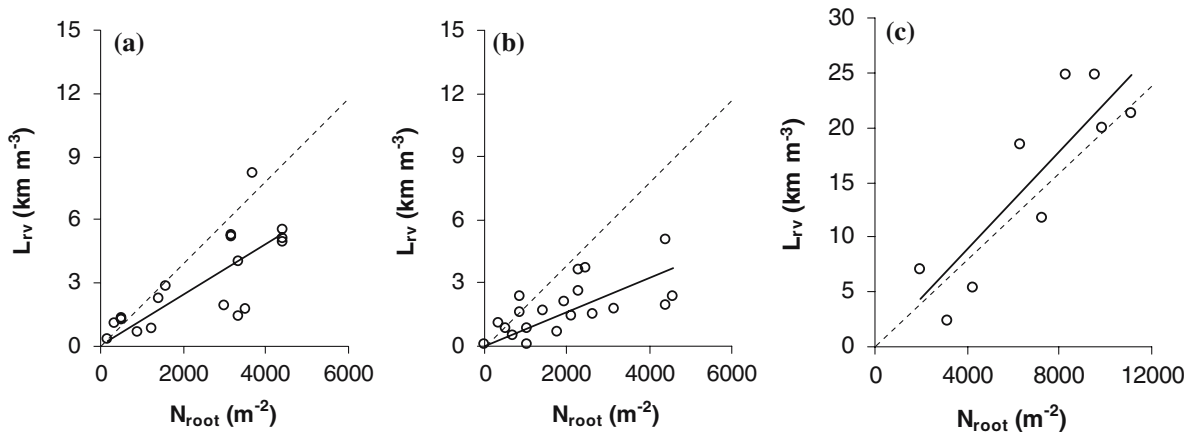


Figure 2. Linear calibration between root counts (N_{root}) and root length density (L_{tv}) for walnut (a), poplar (b), and durum wheat (c). The dashed lines represent the theoretical relationship if roots were randomly oriented in the soil volume.

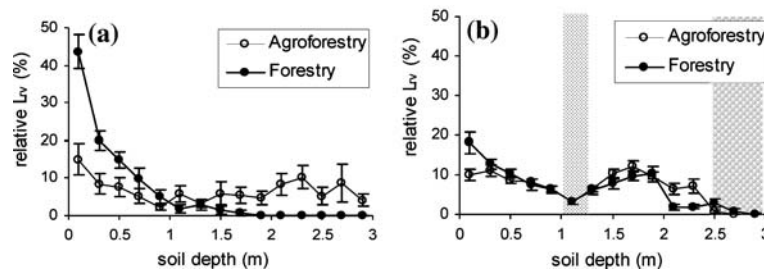


Figure 3. Root distribution profiles of walnut (a) and poplar (b) in the agroforestry and forestry plots measured in 2004. The vertical bars indicate one standard error. The shaded areas indicate the 1.1 m deep sand horizon and the 2.5–3 m deep gravel layer in the poplar stand.

regardless of the position of the soil cores in the plot (Figure 3). In the forestry walnut stand, no roots could be found deeper than 2 m soil depth (Figure 3a), and almost half of the fine roots were situated in the top 20 cm soil layer. The root density decreased very rapidly with soil depth. The root profile of intercropped walnut trees was different: the high root density in the topsoil was not observed, and roots were dense below 2 m depth. This resulted in an almost uniform and unusual root distribution pattern. Both d_{50} and d_{90} were very contrasted ($P < 0.001$) between forestry and agroforestry walnuts (Table 2). Almost all roots of forestry walnuts were situated above 0.9 m depth, while half the roots of intercropped walnuts were below 1.4 m.

The root profiles for poplars in the forestry and agroforestry stands shared a similar pattern (Figure 3b): L_{tv} decreased with depth in the first

meter until the 1.1 m deep sandy layer, then increased in the second meter of soil, and finally stopped at about 2.5 m depth, next to the gravel layer. However, d_{50} for forestry poplars (0.86 ± 0.08 m) was significantly ($P = 0.004$) shallower than that of agroforestry trees (1.21 ± 0.07 m). This indicates that the competition with winter crops also induced poplar root systems to grow into deeper layers. In forestry plots, both d_{50} and d_{90} of walnut trees were significantly shallower ($P < 0.001$) than those of poplar trees.

