Root system development of oak seedlings analysed using an architectural model. Effects of competition with grass

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Abstract

A dynamic 3D model of root system development was adapted to young sessile oak seedlings, in order to evaluate the effects of grass competition on seedling root system development. The model is based on a root typology and the implementation of a series of developmental processes (axial and radial growth, branching, reiteration, decay and abscission). Parameters describing the different processes are estimated for each root type. Young oak seedlings were grown for 4 years in bare soil or with grass competition and were periodically excavated for root system observation and measurements (topology of the root system, length and diameter of all roots with a diameter greater than 0.3 mm). In the fourth year, 40 cm×20 cm×20 cm soil monoliths were excavated for fine root measurement (root density and root length). Root spatial development was analysed on a sub-sample of roots selected on four seedlings. The model was a guideline that provided a complete and consistent set of parameters to represent root system development. It gave a comprehensive view of the root systems and made it possible to quantify the effects of competition on the different root growth processes. The same root typology was used to describe the seedlings in bare soil and in grass. Five root types were defined, from large tap roots to fine roots. Root system size was considerably reduced by grass competition. Branching density was not affected but the branch roots were always smaller for the seedlings grown in competition. Reiteration capacity was also reduced by competition. Cross sectional areas before and after branching were linearly related with a scaling coefficient close to 1, as predicted by the pipe model theory. This relationship was not affected by grass competition.

Introduction

Herbaceous vegetation has been shown to have a significant negative impact on survival and growth of newly planted tree seedlings (Davies, 1985). Experimental evidence suggests that the detrimental effects of grasses result mainly from belowground effects (Balandier et al., 2006; Nambiar and Sands, 1993). Grasses develop a dense and shallow root system located in the same soil horizon as the newly established tree seedlings, which impacts the seedling root system. The spatial distribution of seedling roots is strongly affected by the presence of grass roots: reduction in total root length and biomass (Harmer and Robertson, 2003; Ludovici and Morris, 1997), shifts in the root vertical distribution (Dawson et al., 2001; de Montard et al., 1999) and differences in lateral root expansion (Schaller et al., 2003; Schroth,

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1999) in response to grass competition were frequently reported.

Changes in the spatial distribution of seedling roots in response to grass presence may be related to changes in soil resource distribution. The locally high density of grass roots usually creates a zone of nutrient and water depletion and induces vertical and horizontal gradients of resource availability. Resource depletion generally induces noticeable reduction in seedling root development and gradients in resource availability may induce shifts in seedling root distribution, resulting from the ability of the seedling to favour root growth in nutrient-rich and moist soil patches, therefore avoiding the resource-deprived soil areas already colonised by the grass roots (Maina et al., 2002). Changes in seedling root spatial distribution are not necessarily resource-mediated and may also be caused by the ability of the grass to reduce the development of the tree seedling roots directly through mechanical effects (Baan Hofman and Ennik, 1982) or through allelopathy or non-toxic signals (Gruntman and Novoplansky, 2004).

Regardless of their origin, these competition-induced changes in the root distribution affect the capacity of the seedlings to withdraw water and nutrients from the soil, to escape the competition from the grass and, thus, to establish themselves successfully and to achieve rapid growth. The occupation of soil space by seedling roots is of primary importance for the outcome of belowground competition and the pool of soil resources available to the seedlings is determined by the volume of soil explored by their root system, the density and the spatial pattern of the roots within the rooting volume (Casper and Jackson, 1997; Casper et al., 2003). Our knowledge of the actual spatial distribution of tree seedling roots and their plasticity in response to grass competition is limited and precludes our understanding of tree-grass competition processes.

In this study, we examined the effects of *Deschampsia caespitosa* (L.) Beauv. on the root system development of sessile oak [*Quercus petraea* (Mattus.) Liebl.] seedlings. The highly detrimental effects of grasses on the survival and growth of newly planted oak seedlings have been previously shown by Collet et al. (1999) and by Löf (1999), and although oaks are usually grown at fertile sites, competition for belowground resources

was identified as the major factor limiting seedling establishment (Löf, 2000). *Deschampsia* is a cespitose grass, which was shown to have a strong belowground competitive effect on oak seedlings (Collet and Frochot, 1996; Collet et al., 1996).

In order to analyse the spatial distribution of seedling root systems and their plasticity in response to *Deschampsia* competition, we used the quantitative modelling approach developed by Pagès et al. (2004), which provides a consistent framework with a set of quantitative parameters that represent the architecture of the root system in a dynamic way. The model parameters represent different development processes involved in the root architectural dynamics. The use of the model to analyse oak seedling root systems made it possible: (1) to quantify the effects of grass competition on different development processes and (2) to assess the impact of changes in the different processes on the spatial deployment of the root systems. This work is also a contribution to the estimation and validation of this type of model on the basis of field data on tree root systems.

Materials and methods

Experimental site and plant material

The experiment was conducted near Nancy, in eastern France (alt.: 220 m, lat.: 48°44′ N, long.: 6°14′ E). The site was a former pasture on a pseudogley soil, with a clay horizon at a 30-cm depth. In May 1998, 1-year-old bare root oak seedlings (*Quercus petraea* Matt. Liebl.) were planted at 2.5 m×2.5 m intervals, on a 4500 m² plot. Seedlings ('eastern France' origin) were purchased from a commercial nursery where they had been wrenched at the end of the first growing season. Before planting, each seedling was measured: stem height, basal diameter, number of tap roots (many seedlings had multiple tap roots) and length of the tap roots. As a result of the wrenching in the nursery, most tap roots were between 10 and 15 cm long. Before planting, longer tap roots were cut to a 15-cm-length. Seedlings with no tap roots longer than 7 cm were discarded.

Grass (*Deschampsia cespitosa* L.) was sown over half of the experimental area. During the

first growing season, the grass plot was manually weeded to obtain a complete coverage by *Deschampsia* in autumn 1998. In the second, third and fourth growing seasons (1999–2001), a few manual weeding operations were performed once again to prevent the establishment of other species. In autumn 1998, the root development of the grass was limited, with only a few roots below a 20-cm depth. In July 2000, cylindrical (diameter: 10 cm) soil cores were taken from the surface down to a 75-cm-depth, at nine locations randomly chosen in the grass plot. All soil cores were taken between grass tussocks. Each soil core was split into six 12.5-cm-long samples. The samples were washed, the grass roots separated from oak roots and the grass root length was determined for each sample using the RHIZO image analysis system (Régent Instruments, Quebec, Canada). Mean grass root length density in the six successive 12.5-cm-deep soil horizons was: 1.37, 0.53, 0.29, 0.19, 013 and 0.13 cm cm^{-3}. In June 1999, 2000 and 2001, the grass was cut to a height of 20 cm in a 1-m diameter disc around each seedling, to reduce aboveground interaction between grass and oak seedlings. In the second half of the experimental area, the soil was kept free of any vegetation other than the oak seedlings by regular herbicide control (atrazine and glyphosate). During the 4 years of the experiment, the whole experimental area was continuously irrigated to avoid summer drought. The amount of water required in the grass and in the bare soil plots was determined by gravimetric measurements of soil water content made every two weeks during the summer.

