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Belowground biomass and nutrient content in a 47-year-old Douglas-fir plantation

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Abstract – Biomass and nutrient content of the root system of a Douglas-fir stand were calculated using the regression technique. Nine trees, evenly distributed in the girth classes of the stand, were felled for measurements and sampling. Results were compared to published data. Statistically significant relationships between tree circumference at 1.30 m and root biomass or nutrient content were observed. The root biomass was 58 t of dry matter, which was 18% of the total stand biomass. A linear model characterized the relationships between aerial and belowground biomass of 38 Douglas-fir stands previously described in the literature. This simple relationship is very useful when using estimates of the aerial biomass of a stand to calculate the carbon storage in the belowground compartment. Nutrient concentration in the belowground compartment was lower than in the aerial biomass. However, very fine roots and mycorrhizae were not considered. Contrary to aerial biomass, very few published data were found for belowground biomass, hindering any generalization for the nutrient content of the belowground compartment.

Douglas-fir / root system / C sequestration / nutrient content

Résumé – Biomasse et minéralomasse de la partie souterraine d'un peuplement de Douglas de 47 ans. La biomasse et le contenu minéral du système racinaire d'un peuplement de Douglas ont été estimés au moyen de régressions, à partir d'un échantillonnage destructif portant sur 9 arbres répartis dans toutes les classes de diamètre à 1,30 m du peuplement. Le résultat a été comparé aux données de la littérature. Il existe des relations statistiquement significatives entre le diamètre à 1,30 m d'un arbre et sa biomasse racinaire ou son contenu en éléments nutritifs. Ces relations conduisent à un modèle prévisionnel. Les résultats indiquent que la biomasse racinaire atteint 58 t de matière sèche dans le peuplement étudié, soit 18 % de la biomasse totale du peuplement. La souche et les grosses racines représentent 89 % de cette biomasse. Un simple modèle linéaire relie la biomasse aérienne et la biomasse souterraine pour 38 peuplements de Douglas décrits dans la littérature, ce qui permet de calculer assez facilement le stockage de carbone dans le compartiment souterrain, connaissant la biomasse aérienne d'un peuplement. Pour ce qui concerne les éléments nutritifs, le compartiment souterrain est globalement relativement plus pauvre que le compartiment aérien, mais les très fines racines voire les mycorhizes n'ont pas été prises en compte dans cette étude. Trop peu de données existent pour généraliser l'information.

Douglas / système racinaire / contenu en carbone / minéralomasse

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1. INTRODUCTION

Investigations into the belowground part of plants is necessary for very different purposes:

- characterising the volume of soil from which trees take up their nutrients and delimiting the ecosystem for nutrient budget calculation [3, 22];
- quantifying C and nutrient sequestration in the underground woody structures [2, 6, 13];
- quantifying organic matter released underground into the soil by plants at thinning and/or clearcutting [7];
- quantifying the current turnover of C and nutrients due to root decomposition [1, 8, 16];
- characterising tree anchorage.

Though its significance is globally recognised, a very limited part of the research potential was focused on the root compartment. Not only because excavating root systems is a difficult task , but more probably because we lack an adequate method to properly study the dynamics and functions of this part of the ecosystem, which could represent 25% of a stand total biomass [23].

Several reviews based on the existing database of the literature led to the following conclusions:

- In a stand, there is usually a good relationship between tree diameter and belowground biomass, as it is the case for aerial components [23]. The regression method was consequently very often used to develop biomass tables and quantify root system biomass at the stand level [5, 14, 15, 17, 18, 20, 21]. Prediction at this level is reasonably accurate, depending of course on sample quality. Coarser components are usually accurately quantified whereas finest roots and mycorrhyzae are the most poorly quantified compartments [12], or are not taken into account as their biomass does not enable a good estimation of their activity.
- Even when considering the whole literature, it is not possible to identify general significant trends in terms of explanatory variables such as climate, soil type, forest species or stand age [23]. Dupouey et al. (1999) [6] calculated an expansion factor (ratio between belowground biomass and stand total biomass) based on 200 studies in order to evaluate belowground Ccontent in stands at a national level, but found no discriminating variable, especially stand age. The high variability in the expansion factor (between 1.1 to 1.4) indicates large differences between stands, without us being able to find the factors involved.

It appeared that too few situations had been studied to avoid a confounding effect between explanatory variables: more observation was needed.

