Available online at www.sciencedirect.com
SCIENCE DIRECT
Forest Ecology and Management 222 (2006) 279–295
Forest Ecology and Management
www.elsevier.com/locate/foreco

Carbon concentration variations in the roots, stem and crown of mature *Pinus pinaster* (Ait.)

Didier Bert *, Frédéric Danjon

Unité de Recherche EPHYSE, Dendroécologie et Écologie Forestière, Institut National de la Recherche Agronomique–Bordeaux-Pierroton, 69 Route d'Arcachon, 33 612 CESTAS Cedex, France

Received 20 April 2005; received in revised form 30 September 2005; accepted 7 October 2005

Abstract

Stands of maritime pine (*Pinus pinaster* Ait.) cover about one million hectares of land in south-western France and produce 19% of all French timber, thanks to the intensive management methods employed. Evaluations of carbon fixation and storage in this forest are facilitated by its general homogeneity with respect to soil, climate and tree genetics. However, initial assessments were based on basic values for expansion factors and carbon concentration in the biomass, and more accurate results could be obtained.

The aim of the present study was to estimate the carbon concentration in the 13 main compartments of mature *P. pinaster* shoots and roots, describing sources of variation within these compartments and quantifying precisely the corresponding carbon contents.

The biomass distribution per compartment in the shoots and roots of 12 trees with a range of social status is given. It was obtained by joint architecture and dry weight measurements. The root systems were uprooted with a mechanical shovel and measured by 3D digitizing. Biomass allometric prediction equations per compartment according to girth at breast height were developed. The carbon concentration was analysed in 300 samples from four trees, taking into account their architecture.

The carbon concentration varied largely between compartments and showed a quadratic relationship with relative height in the four stem compartments and in branches and buds. It showed a negative exponential relation with root diameter. The carbon concentration of needles was not related to their age or their relative height in the crown. Carbon concentration variations were in accordance with the tissue chemical composition found in literature. The biochemical concentration of softwoods organs is extensively reviewed in the paper. The weighted mean carbon concentration reached 53.6% in the shoots and 51.7% in the roots. This resulted to 53.2% at tree level. The carbon content in the pine stand was 74 t C per hectare.

Between and within compartment variations in carbon concentration should be considered in carbon content evaluations and in structural–functional models. The underestimation of carbon storage in mature *P. pinaster* stands and sawnwood products reaches 6% when the usual 50% conversion factor is used.

Keywords: Carbon; Maritime pine; Biomass; Structural roots; Biochemistry

1. Introduction

Increasing levels of carbon dioxide in the atmosphere and global climate change have given rise to considerable research on the carbon balance in forest ecosystems, particularly with respect to compliance with the Kyoto protocol. Studies generally require the calculation of fluxes and measurement of storage. Flux measurements in the atmosphere over the canopy enable calculation of the carbon, water and energy balance on a short-term basis, i.e. over a few months or years (Kowalski et al., 2003). Long-term evolutions caused by the ageing of stands, silviculture, and climate change are assessed by measuring carbon contents in trees, the understorey and the soil. Evaluating carbon content (mass of carbon per tree or per ha) in forest trees is mostly based on relationships between tree size and the biomass of its different parts (Parresol, 1999; Dieter and Elsasser, 2002; Porté et al., 2002). The biomass per ha is then converted into a carbon content per ha, using the carbon concentration in the biomass (g of carbon per g of biomass). The value most widely employed is 50%, because the average molecular formula for living plant matter is $CH_{1.44}O_{0.66}$ (Pettersen, 1984). However, some analyses have

* Corresponding author. Tel.: +33 5 57 12 28 44; fax: +33 5 56 68 02 23.
E-mail address: bert@pierroton.inra.fr (D. Bert).

0378-1127/$ – see front matter © 2005 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2005.10.030

shown that the carbon concentration may range from 47 to 59%, as a function of tree compartment or species (Laiho and Laine, 1997; Lamlom and Savidge, 2003). Such a range would produce an uncertainty of about 20–25% in the carbon content of aerial parts in a mature *Pinus pinaster* stand with 160 t biomass ha^{-1}. The accuracy of carbon content assessments has been improved by the estimation of carbon concentration per compartment in some studies, e.g. Ritson and Sochacki (2003) for *P. pinaster* in Australia. However, most sampling protocols have not been able to take account of potential variations within compartments, in particular because of sampling at only one height of the stem.

The Landes de Gascogne forest is an intensively managed forest of Maritime pine (*P. pinaster* Ait.) located in south-western France. It covers 965,000 ha, which represents approximately a third of the surface area of this species worldwide. In France, this forest covers 6.5% of all French forest land but produces 19.2% of the timber (DERF, 2000; Inventaire Forestier National, 2003). Research has therefore been carried out on the Landes de Gascogne ecosystem in order to quantify its carbon balance and carbon contents using forest inventories (Loustau et al., 1999; Pignard et al., 2000; Bosc et al., 2003; Kowalski et al., 2003).

In order to improve carbon content assessments, we have now studied variations in the carbon concentration of maritime pines at the end of the usual 50-year rotation plan applied in this region (Lemoine, 1991). We extracted 300 samples from both aerial parts and coarse roots for elemental chemical analysis, with a view to answering the following important questions:

- How does the carbon concentration vary between tree compartments?
- How does the carbon concentration vary within each type of compartment?
- Can variations be explained by chemical composition?
- What is the average carbon concentration of each compartment, of a whole pine tree or a stand?
- How can these findings be applied to forest inventories?

2. Materials and methods

2.1. Study site

Trees were sampled in a 50-year-old *P. pinaster* Ait. stand in the Landes de Gascogne forest near the hamlet of Bilos, 50 km southwest of Bordeaux (44°29′43″N, 0°57′09″W, 38 m a.s.l.). The whole stand covered 60 ha and was managed by the French National Forestry Agency (ONF). The relief in this region is flat and the soil is a hydromorphic sandy spodosol with a discontinuous hardened iron pan at a depth of about 90 cm (Jolivet et al., 2003). The water table is generally near the surface in winter and at a depth of around 1.50 m at the end of August. The climate is temperate-maritime, with an annual mean temperature of 12.5 °C and about 930 mm of precipitation, skewed towards the winter months.

2.2. Sampling of trees

The stand had a density of 223 trees/ha, a basal area of 25.2 m^2 and a standing volume of 228 m^3/ha. The diameter at breast height (DBH at 1.30 m) of all trees in a square of 9 ha was measured. The mean DBH was 0.38 m, the dominant DBH was 0.42 m, and the dominant height was 20.7 m. Twelve trees were sampled for biomass assessment in order to represent DBH classes containing the same number of trees. For carbon concentration analyses, four of the 12 pines were sub-sampled based on their social status, defined as a percentage within the DBH range (Table 1):

$$\text{Social status} = \frac{\text{DBH} - \text{DBH}_{\min}}{\text{DBH}_{\max} - \text{DBH}_{\min}} \times 100$$

The social status of trees varies from 0 to 100 within a given stand.

The pines were felled in April 2000 and stem analyses were conducted in order to measure the length and circumference of each annual growth unit (AGU) and intra-annual growth cycle in this polycyclic species. AGU 1 was the last year of growth at the top of the tree and AGU 48 the lowest AGU in the stem after felling. The diameters over bark of all branches were measured with an electronic calliper at 5 cm from insertion on the stem (variable referred to as "D5" hereinafter).

2.3. Sampling compartments in trees

For each AGU 8, 12, 16, 18, 24, 32 and 40, we extracted (Fig. 1):

- Four cores for chemical analysis. These were split into heartwood and sapwood on the field, as a function of colour and transparency.
- One cross-section to sample the phloem and bark on a quarter or an eighth of its circumference. The "phloem" compartment had a maximum width 0.7 cm and was in fact made up of phloem, phelloderm and phellogen. The "bark" compartment comprised only phellem, which reached a thickness of 7 cm in this stand.

The low biomass levels in each compartment of the upper crown AGU led to both AGU 1, 2 and 3 being grouped together and AGU 4 and 5. In the living crown, one branch from monocyclic AGU 4, 12 and 18 was sampled and broken down into sub-compartments: wood and bark together, buds, needles from 1997, 1998 and 1999 separately. On pines 1593 and 1363, AGU 12 was bicyclic and the branch from the second cycle was sampled in the same way. Dead branches still inserted on the stem below and within the crown were removed, and one representative sub-sample per tree was analysed.

Root systems were uprooted with a large mechanical shovel and cleaned with a high velocity air jet and hand tools. The root system architecture, including topology and geometry, was measured with a Polhemus 3D digitizer driven by Diplami software (for a full description of the methods employed, see Danjon et al., 1999a,b). All roots with a proximal diameter of

Table 1
Description of the 12 pines sampled for biomass

Pine	1100	1768	1114	1593	1370	1363	1829	1684	1272	1030	1685	1374
Code				1		2			3			4
DBH (cm)	29.8	31.4	32.9	34.3	35.8	36.9	37.7	39.2	41.1	41.7	44.3	45.9
Social status (%)	19.8	25	29.7	33.8	38.7	42.2	44.5	49.5	55.2	57.2	65.3	70.3
Height (m)	18.65	20.65	19.8	22.09	20.25	19.71	20.67	22.57	22.11	18.67	21.29	21.69
Base of the crown relative height (%)	68.6	72.4	65.2	62.2	65.7	60.9	61.4	60.6	68.8	56.1	55.5	60.7
Compartment	Biomass (kg)											
Buds	0.9	0.8	1.7	1.5	1.9	2.2	2.8	2.8	2.0	2.9	3.8	3.1
Cones	6.5	7.1	7.7	8.3	9.0	9.4	9.8	10.5	11.4	11.7	12.9	13.8
Wood + bark dead branches	7.5	3.8	11.6	6.8	8.2	15.0	8.2	13.8	7.8	9.3	16.8	15.9
Wood + bark living branches	22.0	17.7	43.9	36.9	49.9	57.3	76.2	73.2	56.7	84.7	103.0	90.7
Needles	8.8	7.8	17.0	14.2	16.0	20.9	23.9	23.5	17.8	23.2	34.2	25.7
Total crown	**45.6**	**37.2**	**81.9**	**67.6**	**84.9**	**104.8**	**121.0**	**123.7**	**95.6**	**131.8**	**170.7**	**149.2**
Stem heartwood	93.8	99.1	122.0	146.1	132.5	147.9	175.4	205.6	198.9	168.8	245.9	251.4
Stem sapwood	97.0	106.0	121.6	147.1	133.7	154.9	185.1	204.3	196.1	157.4	244.6	244.1
Total stem wood	**190.8**	**205.1**	**243.5**	**293.2**	**266.2**	**302.7**	**360.5**	**409.9**	**395.0**	**326.2**	**490.6**	**495.5**
Stem phloem	6.7	7.3	7.7	8.7	8.3	8.4	9.6	10.6	10.3	8.5	11.2	10.4
Stem bark	39.2	39.7	46.9	51.0	49.6	47.0	53.3	64.4	63.8	55.7	66.8	60.2
Total stem bark	**45.9**	**47.0**	**54.6**	**59.8**	**57.9**	**55.4**	**62.9**	**75.0**	**74.1**	**64.2**	**78.0**	**70.6**
Total stem	**236.7**	**252.1**	**298.1**	**352.9**	**324.1**	**358.1**	**423.4**	**484.9**	**469.1**	**390.4**	**568.6**	**566.1**
Total above ground	**282.3**	**289.2**	**380.1**	**420.6**	**409.0**	**462.9**	**544.3**	**608.6**	**564.7**	**522.2**	**739.3**	**715.3**
Wood taproots	19.3	19.9	25.9	19.0	20.8	34.2	31.0	47.6	23.6	25.5	33.1	57.6
Bark taproots	3.7	3.8	4.9	3.6	3.9	6.1	4.8	8.0	4.2	4.4	5.6	9.8
Total taproot	**23.0**	**23.7**	**30.7**	**22.6**	**24.7**	**40.3**	**35.8**	**55.6**	**27.7**	**29.9**	**38.7**	**67.4**
Wood coarse roots	56.2	26.4	57.8	88.0	92.1	76.0	75.5	121.0	88.9	70.9	159.9	128.8
Bark coarse roots	4.6	2.3	4.8	6.8	7.5	6.3	6.4	9.9	7.4	5.9	13.1	10.6
Total coarse roots	**60.8**	**28.7**	**62.6**	**94.8**	**99.6**	**82.2**	**81.9**	**130.9**	**96.3**	**76.9**	**173.0**	**139.5**
Total roots	**83.8**	**52.4**	**93.3**	**117.4**	**124.3**	**122.5**	**117.7**	**186.5**	**124.0**	**106.8**	**211.8**	**206.9**
Total tree	**366.1**	**341.7**	**473.4**	**538.0**	**533.3**	**585.5**	**662.1**	**795.1**	**688.7**	**629.0**	**951.1**	**922.2**

The codes are for the pines sampled for carbon analyses and are those referred to in Section 3. The biomass of cones was estimated using the equation in Table 3 due to a lack of data on the studied stand.