At planting, seedling mean height and basal diameter were 36 cm and 0.70 cm, respectively. Total height and basal diameter were measured on all seedlings at the end of each growing season. At the end of 1998, a small but statistically significant difference (*t*-test, *P*-value < 0.001) in basal diameter existed between the seedlings grown in bare soil and the seedlings grown with grass (Figure 1). The difference increased in the following two years (*P*-value < 0.001 in 1999 and in 2000), and mean diameter at the end of 2000 was 27 and 18 mm in bare soil and grass, respectively. Average seedling height decreased in 1998 due to a large number of seedlings with stem apical dieback. Statistically significant differences in height between grass and bare soil seedlings

occurred only in 2000 (*P*-value > 0.16 in 1998 and in 1999, *P*-value < 0.001 in 2000).

Root system excavation and measurement

Oak seedlings were periodically excavated for root system description. Seedlings were excavated at 18 dates between June 1998 and October 2000, and eight to 20 seedlings were chosen each time. A total of 225 seedlings were excavated. During the first growing season, the seedlings grown with grass were considered to have a root system development similar to the seedlings in the bare soil because of the limited root development of the grass, and only bare soil seedlings were excavated. During the second and third growing seasons, seedlings from both the grass and the bare soil plots were excavated. At each date, the seedlings were randomly chosen and their average height and basal diameter were close to the average values for the whole experiment (Figure 1).

The root systems were excavated using small hand tools, starting at the stem and progressing along the roots until the root tip was reached. All roots with a diameter greater than 0.3 mm were excavated. Up until August 1999, the extracted root systems were completely described. From September 1999 to October 2000, small root systems were completely described but large root systems were only partially described. On large root systems, all roots with a basal diameter greater than 1 mm were described. Two main roots were chosen on each large root system: one vertical tap root and one large lateral root. On the two roots, all roots with a basal diameter greater than 0.3 mm were described. For each described root, total length, diameter at the base and every 5 cm along the root were measured and the connection to the system (identification of the parental root and position on the parental root) was recorded. After the root systems were described, the seedlings were oven-dried at 85 °C and their roots and shoots were weighed.

In July 2001, four seedlings (two in each treatment) were chosen for measurements on smaller roots. For each seedling, rectangular soil monoliths (approx. 40 cm in length, 20 cm in width and 20 cm in height) were extracted from a group of large lateral roots and from a group of vertical tap roots. A total of 18 monoliths were excavated. The monoliths were washed after
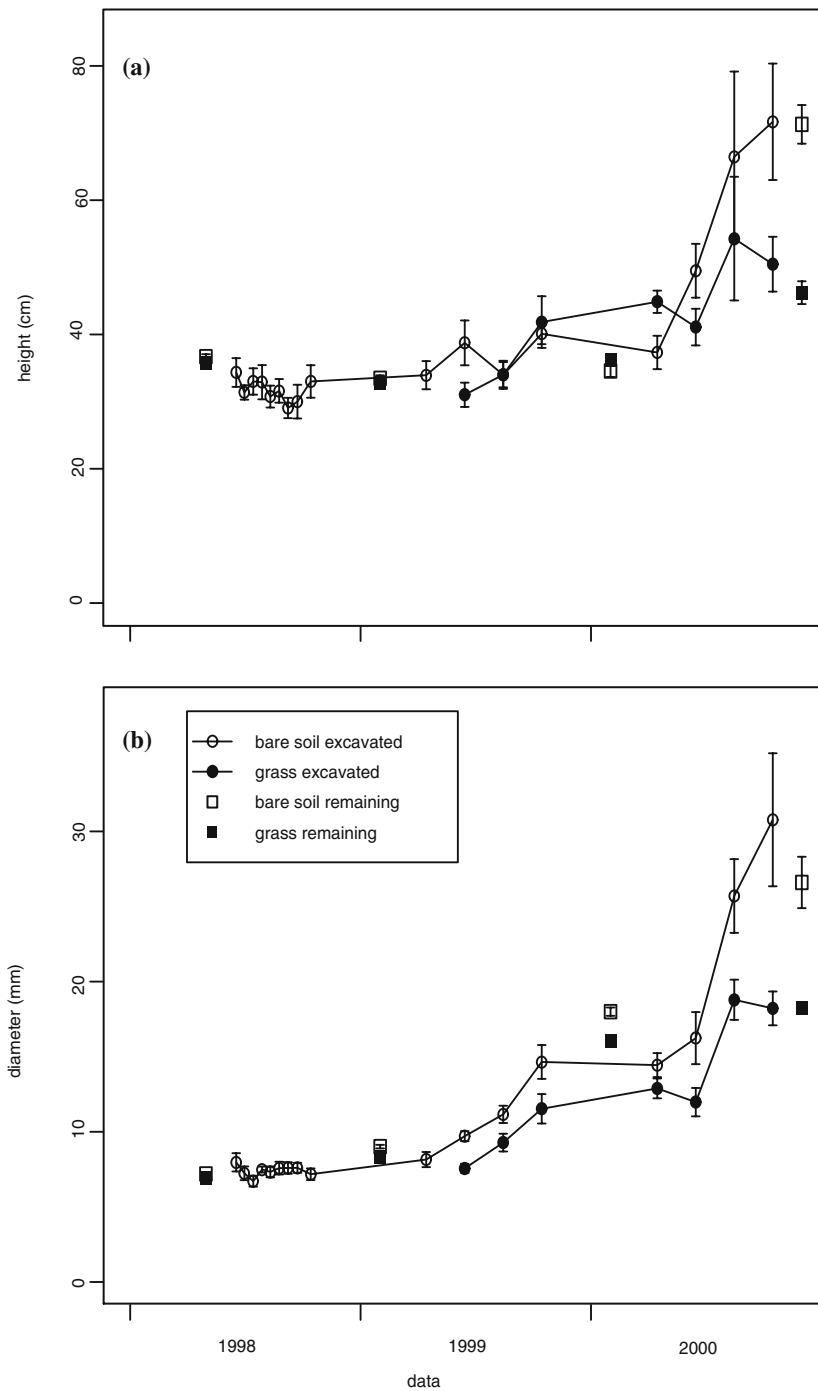
Figure 1. (a) Total height and (b) basal diameter of oak seedlings grown for three years in bare soil or with grass. Values (mean ± SEM) for the excavated seedlings are indicated at each excavation date and values (mean ± SEM) for the remaining (not excavated) seedlings are indicated at the end of each growing season.

a 1-day-soaking in salt-saturated water, and the large roots with all their lateral roots were extracted. The large roots extracted from adjacent monoliths were pieced together and the root sections developed each year from 1998 to 2001 were distinguished by identifying the scars left

each year by the apex death during the winter period. For each root section, the position and the basal diameter of all lateral roots were recorded.

Root system digitisation

In July 2001, four seedlings (two in each treatment) were selected to analyse the spatial development of the roots, using a 3D digitising device (3Space Fastrack, Polhemus, Colchester, VT, USA) (Danjon et al., 1999; Sinoquet and Rivet, 1997) and using 3A software (Adam et al., 1999). Each seedling was excavated using small hand tools. During the excavation, a large lateral root and a large tap root and its successive reiterations were selected on each seedling. On each large root, a subsample of branch roots with different sizes was selected. A total of 190 roots were selected, with a length ranging from 2 to 73 cm. Each root was numbered and labelled. The position of each root was assessed by recording the spatial coordinates of points along the root. The distance between two successive points varied between 2 and 5 cm, depending on root curvature. As the excavation advanced, the coordinates of the points were recorded while the measured points were still in their initial position.