Spatial heterogeneity of root profiles within the walnut agroforestry stand

All data collected show a reduction of the relative L_{tv} in the top horizons in the cropped zone, along with an increase of the root proportion in the deeper horizons (between 1 and 2 m depth)

Table 2. The depths of 50% (d_{50}) and 90% (d_{90}) cumulated root length as indicators of the shape of the rooted profiles calculated for the system level (agroforestry – AF vs. forestry – F), the zone level (tree row – TR vs. cropped zone – CZ), and for the distance of soil core positions from the tree trunk in the cropped zone

Tree species	System	Year of soil coring	Zone	Distance from tree trunk (m)	Depth of sampled profiles (m)	d_{50} (m)	d_{90} (m)	Number of sampled profiles*
Walnut	AF	2002–2003	TR		2	0.42 ± 0.06	1.46 ± 0.08	11
	AF	2002–2003	CZ		2	0.81 ± 0.13	1.54 ± 0.14	11
	F	2004			3	0.27 ± 0.03	0.87 ± 0.11	8
	AF	2004			3	1.41 ± 0.24	2.48 ± 0.09	8
	AF	2004	TR		3	0.86 ± 0.17	2.30 ± 0.12	3
	AF	2004	CZ	2	3	1.29 ± 0.16	2.46 ± 0.10	3
	AF	2004	CZ	4	3	2.41 ± 0.16	2.80 ± 0.06	2
Poplar	F	2004			3	0.86 ± 0.08	1.94 ± 0.05	20
	AF	2004			3	1.21 ± 0.07	2.03 ± 0.04	32
	AF	2004	TR		3	0.96 ± 0.17	1.94 ± 0.11	8
	AF	2004	CZ	1.5	3	1.14 ± 0.10	2.05 ± 0.06	8
	AF	2004	CZ	3	3	1.28 ± 0.11	2.04 ± 0.06	8
	AF	2004	CZ	8	3	1.58 ± 0.08	2.13 ± 0.07	8

The levels of lower-scale experimental factors (season, position) were confounded when computing the average values for higher-scale classification factors (tree species, system, zone).

*Excluding the profiles that contained no roots (no walnut roots could be found at 4 m and 6 m distance in 2002 and 2003. In 2004, roots were found at 4 m distance, but not at 6 m distance).

