Estimation of nutrient content of woody plants using allometric relationships: quantifying the difference between concentration values from the literature and actuals

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Summary

The objective of this study was to evaluate the reliability of allometric methods for assessing biomass and nutrient contents of woody species at the stand scale. Allometric relationships were built from 13 stands of a woody species of moderate height (European gorse: *Ulex europaeus* L.). In eight other stands, the above-ground biomass of the species was estimated using allometric relationships. Total nutrient contents (N, P, K, Ca, Mg) of these eight stands were also computed either with nutrient concentrations obtained from local stratified samples or with values derived from the literature. The estimated above-ground biomass was consistent with the measured values obtained by complete harvest of the stand. The nutrient contents calculated using the local samples were also in agreement with measured values. Conversely, the use of nutrient concentrations values derived from the literature led to significant errors which were up to 104 per cent in the estimation of nutrient contents. We conclude that allometric methods can give reliable and accurate estimates of above-ground biomass and nutrient content of woody species, provided that the values for nutrient concentrations are obtained from local samples and not from average values found in the literature.

Introduction

In recent decades, the sustainable management of forest ecosystems has become a central issue of policy and hence of interest in the research community (Kimmins, 1974; Toman and Ashton, 1995; Fox, 2000; Hunter and Schuck, 2002). Among the many topics related to the sustainable

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management of forests, maintaining the healthy nutrient status of the ecosystem has received particular attention (McMurtrie and Dewar, 1997; Blanco *et al.*, 2005; Sverdrup *et al.*, 2006). A common method to address this aspect of sustainable forestry is to calculate the input–output nutrient budget at the stand scale (Kimmins, 1974; Ranger and Turpault, 1999; Akselsson *et al.*, 2007). In many cases, removal of nutrients through harvesting can represent a considerable proportion of nutrient budgets (e.g. Ranger *et al.*, 2002; Laclau *et al.*, 2005) and thus needs to be estimated accurately. Reliable estimates of nutrient losses caused by biomass exports are even more important in the current context of climate change. With the aim of mitigating climate change, many governments are promoting the use of forest biomass to produce energy (Rhen, 2004). Indeed, biomass could be considered as a good energy supply as the carbon emitted during energy production was previously fixed by vegetation. The carbon balance of biomass is then nil or almost nil when taking into account the fossil fuels indirectly used for biomass production, transport and transformation. However, forest biomass used to produce energy often includes harvest residues (Nunez-Regueira *et al.*, 2005). Including such residues in the exports of biomass can result in a dramatic increase in nutrient losses for forest ecosystems, although the increase in biomass harvest is small (Thompson *et al.*, 1986; Mann *et al.*, 1988; Fahey *et al.*, 1991; Son and Gower, 1992; Yanai, 1998; Sicard *et al.*, 2006). This well-documented effect supports the idea that there is a need for reliable and accurate estimates of the nutrient content of forest biomass. Unfortunately, the measurement of forest biomass and its nutrient composition is time consuming and costly. One way to achieve this other than collecting biomass and nutrient data is to build allometric relationships (e.g. Baskerville, 1972; Ranger *et al.*, 1995). In their study, Arthur *et al.* (2001) described an experiment to test allometric estimates of above-ground biomass and of nutrient contents of a forest. They concluded that the method was accurate for biomass estimates but not for estimates of certain major nutrients such as nitrogen or potassium. Allometric methods are commonly used in forest science to estimate the nutrient content of stands. Consequently, this result is important as the potential unreliability of the allometric approach could discredit the results of many studies. However, Arthur *et al.* (2001) did not collect any samples to determine the nutrient concentration of the different stand compartments (i.e. foliage, branches, trunk). Instead of using the results of direct sampling, the authors used published concentrations to calculate the estimated nutrient contents. If the nutrient concentrations of the stemwood of a given tree species appear to be quite constant whatever the context of the site (Alban, 1979; Augusto *et al.*, 2000, 2008), this is not the case of the nutrient concentrations of the canopy and particularly of the foliage (e.g. Johansson, 1995; Beier *et al.*, 1998; Oleksyn *et al.*, 1999). Therefore, we advance the hypothesis that the discrepancies observed by Arthur *et al.* (2001) between measured and estimated values were not the result of the unreliability of the method but due to the use of inaccurate nutrient concentrations. The objective of the present study was to test this hypothesis. For this purpose, we built allometric relationships for the above-ground tissues of a woody species and calculated the total stand nutrient content (N, P, K, Ca, Mg) using either direct chemical analyses of local tissues or nutrient concentrations based on values published in the literature. We compared these values with those obtained from destructive harvests (including chemical determinations) which enabled us to quantify the potential error in estimating stand nutrient contents when nutrient concentrations from the literature are used instead of *in situ* values.