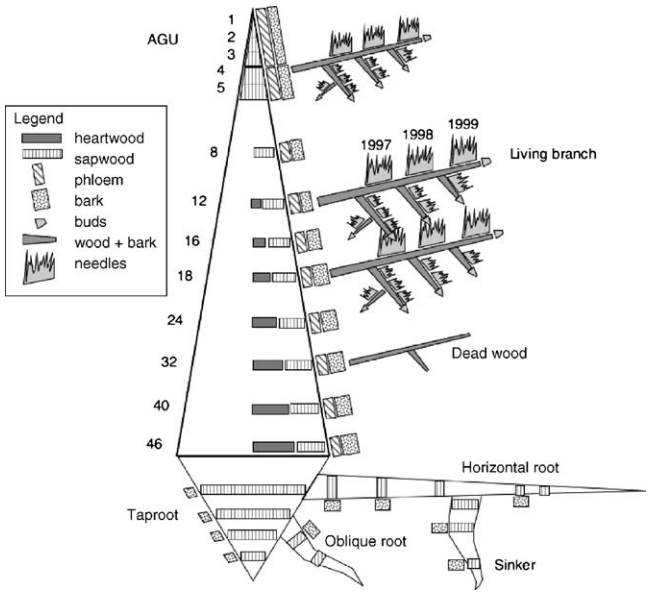

Fig. 1. Diagram of sampled compartments in the aerial parts and coarse roots of the four pines. One branch was also sampled on the second cycle of AGU 12 in two pines. The proportions between compartments are not real on this diagram.

more than 1 cm were measured. Mature *P. pinaster* root systems are mainly made up of a large taproot, surface roots, sinkers and a few oblique roots (Fourcaud et al., 2003a,b; Danjon et al., 2005). A root cross-section was thus sampled for chemical analysis at intervals on the taproot, on one large surface second order root, on one oblique root and on one sinker per tree (Fig. 2). Sampled roots were randomly distributed around the taproot. The position of both ends of each sample was tagged before measurement and recorded during 3D digitizing. Samples were divided between a ''wood compartment'' and a ''phloem + bark compartment'' and their dry weight measured. The following characteristics were computed for each sample using the AMAPmod software (Godin et al., 1997):

- Order of the root (= 1 for the taproot, = 2 for roots inserted on the taproot, = 3 for roots inserted on 2nd order roots, and so on).
- Diameter of the sample.
- Distance between the sample and insertion of the root.
- Horizontal and vertical distances between the sample and the insertion.
- Mean inclination of the root.

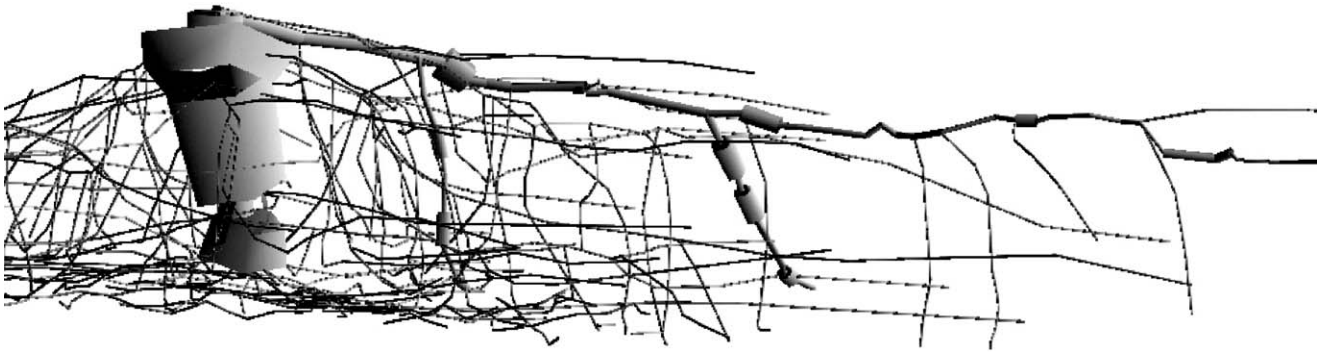

Fig. 2. Diagram of sampled compartments in the root system. 3D AMAPmod reconstruction of roots with orders 1, 2 and 3 of pine 1 – side view. The real diameter was used for segments sampled for carbon content analyses. The diameter of the corresponding axes was divided by 3. The diameter of all other segments was set at 4 mm.

2.4. Chemical analysis of carbon concentration

Lamlom and Savidge (2003) showed that accurate estimates of carbon concentration can only be achieved by reducing wood to a particle size of $\leq$3 mm. Small samples (2 g < weight < 50 g) were directly ground into 0.2 mm powder. Larger samples were first ground in a 10 mm mill and then a subsample was ground in the 0.2 mm mill. Analyses of residual water and carbon concentration were performed by the USRAVE-INRA Laboratory in Bordeaux. The carbon concentration was analysed using the Dumas method with a Leco CN2000 analyser. Two hundred milligrams samples were burned at a high temperature in a closed vial containing pure oxygen and catalysts. After purification, the CO_2 concentration was measured with IR. The carbon concentration was finally corrected in order to take account of the moisture content of the sample exposed to ambient humidity. This type of correction uses the weight difference between 1 g of sample collected at ambient humidity and then after 16 h at 103 ± 2 °C (water accounted for circa 6–7% of weight at 20 °C). The corrected carbon concentration will be referred to below as C_{103} and is expressed as a percentage, e.g. 52% means that 100 g of dry matter at 103 °C contains 52 g of pure carbon.

However, according to standard practice, the biomass was dried at 65 ± 2 °C, and the conversion of biomass into carbon content requires a value for the carbon concentration at 65 °C, referred to as C_{65} in this paper. For this reason, the weight of the samples was measured after drying at 65 °C and then again after drying at 103 °C. The loss was circa 2% (referred to as HUM below), and enabled calculation of the C_{65} value.

$$C_{65} = \frac{C_{103} \times (100 - \mathrm{HUM})}{100}$$

2.5. Accuracy of the analysis

The accuracy of all the steps from sample extraction to the final result for carbon concentration was checked in ten AGU 8 cross-sections from one 15-year-old maritime pine. The mean C_{103} value found was 53.07%, the standard deviation was 0.48% and the confidence interval of the mean was ±0.36% at the 95% level. Uncertainty was therefore sufficiently limited to demonstrate some gradients in the trees.

The influence of the manual handling of small samples was also checked on heartwood cores taken at breast height from a mature pine. The standard procedure consisted in manipulating and breaking the core into pieces by hand and then drying them in a classic paper bag. The alternative method consisted in manipulating the cores with clean gloves, brushing with a metal brush and washing with distilled water, before they were cut into small pieces with a cutter and dried in a Petri dish. Three replicated sets of four mixed cores were analysed for each procedure. The results for C_{103} were:

- Standard procedure: mean = 52.7%, σ = 0.32%.
- Alternative procedure: mean = 52.2%, σ = 0.17%.

The variances were equal and the means did not differ significantly (T-test = 2.21, p = 0.450). Manual handling of the samples did not modify the carbon concentration to a significant extent.

2.6. Statistical analysis of carbon concentration data

As the number of compartments was quite large, complete results are shown for C_{103} and only equations or average values are given for C_{65}. C_{103} values were slightly more consistent between trees when plotted according to their relative position in the stem than in terms of their absolute height aboveground, because the four sampled trees had different stem lengths (Table 1). The results were thus presented using the relative height (RH), which is 0% at ground level and 100% at the top of the tree.

The data for heartwood, sapwood, phloem and bark were analysed using polynomial mixed models for repeated data because of the spatial structure within a given stem (Proc. Mixed in SAS, SAS Institute Inc., Cary, NC, USA). If y_{ijk} was the carbon concentration in compartment i, at relative height j and in tree k, the fitted mixed model could be expressed as:

$$y_{ijk} = \mu + \beta_{0i} + \beta_{1i}\mathrm{RH}_j + \beta_{2i}\mathrm{RH}_j^2 + t_{ki} + \varepsilon$$

where μ is the overall mean, and β_{0i}, β_{1i} and β_{2i} the parameters corresponding to fixed effects of the type of compartment on the model. RH_j and RH_j^2 are the fixed effects of the relative height at the simple and square powers, respectively. t_{ki} is the random effect of the tree within a compartment, because trees were sampled in order to represent a population. ε is the residual error. The four polynomial models were fitted simultaneously. They expressed the carbon concentration according to relative height and its square, as its cube was not significant. This type of analysis can address two principal questions: (1) did the compartments have significantly different carbon concentrations; and (2) how did mean carbon concentrations change as a function of stem length.

Simpler analyses were more pertinent for compartments with less data and a variety of trends. Correlations, comparisons of means, linear and non-linear regressions were applied to these data using SAS. For taproots, surface roots or sinkers, separate stepwise regressions were performed on the diameter of the sample, its cross-section and distances from the insertion. The results of these regressions were used to compute the biomass and carbon content of the 46,387 segments making up the 12 root systems, based on their digitized volume.

The fitted gradients, or the mean value if there was no significant gradient, were then applied to every part of the tree in order to compute the carbon content. For instance, the biomass of sapwood of each AGU was converted into a carbon content using the fitted gradient of C_{65}. The carbon contents of all AGU of the stem were then added together and the total was divided by the total biomass of sapwood in the stem. The result was called the Weighted Mean Carbon Concentration (WMCC), as each part of the stem contributed in proportion to its biomass. The WMCC could be calculated at different levels of aggregation in the different compartments so that it could be used with more or less detailed biomass data. The biomass per ha was estimated from standard allometric relationships calibrated on the data from the studied stand (e.g. Porté et al., 2002).

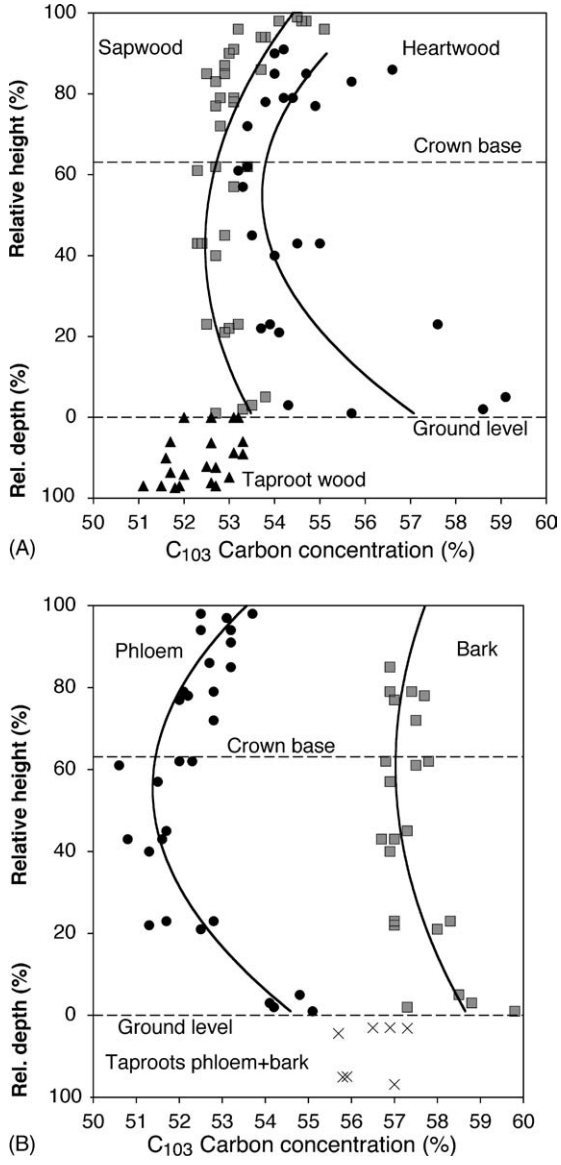

Fig. 3. Carbon concentration C_{103} as a function of relative height for stems (100% = 21.4 m), or the relative depth for taproots (100% = 1 m). The vertical axis has two different scales because of the short length of taproots when compared to stems. The equations for these models are shown in Table 2.