For each digitised root, total length, diameter at the base and every 5 cm along the root were measured and the connection to the system (identification of the parental root and position on the parental root) was recorded.

Root architecture model

The model was adapted from those of Pagès et al. (2004) and Vercambre et al. (2003), which simulate the development of root systems in three-dimensional space. In these models, the various roots are categorised into a limited number of types. Roots in each type have a homogenous behaviour and are characterised by a set of developmental characteristics: axial growth (indeterminate or determinate; growth rate), radial growth, longevity, growth direction (gravitropism) and external aspect (lignified or not lignified).

The model represents the root system as a sequence of cylindrical root segments and calculates the size (length and diameter) and the location of each root segment at each time step, using stochastic submodels to describe elementary growth processes:

• *axial growth*. The length of each root segment within a root is calculated as a negative exponential function of root age according to the following equation:

$$L = A(1 - e^{\frac{-bt}{A}}),$$

where L is the length of the root, t the time after emergence, A the asymptotic root length and b the initial growth rate. These coefficients are drawn from log-normal distributions. The direction of each root segment is determined by a gravitropism parameter and a soil mechanical constraint parameter.

• *radial growth*. The radial growth is modelled on the basis of the pipe model (Shinozaki et al., 1964). The cross sectional area (CSA) of a root at a given branching point is calculated as the sum of the CSAs of the branch roots:

$$S = \alpha \sum s_i,$$

where S is the CSA of the mother root above the branching point, s_i the CSA of the i-th daughter root distal to this point, and α a parameter to be determined (generally close to 1). An initial diameter is given to each root when it is initiated.

• *branching*. Branch roots are assumed to appear acropetally. Two groups of parameters are used to describe the branching process: (i) the inter-branch distance, which is the average distance between two successive branch roots along the mother root, and (ii) the proportion of each root type among the branch roots. The initial growth direction of each branch root is characterised by the radial angle (azimuth drawn from a uniform distribution between 0 and 360°) and the insertion angle (drawn from a normal distribution).

• *reiteration*. A reiteration is defined as a branch root that is located at the apex of its mother root and is the same type as its mother root. Reiteration events occur regularly and lead to the formation of the structural root axes. The reiteration process is described using three parameters: the frequency of reiteration events, the minimal (R_{min}) and the maximal (R_{max}) number of reiterated daughter roots at each reiteration. For each root

and at each reiteration event, the number of reiterated daughter roots is drawn from a uniform distribution between R_{min} and R_{max}.

• *decay*. The parameter used to describe root decay is the necrosis duration. When a root stops growing, it starts to senesce and is trimmed after a period equal to the necrosis duration, unless it still bears living roots.

The parameters describing the growth processes are determined for each root type. Several coefficients characterising individual roots are drawn from probability distributions, which leads to a stochastic representation of the root systems and also provides continuity between the root types.

Root system simulation

The measurements on the excavated root systems were used to parameterise the model for seedlings grown in bare soil and in grass. Forty root systems (20 in bare soil and 20 in grass) were simulated. For each simulated root system, the total volume explored by the roots was calculated as the smallest convex hull containing all the roots, using Qhull software (Barber et al., 1996).

Statistical analysis

Treatment (bare soil or grass) effects on the different variables used to characterise root system development were tested using linear models: *t*-tests were used when testing treatment effects, ANOVAS when testing the combined effects of treatment and root type, regressions when testing relationships between CSAs, and ANCOVAs when testing the effects of treatments or root type on the relationships between CSAs before and after branching. All data preparation, statistical analyses and graphs were performed with the R environment (R Development Core Team, 2005).

Results

Root and shoot biomass

At the last excavation date (October 2000), mean seedling dry biomass was 78 g and 493 g in the grass and bare soil, respectively. The relationship between root and shoot biomass is presented on Figure 2 in comparison with the bisecting line. It shows that small seedlings invested more in the roots than in the shoots and, as the seedlings grew larger, they invested more biomass in the shoots than in the roots, leading to smaller root-shoot ratios for large seedlings. Over the common biomass range, the seedlings grown with grass invested more in their root systems compared to the seedlings grown in bare soil. The data did not make it possible to distinguish the possible effects of seedling age and seedling size on the relationships between shoot and root biomass.

Root typology

Beside the transplanted roots (those which existed at planting), five root types were defined, based on their length, diameter, growth direction, branching and reiteration capacity and lifespan (Table 1). The five root types were classified in decreasing order of growth capacity, from type T1 to type T5. Although each root type presented a large variability, it was characterised by a set of fixed attributes. We considered that the seedlings from both treatments could be described using a single root typology, with root types defined by the same set of qualitative attributes. Two separate simulators were adapted for the seedlings grown with or without grass competition. The two simulators were based on the same root typology and were parameterised using two different sets of quantitative parameters inferred from the analyses of the excavated root systems (Table 2).

The T1 root type represented the tap roots, which are the successive reiteration of the transplanted roots (which are not considered as T1 types in the simulator) and are characterised by their large size (length and diameter), a clearly vertical growth direction, a capacity to emit a considerable number of large lateral roots and a capacity to reiterate. Lateral roots were divided into three types (T2, T3 and T4) according to their size, their growth potential and their ability to reiterate. Their growth direction varied from vertical to strictly horizontal roots, and lateral roots were considered to exhibit an exotropism (a tendency to maintain their initial growth direction). The T5 type represented the fine roots, with no radial growth, no branching and no reiteration capacity.
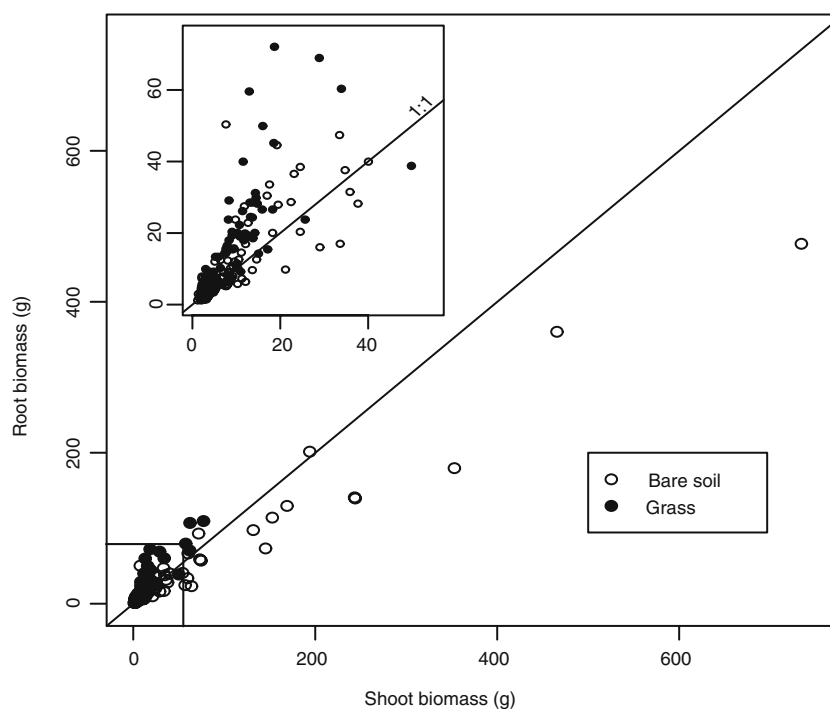
Figure 2. Relationship between root and shoot dry biomass for oak seedlings grown in bare soil or with grass. The data of all excavation dates are pooled. The included graph is a zoom on the smaller seedlings.