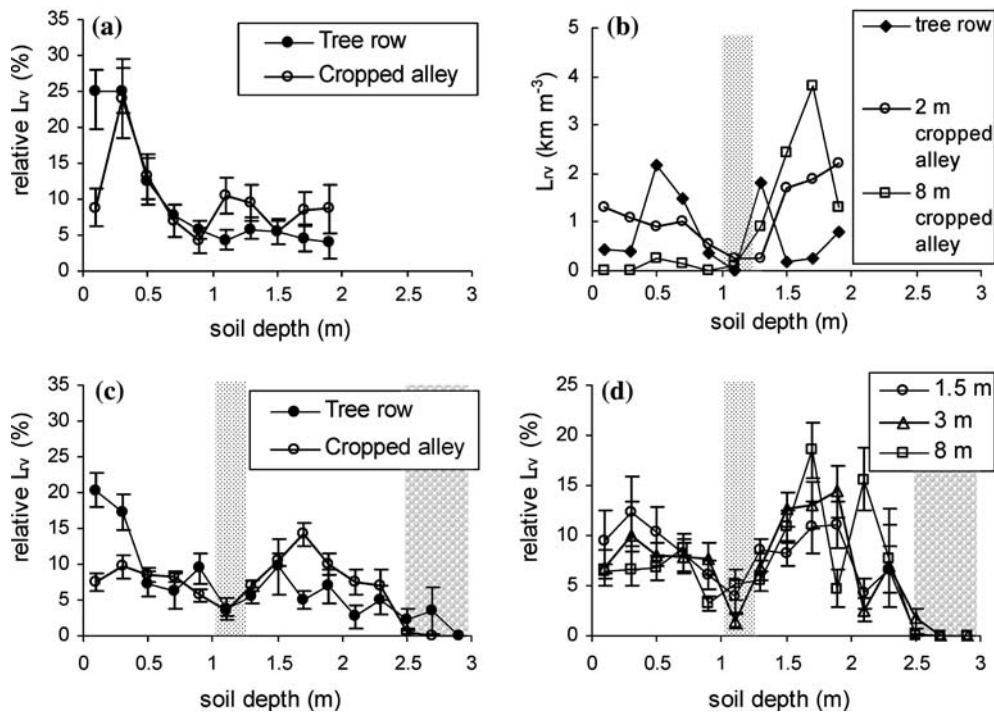


Figure 4. (a) Root distribution profiles of walnut trees with soil depth within tree row and in the cropped alley based on the root observations in year 2002–2003. (b) Fine roots in a poplar agroforestry stand in July 2003. (c) Root distribution profiles of poplar trees within tree row and in the cropped alley, and (d) at three distances from tree trunk in the cropped alley observed in 2004.

Table 3. Effect of the distance from the trunk and of the season on the shape of the rooting systems of poplars in an agroforestry system

Distance from the tree row (m)	D_{50} (m)	d_{90} (m)	Season	d_{50} (m)	d_{90} (m)
0 m (tree row)	1.02a	1.98a	Spring	1.33a	2.11a
1.5 m (crop zone)	1.20ab	2.10a	Summer	1.05b	1.91b
3 m (crop zone)	1.34abc	2.09a	Autumn	1.51a	2.23a
8 m (crop zone)	1.62c	2.16a			

The depths of 50% (d_{50}) and 90% (d_{90}) cumulated root length are compared with a Duncan's test ($\alpha=0.05$). Values with the same letter are not significantly different.

in 2002 and 2003 (Figure 4a), and down to 3 m depth in 2004 (data not shown). However, the patchy pattern of root density resulted in large standard deviations at a given depth and position. Based on the 2002 and 2003 data, d_{50} of walnut trees in the crop zone (0.81 ± 0.13 m) was deeper than within the tree row (0.42 ± 0.06 m) with $P=0.03$. In 2004, based on the root observations in the first 3 m depth, the average d_{50} was 0.86 m deep on the tree row, 1.29 m deep at 2 m distance and 2.41 m deep at 4 m distance in the cropped zone indicating a much deeper rooting system under the cropped zone. No walnut roots could be found at 4 m and 6 m (the middle of the cropped alley) distance in 2002 and 2003. In 2004, roots were found at 4 m distance, but not at 6 m distance indicating that the 7 m tall walnut trees did not explore yet the whole available soil at this stage of their growth. Walnut roots likely developed at very deep soil horizons below the crop rooting zone, and did not colonise the topsoil that was rooted by the wheat crop. Soil tillage was limited to the first 30 cm, and the reduction in tree fine root densities in the first meter cannot be explained only by the mechanical destruction of the roots. To statistically test the effect of the distance from the tree trunk more sampled profiles are required and these will be collected when the walnut trees will be more developed.

Spatial and temporal heterogeneity of root profiles in the poplar agroforestry stand

In July 2003, a strong horizontal gradient of root length density was observed on a single tree (Figure 4b). The poplars canopy covered only 60% of the plot, but the poplar roots did colonise the whole plot: large quantities of fine roots

were found at the centre of the cropped alley (8 m from the tree rows). The highest L_{rv} (3.8 km m^{-3}) was surprisingly recorded at the farthest position from the tree trunk, 8 m from the tree row and at 1.8 m depth (Figure 4b). In the middle of the alley, an unusual vertical profile was observed, with small root length densities in the upper metre and a large increase in fine root length density between 1.0 and 1.6 m in depth. The dry hard soil prevented us to core duplicates in 2003. Subsequent measurements with many replications in 2004 indicated less contrasted root profiles (Figure 4). The impact of the 1.1 m deep sand layer was still clear. Above this layer, root relative densities on the tree row were higher than those in the cropped zone (Figure 4c). Under this layer, the opposite was observed, but the pattern was not as marked as that observed in 2003. Significant root densities were found below 2 m depth, with a higher value observed at 1.7 m depth under the cropped zone. When comparing the profiles at three distances in the crop zone, no significant differences were observed (Figure 4d), which contrasted with that observed in 2003. The general pattern was still that more roots could be found below than above 1 m soil depth. d_{50} increased steadily from the tree row (0.96 m) to the middle of the alley (1.58 m) (Table 2). The effect of distance to the tree row was significant for d_{50} ($P=0.018$) but not for d_{90} ($\alpha=0.05$). The results of the Duncan's test for the comparisons between distances are available in Table 3. Interestingly, the effect of the season was significant both for d_{50} ($P=0.009$) and d_{90} ($P=0.001$). Both d_{50} and d_{90} were shallower in summer than those observed in spring and autumn (Table 3). The effect of season was not significant for forestry trees, neither for d_{50} ($P=0.58$) nor for d_{90} ($P=0.60$).