Materials and methods

Study region and species

The 'Landes' forest covers more than 860 000 ha in southwest France (approximately between 43.5 and 45.5°N and 1.5°W and 0.3°E) and is the largest man-made forest in Europe. It is mainly composed of even-aged stands of maritime pine (*Pinus pinaster* Ait.) growing on very poor and sandy podzosols and arenosols (Trichet *et al.*, 1999) which were previously occupied by pastured heathlands. The site classification, which includes various soil types and understory vegetation, depends mainly on the depth of the water-table. The species studied in the present work

was *Ulex europaeus* L., commonly known as European gorse (hereafter called 'gorse'). It is an evergreen spiny woody species that occurs in all site classes of the Landes forest, except the wettest (Demounem, 1968). Adult gorses can be 4–6 m tall and has a lifespan of 10–30 years (Lee *et al.*, 1986; Rameau *et al.*, 1989; Clements *et al.*, 2001). We chose gorse because (1) its moderate height enabled us to harvest the entire above-ground biomass of complete stands within a moderate budget and (2) the species is of special ecological interest for forest managers due to its ability to fix atmospheric nitrogen (Augusto *et al.*, 2005; Cavard *et al.*, 2007).

Calibration of allometric models

The objective of the calibration was to build models based on at least 10 stands representing a continuous range of density which was representative of the densities found for the studied species. After several field surveys, 13 gorse stands were chosen and sampled (stand density (StDst) = 0.06–13.33 stems m^{-2}). The surface area of the sample plot was adapted to the StDst so as to include at least 10 stems. A total of 241 stems were harvested by cutting them at the soil surface.

For each stem, the diameter was measured with a numeric slide calliper 10 cm from the base (D_{10}; mm). As the stem cross section was not strictly circular, the arithmetic mean of two perpendicular measurements was used as the D_{10} value. Stem basal area (SB_{10}; mm^2) was calculated according to D_{10}. The height of the plant was measured (Ht; cm). The pine needles which were intercepted by the gorse spines during litter fall were delicately removed by hand. The number of broken branches was recorded. Each stem was divided into two compartments: green twigs (GT; g) and woody twigs and stem (WTS; g). The GT compartment was defined as the twigs that support the leaves. In the case of gorse, the leaves are spines. The compartments were oven dried at 65°C until the weight stabilized. Plant above-ground biomass (PAB; g) was the sum of GT and WTS.

The allometric relationships were built using two approaches: (1) the commonly used log(PAB) − log(D_{10}) relationship and (2) a linear relationship between SB_{10} and above-ground biomass (Lovenstein and Berliner, 1993).

With the first method (hereafter called 'logarithmic method'), the PAB was estimated as follows (equation 1; Figure 1a):

$$\log(\mathrm{PAB}) = (0.8717 \times \log(D_{10}^2 \times \mathrm{Ht})) - 3.7676. \quad (1)$$

The decreasing GT : PAB ratio with increasing plant size was previously observed for gorse (Hely and Forgeard, 1998; Puentes and Basanta, 2002). Therefore, equation (2) was used to estimate the biomass of the GT compartment (Figure 1b):

$$\mathrm{GT} = \left(\frac{\mathrm{GT}}{\mathrm{PAB}}\right) \times \mathrm{PAB} = \frac{((0.1271 \times D_{10}) + 2.9655)}{(D_{10} + 4.6989)} \times \mathrm{PAB}. \quad (2)$$

Finally, WTS was estimated with the logarithmic method according to equation (3), corrected according to Baskerville (1972):

$$\mathrm{WTS} = (\exp^{(1)}) - (2). \quad (3)$$

With the second method (hereafter called 'linear method'), we modified the formula proposed by Lovenstein and Berliner (1993) in order to take into account the effect of StDst which caused the WTS–SB_{10} relationship to be non-linear (equation 4; Figure 1c):

$$\mathrm{WTS} = (0.1697 \times \mathrm{StDst}) \times (\mathrm{SB}_{10}^{(1.1777 - (0.0184 \times \mathrm{StDst}))}). \quad (4)$$

In equation (4), the StDst parameter is valid for a limited range of values (2.75–10.00). For stand densities lower than 2.75 or higher than 10.00, the extreme value of the range (i.e. 2.75 or 10.00) is used for the StDst parameter of the equation (4). Beyond these limit values, the StDst showed no more impact on the allometric relationship.