3. Results

3.1. Carbon concentration in the stem: heartwood, sapwood, phloem and bark

The data showed similar vertical variations in the four compartments of the stem (Fig. 3A and B). C_{103} values were higher at the base and top of the stem and at their lowest in the middle. The scatter of values within a single compartment was quite limited, except in heartwood.

The four polynomials of order 2 given by the analysis followed the equation $C_{103} = a + bRH + cRH^2$ (Table 2). Coefficients a, b and c were significant at the 5% threshold, except for RH^2 regarding the bark, where data from the upper part of the stem had to be removed because of difficulties in sampling sufficient pure, thin bark. The coefficients of the polynomials differed significantly from one compartment to another because interactions between the compartment effect and RH or RH^2 were significant. Multiple comparisons of means showed that all compartments were significantly different, except for the sapwood and phloem which only differed significantly when the relative height was more than 50%. These models were used to compute three C_{103} values: (1) at the base of the stem; (2) the minimum value close to the middle of the stem; (3) at the top of the stem. They were, respectively, 57.1, 53.7 and 55.2% in heartwood, 53.5, 52.5, 54.4% in sapwood, 54.6, 51.4, 53.6% in phloem and 58.7, 57.0, 57.7% in bark.

The results concerning C_{65} values were very similar (Table 2). The polynomials also included RH and RH^2 with significant parameters at the 5% threshold, except for bark as seen above. Interactions showed that the four models also differed, and comparisons of means demonstrated a significant

Table 2
This table shows (1) regression models for carbon concentration as a function of relative height (RH, %) in biomass dried at 103 or 65 °C, or (2) the mean and σ for compartments with no significant trend as a function of RH, or (3) the model for WMCC as a function of RH in compartments analysed separately and then grouped, or (4) the model as a function of branch diameter "*D*5" or root "*D*root" (cm)

	Compartment	C_{103} model	C_{65} model
CROWN	Dead wood (2)	54.42% $\sigma = 0.33\%$	53.43% $\sigma = 0.28\%$
	Wood + bark branches (4)	$[5.67/(2.13 + D5)] + 53.5$ or $54.2 + 0.210 + 8.45 \times 10^{-8}(\mathrm{RH} - 50)^{4.2}$	$(0.0198 + D5)/(0.0188D5)$ or $53.3 + 0.165 + 2.65 \times 10^{-11}(\mathrm{RH} - 50)^{6.29}$
	Buds (4)	$52.97 + 0.48D5$ or $53.0 + 0.259(100 - \mathrm{RH})^{0.605}$	$51.72 + 0.42D5$ or $51.8 + 0.195(100 - \mathrm{RH})^{0.641}$
	P	<0.0001	<0.0001
	Needles $\mathrm{year}_{n \text{ to } n-2}$ (2)	54.74% $\sigma = 0.75\%$	53.61% $\sigma = 0.85\%$
	Pollen	One data: 55.7%	One data: 51.9%
STEM	Heartwood (1)	57.2 −0.127RH +0.00115RH^2	56.1 −0.108RH +0.000961RH^2
	P	<0.0001 <0.0001 <0.0001	<0.0001 <0.0001 <0.0001
	Sapwood (1)	53.5 −0.0450RH +0.000588RH^2	53.0 −0.0485RH +0.000532RH^2
	P	<0.0001 0.0157 0.0028	<0.0001 0.0150 0.0049
	Phloem (1)	54.7 −0.120RH +0.00109RH^2	53.0 −0.104RH +0.000927RH^2
	P	<0.0001 <0.0001 <0.0001	<0.0001 <0.0001 <0.0001
	Stem bark (1)	58.7 −0.0551RH +0.000452RH^2	56.8 −0.0504RH +0.000411RH^2
	P	<0.0001 0.0286 0.1150	<0.0001 0.0377 0.1372
	Heartwood + sapwood (3)	Not available	$54.9 - 0.0904\mathrm{RH} + 0.000918\mathrm{RH}^2 - 1.59 \times 10^{-6}\mathrm{RH}^3$
	Phloem + bark (3)	Not available	$56.4 - 0.0447\mathrm{RH} - 0.00123\mathrm{RH}^2 + 6.54 \times 10^{-5}\mathrm{RH}^3 - 1.09 \times 10^{-6}\mathrm{RH}^4 + 5.79 \times 10^{-9}\mathrm{RH}^5$
	Whole stem (3)	Not available	$55.1 - 0.0845\mathrm{RH} + 0.00257\mathrm{RH}^2 - 1.14 \times 10^{-4}\mathrm{RH}^3 + 2.67 \times 10^{-6}\mathrm{RH}^4 - 2.74 \times 10^{-8}\mathrm{RH}^5 + 1.03 \times 10^{-10}\mathrm{RH}^6$
ROOTS	Taproot wood (2)	52.38% $\sigma = 0.67\%$	51.72% $\sigma = 0.61\%$
	Taproot bark + phloem (2)	56.44% $\sigma = 0.65\%$	54.87% $\sigma = 0.80\%$
	Roots wood (4)	$1.89 \exp^{-0.43D\mathrm{root}} + 51.83$	$1.98 \exp^{-0.53\ D\mathrm{root}} + 51.16$
	Roots bark + phloem (2)	56.18% $\sigma = 0.84\%$	54.42% $\sigma = 0.78\%$

"Not available" means that the WMCC could not be calculated because no biomass dried at 103 °C was available. *P* is the likelihood associated with each parameter estimate.

difference between the four compartments. Within a given compartment, the C_{103}-model produced mean carbon concentration values higher than the C_{65}-model by 0.8, 0.6, 1.4 and 1.9% for heartwood, sapwood, phloem and bark, respectively. The carbon concentration increased in line with the hydrophilicity of the organ, because the biomass lost more or less water between 65 and 103 °C.

The use of these models of carbon concentration based on actual biomass data produced the WMCC and the underestimations shown in Table 3. WMCC values ranged from 51.0 to 55.9% in different compartments, depending on their nature and the biomass proportion in the stem. Thus, assuming a 50% carbon concentration in all compartments, a 1.9–10.6% relative underestimation of the carbon content per compartment would result.

The compartments were grouped together and then the WMCC value was calculated for each growth unit, taking account of the proportion of biomass in each compartment and their respective carbon concentrations. Finally, WMCC was fitted to the RH using various polynomials (Table 2). WMCC values were thus 53.3% for wood, 55.2% for whole bark and 53.6% pour the whole stem (Table 3). Finally, using 50% carbon concentration for the stem would result to underestimate by 6.8% the carbon content.

3.2. Carbon concentration in branches: wood and bark pooled

A link was observed between C_{103} values and the branch diameter (Fig. 4A). Branches inserted at the base of either a first or a second intra-annual cycle were very similar and were pooled. The trend was successfully fitted with a non-linear regression allowing extrapolation to the largest diameters of the branch set, i.e. 7.5 cm:

$$C_{103}\,(\%) = \frac{5.67}{2.13 + D5} + 53.5, \qquad \text{with } D5\ (\mathrm{cm})$$

The trend was non-linear because bark thickness increases more slowly than the wood cross section. For this reason, the proportion of bark in the branch volume decreases in a non-linear fashion when the diameter of a branch increases. This gives rise to a downwards carbon concentration trend, because of the lower carbon concentration of the wood.

In order to provide a C_{103} estimation based on the relative height of branches, we applied the previous model to the 981 branches of the 12 pines making up our complete biomass sample, and fitted another non-linear model (Table 2, Fig. 4B). Branches within a whorl have a broad range of diameters at a given height on the stem. It would be therefore more accurate to

Table 3
Mean "weighted mean carbon concentration" (WMCC) in the 12 pines and all compartments dried at 65 °C

Compartment	Mean WMCC (%)	RUE (%)	*a*	*b*	Biomass (t/ha)	Carbon (t/ha)
Buds	53.43	−6.4	1.2	3.10	0.48	0.25
Wood + bark dead branches	53.43	−6.4	7.3	2.01	2.32	1.24
Cones	53.43[a]	−6.4	7.3[b]	1.74[b]	2.20	1.18
Wood + bark living branches	53.46	−6.5	29.6	3.56	12.8	6.85
Needles	53.61	−6.7	12.2	2.50	4.24	2.27
Total crown	**53.49**	**−6.5**	**56.0**	**2.74**	**22.1**	**11.8**
Heartwood	54.39	−8.1	111.6	2.24	37.0	20.1
Sapwood	52.26	−4.3	115.7	2.06	37.1	19.4
Total wood	**53.32**	**−6.2**	**227.3**	**2.15**	**74.2**	**39.5**
Phloem	50.96	−1.9	5.6	1.01	2.01	1.02
Bark	55.90	−10.6	44.0	1.13	11.9	6.65
Total bark	**55.18**	**−9.4**	**51.6**	**1.11**	**13.9**	**7.67**
Total stem	**53.62**	**−6.8**	**278.8**	**1.98**	**88.1**	**47.2**
Total above ground	**53.60**	**−6.7**	**333.9**	**2.13**	**110.2**	**59.0**
Wood taproot	51.72	−3.3	20.4	2.14	6.65	3.44
Bark taproot	54.87	−8.9	3.8	1.83	1.17	0.64
Total taproot	**52.20**	**−4.2**	**24.2**	**2.10**	**7.82**	**4.08**
Wood coarse roots[c]	51.33	−2.6	56.0	2.46	19.4	9.95
Bark coarse roots[c]	54.42	−8.1	4.6	2.48	1.60	0.87
Total coarse roots	**51.57**	**−3.0**	**60.6**	**2.46**	**21.0**	**10.8**
Total roots	**51.74**	**−3.4**	**84.7**	**2.37**	**28.8**	**14.9**
Total tree	**53.21**	**−6.0**	**418.7**	**2.18**	**139.0**	**73.9**

Relative underestimation (RUE) of the actual carbon content using 50% as the carbon concentration. Example: 1000 kg of aerial stem biomass × 53.62% = 536.2 kg of carbon; relative underestimation = [(1000 × 50%) − 536.2]/536.2 = −6.7%. Parameters of the allometric equation giving the biomass in kg from the Girth at Breast Height (GBH) (m): biomass = $a\mathrm{GBH}^b$. Estimated biomass and carbon stock per ha.

[a] WMCC of dead wood because of the lack of data for cones.

[b] Equation established on a 32-year-old stand and applied to the studied 50-year-old stand.

[c] Taproot excluded.

use the model based on the branch diameters than that based on relative height, despite the significant correlation between *D*5 and relative height ($r = -0.773$, $p < 0.001$, $n = 981$).

3.3. Carbon concentration in needles

C_{103} values showed no significant trend as a function of height in the crown; for example, the correlation was 0.093 ($p = 0.751$) for needles which had grown in 1999 (Fig. 5A). Likewise, neither the DBH nor the total height of the stem, the length of the crown or radial growth during the four years prior to felling were related to the carbon concentration of needles. The four pines were not ordered in the same way as a function of the year of the needles considered (Fig. 5B). These results thus suggested that the carbon concentration was not related to position in the crown, the age of needles or the size of the pine. In this situation, WMCC was the arithmetic mean of the data, i.e. $C_{65} = 53.61\%$, $\sigma = 0.85\%$, $n = 53$ (Table 3). Underestimation could be calculated at about 6.7% if 50% were used to convert needle biomass into carbon content.