Table 1. Root typology defined for oak seedlings, characterising axial and radial growth, tropism, longevity, reiteration ability, and branching pattern for each root type

	T1	T2	T3	T4	T5
Description	Tap	Large lateral (reiterated)	Large lateral (not reiterated)	Small lateral	Fine
Axial growth	Indeterminate	Indeterminate	Indeterminate	Determinate	Determinate
Radial growth	High	High	High	Low	No
Tropism	Positive gravitropism	Exotropism	Exotropism	Exotropism	Exotropism
Mortality	Perennial	Perennial	Perennial	Abscission	Abscission
Reiteration	Very frequent	Frequent	Never	Never	Never
Branching: carried types	T2–T3–T4–T5	T2–T3–T4–T5	T3–T4–T5	T4–T5	None

T1: Tap roots, T2: Large lateral roots with reiteration, T3: Large lateral roots without reiteration, T4: Small lateral roots, T5: Fine roots.

Reiteration

Reiteration frequency was evaluated on the tap roots and on the lateral roots. Lateral roots were separated according to their length into 'long laterals' (length ≥5 cm) and 'short laterals' (length < 5 cm).

When pooling all excavated roots (regardless of the excavation date and the root age), we observed that 60% and 64% of the tap roots reiter- ated in bare soil and in grass, respectively. The number of branch roots at each reiteration event ranged between one and four. Average values (including the roots that did not reiterate) were 1.06 and 1.13 for the seedlings grown in bare soil and in grass, respectively. The proportion of roots that reiterated was 25% and 18% for long lateral roots, and 4% and 2% for short lateral roots, in bare soil and in grass, respectively. For the long lateral roots, the number of branch roots

Table 2. Model parameters adjusted for the different root types

Description	Bare soil					Grass				
	T1	T2	T3	T4	T5	T1	T2	T3	T4	T5
	Tap	Large lat.	Large lat.	Small lat.	Fine	Tap	Large lat.	Large lat.	Small lat.	Fine
Angle of insertion (rad)	0.5 (0.1)	1.46 (0.08)	1.46 (0.08)	1.46 (0.1)	1.46 (0.1)	0.5 (0.1)	1.46 (0.08)	1.46 (0.08)	1.46 (0.1)	1.46 (0.1)
Axial growth										
A, asymptotic length (cm)	100 (0)	100 (0)	100 (0)	3 (1.5)	1 (0.4)	100 (0)	100 (0)	100 (0)	3 (1.5)	1 (0.4)
b, initial growth rate (cm day^{-1})	0.4 (0.35)	0.35 (0.35)	0.35 (0.35)	0.35 (0.18)	0.2 (0.1)	0.4 (0.35)	0.35 (0.35)	0.35 (0.35)	0.35 (0.18)	0.2 (0.1)
Radial growth										
α, radial growth parameter	1.01	1.01	1.01	1.01	–	1.01	1.01	1.01	1.01	–
Root apical diameter (mm)	1.3	1.3	1.3	0.4	0.2	1.3	1.3	1.3	0.4	0.2
Time necrosis (day)	∞	∞	∞	1000	100	∞	∞	∞	1000	100
Reiteration										
Frequency	Each winter	Each Winter	Never	Never	Never	Each winter	Each winter	Never	Never	Never
Min.–max. number of branch roots	0–2	0–2	–	–	–	0–2	0–2	–	–	–
Branching										
Distance between branch roots (mm)	3.4	3.4	3.4	3.4	–	3.4	3.4	3.4	3.4	–
Root type proportion (%)										
T2	4	1	0	0	–	1.5	0.5	0	0	–
T3	7	1.3	2.3	0	–	4.5	1.2	1.7	0	–
T4	9	0.7	0.7	3	–	7	1.3	1.3	3	–
T5	80	97	97	97	–	87	97	97	97	–

T1: Tap roots, T2: Large lateral roots with reiteration, T3: Large lateral roots without reiteration, T4: Small lateral roots, T5: Fine roots.
Parameters were adjusted separately for oak seedlings grown in grass or in bare soil. Mean and standard deviation are indicated for the insertion angle and the axial growth parameters, the minimal and maximal numbers are indicated for the number of reiteration branch roots and constant value is indicated for all other parameters. See text for parameter definition.

at each reiteration event ranged between one and three. Average values (including the roots that did not reiterate) were 0.41 and 0.27 for the seedlings grown in bare soil and in grass, respectively.

Observations made on seedlings excavated in spring showed that reiteration events occurred during the winter on all roots. Observations made on seedlings excavated during the growing season showed that reiteration also occurred during the growing season on the tap roots, but less frequently. However, since root age was very difficult to evaluate, it was not possible to date the roots and therefore to determine the relative importance of the reiteration events occurring in the winter or during the growing season.

In the model, reiteration events occurred once a year in the winter for all roots. For the tap roots (T1), the number (min., max.) of reiterated branch roots at each reiteration event was set to (0, 2). For the lateral roots, the numbers were set to (0, 2) for the T2 roots and reiteration was impossible for the T3 roots. The exact number of reiterated branch roots observed on the excavated seedlings in bare soil and in grass were obtained by adjusting the proportion of T2 and T3 roots during the branching process.

Branching

Total branching density, evaluated on the monoliths extracted in 2001, was similar for the two treatments and was similar for tap roots and large lateral roots: an ANOVA ($n = 37$) showed no statistically significant effect of treatment (P-value = 0.052), root type (P-value = 0.65) and root type-treatment interaction (P-value = 0.72). The mean values observed in 2001 were: 3.2, 2.9, 3.1, 2.3 roots cm^{-1}, for the root segments developed in 1998, 1999, 2000 and 2001, respectively, for all treatments and all root types pooled. Since no clear pattern of root decay between 1998 and 2001 was observed, an average root density of 2.9 roots cm^{-1} was considered for all roots, regardless of the treatment, root type or root age. The corresponding parameter in the model (inter-branch distance) was set to 0.34 mm for all root types.

An analysis of variance showed statistically significant (P-value < 0.001, $n = 1261$) but small differences in the branching angle between the two treatments (88.6° and 85.1° in the grass and bare

soil, respectively), and between the root types (90° and 84° for the tap and lateral roots, respectively). No relationship between the basal diameter of the branch and its branching angle was observed. In the model, a constant value of 85° was used for the emergence angle of all root types.