The objective of the present work was to quantify the belowground biomass and nutrient content of a Douglasfir stand and to correlate it with aerial biomass accumulation. Compilation of the data for Douglas-fir found in the literature (38 case studies) was performed in order to check whether there was a simple regression line. It will be interesting to predict the belowground biomass of a stand using the aerial biomass measurement alone, as it is usually the available information.

2. MATERIALS AND METHODS

2.1. The study site is located in the Beaujolais mountains, 40 km NW of Lyon (France)

The forest stand is a plantation of Douglas-fir (*Pseudotsuga menziesii* Mirb.). Trees were 47 years old when root-systems were excavated. Measurement of aerial biomass was performed in 1992 [19]. In 1999, stand increment between 1992 and 1999 was estimated from circumference at breast height (C_{130}) inventory, and from application of biomass and nutrient tables calculated in 1992. The main characteristics of the ecosystem are the following:

- altitude: 750 m;
- mean annual rainfall: 1 000 mm;
- mean annual temperature: 7 °C;
- geology: volcanic tuff dated from the Visean period;
- soil: Typic Dystrochrept, acidic and desaturated (mean characteristics are presented in *table I*);
- stand: Douglas-fir plantation on a previously afforested site on a former agricultural land (mean stand characteristics are presented in *table II*).

2.2. Stand biomass and nutrient content measurements

The method used was described by Ranger et al. (1992, 1995) [18, 19]. The main steps were the following:

forest inventory on an area depending on mean tree size;

	Par	ticle size distrib	oution					Total	element		Free e	lement
soil layer (cm)	Clay %	Silt %	Sand %	Org. Mat. (%)	N org.(%)	C/N	Ca tot. (%)	Mg tot. (%)	K tot. (%)	P ₂ O ₅ tot.(%)	Al Tamm (%)	Fe DCB (%)
A1Ap 0-15	19.9	43.6	36.6	5.7	0.27	12.3	0.10	0.50	3.12	0.13	0.66	0.97
Ap2 15-30	19.5	44.6	36.0	3.8	0.20	11.2	0.12	0.59	3.25	0.14	0.55	0.95
A(B) 30-45	23.6	44.9	31.6	1.6	0.09	10.8	0.10	0.65	3.33	0.13	0.37	0.91
(B)1 45-65	22.0	41.9	36.2				0.14	0.74	3.46	0.12	0.29	0.90
(B)2 65-85	18.5	39.7	41.9				0.11	0.82	3.67	0.12	0.23	0.80
(B)/C 85-105	14.8	38.3	46.9				0.13	0.85	3.68	0.10	0.17	0.78
C1 105-115												
		Exchangeable element										
soil layer (cm)	pH(H ₂ O)	K (cmol _c kg ⁻¹)	Ca (cmol _c kg ⁻¹)	Mg (cmol _c kg ⁻¹)	Mn (cmol _c kg ⁻¹)	Fe (cmol _c kg ⁻¹)	Na (cmol _c kg ⁻¹)	Al (cmol _c kg ⁻¹)	BC (cmol _c kg ⁻¹)	BC/CEC(%)	CEC (cmol _c kg ⁻¹)	P ₂ O ₅ avail. (%)
A1Ap 0-15	4.4	0.24	1.12	0.17	0.20	0.02	0.05	5.94	1.64	20.3	8.1	0.02
Ap2 15-30	4.4	0.13	0.21	0.05	0.06	0.00	0.06	4.84	0.49	8.9	5.5	0.02
Ap(B) 30-45	4.4	0.11	0.17	0.05	0.05	0.00	0.06	4.68	0.43	8.1	5.3	0.02
(B)1 45-65	4.4	0.15	0.14	0.04	0.05	0.00	0.05	4.47	0.43	8.5	5.1	0.02
(B)2 65-85	4.4	0.13	0.14	0.04	0.03	0.00	0.06	4.27	0.43	8.9	4.8	0.02
(B)/C 85-105	4.4	0.12	0.13	0.07	0.04	0.00	0.05	4.44	0.42	8.3	5.1	0.01
C1 105-115	4.4	0.13	0.03	0.04	0.02	0.00	0.02	4.36	0.27	5.6	4.8	0.02

Table I. Main soil characteristics for the 60 year-old stand. (Data supplied are for air-dry material except for granulometry and total analysis expressed for 105 °C dried material).

Table II. Main stand characteristics.