3.4. Carbon concentration in buds

C_{103} values decreased with height in the crown in the four pines. C_{103} was also well correlated with branch diameter ($r = 0.742$, $p = 0.006$, Fig. 6A, Table 2). The linear relationship according to *D*5 was applied to the diameter inventory of the 981 branches of the 12 pines. The C_{103} values were then fitted using an allometric model, so as to enable determination of the carbon concentration when *D*5 is not known (Fig. 6B, Table 2).

In order to estimate the WMCC of buds in a tree, our model for the biomass of buds per branch was:

$$\text{Biomass (g)} = 1.741 D5^{2.599} \mathrm{RH}^{0.251}$$

The bud biomass of each branch was then multiplied by C_{65} and the WMCC calculated for each pine. The mean of 12 WMCC was 53.43% and the mean underestimation of carbon content would be 6.44% with 50% as the carbon concentration.

3.5. Carbon concentration in the wood and bark of dead branches

Sampled trees 1–4, respectively, corresponded to the following C_{103} values: 54.5, 54.8, 54.4 and 54.0%. The values were within the range of measurement uncertainty and no trend in line with DBH could be considered as significant. Therefore, the average C_{103} value was 54.42% with $\sigma = 0.33\%$, and the

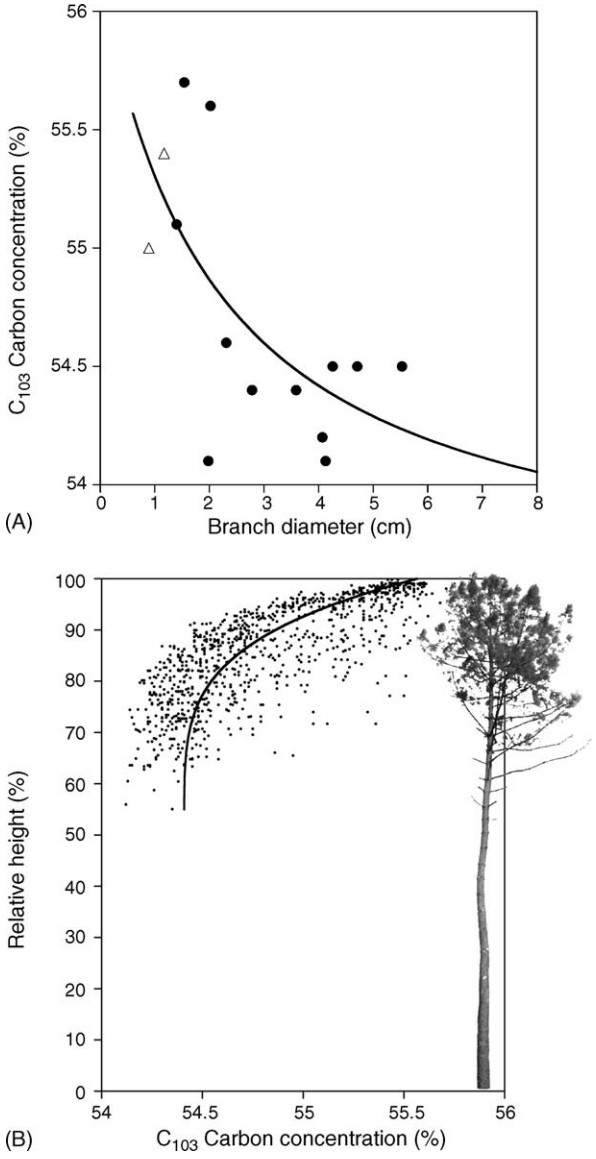

Fig. 4. Carbon concentration C_{103} as a function of branch diameter close to the insertion (D5), or relative height on the stem (100% = 21.4 m). On (A), the black circles are for branches inserted at the base of the first cycle or monocyclic annual growth unit, and the white triangles are for branches inserted at the base of the second cycle. The equations for these models are shown in Table 2.

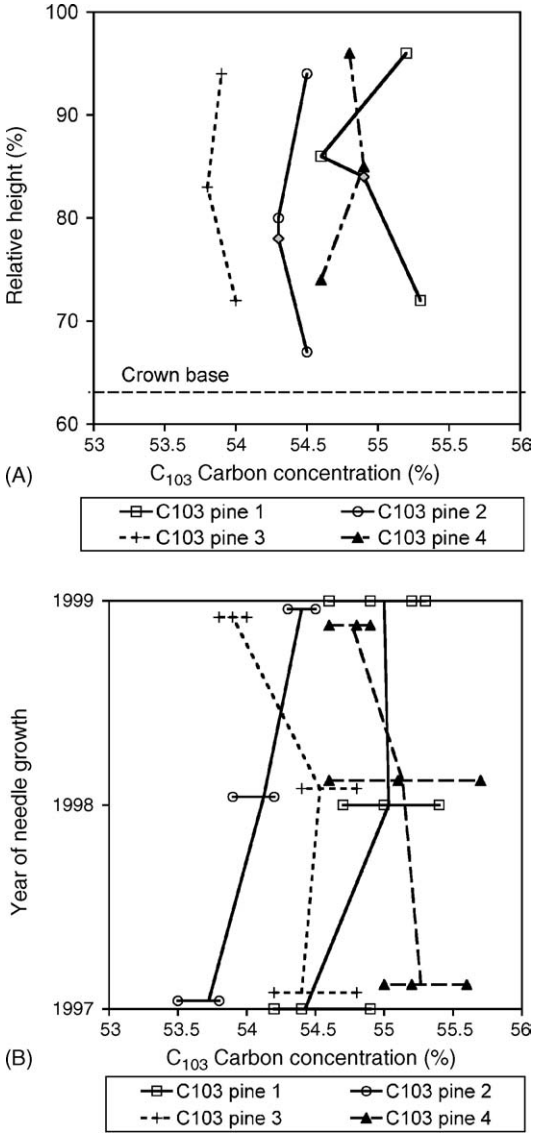

Fig. 5. Carbon concentration C_{103} as a function of relative height or year of growth for needles. (A) the grey rhombuses are for branches inserted at the base of the second cycle. (B) the dots are slightly shifted on the y axis for improved display. The lines join up the means for each year for a given pine.

average C_{65} value was 53.43 with $\sigma = 0.28\%$. Underestimation reached 6.4% when compared with the result using 50% as the carbon concentration.

3.6. Carbon concentration in roots: wood and bark

The C_{103} values for taproot wood and trunk sapwood were similar, certainly because the taproot is a continuation of the trunk axis (Fig. 3A). However, a t-test comparison of means between the 21 values from taproots and the 16 values from stems below the crown showed that C_{103} was significantly lower in the taproot, by 0.54% ($t = 2.78$, $p = 0.009$). Neither C_{103} nor C_{65} values showed any significant trend at the 5% level as a function of the depth or diameter of the taproot. The WMCC for this wood was therefore the C_{65} mean, i.e. 51.72% with $\sigma = 0.61\%$.

C_{103} values from the complete bark of the taproot were intermediate between the carbon concentration of stem phloem and bark, because the two compartments were not separated (Fig. 3B). As no trends were seen in these data, the WMCC for the complete bark was considered to be the mean of the seven samples: 54.87%, $\sigma = 0.80\%$.

In the wood of 2nd to 4th order roots, the diameter of root samples was more closely linked to C_{103} than either the cross section area of the root, the distance from the root base, or depth in the soil. Surface roots and sinkers exhibited the same results, which were then pooled. The relationship was non-linear and showed that C_{103} increased from the base of the root to the tip,

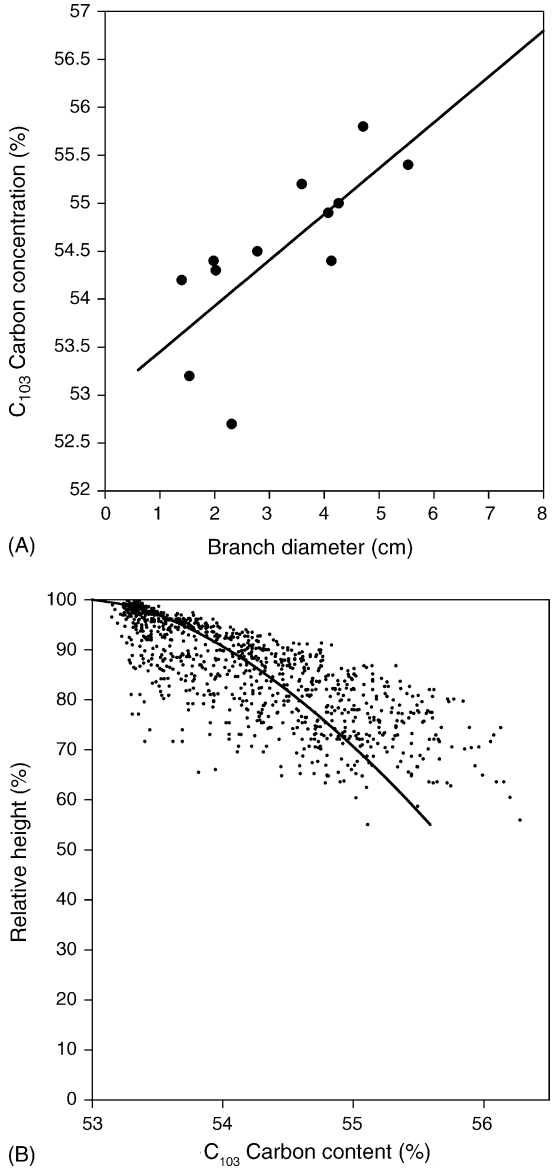

Fig. 6. Carbon concentration C_{103} for buds as a function of branch diameter close to the insertion (D5) or relative height. The equations are shown in Table 2.

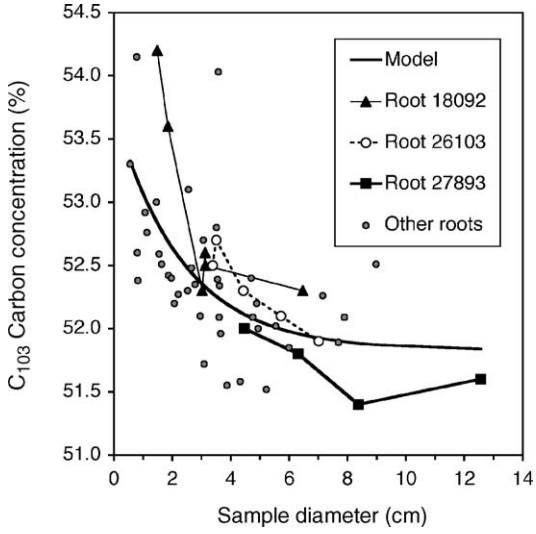

Fig. 7. Carbon concentration C_{103} in the wood of roots other than taproots as a function of the diameter of the root sample. Lines join up the data for three roots. The C_{103} model is shown in Table 2.

either within a given root, in horizontal or vertical roots or within the whole set of data (Fig. 7, Table 2). The trend is particularly clear for root sections with diameter of less than 4 cm. In thicker sections, the carbon concentration seemed to be relatively constant, as was found in taproots.

In the complete bark of 2nd to 4th order roots, an increasing trend between diameter and carbon concentration may have been similar to that found in the stem, where the diameters were within the same range as the roots. However, that relationship was significant for neither C_{103} ($r = 0.415$, $p = 0.124$, $n = 15$) nor C_{65} ($r = 0.413$, $p = 0.126$), and mean C_{103} and C_{65} values were 56.18% and 54.42%, respectively (Table 2).

The WMCC value for the entire root system was yielded by applying the previous results to all 46,000 root segments: 51.74% ($\sigma = 0.07\%$). The mean underestimation would be 3.4% with a carbon concentration of 50% (Table 3).