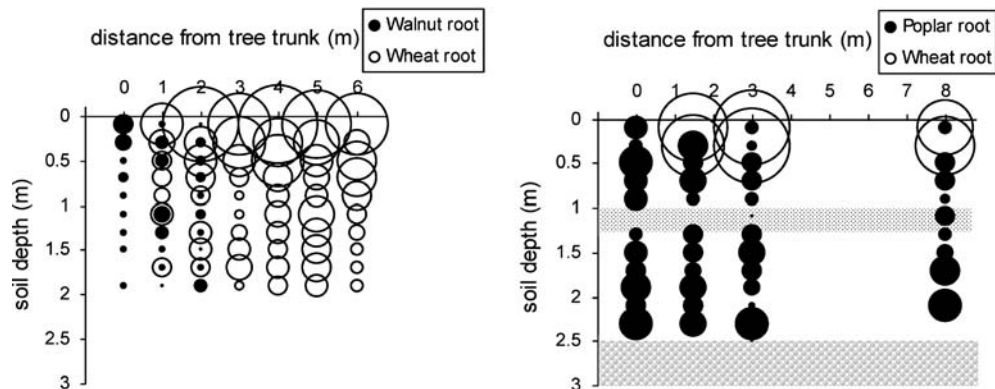


Figure 5. Compared root distributions of durum wheat and trees in the walnut agroforestry plot observed in spring 2002 (left, Grazzia variety) and in the poplar agroforestry plot observed in spring 2004 (right, Allure variety). The bubble sizes are proportional to the observed root length densities.

Distribution of crop root length density

Root profiles of the wheat crop were different between the two sites (Figure 5). At the walnut site, wheat roots were found down to 1.8 m depth, with $d_{50}=0.4$ m and $d_{90}=1.2$ m, respectively. By contrast, the wheat root system was more superficial at the poplar site, with hardly any roots found below 0.5 m depth (d_{50} was 0.15 m and d_{90} was 0.30 m).

Discussion

Most fine root distribution studies of trees are limited to the top layers of the soil, due to the heavy work involved. Soil coring is preferred when a non-destructive method is required, but coring below 1 m is difficult and is seldom applied. Most authors therefore explored a limited depth, such as 0.5 m in Bayala et al. (2004), Millikin and Bledsoe (1999), Rowe et al. (2001); 0.8 m in Moreno-Chacon and Lusk (2004) and Olsthoorn et al. (1999); 1 m in Purbopuspito and van Rees (2002); 1.5 m in Smith et al. (1999) and 2 m in Moreno et al. (2005) and Radersma and Ong (2004). In both our plots, the alluvial water table was 3–4 m deep at the end of the summer, calling for exploring the tree root profiles to a depth of 3 m.

The calibration factor of the core break method

The r^2 values of the calibration equation were lower for poplar and walnut than for durum

wheat. Similarly low r^2 were observed for oaks in a Mediterranean savannah (Moreno et al., 2005). Low r^2 values were likely due to the patchiness of tree rooting system. Root patchiness at the 10 cm scale was clear from our observations. It often happened that a clump of fine roots was present in the soil core, but did not extend up to the plan of observation. This is not concerning as long as it does not induce a bias in the use of the correlation, but it calls for more profiles to be sampled. The wheat root system was more regularly distributed in the crop root zone.