Number of trees per ha	Mean tree circumference	Mean tree basal area	Basal area per ha	Mean stand height
350	137 cm	0.154 m ²	46 m ²	31 m

- selection of 12 trees belonging to every girth class derived from the inventory;
- destructive sampling for volume, biomass, water and nutrient content;
- calculation of biomass and nutrient content tables;
- application of the tables to the stand inventory to estimate stand biomass and nutrient content on a hectare basis.

2.3. Root system

2.3.1. Excavation

The selected trees were fallen to collect the whole root system. Nine trees classified according to girth classes derived from the stand inventory, were selected. Approximatively one metre deep trenches were dug halfway between each neighbouring tree. The tree was attached with a cable and pulled with a tackle. A mechanical digger was used to fell the tree. The root system was manually cleaned for fine root collection. The stem was cut and the remaining part of the root system was then lifted using the mechanical digger. Earth and stones were then removed using a high pressure cleaner. Three root classes were defined: (i) fine roots with a diameter below 1 cm, (ii) medium roots with a diameter between 1 and 4 cm and (iii) large roots with a diameter over 4 cm. The remaining part, which we called "stump", was in fact the stump and the taproot; part of the stump belongs to the aerial biomass, but is not generally harvested.

Big roots cut by the excavator or left in the outer part of the trench were collected. In the present study, accurate observation of the trenches showed that very few roots were outside the inner volume limited by the trenches, probably because the plantation was initially denser than at the time of the experiment.

All the fresh belowground compartments were weighed after cleaning, and appropriate representative samples were collected: three disks, two centimetre thick, were collected in the different classes of roots.

2.3.2. Sample treatments

Once collected and put in a plastic bag after having recorded fresh weight, the samples were oven-dried to a constant weight at 65 °C. Total N was measured by colorimetry after Kjeldahl mineralisation, P, K, Ca and Mg contents were measured after acid digestion of the finely ground material, by ICP spectrophotometry.

2.3.3. Calculation of belowground biomass and nutrient content tables

The same procedure was used as for measuring aerial biomass [19]. Tables were calculated trying to (i) eliminate bias, (ii) minimise the root mean square error and (iii) maximise the adjusted R^2 value. These tables were then applied to the stand inventory to calculate the belowground biomass on a hectare basis.

Unistat software was used for statistical analyses.

3. RESULTS AND DISCUSSION

3.1. Biomass and nutrient content tables

Provisional tables were obtained for biomass and nutrient content in the belowground compartment of the stand. Second degree polynomial regression using diameter at breast height as an explanatory variable was consistent with the observations and resulted in R^2 coefficient equal to 0.86.

As generally observed when similar calculations were performed for the different stand compartments, R^2 values were statistically different of zero at the 1% probability level for larger compartments (i.e. large roots) but not for smaller ones (i.e. fine roots). This can be explained by the fact that tree diameter is a cumulative variable, as is the case for larger compartments, but this is not the case for the finest roots, the behaviour of which mostly depends on the current tree development.

The situation was identical for nutrient content, with R^2 values ranging from 0.5 to 0.9. A rather low coeffi-

cient was observed for Ca, due to large variability between trees for this element.

The tables calculated for biomass and nutrient content of the belowground compartment are presented in *table III*.

3.2. Belowground biomass of the stand compared to the aerial part

Total belowground biomass of the stand amounted to 58 t of dry matter per ha, which represents approximatively 29 t of C for an aerial biomass of 272 t (*table IV*). This represents about 18% of the stand total biomass. The basal stem, usually not harvested, was included in the belowground biomass. Stump and large roots represented 89% of the belowground compartment, in which the aerial basal stem could represent about 15%. The finest roots represented less than 4%. The proportion of bark was about 15% for larger compartments, i.e. stump and large roots (on a dry weight basis), but was not quantified for medium and fine roots.

It is useful to compare the belowground biomass which is generally not harvested with the aerial slash, potentially easier to remove from the site (including silvicultural practices such as removing or burning stand harvest residues). In the present situation needles and branches represented about 12% of the stand total
 Table III. Main biomass and nutrient content tables calculated for belowground compartments.