Then, GT was estimated according to equation (5) (Figure 1d):

$$\mathrm{GT} = 0.343 \times \mathrm{SB}_{10}. \quad (5)$$

Finally, PAB was estimated with the linear method as the sum of WTS and GT:

$$\mathrm{PAB} = (3) + (4). \quad (6)$$

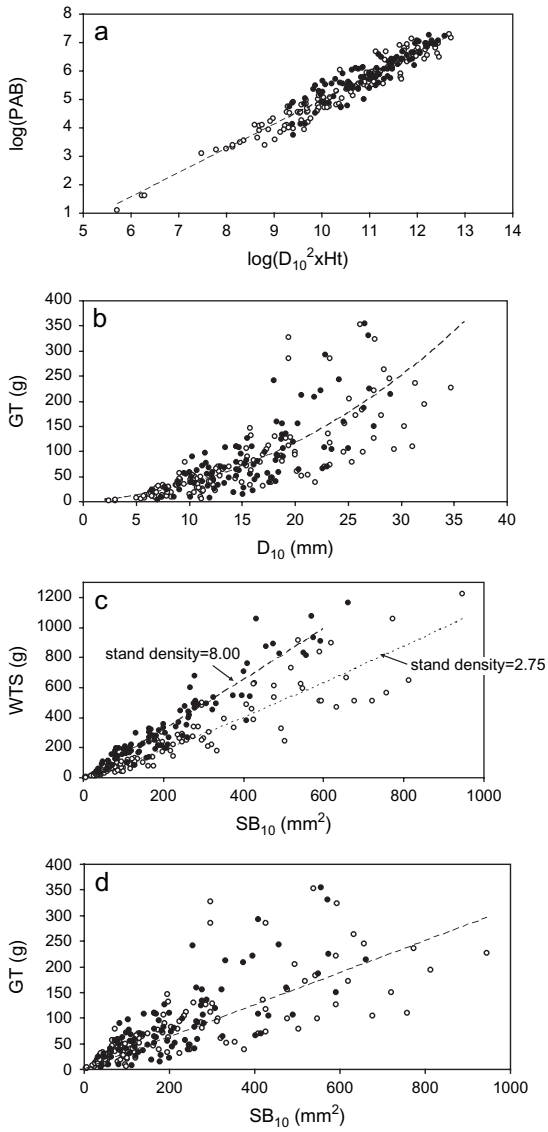

Figure 1. Allometric relationships used to estimate the above-ground biomass of the plant. D10: stem diameter (mm) measured 10 cm from its base; SB_{10} (mm^2) at 10 cm from its base; open circles: stem from a stand with a low to moderate density (0–5 stems m^{-2}; 145 stems from eight stands); closed circles: stem from a stand with a moderate to high (5–14 stems m^{-2}; 96 stems from five stands); lines: allometric relationships (see equations 1–6 in the text for Figure 1a–d).

Validation of model and estimation of nutrient content

The objective was to find at least 10 homogeneous stands of gorse (with a minimal surface area of 100 m^2) and with a continuous and representative range of density to validate the allometric relationships. Unfortunately, no homogeneous stand of at least 100 m^2 was found for the highest values of the StDst range and only eight stands were selected (StDst: 0.05–3.50 stems m^{-2}). These stands were different from the 13 stands used to calibrate the allometric relationships. The surface area of the sample plots was adapted to the local density of gorses and ranged from 160 to 600 m^2. A sample plot was set in the centre of the gorse stand. In each sample plot, all living gorses more than 10 cm tall were cut at the soil surface and transported to the laboratory. A total of 1268 stems were harvested. D_{10} and Ht were measured. The number of broken branches was recorded and the pine needles were removed by hand.

Measured above-ground biomass of the stand

After measurement of Ht and D_{10}, all the gorses from each sample plot were crushed with a Destrian-HMix and a BroiMix-12p and homogenized, and fresh weight (FW) was assessed. Five subsamples were collected to determine the water content (dried at 65°C until weight was constant). The measured stand above-ground biomass (SAB; g m^{-2}) of the sample plot was then calculated using the total FW and dry matter content obtained after drying.

Estimated above-ground biomass of the stand

PAB was calculated according to the two methods described above (equations 1 and 6). The estimated SAB; g m^{-2} was calculated as the sum of the above-ground biomass of all individual plants (SAB = $\sum$PAB).

Measured above-ground nutrient content of the stand

Five subsamples were collected from the crushed and homogenized fresh biomass and used to determine the mean nutrient concentrations of the stand. This method of estimation of the nutrient concentration is hereafter referred to as 'Total Harvest'. Nitrogen concentrations were determined by thermal conductimetry (Horneck and

Miller, 1998). For P, K, Ca and Mg, analyses were performed by dry acid digestion (Pinta, 1971) followed by inductively coupled plasma spectrophotometry (Masson and Esvan, 1995) calibrated with certified references. The nutrient content of the stand was calculated by multiplying the measured dried biomass (crushed) of the stand by the nutrient concentrations.