The calibration factor estimated for durum wheat was in the range of values published for maize (0.8–1.1, van Noordwijk et al., 1995) or for cotton and sorghum (0.7–1.2, Bennie et al., 1987), and indicated that wheat fine roots have no preferential orientation. Nonetheless, Bragg et al. (1983) reported a value of 2.2 for oat and Drew and Saker (1980) surprisingly observed much higher values ranged between 2.1 and 4.4 for winter wheat. The low calibration factors for both poplar and walnut indicated preferentially vertically oriented fine root systems (Drew and Saker, 1980). The poplar fines roots were the most vertically oriented.

Effect of winter intercrops on tree root systems

We observed a strong effect of the winter crops in a Mediterranean climate on the tree root systems after 10 years of intercropping. This effect was not limited to the mechanically disturbed

topsoil, but extended to deep horizons below the crop rooted soil volume. Yocum (1937) reported the root system of 3-year-old apple trees turned downward due to the presence of a summer crop (maize) and spread laterally below the maize root system at 2.4 m soil depth. Unfortunately, no comparison with the rooting system in a tree-only control plot was mentioned. The high plasticity observed in our experimental plots was also documented by other authors such as Bayala et al. (2004) or Singh et al. (1989) in the dry tropics; Livesley et al. (2000) or Lose et al. (2003) in the humid tropics; and Dawson et al. (2001) in temperate conditions. However, none of those studies observed inverted root profiles like the ones documented here for poplar (year 2003) or walnut (year 2004) in the cropped zone. Uniform profiles with depth were however recently observed by Moreno et al. (2005) in low-density oak stands in a Mediterranean climate in Spain, but no tree-only control was available.

When comparing walnut and poplar fine root profiles, we can conclude that the impact of the same winter wheat crop in the same climatic zone was more pronounced for walnut as compared to poplar. Tree phenology, crop rooting profiles and tree size may contribute to explain these differences. The phenology of walnut and poplar trees is very different. I-214 hybrid poplar trees open their buds after a 430 °C sum of temperature (base temperature = 0 °C) after January 1st, while walnut trees need 720 °C. The consequence is a 6-week difference in leaf phenology. Therefore, the wheat crop extracts much more water from the topsoil layers before the walnut trees start to shade, transpire and extend their root system. Walnut trees therefore encounter dry topsoil that reduces the benefit of colonising this upper soil horizon. In comparison, the poplar trees can explore the topsoil that has not yet been completely dried by the wheat crop. By shading the crop earlier, they also reduce crop transpiration rates, which in turn maintains soil humidity in the top layers.

Much deeper rooting profiles of wheat were observed on the silty soil of the walnut experiment than on the sandy soil of the poplar experiment (Figure 5). The very sandy soil and frequent rains during the wheat growing season at the poplar site may partially explain the shallow rooting pattern of the wheat. At the walnut

site, we observed that the wheat used the vertical macropores resulting from the decay of the tap-roots of the rapeseed break-crop to colonise deep horizons. It is however noticeable that the strong displacement of walnut tree roots towards deeper horizons is observed where a deep rooting pattern of the wheat is observed, while the poplar roots were displaced downwards to a lesser extent as the wheat crop has a shallower rooting pattern. Average wheat biomass and yield during the ten years of intercropping were higher in the walnut plot than in the poplar plot, resulting in larger water extraction (data not shown). This may also contribute to more pronounced spring soil water depletion in the walnut plot, which probably forced the tree roots to move downward. The depth of the water table was however similar in the two experiments.

We observed a temporal variation of poplar rooting pattern in 2004. Trees developed more superficial rooting systems in summer than in spring or autumn. After the wheat harvest in June, the stubble ploughing leaves a bare soil in summer very favourable to the infiltration of the few summer rains. Without any competitor, the poplar root system may colonise progressively the superficial soil layers in the crop zone after the crop harvest. However, the deeper rooting systems observed in autumn indicate that this summer trend is temporary, probably because the water resources in the top layers are rapidly exhausted, inducing the tree root systems to tap again the subsoil water reserves. This hypothesis is supported by the fact that the effect of the season was not significant for forestry trees.