Equation	R^2
Total belowground biomass (including stump)	
$TBB = 0.000155 X^2 - 0.0908243 X$	0.87
Stump biomass (bark + wood)	
$SB = 0.00006147 X^2 - 0.02911105 X$	0.88
large root biomass (bark + wood) $IR = 0.000085234 X^2 = 0.0633035 X$	0.80
Medium root biomass (bark + wood)	0.00
$MR = 0.000010785 X^2 - 0.0051797 X$	0.79
Fine root biomass (bark + wood)	
FRB = -0.000002982 + 0.00846496 X	0.04

Nutrient content of the total belowground compartments					
Ν	$= 0.00002391 \ X^2 - 0.01258838 \ X$	0.89			
Р	$= 0.0000011661 X^2 - 0.00004165 X$	0.88			
Κ	$= 0.00000799 \ X^2 - 0.00029069 \ X$	0.80			
Ca	$= 0.00001259 \ X^2 - 0.0007908 \ X$	0.67			
Mg	$= 0.00000099 \ X^2 - 0.00000365 \ X$	0.72			

Data expressed in kg of dry matter at 65 °C for biomass and in g of dry matter at 65 °C for nutrients. X = Circumference at 1.3 m in mm.

Table IV. Aerial and belowground compartmented biomass and nutrient content of the 47-year-old Douglas-fir stand (data in t per ha of dry biomass at 65 °C and in kg per ha of dry matter for nutrients).

	Biomass	Ν	Р	K	Ca	Mg	Biomass	Ν	Р	K	Ca	Mg
							b%(a+b)	b%(a+b)	b%(a+b)	b%(a+b)	b%(a+b)	b%(a+b)
Needles	13.6	207	12.9	58.2	66.3	14.1	4.1	32.5	27.7	14.9	21.1	27.3
Branches	25.9	93.7	9.4	58.3	79.6	9.8	7.8	14.7	20.2	15.0	25.4	19.0
total crown	39.5	301	22.3	117	146	23.9	11.9	47.2	48.0	29.9	46.5	46.2
Stembark	29.7	116	14.4	84	61.2	10.7	9.0	18.2	31.0	21.5	19.5	20.7
Stemwood	203.2	125	4.3	152	62.1	11	61.4	19.7	9.2	39.0	19.8	21.3
total stem	232.9	241	18.7	236	123	21.7	70.4	37.9	40.2	60.6	39.3	42.0
total aerial (a)	272.4	542	41	353	269	45.6	82.4	85.1	88.2	90.5	85.9	88.2
stumps	26.1	38.3	2.1	13.8	15	2	7.9	6.0	4.5	3.5	4.8	3.9
large roots	25.5	38.4	2.1	14.8	22.3	2.5	7.7	6.0	4.5	3.8	7.1	4.8
medium roots	4.6	10.4	0.7	5.1	4.6	0.8	1.4	1.6	1.5	1.3	1.5	1.5
fine roots	2.1	7.7	0.6	3.4	2.4	0.8	0.6	1.2	1.3	0.9	0.8	1.5
total roots (b)	58.3	94.8	5.5	37	44.3	6.1	17.6	14.9	11.8	9.5	14.1	11.8
total (a+b)	330.7	636	46.5	390	314	51.7	100	100	100	100	100	100





Figure 1. Relationship between above ground and below ground biomass for 38 case-studies of Douglas-fir stands published in the literature (\blacksquare). The present stand is figured by \Box .

biomass, which is much less than the 18% of the belowground total biomass, especially since fine and very fine roots were underestimated (the method used did not allow to harvest very fine roots).

The data found in the literature concerning Douglasfir stands on 38 sites were compiled. *Figure 1* presents the relationship between aerial and belowground biomass for the stands of these 38 study sites. A significant tendency towards a linear relationship between these two compartments ($R^2 = 0.94$) indicates that the proportion of belowground biomass is rather constant at 20%, which is consistent with the conclusion of Vogt et al. (1996) [23]. The location of the study site (presented with a specific figure on *figure 1*) is fully consistent with this general relationship.

There was some variability but it seemed rather constant in absolute value for the whole range of stands. In these conditions, the relative error is acceptable for stands with a biomass over 250 t per ha (about 20% of the mean value), but is too high for stands with low biomass (50% of the mean value). This variability originates both from real divergence from the above relationship, and, to the fact that very different methods used.

Nevertheless, this seems to indicate a relative independence of the belowground/aerial biomass ratio of Douglas-fir from parameters such as stand age or site ecology. This could be linked to the relatively limited ecological range of this species which does not tolerate

Table V. Mean concentrations of major nutrients for the belowground compartments of the 47-year-old Douglas-fir stand in the Beaujolais (data in% of dry matter at 65 °C).