The branching density was also examined on the root systems excavated in 2000. Only roots with a basal diameter greater than 0.3 mm were taken into account. Lateral roots were separated according to their length into 'long laterals' (length ≥5 cm) and 'short laterals' (length < 5 cm). A series of *t*-tests indicated that branching density was similar in the two treatments for all root types (P-value > 0.35 for all four root types), and decreased from 1.6 roots cm^{-1} for the transplanted roots to 0.13 roots cm^{-1} for the tap roots, 0.03 roots cm^{-1} for the large lateral roots, and 0.005 roots cm^{-1} for the small lateral roots. However, for all root types, the length of the branch roots was significantly lower in the grass than in the bare soil seedlings, resulting in a significantly higher proportion of short laterals in the seedlings in competition with grass: the proportion of short laterals was 0.42 and 0.27 for the transplanted roots (P-value < 0.0001), 0.59 and 0.40 for the tap roots (P-value = 0.003), 0.76 and 0.43 for the large lateral roots (P-value < 0.001), for the seedlings grown in grass and in bare soil, respectively. In the model, the proportion of T5 roots was calculated as the ratio between the total density observed on the excavated root systems and the density observed on the monoliths; the proportion of T1, (T2 + T3) and T4 were calculated from the relative importance of the various root types observed on the excavated root systems. The relative proportion of T2 and T3 was adjusted to obtain a number of reiterated branch roots on the lateral roots at each reiteration event in the simulated root systems, similar to the number of reiterated branch roots observed in the excavated root systems.

Cross sectional area and radial growth

The relationship between CSAs before and after branching was evaluated by splitting the roots into 5-cm-long segments and analysing the relationship between the CSA of the proximal end of the segment and the sum of the distal segment end CSA and the branch CSAs (Figure 3). The relationship on all data pooled was close to
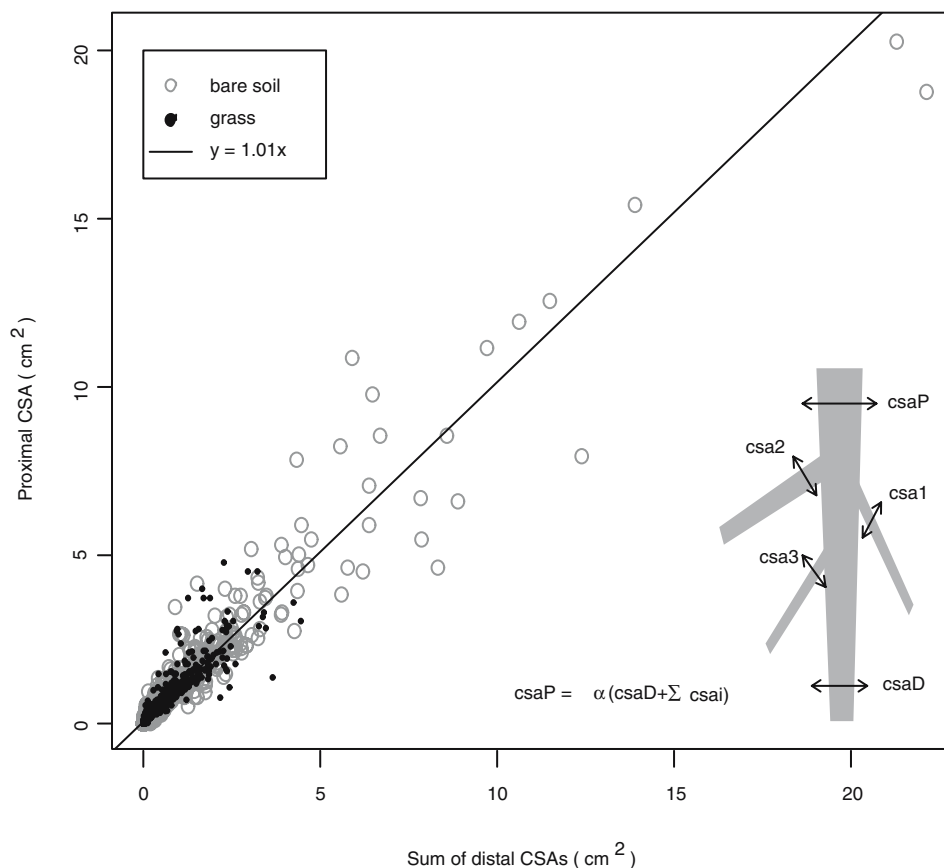
Figure 3. Relationship between the cross sectional area (CSA) of the main root (proximal end of the root segment: csa$P$) and the sum of the branch CSAs (distal end of the root segment and of all branch roots: csa$D + \sum$ csa$_i$) for oak seedlings grown in bare soil or with grass. The data of all excavation dates are pooled. The line associated with the model fitted on the data is drawn.

linear (α estimate: 1.01, SE: 0.0018, P-value: < 0.001). The large number of observations made the deviation from linearity significant and the use of linear models to compare groups of data spanning different ranges impossible. However, when limiting the comparison to the range common to both treatments (sum of proximal CSAs < 4 cm^2), an analysis of covariance did not reveal any statistically significant effect of the treatment (P-value < 0.34). Similarly, no statistically significant effect of the root type (tap root or lateral root) appeared in an analysis of covariance (P-value < 0.24) over the range common to both root types (sum of proximal CSAs < 2 cm^2).

The radial growth parameter (α) was set to 1.01 for all roots. In the model, the radial growth of a root is linked to the appearance of branch roots and therefore depends on the apical diameter of all the distal roots. The apical

diameter of the different root types, measured on 1-year-old oak seedlings grown in transparent root boxes for several months (unpub. data) was set to 1.3 mm for the tap root and the large lateral roots, to 0.4 mm for the small lateral roots and to 0.2 mm for the fine roots.