Estimated above-ground nutrient content of the stand

The nutrient content of the gorse stand (mg-nutrient m^{-2}) was estimated by multiplying the biomass of a compartment (GT or WTS; g m^{-2}) with its nutrient concentration (mg-nutrient g^{-1}). The nutrient concentrations were estimated from local field sampling or using values cited in the literature:

1. Local field sampling: five GT and five WTS samples were collected from five plants of different sizes. The samples were oven dried, ground and weighed before analysis. Nutrient concentrations were determined using the same methods as above. This method of estimation of the nutrient concentration is hereafter referred to as 'Field Sampling'.
2. Literature review: we investigated the literature and found only six references presenting nutrient concentrations of the study species: Egunjobi (1971b), Gehu-Franck (1974), Forgeard (1977), Lambert *et al.* (1989), Soto *et al.* (1997) and Mitchell *et al.* (2000). Mean values of nutrient concentrations of GT and WTS are presented in Table 1. References including gorse in New Zealand (Egunjobi, 1971b; Lambert *et al.*, 1989) were considered as not representative of our study context because this species is invasive in many ecological conditions in this country. The other references all had similar soil conditions, land use, ages of gorse and were all located near the Atlantic coast of Western Europe under temperate climate (Table 1). Consequently, the nutrient concentrations of GT and WTS of four references (Gehu-Franck, 1974; Forgeard, 1977; Soto *et al.*, 1997; Mitchell *et al.*, 2000) were considered as the most reliable for our purpose (hereafter referred to as 'Literature Selection') and the means of these four sets of data were used as estimated concentrations.

Table 1: Nutrient concentrations of above-ground compartments of *Ulex europaeus*

Reference	Location	Climate	Soil	Site	Mean age of gorses	Tissue	N (mg g^{-1})	P (mg g^{-1})	K (mg g^{-1})	Ca (mg g^{-1})	Mg (mg g^{-1})
Lambert *et al.* (1989)	New Zealand	Temperate	Slightly acidic, organic	Perennial pastures	3–5 years	GT	19.0	1.10	10.0	3.2	1.3
						WTS	13.0	0.80	9.0	2.8	1.2
Forgeard (1977)	Western France	Temperate Atlantic	Acidic sandy	Pastured heathland	4–6 years	GT	18.4	0.73	6.8	1.4	1.7
						WTS	7.8	0.17	2.1	1.0	0.8
Egunjobi (1971b)	New Zealand	Temperate	Leached argilized	Post-fire regeneration	6–7 years	GT	16.3	0.71	6.6	3.2	2.2
						WTS	6.0	0.21	2.8	1.2	0.8
Gehu-Franck (1974)	Western France	Temperate Atlantic	Acidic sandy	Abandoned heathland	7–10 years	GT	21.3	–	9.4	4.4	1.7
						WTS	7.6		2.2	0.9	0.6
Mitchell *et al.* (2000)	Southern England	Temperate Atlantic	Acidic sandy	Abandoned heathland	7–9 years*	AGB†	11.3	0.08	2.6	1.7	0.9
Soto *et al.* (1997)	North Western Spain	Temperate Atlantic	Acidic sandy loam	Post-fire regeneration	8 years	GT	11.8	0.50	4.6	2.3	1.6
						WTS	5.2	0.20	2.9	1.0	0.6
Present study	Western France	Temperate Atlantic	Acidic sandy	Pine stands on former heathland	5–6 years	GT	16.7	0.61	5.4	2.2	1.2
						WTS	5.9	0.16	1.5	0.9	0.5

* Estimated according to plant height and to growth curves (Lee *et al.*, 1986; L. Augusto, C. de Lavaissière, L. Jordan-Meille and M.R. Bakker).
† The above-ground biomass (AGB) was analysed as a single tissue (GT and WTS crushed and pooled together).

In addition, the use of a mean derived from data in the literature was also tested as a third method to estimate the nutrient concentration of the stands (hereafter referred to as 'All Literature'). In other words, the use of all six references in a non-selective way was also tested.

No error term of the nutrient concentrations was found in any of the six references.

Statistical analysis of data

The reliability and the accuracy of the three methods (All Literature, Literature Selection and Field Sampling) to estimate the nutrient concentrations of the above-ground biomass of the stands were tested as follows. The results of the estimated nutrient content of the stands were plotted *vs* the measured nutrient content (concentrations determined with the Total Harvest method). The scatter plots dedicated to the evaluation of the methods were of the $y = f(\hat{y})$ form as requested by Piñeiro *et al.* (2008), where y and $\hat{y}$ are the measured value and the estimated value, respectively. We followed the methodology of Mayer and Butler (1993) for statistical validation of estimated *vs* measured data, using a parametric paired t test for means and linear regression analysis testing for zero intercept and unit slope (including a simultaneous test of both conditions). The mean error of prediction (MEP) of the methods of estimation of the nutrient content was calculated according to Wallach and Goffinet (1987): $\mathrm{MEP} = \sqrt{\frac{1}{n-1}\sum_{1}^{n}(y-\hat{y})^2}$.

The modelling efficiency (ME) was quantified as follows (Mayer and Butler, 1993): $\mathrm{ME} = 1 - \frac{\sum(y_i - \hat{y}_i)^2}{\sum(y_i - \overline{y})^2}$, where $\overline{y}$ is the mean of observed values.