4. Discussion

4.1. Carbon concentration varied within and between compartments

The carbon concentration in mature *P. pinaster* is highly variable, since C_{103} values ranged from 50.6 to 60% in the present data. Compartments exhibited different carbon concentrations and in general, some gradients were seen to be related to position within the tree or the size of the tree part (Fig. 8). The carbon concentration increased from the phloem to sapwood and heartwood, reaching its maximum in the bark. Dead wood and needles did not display any trend and had respective carbon concentrations of 54.4 and 54.7%. Wood and bark together from living branches exhibited a trend which declined with branch diameter at the insertion, from circa 55.7 to 54%. This gradient led to an increasing trend with height. Conversely, buds were richer at the base of the crown (56%) than at the apex (53%). The phloem and bark together (i.e. the complete bark) of taproots showed no trend with depth, similar to taproot wood, which is also slightly poorer than the sapwood in the stem. In 2nd to 4th order of branching roots, the carbon concentration of wood fell with the diameter of the axis. No significant trend was seen in the complete bark of such roots. Finally, the weighted mean carbon content of whole 50-year-old pines was 53.21%, $\sigma = 0.07\%$, and the mean relative underestimation of the carbon content would be 6.0% taking 50% as carbon concentration.

Previous studies had shown that carbon concentration could vary both between hardwood and softwood species and between softwood species. For example, the mean stem carbon concentration of 32 species of tropical trees ranged from 44.4 to 49.4% (Elias and Potvin, 2003), 47.5% being the mean value of a chronosequence of *Fagus sylvatica* in France (Huet et al.,

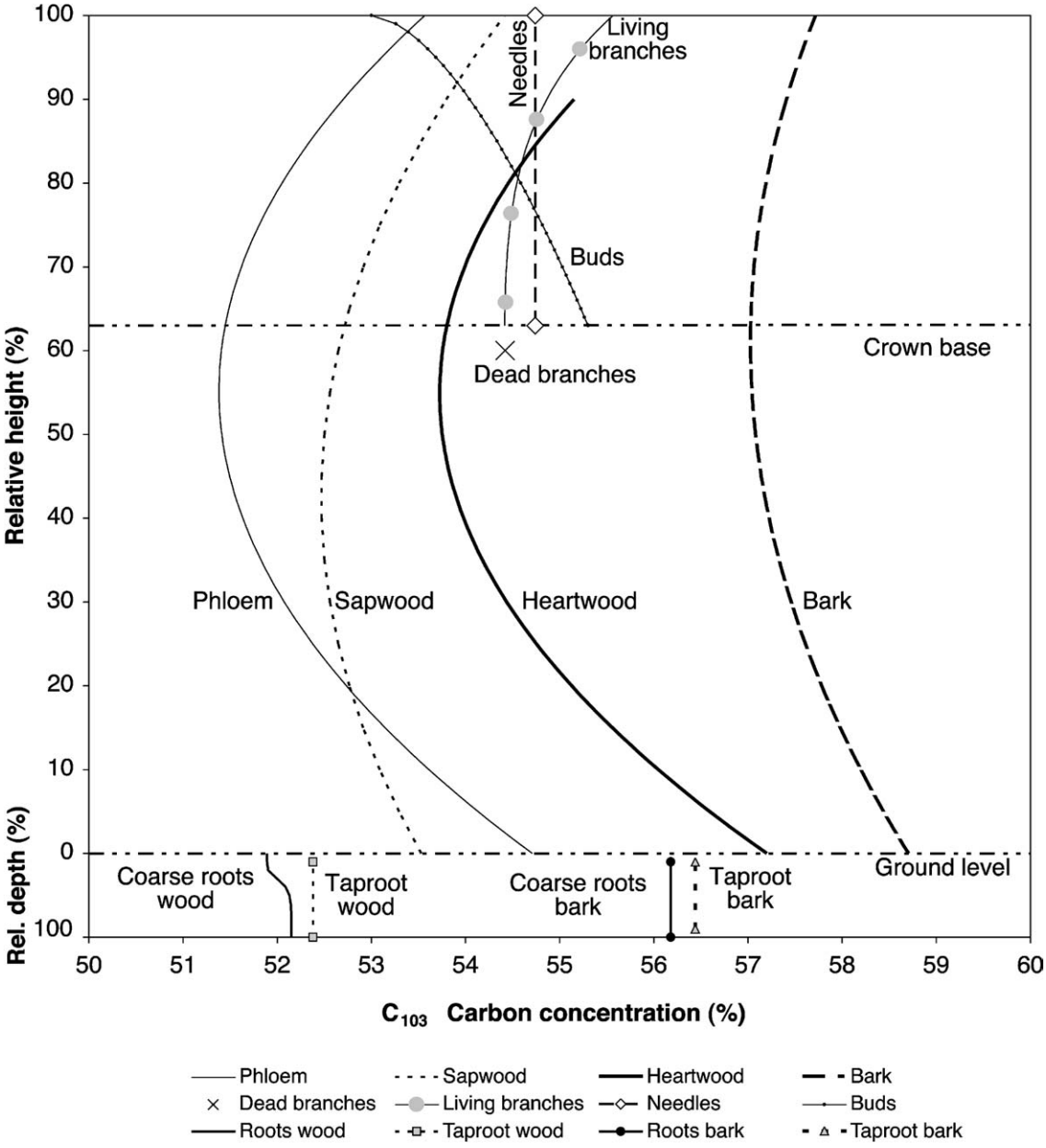

Fig. 8. Carbon concentration C_{103} as a function of relative height for stems (100% = 21.4 m), or relative depth for taproots (100% = 1 m). The equations are shown in Table 2. This figure summarizes the fitted variations within and between compartments.

2004), while it ranged from 48 to 54.4% in the wood of temperate pines (Matthews, 1993). The carbon concentration of heartwood ranged from 47.2 to 55.2% in samples which were probably collected at different heights from the stems of 19 North-American softwood species (Lamlom and Savidge, 2003). Of the different factors for variation, the species effect can be illustrated by the following differences between *Pinus sylvestris* (Janssens et al., 1999) and *P. pinaster*, respectively (this study): the carbon concentration was 48.9% versus 53.6% in stems, 51.6% versus 53.5% in living branches, 48.2% versus 53.6% in needles, 49.4% versus 52.2% in coarse roots and 52.6% versus 51.6% in medium roots. However, such comparisons may be complicated because of differences in area, silviculture techniques, sampling methods and chemical analyses.

Carbon concentration data are still very scanty with respect to *P. pinaster*. Ritson and Sochacki (2003) analysed 61 samples of composite aerial and root parts from Australia which were oven-dried at 70 °C. The mean values were lower than ours, e.g. 49.7% for Australian stems compared to the WMCC of 53.6% shown in Table 3. As the physicochemical analysis methods were the same in both studies, these differences may be due to different sampling methods, stand ages (1–47 years-old for Australian trees versus 50 for the present data), pedoclimatic conditions, or provenance (Portuguese provenance in Australia versus French provenance in our study). Indeed, another study

on a Portuguese *P. pinaster* stand found a value of 47.1% for stemwood (Balboa et al., 2005).

4.2. Carbon concentration is driven by chemical composition

Biomass is a complex plant matter, mainly composed of organic molecules with varying proportions of carbon. The following paragraphs consider the main components of softwood trees and their carbon concentration, focusing on *P. pinaster* when possible. In most cases, the sum of the percentages of different components differs slightly from 100% because the extractions were not performed successively on the same sample, and the chemical methods are not perfectly specific to one type of molecules. The weight proportion of carbon in a molecule will be referred to as C%, e.g. C% = 27.3% in CO_2.

4.2.1. Main biochemical components of softwoods

The chemical composition of wood varies as a function of tree part (root, stem or branch), type of wood (normal, tension or compression), geographical location, climate and soil conditions (Pettersen, 1984; Timell, 1986; Romberger et al., 2004). Many analytical data have shown that there are two principal chemical components in wood: lignin (18–35% biomass) and holocellulose (65–75%) made up of α-cellulose and hemicelluloses. Minor amounts of extraneous materials, mostly in the form of organic extractives and inorganic mineral (ash), are also present in wood, and usually account for 4–10% of biomass. Lignin and holocellulose are complex, polymeric materials and their chemical formula is not unique.

Lignin gives rigidity to the cell walls and enables terrestrial plants to develop upright forms. Softwood lignin is a phenolic polymer in which monomeric guaiacylpropane units ($C_{10}H_{14}O_3$, i.e. C% = 65.9%) are the major component (>90%) (Pettersen, 1984; Higuchi, 1997). Elemental analysis of *Picea abies* milled wood lignin indicates a composition of $C_9H_{7.92}O_{2.40}(OCH_3)_{0.92}$, i.e. 66.0% of carbon (Pettersen, 1984). Based on studies of biosynthesis and the analysis of various linkage types and functional groups, structural formulas for lignin have been constructed. That suggested for softwood lignin consists of 16 phenylpropane units and represents only a segment of the lignin macromolecule (Adler, 1977): $C_{162}H_{175}O_{60}$, i.e. 63.1% of carbon. It can therefore be considered that the carbon concentration of lignin is within the range of 63–66%.

α-Cellulose is a glucan polymer consisting of linear chains of 1,4-β-bonded anhydroglucose units which can be summarized as $(C_6H_{10}O_5)_x$, so that C% = 44.4%. Hemicelluloses are intimately associated with cellulose and appear to act as a structural component in the plant. Hemicelluloses are mixtures of polysaccharides synthesized in wood almost entirely from glucose, mannose, galactose, xylose, arabinose, 4-*O*-methylglucuronic acid, and galacturonic acid. Galactoglucomannans are the principal hemicelluloses found in softwoods, about 20% (Sjoestroem, 1993), and contain 42–46% of carbon. In addition to galactoglucomannans, softwoods contain an arabinoglucuronoxylan (5–10%), with 45.2% of carbon. Finally, α-cellulose and hemicelluloses can be considered to include 44% of carbon.

The extractives are composed by fats, waxes, alkaloids, proteins, simple and complex phenolics, simple sugars, pectins, mucilages, gums, resins, terpenes, starches, glycosides, saponins and essential oils. They contribute to wood properties such as colour, odour and decay resistance (Sjoestroem, 1993). Their composition is very varied and gives rise to very different carbon concentrations ranging from 40 to 88%, although most are higher than 60%.

As the carbon concentrations of these components differ, their relative proportions modify the carbon concentration in different parts of the tree. The principal factor is the lignin to holocellulose ratio because of its broad variations in softwoods, in particular, as well as an enrichment in some extractives in some compartments.

4.2.2. Stem wood

Within stem wood, four gradients are combined to modulate the carbon concentration of the wood: normal versus compression, juvenile versus mature, heartwood versus sapwood and early versus latewood (Fig. 9).

Normal softwood contains 26–32% lignin, while the lignin content of compression wood is 35–40% (Sjoestroem, 1993).

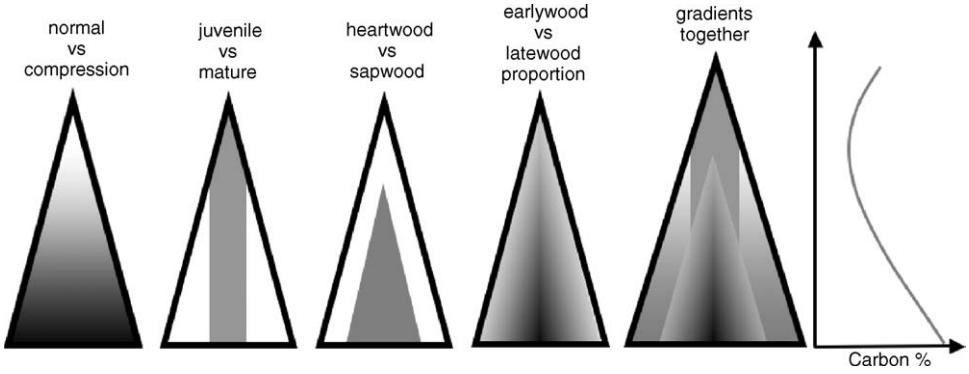

Fig. 9. Diagram of four carbon concentration gradients within the stem. The colour is darker at higher carbon concentrations. Compression wood is mainly found in at the base of the stem. Juvenile wood constitutes the 15 tree-rings at the pith. Heartwood is found in the core of the stem. Earlywood proportion decreases in line with the current age of the tree ring. The curve plots changes to the percentage of carbon in stem wood as a function of height.