		Ν	Р	Κ	Ca	Mg
Stump wood	М	0.119	0.005	0.042	0.025	0.006
	SD	0.021	0.001	0.010	0.003	0.001
Stump bark	М	0.334	0.027	0.140	0.255	0.021
	SD	0.060	0.004	0.017	0.063	0.005
Large roots wood	М	0.121	0.005	0.040	0.026	0.071
	SD	0.013	0.002	0.010	0.003	0.014
Large roots bark	М	0.314	0.029	0.157	0.387	0.027
	SD	0.033	0.004	0.024	0.141	0.005
Medium roots total	М	0.251	0.016	0.118	0.099	0.019
	SD	0.060	0.005	0.022	0.023	0.005
Fine roots total	М	0.442	0.032	0.195	0.133	0.043
	SD	0.047	0.005	0.033	0.055	0.007

M = mean; SD = square deviation.

calcareous, very dry and hydromorphic soils. On the one hand, the biomass approach conceals the effect of stand age and ecological parameters, as an identical biomass can be achieved over a period depending on soil fertility which regulates stand production. On the other hand, biomass and morphology of the root system are not necessarily related. It could be assumed that soil type interferes with morphology but not necessarily with the biomass of the root system.

3.3. Nutrient content of the belowground compared to the aerial part

The concentrations of the different compartments of the stand belowground biomass are presented in *table V*. Concentration increased for all elements when compartment size decreased, i.e. from large to fine roots [10]. Similarly to aerial compartments, root bark was far more concentrated than root wood.

Comparing aerial and belowground concentration of nutrients showed that belowground compartments were less concentrated than aerial ones. For example concentration in fine roots (as collected in this study) were not significantly higher than in large branches, except for Ca.

At the stand level, the nutrient content of the belowground compartment represents for N, P, K, Ca and

Mg respectively: 14.9, 11.8, 9.5, 14.1 and 11.8% of the stand total biomass (*table IV*). These values are relatively low, indicating the presence of a larger quantity of poorly mineralised woody structures. Nevertheless, it is necessary to consider that very fine roots were excluded from this sampling and that their concentrations were higher, closer to those of leaves [12]. These authors, calculating a total budget for fine roots, concluded that the later could represent one third of the net primary production of trees.

It is rather difficult to compare these data with the studies already published. Cole and Rapp (1980) presented only one measurement for Douglas-fir in their compilation of IBP sites. It concerned a 450-year-old native stand from Oregon (USA) [11], which is not directly comparable with a 47-year-old plantation in Europe. We measured the nutrient content of an 85-year-old spruce plantation in the Vosges mountains, eastern France [18]. The belowground biomass of this stand was relatively similar in absolute value (62 vs. 58 t), but regarding nutrient content, N content only was similar (112 vs. 95 kg). K was twice higher, P and Ca 3 times and Mg 4 times higher. In both cases, tree nutrition was optimal according to foliar diagnosis but it was impossible to determine whether luxury consumption of elements other than N occurred, depending on nutrient availability in the soil [18, 19].

Nutrient content absolute value of the belowground biomass was quite high for N, K and Ca. The depletion of these nutrients due to harvesting is only a theoretical problem in the present situation because roots are never harvested. It is interesting to focus on the contribution of the decaying root system to the nutrition of the future stand after harvesting. This is rarely taken into account with the available pool of nutrients, contrarily to the forest floor. Feger et al. (1988) showed how this disturbs the present function of the ecosystem when leading to overnitrification.

4. CONCLUSION

The relationship between aerial and belowground biomass indicates that extrapolation from aerial biomass makes it possible to evaluate the sequestration of C and nutrients in the belowground of a Douglas-fir stand. It is necessary to check this assumption for other species.

This result is probably due to the specific autecology of Douglas-fir, which has a limited ecological amplitude.

Increasing the accuracy of this relationship is necessary and possible, but a considerable effort of measurement will be needed to identify the significance of the different parameters involved in forest production.

Root system biomass represents about 20% of the stand total biomass, but nutrient sequestration is more limited when very fine roots and symbionts are not considered. The latter compartments are of great importance to current soil functioning but not to input-output budgets, because they are never removed.

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REFERENCES

[1] Bakker M.R., Effets des amendements calciques sur les racines fines de chênes (*Quercus petraea* et *robur*) : conséquences des changements dans la rhizosphère. Thèse de doctorat, sciences de la terre, Université Henri Poincaré-Nancy I, 1998, 291 p. + annexes.

[2] Cairns M.C., Brown S., Helmer E.H., Baumgardner G.A., Root biomass allocation in the world's upland forests, Oecologia 111 (1977) 1–11.