ME ranges from 0 (model not better than $\overline{y}$) to 1 (perfect relationship).

The estimation error of nutrient content was calculated as the $((\hat{y}_i/y_i) - 1)$ value (expressed in per cents), where y and $\hat{y}$ are the measured value and the estimated value, respectively. The mean estimation error for the eight stands was presented in the Results section as the arithmetic mean (±1 SE) of the eight estimation errors (in per cent).

As no error term of the nutrient concentration was found in the few references in the literature dedicated to gorse, it was not possible to calculate any confidence interval of the estimated nutrient content of the above-ground biomass of the stands.

Results

Above-ground biomass of the stand

The mean value of D_{10} ranged from 10.0 to 20.6 mm for each of the eight plots used for validation. The corresponding values for plant height ranged from 92 to 204 cm. The height of the tallest plant in each plot ranged between 235 and 380 cm. The contribution of chlorophyllian tissues to SAB was relatively constant among the plots: 26–35 per cent.

The estimates of SAB of the eight stands calculated with the allometric relationships were compared with the measured values (Figure 2) and there was no significant difference ($P \geq 0.304$)

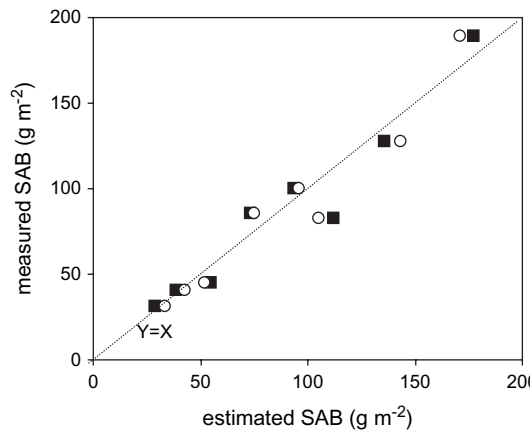

Figure 2. Validation of the allometric approach used to estimate the above-ground biomass of the stand. SAB calculated as the sum of the aboveground biomass of all the individuals of the stand (SAB = ∑PAB); open circles: SAB calculated with PAB values estimated according to the logarithmic method (equation 1 in the text); closed squares: SAB calculated with PAB values estimated according to the linear method (equation 6).

according to a parametric paired *t* test. Using less than 13 stands for the calibration of the allometric relationships led to increasing errors in the estimated SAB with a decrease in the number of stands and hence with a decrease in the range of the StDst. The error reached 54 per cent of the measured SAB when only one stand was used for the calibration of the allometric relationships (data not shown).

The accuracy and the reliability of the estimates calculated with the logarithmic approach (equation 1: MEP = 13; error of estimation = 5 per cent ± 5 per cent; ME = 0.92) were similar to those calculated with the linear approach (equation 6: MEP = 14; error of estimation = 3 per cent ± 7 per cent; ME = 0.98). It is noticeable that the latter method overestimated quite much (+36 per cent) the SAB of one stand (Figure 2; measured SAB = 82 g m^{-2}, estimated SAB: equation 1 = 105 and equation 6 = 112 g m^{-2}). This stand had the highest proportion of damaged stems (26 per cent of the stems having at least one broken branch; data not presented).

Since the two methods of estimation of the plant biomass gave very similar results, we subsequently used results for stand above-ground biomass from only one method (linear method: equation 6).

Above-ground nutrient content of the stand

The nutrient content of the eight stands used for the validation of the methods was estimated according to the three methods described in the Materials and Methods section (Field Sampling, Literature Selection and All Literature) and compared with measured nutrient content (Total Harvest). The main results for the nutrient content of SAB were summarized in Table 2. The measured contribution of the GT compartment to the nutrient content of SAB was in the following ranges: 50–61, 55–67, 55–71, 39–59 and 43–60 per cent for N, P, K, Ca and Mg, respectively.

Table 2: Estimation of the nutrient content (N, P, K, Ca, Mg) of the above-ground biomass of the stand