For normal pine wood, the literature gives a lignin content of 25–30% (Pettersen, 1984; Kim et al., 1989). Normal wood in *P. pinaster* is within this range (26–27%), whereas its compression wood has a higher lignin content of 37% (Chantre and Da Silva Perez, 2002). The proportion of compression wood in the 12 pines of the present study was visually measured as a relative area on cross sections according to height in the stem. Using this method, it was found to range mainly between 20 and 50%. The mean value was 27–30% below the living crown, which then dropped close to 0% at the middle of the crown. Similar variations have been measured in other stands of *P. pinaster* and related to stem straightness (Radi and Castéra, 1992; Alteyrac et al., 1999). This high proportion of compression wood generally originates from poor stem straightness and may partly explain the carbon concentration values of more than 50% found in *P. pinaster*.

Juvenile wood is produced in the crown and its characteristics differ from those of mature wood produced below the crown (Romberger et al., 2004). Analyses of juvenile wood cross-sections taken at breast height in 591 14-year-old *P. pinaster* trees located in the same region as our study site gave the following mean composition: lignin: 29% of dry weight, α-cellulose: 46.4%, hemicellulose: 24.2%, and extractives: 7.2% (Pot et al., 2002). A similar type of genetic trial enabled the analysis of eighty 9-year-old *P. pinaster* trees and concluded as to lignin: 26.6%, α-cellulose: 44.3%, and extractives: 10% (Markussen et al., 2003). Such wood has a higher lignin and extractives concentration than adult wood and will therefore have a higher carbon concentration. This partly explains the higher carbon concentration found in heartwood.

The chemical and structural differences between sapwood and heartwood are known for some species. The most important changes which occur during the transformation of sapwood into heartwood in *Pinus* sp. include the loss of stored starch in ray parenchyma cells, death and lignification of parenchyma cells and the deposition of extractives. The border between sapwood and heartwood in pines is detected visually by the darker colour of heartwood, which is caused by higher levels of extractives, and in particular phenolic constituents (C% > 60%). In *Pinus contorta* var *latifolia* and *murrayana*, the extractives content of heartwood was found to be significantly higher than that of sapwood (3.30% versus 2.03%) and higher at the base of the stem (Campbell et al., 1990). One early analysis of carbon concentration in *P. sylvestris* at ground level in heartwood and sapwood indicated 54.38 and 50.18%, respectively (Daube, 1883). This 4.2% difference was similar to the 3.1% that we found at the same height. In *P. sylvestris*, Sjoestroem (1993) and Bergstrom (2003) showed that concentrations of free fatty acids (C% = 65–77%), resin acids (C% = 75%) and pinosylvin (C% = 79%) were higher in heartwood than in sapwood, while the triglyceride (C% = 65–77%) concentration was considerably lower, and starch (C% = 44.4%) was absent from heartwood. No seasonal variations could be found. Together with the lignification of heartwood, these changes are in agreement with the higher carbon concentration of heartwood and they probably occur in other species of pines, such as *P. pinaster*.

The carbon concentration of earlywood was found to be higher than in corresponding latewood in seven North-American hardwood and softwood species (Lamlom and Savidge, 2003). Like for other softwoods (e.g. *P. sylvestris* in Gindl, 2001), the latewood of *P. pinaster* has consistently higher levels of cellulose and lower levels of lignin than earlywood (Chantre and Da Silva Perez, 2002). Moreover, the ring-width latewood proportion of the pines we studied increased from the pith to the cambium from 20–30% to 40–70% at breast height, with annual variations which were probably related to climate (Lebourgeois, 2000). Both characteristics would lead to a decreasing radial trend of the carbon concentration from pith to bark.

To summarize, the higher carbon concentration in conifers fits well with their higher lignin content, which is approximately equal to 30%, versus approximately 20% in hardwoods (Lamlom and Savidge, 2003). Overall, the wood of *P. pinaster* is known by paper pulp makers to be richer in lignin and extractives and also poorer in holocellulose than other French softwoods (Chantre and Da Silva Perez, 2002). Such characteristics lead to a higher carbon concentration in the wood. The differences we found between heartwood and sapwood could be explained by three main factors: (1) the higher lignin concentration in juvenile wood than in adult wood; (2) the higher concentrations in extractives and lignin in heartwood than in sapwood; and (3) the higher lignin concentration in earlywood than in latewood, coupled with a radial variation of their proportion in tree rings. The vertical gradients in carbon concentration could result from variations of these factors according to height in the stem, including in first place the proportion of compression wood (Fig. 9).

4.2.3. Stem bark

Bark contains a similar range of chemical constituents to wood. Thus, cellulose, hemicelluloses and lignin plus extractives (including fats, sterols, terpenes, various polyphenols, etc.) are present. However, the development of specialised bark tissues also produces polymeric materials peculiar to bark (Ellis, 1973), and the bark cellulose content is half that of wood (Labosky, 1979; Vazquez et al., 1987). Conifer bark contains high levels of polyphenolic compounds, both as extractives and cell-wall components (phenolic acids). Polyphenolic tannins consist of leucocyanidin and catechin at different degrees of polymerization (Hergert, 1960; Porter, 1974). Similarly, they contain high levels of carbon (59–62%). Lignin is also present and inextricably mixed with phenolic acids (Ellis, 1973; Labosky, 1979). Together they constitute more than 40% of dry weight. A small percentage of suberin is also found in cork cell walls. Suberin is a complex lignin-like phenolic polymer built from fatty acid glycerides with a higher carbon concentration (C% ≈ 73%).

Due to its high levels of extractives, lignin and tannins, bark is that part of the pine with the highest carbon concentration. The WMCC was 55.9% in the studied *P. pinaster*, which is almost equivalent to the 54.9% found as a mean in various pine barks (Anonymous, 1972 in Ragland et al., 1991), and slightly higher than the 53.3% found in *P. radiata* in Australia (Gifford,

2000a). The bark of fifty 25-year-old *P. pinaster* trees in Portugal contained 11.4% total extractives, 1.5% suberin, 43.7% lignin-polyphenolics, and 41.7% holocellulose (Nunes et al., 1996). Another study on Portuguese *P. pinaster* concluded ca. 17% total extractives, ca. 44% lignin–polyphenolics, ca. 39% holocellulose and ca. 1% ash (Fradinho et al., 2002). Taking 44, 64, 73 and 75% as the respective carbon concentrations in these chemical compounds, these levels give rise to a bark carbon concentration ≈56% at breast height in the first case and 57.4% in the second case. This is close to the 56.3% produced by our model for a 10% relative height (Table 2).

4.2.4. Stem phloem

Phloem is made up of almost non-lignified sieve cells, and it acts as a transport agent for the results of photosynthesis (Sjoestroem, 1993; Matthews, 1993). Most photosynthates are sugars and include 40% carbon. Both characteristics are in agreement with the lowest carbon concentration found in the stem. Furthermore, the sugar concentration may exhibit a vertical gradient as a function of height, with minimum levels in the central part of the stem and maximum values at the apex and ground level (Pate et al., 1998). If, as a result of further checks, this type of gradient is shown to exist, it would be similar to the carbon concentration trend demonstrated during the present study (Fig. 3B).

4.2.5. Wood, bark, and needles of living branches

In the crown, the decreasing trend exhibited by the carbon concentration of wood and bark together in branches as a function of their diameter (Fig. 4A) has also been found in *Pinus radiata* with the same range of diameters (Gifford, 2000a). The carbon concentration of wood and bark of living branches is 53.5%, and similar to the mean value of 53.6% seen in needles. The same result was found in *P. radiata,* with values of 51.4 and 51.1%, respectively (Gifford, 2000a). Carbon analyses carried out in *Pinus strobus*, *P. resinosa* and *P. elliottii* foliage resulted in carbon concentrations of 51.9, 51.9 and 50.23%, respectively (Newman et al., 1994), which is slightly lower than the WMCC of 53.6% obtained for *P. pinaster* (Table 3). Some lower values have also been found in needles from *Pinus palustris*, *P. taeda* and *P. virginiana*, i.e. 47.9, 49.8, and 49.3%, respectively (Niinemets et al., 2002).

Compared with the wood composition of softwoods species, the chemical composition of needles is globally similar in terms of lignin concentration (22–27%), but lower with respect to α-cellulose (36–41%) and higher in ash and extractives levels (6–10%) (Newman et al., 1994; Bolster et al., 1996). Needles also contain more proteins, which have a mean carbon concentration of close to 53.5% (Niinemets et al., 2002). More specifically, the foliage of *P. pinaster* is made up of 3.1% ash, 24.4% lignin, 44.9% holocellulose, 7.45% proteins and 24.4% extractives (Vazquez et al., 1995). The latter are mainly composed of fats (C% > 70%), waxes (C% > 80%), tannins and phenolic compounds (C% > 70%). Compared with other species, the needles of *P. pinaster* appear to be poor in cellulose, within the mean for lignin and protein content, and rich in extractives with a high carbon concentration. Such characteristics are in agreement with their higher carbon concentration.

The carbon concentration in needles may be proportional to irradiance, i.e. the relative height in the crown, as has been shown in *P. palustris*, which is very intolerant to shade, but not in *P. taeda* and *P. virginiana* as they are more shade-tolerant (Niinemets et al., 2002). The LAI of *P. pinaster* stands is low and does not modify irradiance sufficiently to produce significantly different photosynthetic characteristics of mature needles within the crown (Porté and Loustau, 1998). Therefore, the vertical homogeneity of light conditions may explain the lack of trend in carbon concentration as a function of height (Fig. 5A).

4.2.6. Buds

The gradient of carbon concentration in buds was seen to decrease with height and branch diameter (Fig. 6). Two compatible hypotheses can be advanced to interpret this relationship. Firstly, the carbon concentration of buds may depend on the proportion of different types of compounds, as is the case in other compartments. At present, no data are available on the chemical composition of buds as a function of their position in the crown. Secondly, the carbon concentration of buds may be due to their mean pollen content. The bud compartment studied was indeed a pool of vegetative buds and sexual buds. Samples were collected in the field in April, prior to pollen dissemination. They seemed to contain more pollen in the lower part of the crown than in the upper part. This is in agreement with the fact that female flowers are located at the ends of the 3–4 upper whorls, and lower whorls mainly produce male flowers. The sole carbon concentration measured in pollen was $C_{103} = 55.7\%$ and $C_{65} = 54.1\%$. This value fits well with the mean carbon concentration of buds at the base of the crown and would support the second hypothesis. Based on these data, we cannot conclude as to a possible generalization of the observed gradient and it may be partly related to phenology.

4.2.7. Root wood

During the present study, the WMCC values for the wood of taproots or coarse roots were 51.7 and 51.3%, which was close to the value of 52.3% found in sapwood. On average, Gifford (2000b) also found similar carbon concentrations in the woody roots (50.4%) and sapwood (49%) of *P. radiata* in Australia. No trend was seen regarding carbon concentration values as a function of root diameter when the diameter of *P. pinaster* roots was greater than 4 cm (Fig. 7), or in taproots (Fig. 3A). Gifford (2000b) achieved the same result for *P. radiata* with the same range of root diameters. The significant but slight difference of −0.54% in the carbon concentration of wood between the taproot and sapwood may be related to the starch concentration. The pines were sampled in April, when the starch content could be high in taproots. Starch has a low carbon concentration (C% = 44.4%) and has been shown to account for 7% of root dry weight in *Pinus elliottii* in March and April (Gholz and Cropper, 1991). Such an increase in carbohydrates may be able to reduce the carbon concentration in taproots and coarse roots by 0.5–1%.

4.3. Possible effects on carbon concentration of age, genetic breeding and silvicultural techniques

In order to evaluate the generalization of our results to different applications, the variations in chemical composition published in the literature can be considered as proxy data for carbon concentration variations.