The average size of the two tree species after 10 years of growth was different: walnut trees were 7 m tall, and their canopy covered only 30% of the intercropped plot, while the poplar trees were 20 m tall and their canopy covered 70% of the intercropped plot. The vertical projection of rooted volume was 60% of the plot surface for walnut trees while poplars explored 100%. Having colonised the whole soil volume under the cropped zone, the frontier for poplar roots was clearly the crop-rooted zone, where almost no poplar roots could be found during the first 5 years. This may explain the difference between the root profiles measured in 2003 (strong distortion) and 2004 (reduced distortion). We may now be in a process of homogenisation of

the root densities over the whole finite soil volume. Competition for water with the crop is probably the main driver of the tree root distortion in this dry Mediterranean climate.

Root plasticity as a response to heterogeneous soil conditions

Dupraz et al. (1999) measured the soil water content both in the agroforestry and forestry plantations at Restinclières when the walnut trees were 4 years old. In the agroforestry plots, they found that the soil water content fluctuated over time with a very different pattern in the tree row and in the crop zone. This resulted from the large difference in phenology between the trees and the winter wheat intercrop. In the agroforestry plots, both walnut and poplar trees therefore grow in heterogeneous soil conditions that result both from horizontal gradients due to the different extraction dynamics by the plants and vertical gradients due to soil properties.

Many predicted a poor growth of the trees in our experiments as a result of the wheat competition. But on the contrary, tree growth was impressive, suggesting that below-ground competition with the crops was not limiting. However, the resource acquisition by the crops is high and suggests a high level of below-ground competition. Dupraz et al. (1999) suggested a hypothesis that the competition with intercrops might have an important effect on the development of tree rooting systems. Our results show that both walnut and poplar trees were able to adapt to the wheat competition by displacing their root system to deep soil horizons and/or by extending laterally below the crop zone. This effect of the competition was not anticipated to be that strong, and is essential in designing efficient agroforestry systems with a high degree of complementarity between the trees and the crops. While minimising competition, deep tree root systems provide also a 'safety-net' service by capturing nutrients leached from the topsoil. They also capture nutrients from deep soil alteration, which is often referred to as a 'nutrient-pumping' effect (Cannel et al., 1996; van Noordwijk et al., 1996). Most of the alluvial soils in the Mediterranean area of Europe are intensively cultivated, and

both effects are welcome to avoid the pollution of alluvial water table that are crucial for human needs.

The plasticity of the root systems of different tree species is difficult to quantify, but some authors have shown that different tree species may react differently to the same crop competition. Livesley et al. (2000) compared the root systems of *Senna spectabilis* and *Grevillea robusta* trees before and after maize intercropping in Kenya. Interestingly, intercropped *Senna* trees experienced a global diminution of their root densities at every depth, while *Grevillea* trees displayed a reduction in the upper layers and an increase in the deeper layer. This may be interpreted as a higher plasticity of *Grevillea* trees.

However Radersma and Ong (2004) clearly demonstrated that water extraction and L_{rv} are not systematically correlated. A dynamic model is required to predict accurately water extractions by root systems in heterogeneous soil conditions. It is tempting to conclude that the wheat crop displaced the tree roots by predated on the water resource before the trees were active. Most studies on below-ground competition also claimed that the 'winner' plants are likely to be those depleting the resources before competing plants do (De Kroon et al., 2003). It has also been recognised that the most important obstacle to root penetration is the mechanical impedance of dry soils (Clark et al., 2003). A dynamic water budget is required to demonstrate that spring rains could not in our climate maintain attractive conditions in the topsoil under wheat cultivation, and soil water measurements are currently being undertaken to validate this model.

Consequences on modelling tree root dynamics

The simulation of plastic tree root systems clearly calls for a flexible root model. It should be able to simulate any shape of the rooted volume (including non symmetrical shapes), and any density distribution of the fine roots inside this volume. It should be driven by local soil conditions at a time step relevant for root colonisation processes. We found only two models that address the issue of a dynamic modelling of the whole tree root system in the literature: HyPAR (Mobbs et al., 1999) and WaNuLCAS (van Noordwijk and Lusiana, 2000). The HyPAR model

assumes a conical shape of the rooted volume where the maximum lateral extension and maximum rooting depth are simply proportional to tree height. This model ignores the effect of possible horizontal soil heterogeneity in the modelling of tree root extension. The tree root system modelled by HyPAR is therefore completely symmetrical around the trunk axis. Within the rooted volume, fine and coarse tree root distributions are modelled according to an exponential decrease of root density with soil depth and lateral distance from tree trunk.