Method of estimating the concentration	Nutrient	Nutrient content in SAB (mg m^{-2})		Error of estimation relative to the Total Harvest method (%)	
		Mean value	Range	Mean value	Range
Total Harvest	N	803 ± 176	281–1816	–	–
	P	25 ± 6	9–63	–	–
	K	247 ± 75	64–723	–	–
	Ca	123 ± 34	41–333	–	–
	Mg	66 ± 17	23–172	–	–
Field Sampling	N	784 ± 167	265–1621	−2 ± 5	−18 to +19
	P	25 ± 5	8–54	−1 ± 5	−15 to +25
	K	249 ± 70	55–601	+4 ± 12	−17 to +67
	Ca	116 ± 29	39–285	−1 ± 8	−27 to +27
	Mg	61 ± 14	22–145	−4 ± 5	−24 to +19
Literature Selection	N	852 ± 169	273–1649	+8 ± 5	−9 to +34
	P	26 ± 5	8–51	+8 ± 7	−19 to +46
	K	319 ± 63	102–615	+54 ± 16	−15 to +126
	Ca	125 ± 25	40–240	+12 ± 9	−28 to +45
	Mg	82 ± 16	26–158	+31 ± 9	−8 to +61
All Literature	N	926 ± 184	297–1799	+17 ± 6	−1 to +45
	P	40 ± 8	13–78	+64 ± 11	+25 to +121
	K	424 ± 85	136–827	+104 ± 21	+14 to +197
	Ca	158 ± 31	51–307	+42 ± 11	−8 to +82
	Mg	91 ± 18	29–177	+47 ± 10	+3 to +80

Mean values are presented ±1 SE. Errors of estimation were calculated relatively to the Total Harvest method (see the Materials and Methods section for details).

When nutrient concentrations from Field Sampling were used, the estimated nutrient contents of the stand were in agreement with measured values (Figure 3; Table 2). The estimated : measured ratio was not significantly different from 1.0 for any of the nutrients studied ($P \geq 0.458$). Moreover, none of the statistical tests commonly used for validation showed any significant difference between estimated and measured values (Table 3).

Using a selection of the data available in the scientific literature (Literature Selection) also provided reasonably good estimates of the nutrient content even if there was a significant error for Mg content (Figure 3; Table 3). The values estimated with this method were less accurate than those obtained with Field Sampling. Indeed, ME was lower (0.61–0.91) with Literature Selection than with Field Sampling (0.79–0.93; Table 3). In the same way, the MEP was 15–109 per cent higher with Literature Selection (ratio of the MEP of the Table 3).

Using nitrogen concentrations with the All Literature, a marked overestimation of the nutrient contents was observed for P, K, Ca and Mg (Figure 3; Table 2). The discrepancy between the measured nutrient content and the estimated nutrient content was mainly due to overestimation of the nutrient concentrations in the WTS compartment (4–46 per cent and 35–162 per cent overestimation in GT and WTS, respectively). The estimated : measured ratio of the nutrient content of the stand was significantly different from 1.0 for all the nutrients studied ($P \leq 0.001$). These significant errors were confirmed by the simultaneous F test for bias and the parametric paired t test for all the nutrients (Table 3). The MEP increased by +52 to +304 per cent when All Literature values were used rather than values from Field Sampling (ratio of the MEP of the Table 3). The ME of the All Literature method was much lower (0.51–0.87) than that of the Field Sampling method (Table 3).

Discussion

In contrast to the logarithmic model (Harms and Langdom, 1976), the linear model type needs to be calibrated according to StDst. Lovenstein and Berliner (1993) did not observe this result as their range of StDst was narrow (0.06–0.13 trees m^{-2}; 0.06–13.33 stems m^{-2} in the present study). The effect of StDst on the PAB : SB_{10} ratio is supposed to be due to a variation in the permeability of sapwood (see Lopez-Serrano *et al.*, 2005). Indeed, the commonly observed linear relationship (e.g. Morataya *et al.*, 1999; Medhurst and Beadle, 2002) between biomass and sapwood area of the stem ($\approx SB_{10}$ for gorse) is often explained as the result of the limitation of the biomass development by the sap flow and so of the sapwood capacity (Shinozaki *et al.*, 1964). Once calibrated according to StDst, our results were consistent with those of Lovenstein and Berliner (1993) as they showed that the linear model type gave estimates of above-ground biomass of similar quality as the logarithmic model type. From the present study, we concluded that allometric methods in general are reliable to estimate the above-ground biomass of woody species at the stand scale (Arthur *et al.*, 2001).

The discrepancy between the concentrations reported in the literature and field measurements was larger for the WTS compartment than for the GT compartment. In the same way, values reported in the literature were more heterogeneous for the WTS compartment than for the GT compartment. Indeed, the woody twigs of gorse represented a small proportion of the WTS biomass (6–13 per cent; Egunjobi, 1971a) but represented a significant contribution to the WTS nutrient content (20–29 per cent; Egunjobi, 1971b). As illustrated by Augusto and Bert (2005), any unbalanced sampling of a heterogeneous compartment, like gorse WTS, could lead to errors in estimating the mean nutrient concentration of the compartment concerned. Hence, a possible heterogeneity among the literature references in the sampling design of the WTS compartment may have caused the high coefficient of variation and the marked discrepancy between direct measurements and the values cited in the literature. An appropriate sampling design is crucial in studies that aim to quantify the pools of nutrients in forest biomass (Bert and Danjon, 2006) and is one of the preconditions for reliable estimation of forest nutrient content. Moreover, in woody species, there is a negative relationship between the dimension of the stem and the branches and their nutrient concentration (Augusto *et al.*, 2008). This trend can be seen in Table 1 showing that the youngest