4.3.1. Tree age effect

Tree age affects the sapwood/heartwood ratio (Pinto et al., 2004) and the amount of juvenile and mature wood. Consequently, the stem of a young tree will be more similar to the upper part of an old tree than to its lower part. Therefore, the regression models found with 50-year-old pines could be applied to younger pines in their upper range of relative height. For that, the 100% relative height in Fig. 3 would correspond to 21.4 m (mean height of the four studied pines). The relative height, RH_i, of a piece of wood located at H_i metres from the ground in a pine with a total height (TH) can thus be expressed as:

$$RH_i = 100 \times \frac{(21.4 + H_i - TH)}{21.4}$$

If the pine is taller than 21.4 m, the carbon concentrations are satisfactorily predicted as a function of height despite the fact that some relative heights will be negative and some greater than 100%. The carbon concentrations in 10 samples of sapwood from a 16-year-old *P. pinaster* were only 1% lower than the model prediction, and the trend as a function of relative height was in good agreement with the hypothesis. Furthermore, the 10 repeated measures used previously to assess the precision of our analyses were performed on the AGU 8 of one 15-year-old maritime pine and their mean C_{103} value was 53.07%. This could be plotted satisfactorily with the data for the upper parts of older pines in Fig. 3A, with 72% as the relative height.

In *P. radiata* bark, factors related to tree age reduced the level of total extractable material in the bark from 32.1% at 16-year-old to 20% at 40-year-old, expressed as a percentage by weight of air-dried bark (Markham and Porter, 1973). Conversely, no clear relationship was found between tree age and total extractives at breast height in *Pinus taeda*, *echinata*, *elliottii* and *virginiana* (Labosky, 1979). The lack of data for *P. pinaster* prevents clear interpretation of the gradient in Fig. 3B in biochemical terms. However, the age of bark located on a given growth unit of a stem probably modifies its composition and an interaction may exist with the age of the tree. The bark of maritime pine is an accumulation of layers of rhytidome formed at successive ages, with a continuous desquamation of the outermost layers which may form part of an ''age effect''. Variations in carbon concentration as a function of height may originate partly from these dynamics.

4.3.2. Genetic breeding

Donaldson (1993) showed that the percentage of lignin in the cell corner middle lamina of *P. radiata* was genetically controlled. The genetic improvement of maritime pine started in the 1960s and about a third of stand regeneration is achieved with genetic material presenting a significant genetic gain in terms of growth and stem straightness (Baradat and Pastuzka, 1992). Medium heritabilities ($h^2 > 0.3$) have been observed for the lignin and α-cellulose contents, while no significant genetic effects have been detected for hemicellulose or water extractives (Pot et al., 2002). Because of biomechanics (Fourcaud et al., 2003a,b), an improvement in stem straightness is likely to lower the proportion of compression wood and the carbon concentration. Potential selection of a lower lignin content for paper pulp production will also reduce the carbon concentration. Nevertheless, these variations will be counterbalanced by an increased proportion of juvenile wood and other changes due to better radial and height growth (Danjon, 1994; Cucchi and Bert, 2003).

4.3.3. Silvicultural techniques

The effect of the number of trees per ha on the chemical composition of wood have not yet been extensively studied. Stand density did not appear to be consistently related to lower or higher klason lignin, holocellulose and α-cellulose values in the wood of *P. taeda,* but levels of alcohol–benzene extractives were significantly higher in plots with the most trees (Shupe et al., 1996). Similarly, the heartwood of slow-growing large trees was generally darker and contained greater amounts of extractives than the heartwood of young, fast-growing trees (Hillis, 1987 in Higuchi, 1997).

The stand considered during the present study was a monospecific pine stand structured in 2.5 m wide strips, 6 m apart, and was representative of a large majority of stands in the Landes region. Such a spatial structure induced poor stem straightness on most pine trees, mainly in moist sites with shallow rooting. Since the 1970s, maritime pine stands in the Landes de Gascogne forest have generally been established in lines. This has resulted in more symmetric inter-tree competition and better stem straightness. It is therefore likely to lower the carbon concentration in wood due to the lower proportion of reaction wood. Since the 1980s, improved seedlings are planted and their stem straightness is even better. Nevertheless, the better growth of such stands will obviously decrease the length of the rotation and allow a higher carbon fixation rate thanks to the higher yield.

4.4. Application to forest inventories

It is important to distinguish between percentage carbon concentration in the biomass and the relative error concerning carbon content estimates. The impact of each percent around 50% in carbon concentration is doubled when it comes to the accuracy of the final carbon content: 51% compared to 50% is only 1% greater in terms of carbon concentration but $[(100 \times 0.50) - (100 \times 0.51)]/(100 \times 0.51) \sim -2\%$ in terms of the relative error concerning the carbon content.

Some earlier estimates produced a negative bias regarding the true carbon levels stocked in forests. For the above-ground parts of *P. sylvestris* in Finland, a conversion factor of 50% would have lead to an average 5.6% smaller carbon content

value than that obtained using measured C concentrations (Laiho and Laine, 1997). In the stand we analysed during the present study, the underestimation of aboveground parts was similar, i.e. 6.7% (Table 3). However, carbon content assessments are of importance to larger areas (such as a region or country) than a single stand. Thus some of the methods recommended by the IPCC are based on National Forest Inventories (NFI) which give the standing volume V forests in entire regions (Pignard et al., 2000). The carbon content, often called carbon stock, for a species is calculated as:

$$\mathrm{St} = V \times D \times \mathrm{FEB} \times \mathrm{CAR}$$

where V is the commercial wood volume over bark (m^3) measured by the NFI, i.e. the volume of stem over bark with a top tree diameter equal to 7 cm. Among various methods, it is possible to approximate the shape of the stem using two logs described by three over-bark diameters and two lengths. D is the basic wood density at 105 °C (t m^{-3}), FEB is the expansion factor converting the biomass of stem into the total biomass of roots and aboveground tree parts, and CAR is the carbon concentration of the biomass. For French softwoods, the following values are used (Löwe et al., 2000): $D = 0.43$, FEB = 1.6, CAR = 0.5. Data from the present study enabled a comparison of previous average values with actual volume, biomass and carbon measurements. Firstly, V was compared with an accurate measurement of stem volume using about 40 diameters and annual growth unit lengths. In these 12 pines, V was on average 5.8% larger than the actual volume because this method is not specific to the tapering of maritime pine in general, and to the studied pines in particular. Secondly, D was calculated as the total biomass of wood, phloem and bark dried at 105 °C in the entire sample of pines divided by the sum of their actual volume over bark. The weighted mean stem basic density was thus 0.36 t m^{-3}. The mean national value of 0.43 would therefore lead to a 19.3% overestimation of the carbon content. Such a discrepancy is due to the considerable thickness of maritime pine bark, which contains numerous fissures. Thirdly, the expansion factor FEB was calculated as the ratio between total biomass and stem biomass for the whole sample. The weighted mean was 1.56 and FEB was not correlated with DBH ($r = 0.49$, $p = 0.10$). Thus, on average, the use of 1.6 would provide a correct estimate of the carbon content. Moreover, the ratio between total woody biomass and aboveground woody biomass, referred to as the root expansion factor (REF), was equal to 1.26 for this stand, which is within the normal range for softwood stands as a function of age, species and site (Dupouey et al., 1999). Finally, the total carbon content computed for this stand using the national values for D, FEB, CAR and volume assessment was 11.8% higher than the stock yielded using our estimation methods.

In order to simplify the assessment of carbon content for large areas, it is convenient to estimate a coefficient equivalent to $D \times \mathrm{FEB} \times \mathrm{CAR}$ and multiply it by the volume provided by the NFI. For the 50-year-old stand studied, this coefficient was 0.308 tC m^{-3} and could be applied to the whole stand as it was not significantly correlated with the circumference at breast height.

The key points requiring further investigations if this method is to be applied at a regional scale are the effect of growth on biomass allocation and carbon concentration, i.e. the effect of age, site and increment rate under the influence of thinning, genetic breeding, fertilization and global changes.

5. Conclusion

The present study offers the first comprehensive description of intra-tree variations in carbon concentration at the whole tree level. This work highlights marked differences between compartments and gradients within the compartments of a 50-year-old *P. pinaster* stand. The carbon concentration was higher than 50% in all aboveground parts and roots, and was not related to the tree size. Carbon concentration data were generally in agreement with the chemical composition and gradients of tree parts published in the literature.

The soil, climate, stand management and tree genetics in the Landes de Gascogne forest are fairly homogeneous. It is therefore likely that the present results will be valid for many mature stands in this forest. They suggest that the standard 0.5 coefficient cannot be recommended to estimate carbon sequestration in mature *P. pinaster* forest stands in south-western France, based on forest inventories. Moreover, the reliability of carbon allocation data in structural functional models will be improved by more accurate carbon content estimations (e.g. Dewar and Cannell, 1992). These tools are used to predict carbon storage and export of forest ecosystems as a function of stand management and environmental variations.

An accurate estimate of carbon content is also a key element in the life cycle assessment (LCA) of products, i.e. quantification of all environmental impacts from raw material acquisition to final disposal. Shifting the stem wood carbon concentration from 50 to 53.3% in the LCA of end-products originating from Aquitaine *P. pinaster* stands will improve their life cycle balance. This improvement will be even greater for sawn wood-based products (i.e. mainly flooring and skirting), because they are produced from lower stem parts where the carbon concentration is higher. These products have the longest lifespan and therefore constitute an efficient carbon storage.

Finally, sampling strategies for future assessments of carbon content variations between stands will benefit from this intensive within-stand characterization.

Acknowledgements

Technical assistance was mainly provided by F. Lagane, F. Bernier, M. Curtet, B. Issenhuth, C. Espagnet and H. Bignalet. We would also like to thank P. Montpied, J.-L. Dupouey, M. Courtade and many colleagues in Bordeaux for their helpful comments. Financial support was provided by the CarboAge UE project EVK2-CT-1999-00045 and the 1999' windstorm emergency fund at INRA, the French government via the ECOFOR organisation and the Conseil Régional d'Aquitaine. The Office National des Forêts managed the stand owned by the Commune de Salles.

References

Adler, E., 1977. Lignin chemistry—past, present and future. Wood Sci. Technol. 11, 169–218.

Alteyrac, J., Fourcaud, T., Castéra, P., Stokes, A., 1999. Analysis and simulation of stem righting movements in Maritime pine (*Pinus pinaster* Ait.). In: Proc. Connection between Silviculture and Wood Quality Through Modelling Approaches and Simulation Software, Third Workshop of IUFRO Working Party S5.01–04, La Londe-Les-Maures, France, 5–12 September 1999, pp. 105–111.

Anonymous, 1972. Steam/Its Generation and Use. The Babcock and Wilcox Co., New York.

Balboa, M., Rodríguez-Soalleiro, R., Alvarez-Gonzalez, J., Merino A., 2005. Temporal variations and distribution of carbon stocks in above-ground tree biomass of *Pinus radiata* and *Pinus pinaster* pure stands under different silvicultural alternatives. IUFRO Conference: Sustainable Harvest Scenarios in Forest Management, Slovakia, 25–27 August 2004.

Baradat, P., Pastuzka, P., 1992. Le pin maritime. In: Gallais, A., Bannerot, H. (Eds.), Amélioration des espèces végétales cultivées. Objectifs et critères de selection. INRA ed. Versailles, France, pp. 695–709.

Bergstrom, B., 2003. Chemical and structural changes during heartwood formation in *Pinus sylvestris*. Forestry 76, 45–53.

Bolster, K.L., Martin, M.E., Aber, J.D., 1996. Determination of carbon fraction and nitrogen concentration in tree foliage by near infrared reflectance: a comparison of statistical methods. Can. J. For. Res. 26, 590–600.

Bosc, A., Loustau, D., De Grandcourt, A., 2003. Variability of stem and branch maintenance respiration in a *Pinus pinaster* tree. Tree Physiol. 23, 227–236.

Campbell, A.G., Kim, W.J., Koch, P., 1990. Chemical variation in lodgepole pine with sapwood/heartwood, stem height, and variety. Wood Fiber Sci. 22, 22–30.

Chantre, G., Da Silva Perez, D., 2002. Variabilité naturelle des fibres du maritime et conséquences industrielles. In: ARBORA, Bordeaux, France ed., Proceedings «Pin maritime: De la fibre aux matériaux», Bordeaux, March 2002, pp. 36–61.