The WaNuLCAS model divides a 2D soil into 4 zones and 4 layers per zone depending on the distance to the tree trunk. It also assumes a negative exponential decrease of fine and coarse tree root distribution with distance from the tree trunk but inside an elliptical shape of the rooted volume. It takes into account the effect of local soil conditions on the two dimensions of the rooted volume (depth and extension). This allows the prediction of deep and narrowing root systems if the topsoil is dry, or extended and superficial root systems if the topsoil is humid. But the fine root distribution inside the rooted volume continues to decrease exponentially with distance from the tree stem.

Both models would fail to describe correctly the rooting patterns of the walnut trees and poplars in our Mediterranean agroforestry systems, and would not predict correctly the below-ground competition with the wheat crop. The assumed monotonic distribution of fine root densities with distance to the tree stem may be well adapted to pure stands of trees (as it is often for pure crops) but it is not valid for low-density tree stands with intercrops as found in our study. This is well illustrated by the fact that the highest L_{rv} of poplar was measured at the farthest distance from the tree trunk (in the middle of the cropped alley, and at 2 m depth). Any model that forces the root distribution to follow a given theoretical root distribution function would not correctly predict the dynamic complexity of the root system in a heterogeneous soil.

The ability to fully take into account local soil conditions should thus be the main feature of an integrated tree root growth model. Accumulating evidence suggests that all root systems are significantly affected by resource heterogeneity in soils (Fitter et al., 2000; Hutchings and

John, 2004), and that special attention should be directed towards modelling of 3D tree or plant root growth since the natural environment is usually patchy in every direction. For cultivated systems, the model should be able to simulate correctly the impact of soil tillage or root trenching, and processes like lateral root re-colonisation after root trenching or upward root growth (e.g. reported by Huxley, 1999; Schroth, 1995; Singh et al., 1989). To correctly address the impact of root pruning, the topology of the main coarse roots should be included. Currently, no such tree root model is available. More work is needed to design such a model that could predict both root dynamics and water and nutrients capture by a tree in a 3D heterogeneous soil.

Conclusion

Soil coring to 3 m depth and analysing the samples with the core-break method was an effective method to document the rooting pattern of trees grown in contrasting conditions. While the above-ground part of the trees looked very similar in both forestry and agroforestry stands, our measurements show that the below-ground part of the trees was significantly modified by the annual crop competition. Deep and unusual vertical root profiles were documented for agroforestry trees, including profiles with increasing root densities with depth. This was interpreted as the result of a high degree of plasticity to sense and adapt to heterogeneous soil conditions that resulted mainly from crop competition.

The root system of walnuts was the most sensitive to crop competition, and developed towards deeper soil layers or extended laterally below the crop-rooting zone. The poplar root system was less distorted, but was influenced by sandy or gravel layers. The need for a model that could correctly predict the root growth of a perennial plant in a 3D heterogeneous soil environment was underlined. Existing models assume a fixed shape of the rooted volume and they predict L_{rv} as a function of depth and distance to the tree. In our conditions, L_{rv} could not be predicted as a function of depth and distance: significantly different profiles were observed at the same distance from the tree stem on the tree row and in the cropped alley. A 3D model of root

dynamics is therefore required. Natural environments are indeed always patchy rather than uniform (Hutchings and John, 2004), and such a model could have many applications.

The ability of walnut and poplar root systems to adapt to the wheat competition by distorting their root architecture is an essential feature in order to achieve efficient agroforestry systems with a high degree of complementarity between trees and crops (Cannell et al., 1996). While minimising competition, deep tree root systems provide environmental benefits: a 'safety-net' service by capturing nutrients such as nitrates leached from the top soil and a capture of nutrients from deep soil layers, which is often referred to as a 'nutrient-pumping' effect (van Noordwijk et al., 1996). Most of the alluvial soils in the Mediterranean area of Europe are intensively cultivated, and both effects are welcome to avoid the pollution of alluvial water tables.

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