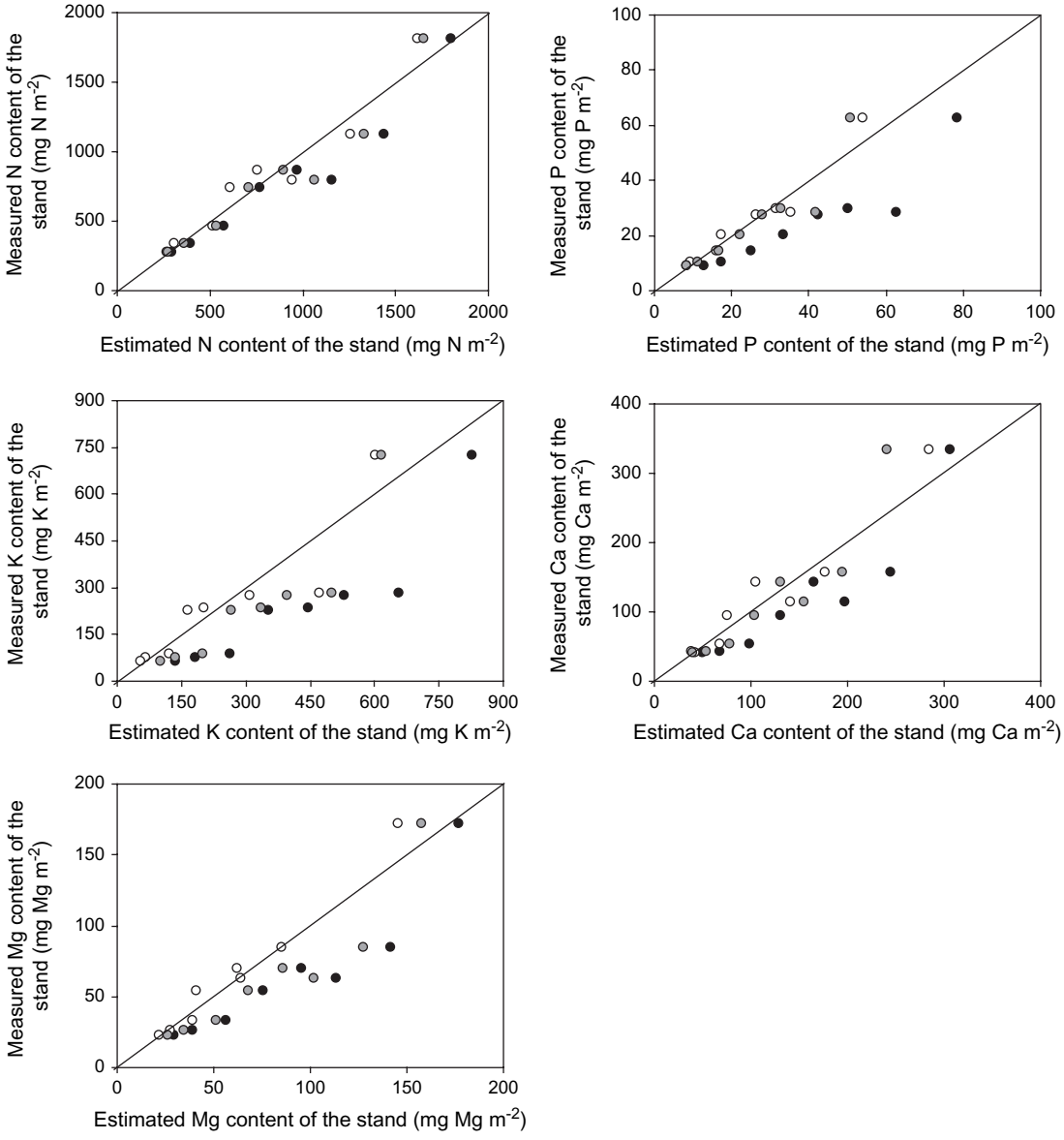

Figure 3. Estimated and measured N, P, K, Ca and Mg contents of the stand. Estimated nutrient content of the stands calculated using values of nutrient concentrations from (1) field sampling (open circles; each of the eight sampled stands had its own concentration values; Field Sampling method in the text); (2) a selection of references found in the scientific literature (grey circles; the mean concentration value calculated from selected references (n = 4) was assigned to all eight stands sampled; Literature Selection method) and (3) all references in which *Ulex europaeus* was studied (closed circles; the mean value calculated from all references (n = 6) was assigned to all eight stands sampled; All Literature method). Measured nutrient content of the stands calculated using values of nutrient concentrations obtained with the Total Harvest method.