Root length distribution

Mean values of the tap root length were similar in both treatments, as shown by a series of *t*-tests performed at each excavation date (P-value: 0.10 and 0.12, n: 177 and 112, in June 1999 and Oct. 2000, respectively). Between June 1999 and Oct 2000, mean root length increased from 11.7 to 20.2 cm (Figure 4). Statistically significant differences in lateral root length between seedlings in grass or in bare soil occurred at most dates, as shown by a series of *t*-tests (P-value: < 0.001, n:
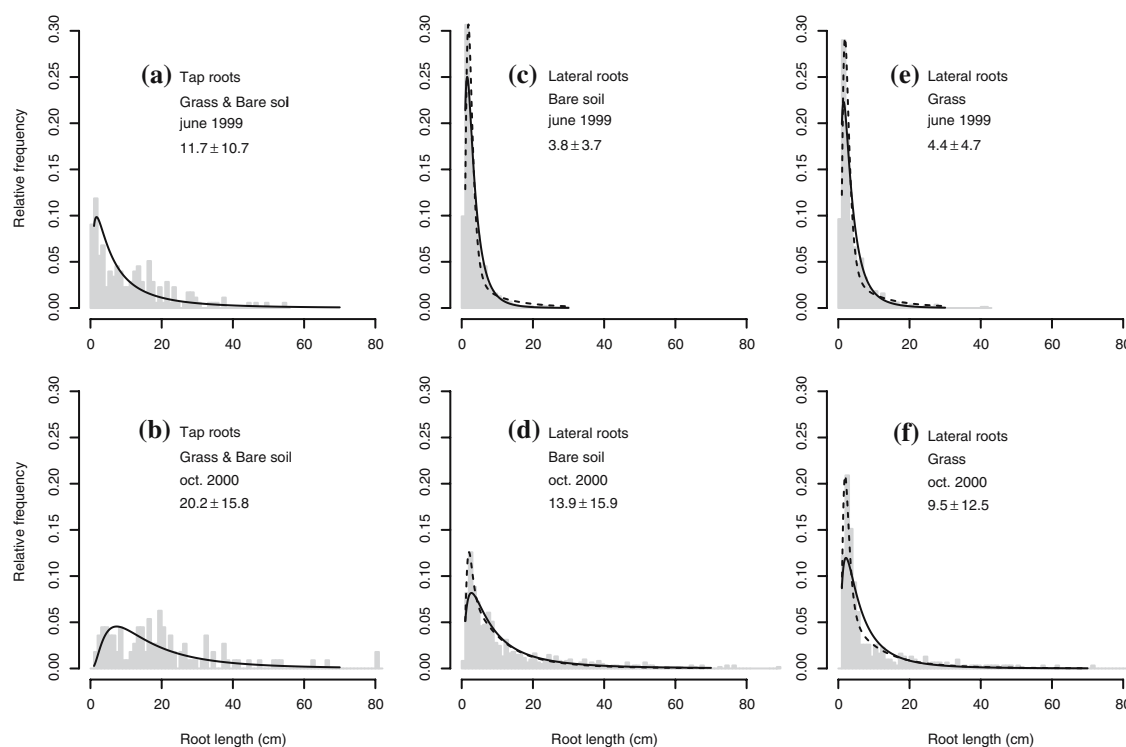
Figure 4. Distribution frequency of the length of the tap roots (a, b) and the lateral roots (c–f) for oak seedlings excavated in June 1999 (a, c, e) and October 2000 (b, d, f). The data from the seedlings grown in bare soil and in grass were pooled for the tap roots and separated for the lateral roots. For each distribution, mean and standard deviation (mean ± SD) are indicated and the density of the corresponding log-normal distribution is drawn (solid line). For the lateral roots, the weighted sum of the density of two log-normal distributions is drawn (dotted line). The mean and standard deviation of the two log-normal distributions are: mean-$\log_1 = 2.25$, $sdlog_1 = 0.88$, $meanlog_2 = 0.84$, $sdlog_2 = 0.47$.

1839 and 923, in June 1999 and Oct. 2000, respectively). The difference was small in June 1999 (3.8 cm and 4.4 cm in bare soil and grass, respectively) and subsequently increased as the roots became longer in the two treatments (13.9 and 9.5 cm in bare soil and grass, respectively, in October 2000).

Root length distributions were clearly I-shaped, except for the tap roots in October 2000. At each date, a log-normal distribution was fitted on the data using the mean and standard deviation of the measured roots. Data from both treatments were pooled for the tap roots and separated for the lateral roots. The fit did not appear to be very adequate although it was better in lateral roots.

In order to be consistent with the model where lateral roots were divided into two types (large and small), we tested if the root length data could be fitted as the sum of two log-normal distributions. A second series of distributions was fitted on the data, as the weighted sum of two log-normal distributions representing a sub-population of short roots and a sub-population of long roots. For the lateral roots, the best fits were obtained using the following parameters: mean = 2.6 and s.d. = 1.3 for short roots, mean = 14.0 and s.d. = 15 for long roots. For each data set, the weighted sum was calculated, weighting (proportion of large roots) being adjusted to best fit the data. The weighting was set to 0.28 and 0.32 (June 1999) and 0.78 and 0.55 (October 2000) for the seedlings grown in bare soil and in grass, respectively. Fits obtained on the lateral roots were adequate, showing that the observed distribution of lateral root length could be modelled as the sum of two log-normal distributions. For the tap roots, fits obtained by adding two distributions were not better than those with a single distribution (not shown).

In the model, axial growth parameters (asymptotic length and initial growth rate) were fixed for each root type and remained constant over the whole simulation period. For each root type, axial growth parameters were chosen to obtain a simulated root length distribution at the end of the simulation period (3 years), similar to an average distribution observed over the 1999–2000 period. Distribution for tap roots (T1 type) was characterised by a mean value of 14 and a s.d. value of 10 for both treatments. Distribution for lateral roots (T2 + T3 + T4 types) was constructed as the sum of the two log-normal distributions observed for short roots (T4 types, mean = 2.6, s.d. = 1.3) and long roots (T2 + T3 types, mean = 14.0, s.d. = 15), the weighting factor that determines the relative importance of short and long roots resulting from the branching and reiteration processes. The resulting distributions for simulated 3-year-old root systems growing in bare soil or in grass were similar to those obtained from the excavated root systems (not shown).

Root growth direction

Root growth direction data were used to adjust parameters (geotropism type, geotropism intensity coefficient and soil mechanical constraint coefficient). Due to the small number of seedlings and roots selected for digitisation, it was not possible to make a good statistical analysis of parameter variability. Average root growth direction, defined as the vertical angle of the line joining root insertion to root tip, was calculated for each digitised root and mean values were calculated for tap roots, large lateral roots and short lateral roots. The calibration of the geotropism parameters determines average root growth direction, thus, the total volume explored by the simulated root systems. For each root type, the geotropism parameters were adjusted for the simulated average growth direction of the different root types to equal the observed growth direction, in order to obtain realistic values for the simulated explored volume. The soil mechanical constraint parameters
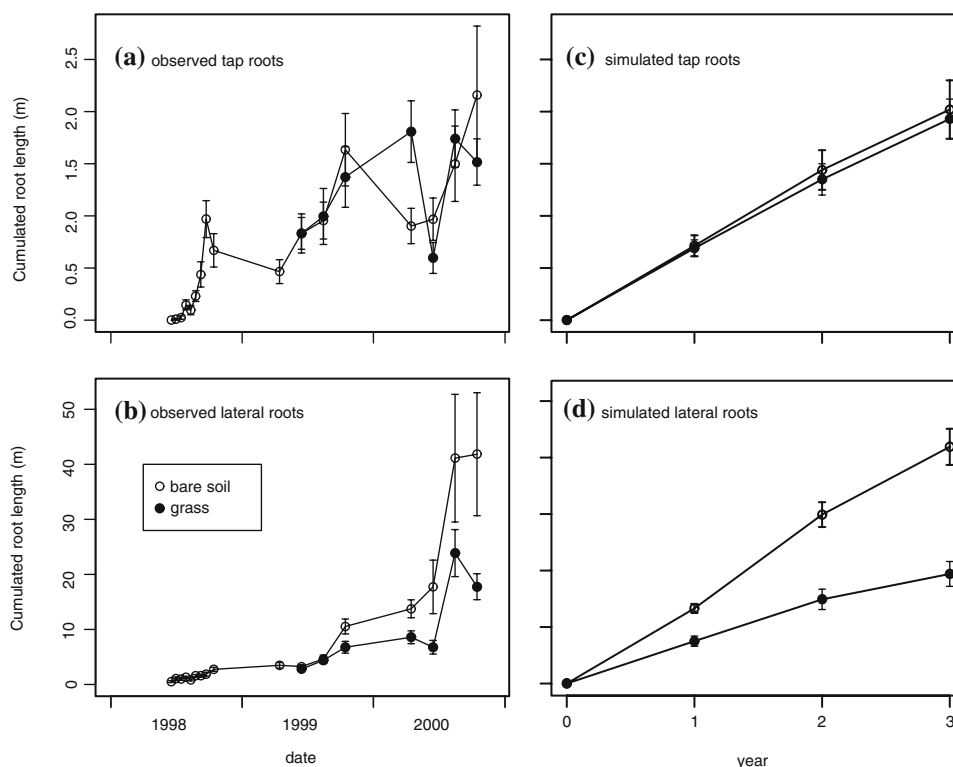

Figure 5. Cumulated root length (mean ± SEM) of the tap roots and the lateral roots for excavated ($n = 8$–20) and simulated ($n = 20$) oak seedlings grown for three years in bare soil or with grass.

were adjusted for the simulated root trajectories to be visually similar to the observed root trajectories. The soil mechanical constraint parameter mainly affects the visual aspect of the simulated root system, and not the average root trajectories.