Cucchi, V., Bert, D., 2003. Wind-firmness in *Pinus pinaster* Ait. stands in Southwest France. Influence of stand density, fertilisation and breeding in two experimental stands damaged during the 1999 storm. Ann. For. Sci. 60, 209–226.

Danjon, F., 1994. Observed selection effects on height growth, diameter and stem form in maritime pine. Silvae Genet. 44, 10–19.

Danjon, F., Fourcaud, T., Bert, D., 2005. Root architecture and windfirmess of mature Pinus pinaster (Ait.) New Phytol. 168, 387–400.

Danjon, F., Bert, D., Godin, C., Trichet, P., 1999a. Structural root architecture of 5-year-old *Pinus pinaster* measured by 3D digitising and analysed with AMAPmod. Plant Soil 217, 49–63.

Danjon, F., Sinoquet, H., Godin, C., Colin, F., Drexhage, M., 1999b. Characterisation of structural tree root architecture using 3D digitising and AMAPmod software. Plant Soil 211, 241–258.

Daube, W., 1883. Chemische Analysen des Kern- und Splintholzes wichtiger Waldbäume. Forstliche Blätter 20, 177–192.

DERF, 2000. Indicators for the sustainable management of French forests. Ministère de l'Agriculture et de la Pêche, Paris.

Dewar, R.C., Cannell, M.G.R., 1992. Carbon sequestration in the trees, products and soils of forest plantations: an analysis using UK examples. Tree Physiol. 11, 49–71.

Dieter, M., Elsasser, P., 2002. Carbon stocks and carbon stock changes in the tree biomass of Germany's forests. Forstwiss. Centralbl. 121, 195–210.

Donaldson, L.A., 1993. Lignin distribution in wood from a progeny trial of genetically selected *Pinus radiata* D. Don. Wood Sci. Technol. 27, 391–395.

Dupouey, J.-L., Pignard, G., Badeau, V., Thimonier, A., Dhôte, J.-F., Nepveu, G., Bergès, L., Augusto, L., Belkacem, S., Nys, C., 1999. Stocks et flux de carbone dans les forêts françaises. C. R. Acad. Agric. Fr. 85, 293–310.

Elias, M., Potvin, C., 2003. Assessing inter- and intra-specific variation in trunk carbon concentration for 32 neotropical tree species. Can. J. For. Res. 33, 1039–1045.

Ellis, E., 1973. Bark chemistry, composition and reactions. In: School of Forestry, Univ., Canterbury, Christchurch, New Zealand ed., Proceedings ''Bark Utilisation Symposium'', pp. 55–73.

Fourcaud, T., Blaise, F., Lac, P., Castéra, P., De Reffye, P., 2003a. Numerical modelling of shape regulation and growth stresses in trees. Part II. Implementation in the AMAPpara software and simulation of tree growth. Trees 17, 31–39.

Fourcaud, T., Danjon, F., Dupuy, L., 2003. Numerical analysis of the anchorage of Maritime pine trees in connection with root structure. In: Ruck, B., Kottmeier, C., Mattheck, C., Quine, C., Wilhelm, G. (Eds.), Proceedings Int. Conf. ''Wind Effects on Trees'', Universität Karlsruhe, Germany, 16–18 September 2003, pp. 323–330.

Fradinho, D.M., Pascoal Neto, C., Evtuguin, D., Jorge, F.C., Irle, M.A., Gil, M.H., Jesus, J.P., 2002. Chemical characterisation of bark and of alkaline bark extracts from maritime pine grown in Portugal. Ind. Crops Prod. 16, 23–32.

Gholz, H.L., Cropper Jr., W.P., 1991. Carbohydrate dynamics in mature *Pinus elliottii* var. *elliottii* trees. Can. J. For. Res. 21, 1742–1747.

Gifford, R.M., 2000a. Carbon content of above-ground tissues of forest and woodland trees. Australian Greenhouse Office, National Carbon Accounting System, Technical Report 22, 18 pp.

Gifford, R.M., 2000b. Carbon content of woody roots. Revised analysis and a comparison with woody shoot components. Australian Greenhouse Office, National Carbon Accounting System, Technical Report 7, 11 pp.

Gindl, W., 2001. The effect of varying latewood proportion on the radial distribution of lignin content in a pine stem. Holzforschung 55 (5), 455–458.

Godin, C., Costes, E., Caraglio, Y., 1997. Exploring plant topological structure with the AMAPmod software: an outline. Silva Fenn. 31, 355–366.

Hergert, H.L., 1960. Chemical composition of tannins and polyphenols from conifer wood and bark. For. Prod. J. 57, 610–617.

Higuchi, T., 1997. Biochemistry and Molecular Biology of Wood. Springler–Verlag, Berlin, Germany.

Huet, S., Forgeard, F., Nys, C., 2004. Above- and belowground distribution of dry matter and carbon biomass of Atlantic beech (*Fagus sylvatica* L.) in a time sequence. Ann. For. Sci. 61, 683–694.

Inventaire Forestier National, 2003. Massif des Landes de Gascogne. 3e inventaire 1998–1999–2000. IFN Bordeaux, France.

Janssens, I.A., Sampson, D.A., Cermak, J., Meiresonne, L., Riguzzi, F., Overloop, S., Ceulemans, R., 1999. Above- and belowground phytomass and carbon storage in a Belgian Scots pine stand. Ann. For. Sci. 56, 81–90.

Jolivet, C., Arrouays, D., Lévèque, J., Andreux, F., Chenu, C., 2003. Organic carbon dynamics in soil particle-size separates of sandy spodosols when forest is cleared for maize cropping. Eur. J. Soil Sci. 54, 257–268.

Kim, W.J., Campbell, A.G., Koch, P., 1989. Chemical variation in lodgepole pine with latitude, elevation, and diameter class. For. Prod. J. 39, 7–12.

Kowalski, A., Sartore, M., Burlett, R., Berbigier, P., Loustau, D., 2003. The annual carbon budget of a French pine forest (*Pinus pinaster*) following harvest. Global Change Biol. 9, 1051–1065.

Labosky, P., 1979. Chemical constituents of four southern pine barks. Wood Sci. 12, 80–85.

Laiho, R., Laine, J., 1997. Tree stand biomass and carbon content in an age sequence of drained pine mires in southern Finland. For. Ecol. Manage. 93, 161–169.

Lamlom, S.H., Savidge, R.A., 2003. A reassessment of carbon content in wood: variation within and between 41 north American species. Biomass Bioenerg. 25, 381–388.

Lebourgeois, F., 2000. Climatic signals in earlywood, latewood and total ring width of Corsican pine from western France. Ann. For. Sci. 57, 155–164.

Lemoine, B., 1991. Growth and yield of Maritime pine (*Pinus pinaster* Ait.): the average dominant tree of the stand. Ann. Sci. For. 48, 593–611.

Loustau, D., Berbigier, P., Granier, A., Brunet, Y., Bariac, T., Valentini, R., 1999. Mesure du bilan de carbone des forêts européennes: cas des sites français du projet EUROFLUX. C. R. Acad. Agric. Fr. 85, 261–270.

Löwe, H., Seufert, G., Raes, F., 2000. Comparison of methods used within Member States for estimating CO_2 emissions and sinks according to UNFCCC and EU Monitoring Mechanism: forest and other wooded land. Biotechnol. Agron. Soc. Environ. 4, 315–319.

Markham, K.R., Porter, L.J., 1973. Extractives of *Pinus radiata* bark. 1. Phenolic components. N. Z. J. Sci. 16, 751–761.

Markussen, T., Fladung, M., Achere, V., Favre, J.M., Faivre-Rampant, P., Aragones, A., Perez, D.D., Harvengt, L., Espinel, S., Ritter, E., 2003. Identification of QTLs controlling growth, chemical and physical wood property traits in *Pinus pinaster* (Ait.) Silvae Genet. 52, 8–15.

Matthews, R.W., 1993. The carbon content of trees. For. Comm. Tech. Paper 4, 21 pp.

Newman, S.D., Soulia, M.E., Aber, J.D., Dewey, B., Ricca, A., 1994. Analyses of forest foliage. I. Laboratory procedures for proximate carbon fractionation and nitrogen determination. J. Near Infrared Spectrosc. 2, 5–14.

Niinemets, U., Ellsworth, D.S., Lukjanova, A., Tobias, M., 2002. Dependence of needle architecture and chemical composition on canopy light availability in three North American *Pinus* species with contrasting needle length. Tree Physiol. 22, 747–761.

Nunes, E., Quilho, T., Pereira, H., 1996. Anatomy and chemical composition of *Pinus pinaster* bark. IAWA J. 17, 141–149.

Parresol, B.R., 1999. Assessing tree and stand biomass: a review with examples and critical comparisons. For. Sci. 45 (4), 573–593.

Pate, J., Shedley, E., Arthur, D., Adams, M., 1998. Spatial and temporal variations in phloem sap composition of plantation-grown *Eucalyptus globules*. Oecologia 117, 312–322.

Pettersen, R.C., 1984. The chemical composition of wood. In: Rowel, R.M. (Ed.), The Chemistry of Wood. Advances in Chemistry Series 207, American Chemical Society, Washington, DC, USA, pp. 57–126.

Pignard, G., Dupouey, J.-L., Arrouays, D., Loustau, D., 2000. Carbon stocks estimates for French forests. Biotechnol. Agron. Soc. Environ. 4, 285–290.

Pinto, I., Pereira, H., Usenius, A., 2004. Heartwood and sapwood development within maritime pine (*Pinus pinaster* Ait.) stems. Trees—Struct. Funct. 18, 284–294.

Porté, A., Loustau, D., 1998. Variability of the photosynthetic characteristics of mature needles within the crown of a 25-year-old *Pinus pinaster*. Tree Physiol. 18, 223–232.

Porté, A., Trichet, P., Bert, D., Loustau, D., 2002. Allometric relationships for branch and tree woody biomass of maritime pine (*Pinus pinaster* Ait.) For. Ecol. Manage. 158 (1–3), 71–83.

Porter, L.J., 1974. Extractives of *Pinus radiata* bark. 2. Procyanidins constituents. N. Z. J. Sci. 17, 213–218.

Pot, D., Chantre, G., Rozenberg, P., Rodrigues, J.C., Jones, G.L., Pereira, H., Hannrup, B., Cahalan, C., Plomion, C., 2002. Genetic control of pulp and timber properties in maritime pine (*Pinus pinaster* Ait.) Ann. For. Sci. 59, 563–575.

Radi, M., Castéra, P., 1992. Qualification de la forme de deux pins maritimes en liaison avec la structure de leur bois. Ann. Sci. For. 49, 185–200.

Ragland, K.W., Aerts, D.J., Baker, A.J., 1991. Properties of wood for combustion analysis. Bioresour. Technol. 37, 161–168.

Ritson, P., Sochacki, S., 2003. Measurement and prediction of biomass and carbon content of *Pinus pinaster* trees in farm forestry plantations, southwestern Australia. For. Ecol. Manage. 175, 103–117.

Romberger, J.A., Hejnowicz, Z., Hill, J.F., 2004. Plant Structure, Function and Development. A Treatise on Anatomy and Vegetative Development with Special Reference to Woody Plants. The Balckburn Press, Caldwel, New Jersey, USA.

Sjoestroem, E., 1993. Wood Chemistry. Fundamental and Applications. Academic Press, London, England.

Shupe, T.F., Choong, E.T., Yang, C.H., 1996. The effects of silvicultural treatments on the chemical composition of plantation-grown loblolly pine wood. Wood Fiber Sci. 28, 295–300.

Timell, T.E., 1986. Compression Wood in Gymnosperms. Springer–Verlag, Berlin, Germany.

Vazquez, G., Antorrena, G., Gonzalez, J., Freire, S., 1995. Studies on the composition of *Pinus pinaster* foliage. Bioresour. Technol. 51, 83–87.

Vazquez, G., Antorrena, G., Parajo, J.C., 1987. Studies on the utilization of *Pinus pinaster* bark. Wood Sci. Technol. 21, 65–74.