[3] Canadel J., Jackson R.B., Ehleringer J.R., Mooney H.A., Sala O.E., Schulze E.D., Maximum rooting depht of vegetation types at the global scale, Oecologia 108 (1997) 583–595.

[4] Cole D.W., Rapp M., Elemental cycling in forest ecosystems, in: Reichle D.E. (Ed.), Dynamic properties of forest ecosystems, IBP programme, Cambridge University Press, 1980, p. 341–409.

[5] Drexhage M., Chauviere M., Colin F., Nielsen C.N.N., Developpement of structural root architecture and allometry of Quercus petraea, Can. J. For. Res. 29 (1999) 600–608.

[6] Dupouey J.L., Pignard G., Badeau V., Thimonier A., Dhôte J.F., Nepveu G., Berges L., Augusto L., Belkacem S., Nys C., Stocks et flux de carbone dans les forêts françaises, C. R. Acad. Agric. No. 6 (1999) 293–310.

[7] Fahey T.J., Hugues J.W., Pu M., Arthur M.A., Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest, For. Sci. 34 (1988) 744–768.

[8] Fahey T.J., Hugues J.W., Fine roots dynamics in a northern hardwood forest ecosystem, Hubbard Brook experimental forest, NH. J. Ecol. 82 (1994) 533–548. [9] Feger K.H., Historical changes in catchment use, in: Barth H. (Ed.), Effects of land use in catchments on the acidity and ecology of natural surface waters, CEC, Air pollution report 13 (1988) 65–74.

[10] Gordon W.S., Jackson R.B., Nutrient concentrations in fine roots, Ecology 81 (2000) 275–280.

[11] Grier C.C., Cole D.W., Dyrness C.T., Frederiksen R.I., Nutrient cycling in 37 and 450-year-old Douglas-fir ecosystems, in: Integrated research in the coniferous biome, Coniferous biome bulletin No. 5, University of Washington, Seattle WA, 1974, pp. 21–34.

[12] Jackson R.B., Mooney H.A., Schulze E.D., A global budget for fine root biomass, surface area, and nutrient contents, Proc. Natl. Acad. Sci. USA 94 (1997) 7362–7366.

[13] Jackson R.B., Canadel J., Ehleringer J.R., Mooney H.A., Sala O.E., Schulze E.D, A global analysis of root distributions for terrestrial biomes, Oecologia 108 (1996) 389–411.

[14] Kapeluck P.R., van Lear D.H., A technique for estimating below-stump biomass of mature loblolly pine plantations, Can. J. For. Res. 25 (1995) 355–360.

[15] Lemoine B., Ranger J., Gelpe J., Distribution qualitative et quantitative des éléments nutritifs dans un jeune peuplement de Pin maritime (*Pinus pinaster* Ait.), Ann. Sci. For. 45 (1988) 95–116.

[16] Praag (van) H.J., Sougnez-remy S., Weissen F., Carletti G., Root turnover in a beech and a spruce stand of the Belgian Ardennes, Plant Soil 105 (1988) 87–103.

[17] Ranger J., Recherches sur les biomasses comparées de deux plantations de pin laricio de Corse avec ou sans fertilisation, Ann. Sci. For. 35 (1978) 93–115.

[18] Ranger J., Cuirin G., Bouchon J., Colin-Belgrand M., Gelhaye D., Mohamed Ahamed D., Biomasse et minéralomasse d'une plantation d'épicéa commun (*Picea abies* Karst.) de forte production dans les Vosges (France), Ann. Sci. For. 49 (1992) 651–668.

[19] Ranger J., Marques R., Colin-Belgrand M., Flammang N., Gelhaye D., The dynamics of biomass and nutrient accumulation in a Douglas-fir (*Pseudotsuga menziesii* Franco) stand studied using a chronosequence approach, For. Ecol. Manage. 72 (1995) 167–183.

[20] Santantonio D., Hermann R.K., Overton W.S., Root biomass studies in forest ecosystems, Pedobiologia., Bd. 17., S. (1977) 1–31.

[21] Satoo T., Madgwick H.A.I., Forest Biomass. Forestry Sciences. Martinus Nijhoff/DR W. Junk publishers, The Hague, 1982.

[22] Stone E.L., Kalish P.J., On the maximum extent of tree roots, For. Ecol. Manage. 46 (1991) 59–102.

[23] Vogt K.A., Vogt D.J., Palmiotto P.A, Boon P., O'Hara J., Asbjomsen H., Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species, Plant Soil 187 (1996) 159–219.

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