Root system simulation

Twenty root systems in bare soil and twenty in grass were simulated using the root typology indicated in Table 1 and the parameter values indicated in Table 2. The quality of the simulation was evaluated by comparing the total root length (tap roots and lateral roots) and the basal diameter for 3-year-old simulated and measured root systems. Since both variables result from the adjustment of several parameters (root length

results from axial growth, branching, reiteration and necrosis processes, and basal diameter results from the same set of processes in addition to radial growth processes), they reflect the overall simulation quality.

The cumulated length of the tap roots (Figure 5) showed significant variability between two successive excavation dates, but the general trend is an increment throughout 1998 and 1999 and a lower increment in 2000. Tap root length was similar for the seedlings in the grass and the bare soil treatments. The cumulated length of the lateral roots increased continuously over the whole measurement period in both treatments. A series of *t*-tests performed at each excavation date revealed statistically significant differences appearing at the end of 2000 between the seedlings grown in bare soil and in grass. In October 2000, lateral root length was twice as great in the
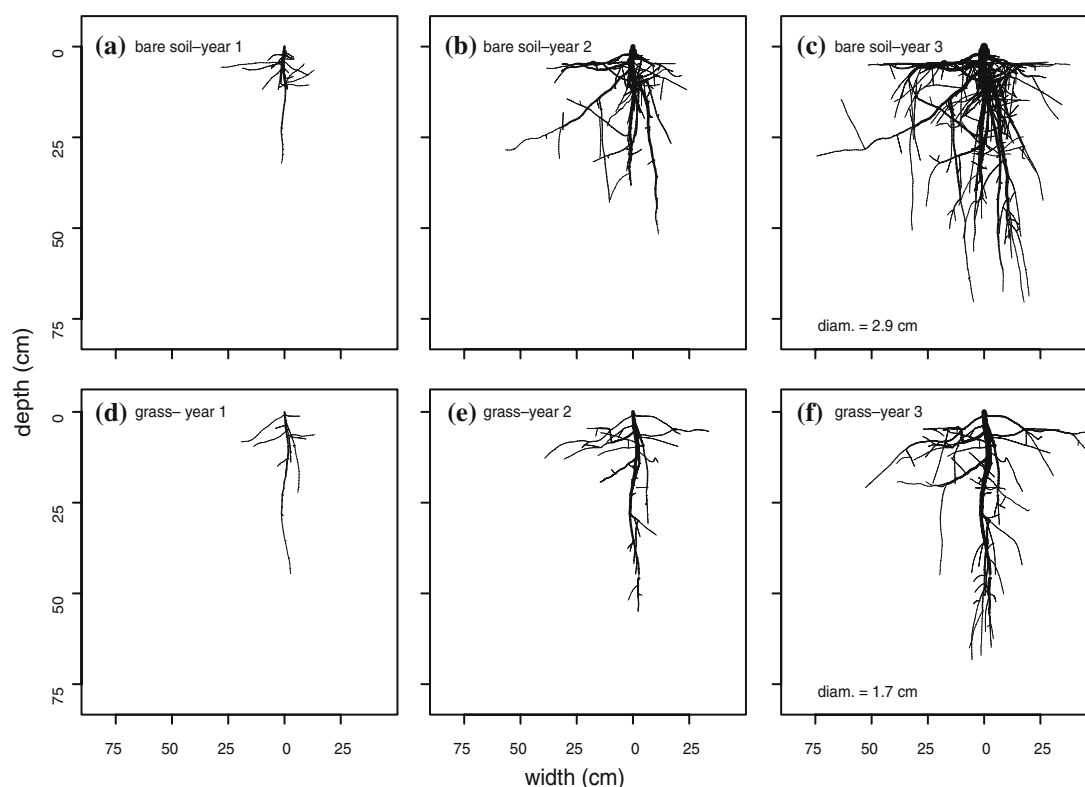

Figure 6. Vertical projection of simulated root systems of seedlings grown in bare soil (a–c) and in grass (d–f). In each treatment, the seedling with a basal diameter after 3 years closest to the mean basal diameter measured on the excavated seedling, was chosen among 20 simulated seedlings. For each seedling, the root system at the end of the first (a, c), the second (b, e), and the third (c, f) growing season is drawn. The basal diameter of the simulated root system at the end of the third growing season is indicated for each seedling.

seedlings grown in bare soil (40 m) as in the seed-lings grown in grass (20 m).

After 3 years, the simulated root systems (Figure 5) had a cumulated tap and lateral root length very similar to those of the measured root systems, for the seedlings grown in grass and for the seedlings grown in bare soil. However, the time-course of root length was different for the simulated root systems, the increase in root length being constant over the 3 years in the model.

Mean seedling diameter at the end of the third growing season was 2.9 and 1.9 cm on the bare soil and grass simulated seedlings, respec-tively, which is similar to the values measured on the excavated seedlings (2.6 and 1.8 cm on the excavated seedlings grown in bare soil and in grass, respectively; Figure 1).

In each treatment, the average simulated root system was determined as the root system whose basal diameter after 3 years was the closest to the mean basal diameter of the excavated seed-lings at the end of 2001. The horizontal projec-tion of the average simulated root systems (Figure 6) shows that the maximal depth and the horizontal extension of the root systems increased over the 3 years but did not differ between the two treatments. Mean maximal depth, calculated for the 20 3-year-old simulated root systems, was 72 and 80 cm, and mean hori-zontal extension was 72 and 84 cm, for the seed-lings in bare soil and in grass, respectively. The similarity in vertical and horizontal extension be-tween the seedlings in bare soil and in grass was also observed (although not measured) on the excavated seedlings.

Mean total volume explored by the simulated root systems (calculated as the smallest convex hull containing all the roots) was larger for the seedlings in bare soil (0.37 m^3) than for the seed-lings in grass (0.23 m^3) and differences were statis-tically significant, as shown by a t-test (P-value = 0.006).

Discussion

The present study confirms some characteristics of root system growth pattern for young oak seedlings already described in previous studies. Oak seedlings develop strong tap roots that have a rapid (Harmer, 1990; Pagès and Serra, 1994) and orthogeotropic (Riedacker et al., 1982) growth. Harmer (1990) reported an average elon-gation rate of 0.6 cm day^{-1}, which is close to our value (0.4 cm day^{-1}), whereas Pagès and Serra (1994) reported higher values (1.5–2.5 cm day^{-1}). These two studies were made on seedlings grown in root observation boxes and reported root elongation rate values obtained by instantaneous measurements (1 to 3-day root elongation). On the contrary, in our study, the seedlings were grown under natural conditions and values were obtained by averaging root length over the dura-tion of the whole growing period, which may explain the slightly lower values obtained here compared to Pagès and Serra (1994). In a previ-ous study under natural conditions, Löf (2000) observed that sessile oak seedlings grown with or without grass competition had much deeper roots systems after 3 years. In the present study, soil texture (compact clay) probably reduced root penetration and limited seedling rooting depth. As described by Mauer et al. (2002), tap roots showed a high reiteration capacity, leading to the formation of a root system with successive substitutive tap roots.

Individual roots showed a wide range of growth patterns (defined by a combination of axial and radial growth rates, growth direction, reiteration and branching capacity, and mortality characteristics) and the transition between growth patterns appeared to be continuous, as it was shown for first-order lateral roots on young oak seedlings (Pagès, 1995) and for complete root systems on peach trees (Vercambre et al., 2003). Despite the large variability and the con-tinuous nature of the observed variability, the categorisation of the roots into a small number of types was possible and represented the root systems well. The stochastic approach used to characterise some of the parameters made it pos-sible to break off the discretisation inherent in the concept of root typology.

Cross sectional areas before and after branch-ing were linearly related, with a scaling coeffi-cient (α) close to 1, as predicted by the pipe model theory (Shinozaki et al., 1964). This rela-tionship had not been previously tested on oak root systems but was shown to be a general property of plant development and had previ-ously been demonstrated for root systems on

other tree species (Oppelt et al., 2000, 2001; Ozier-Lafontaine et al., 1999; Spek, 1997; van Noordwijk and Purnomosidhi, 1995; Vercambre et al., 2003). In these studies, the scaling coefficient ranged between 0.9 and 2.0. This relationship may be used in root development models to simulate radial growth either by progressing upwards in the root system and by calculating mother root CSA from the CSAs of the branch roots as in our model, or by progressing downwards in the root system and by calculating the CSAs of the branch roots from the mother root CSA (Ozier-Lafontaine et al., 1999; Spek, 1997; van Noordwijk et al., 1994). In the upward procedure, radial growth of proximal roots results from the appearance of new distal roots and plant basal diameter increments can be simulated from the development of the root system. In the downward procedure, seedling basal diameter – or the diameter of the main proximal roots – is the main input value of the model and is used to calculate total root system size.

Oak seedling growth was strongly affected by competition from *Deschampsia*, in accordance with other studies reporting similar reduction in oak biomass in response to grass root competition (Collet et al., 1996; Löf et al., 2004; Löf and Welander, 2004). Both shoot and root biomasses were affected. A slightly higher allocation to roots in the seedlings grown with grass was shown, suggesting biomass allocation adjustments (McConnaughay and Coleman, 1999), in response to belowground resource limitation induced by grass root competition. These changes in biomass allocation patterns were observed in addition to an ontogenetic drift (Coleman and McConnaughay, 1995), where, proportionally, small seedlings allocated more biomass to roots than large seedlings did.

Differences between the root systems of seedlings grown in bare soil or with grass were mainly dimensional: none or only slight differences were observed in branching density, reiteration capacity or in the radial growth process. In the model, the main differences resulted from the proportion of the different root types among the branch roots, inducing a larger proportion of short roots, a smaller number of roots, and a reduced root system size for the seedlings grown with grass. These findings are consistent with previous results on the effects of root competi-

tion on the development of tree seedlings: Glenn and Welker (1989) showed a reduction in fine root length (1-year-old *Prunus persica* L. grown with *Festuca arundinacea* Schreb.), Collet (1994) a reduction in total root length (3-year-old sessile oaks grown with Deschampsia), Parker and Meyer (1996) a reduction in root density (1-year-old *Prunus persica* L. grown with several grasses), Ludovici and Morris (1996, 1997) a reduction in root extension rate and root length density (*Pinus taeda* L. grown with *Digitaria* spp.), Harmer and Robertson (2003) a decline in the total number of root tips (newly germinated *Fraxinus excelsior* L., *Sorbus aucuparia* L., and *Acer Pseudoplatanus* L. grown with a herbaceous mixture), and Balandier et al. (2005) a reduction in total root elongation (10-year-old *Prunus avium* L. grown with a herbaceous mixture).

All of these studies indicated a strong decrease in root growth but none of them gave a comprehensive view of root system development or made it possible to understand which root development processes were affected by competition. The model was a guideline that provided a consistent set of parameters to represent root system development, making it possible to obtain a complete description of the root systems and to quantify the effects of competition on the different root growth processes.

The model combines several submodels whose parameters were estimated by a series of statistical procedures to fit the observed data. Individual and direct validation of the submodels would have required excavating and observing an additional set of seedlings, which was not possible. Instead, an overall model validation was performed by comparing prediction of two global criteria – cumulated root length and seedling basal diameter – with observed values, following recommendations by Brown and Kulasiri (1996) who observed that variables reflecting higher level attributes are more informative for model validation than simple specific variables. Although no model calibration (adjustment of parameter values in order for the predicted root system characteristics to match the observed characteristics) was made after the submodel parameters had been estimated, simulated values for cumulated root length and seedling basal diameter were very close to observed values. Since these two criteria integrate the results from

all submodels (axial and radial growth, branching, reiteration, mortality), this suggests a good predictive ability of the model, at least in its morphological and topological aspects.

The geometrical aspects of the model were evaluated through a visual comparison of the simulated and observed root systems. Because of this crude validation of geometrical aspects, we restricted the analysis of the effects of competition on seedling spatial root distribution to the comparison of the soil volume explored by the root systems. We showed that although maximum vertical and horizontal extension were not affected by grass competition, in agreement with observations by Löf (2000) and Löf and Welander (2004), explored soil volume was one third smaller for the seedlings grown with grass competition, in accordance with the lower number of large structural roots produced.

The objective of our study was to adapt a root development model that could serve as a basis for a functional model of grass-tree root competition. Such a model should provide fine-scale 3D dynamic representation of the roots (Biondini, 2001; Mou et al., 1995) that needs to be validated on the basis of field observations before the root model can be integrated into a competition model. It is possible to directly validate the capacity of the model to simulate realistic root distribution patterns by comparing observed and simulated root maps or root profiles (Ozier-Lafontaine et al., 1999; Pellerin and Pagès, 1996). Another option that could prove to be more efficient (Brown and Kulasiri, 1996), is to validate it indirectly by comparing variables reflecting high level attributes, such as plant water and nutrient uptake or plant growth.

Although the model was parameterised to analyse the response of oak seedlings to grass competition, it is based on a generic model of root development (Pagès et al., 2004) that should allow it to be used for other applications, i.e., to examine fertiliser uptake efficiency, disease spread (Brown et al., 1997) or to compare nursery practices (Jacobs et al., 2003), provided the necessary calibration is performed.

Acknowledgements

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