Table 3: Statistical validation of the methods of estimation of the nutrient concentration (N, P, K, Ca, Mg) in the above-ground biomass of the stand

Method of estimating the concentration	Nutrient	Slope	Intercept	Simultaneous *F* test for bias	Parametric paired *t* test	MEP	ME
Field	N	1.03***	−1.2 (ns)	$P = 0.890$ (ns)	$P = 0.666$ (ns)	126	0.93
Sampling	P	1.08***	−1.2 (ns)	$P = 0.728$ (ns)	$P = 0.729$ (ns)	5	0.91
	K	0.97**	3.3 (ns)	$P = 0.987$ (ns)	$P = 0.929$ (ns)	91	0.79
	Ca	1.11***	−7.3 (ns)	$P = 0.581$ (ns)	$P = 0.550$ (ns)	28	0.89
	Mg	1.19***	−6.6 (ns)	$P = 0.053$ (ns)	$P = 0.226$ (ns)	12	0.91
Literature	N	1.00***	−51.5 (ns)	$P = 0.662$ (ns)	$P = 0.345$ (ns)	145	0.91
Selection	P	1.05**	−2.5 (ns)	$P = 0.884$ (ns)	$P = 0.668$ (ns)	7	0.78
	K	1.07**	−95.3 (ns)	$P = 0.193$ (ns)	$P = 0.063$ (ns)	121	0.61
	Ca	1.25**	−34.0 (ns)	$P = 0.546$ (ns)	$P = 0.888$ (ns)	43	0.63
	Mg	0.97***	−13.8 (ns)	$P = 0.152$ (ns)	$P = 0.045$*	25	0.74
All	N	0.92***	−50.5 (ns)	$P = 0.116$ (ns)	$P = 0.042$*	191	0.87
Literature	P	0.70**	−2.9 (ns)	$P = 0.002$**	$P = 0.003$**	19	0.55
	K	0.81**	−96.1 (ns)	$P = 0.005$**	$P = 0.002$**	215	0.51
	Ca	0.99**	−33.9 (ns)	$P = 0.122$ (ns)	$P = 0.032$*	53	0.70
	Mg	0.87***	−13.7 (ns)	$P = 0.026$*	$P = 0.007$**	33	0.68

'Slope' and 'intercept': the parameters of the linear regression between the estimated nutrient content of the stand and its measured nutrient content are presented. Parameters followed by *, ** or *** are significantly different from zero at $P < 0.05$, $P < 0.01$ or $P < 0.001$, respectively. In other cases, ns indicates non-significant differences; 'Simultaneous *F* test for bias': a Fisher test was used to test for zero intercept and unit slope (including a simultaneous test of both conditions) of the linear regression. Probability values followed by *, ** or *** were significant at $P < 0.05$, $P < 0.01$ or $P < 0.001$, respectively, and indicated a significant deviation of estimated nutrient content *vs* measured nutrient content; 'Parametric paired *t* test', 'MEP' and 'ME': test of differences between estimated nutrient content and measured nutrient content (see the Materials and Methods section for details).

stand (Lambert *et al.*, 1989) had much higher nutrient concentrations in the WTS compartments than those of the older stands. This difference was particularly high for K (Table 1). The contribution of this young stand to the errors quantified with the All Literature method underlines the fact that climate, soil properties, location and land use are not the only selection criteria for relevant references when a nutrient concentration value is required. Indeed, the stands cited in the literature should also be at a similar development stage as the stands to which an estimated nutrient concentration is assigned. When this selective approach is used (Literature Selection in the present study), the estimates are likely to be significantly more reliable and accurate, as were our estimated values for gorse. Although the nutrient content values were reasonably accurate, the associated prediction error was still higher than that in the case of estimates based on Field Sampling. Moreover, it should be noticed that the number of replicates of our study was quite low ($n = 8$ stands) because of the low occurrence of homogeneous dense stands in our study region. So, our experimental design could have been not strong enough to detect significant biases of low magnitude for the Literature Selection method and, to a lesser extent, for the Field Sampling method.

Arthur *et al.* (2001) concluded from their validation work that using allometric relationships to estimate above-ground biomass and nutrient content at the stand scale would lead to significant errors in the latter. Our results were consistent with those of these authors (Arthur *et al.*, 2001) but we do not share their interpretation. Indeed, as previously observed, the allometric method gives reliable and accurate estimates of the above-ground biomass of the stands. Similarly, the nutrient content of the stands significantly differed from measured values when the nutrient concentrations were based on values collected with the All Literature method. In both studies, this was

most apparent for potassium contents. However, when the nutrient concentration values were determined using stratified field sampling, that is to say one sampling operation for each type of tissue, there was good correspondence between estimated and measured nutrient contents at the stand scale. Our conclusion is that the allometric approach is a reliable and accurate method to estimate both the above-ground biomass and the nutrient content of woody species at the stand scale, provided (1) direct determination of the nutrient concentrations is included and (2) the allometric relationships take into account all stand variability such as the silvicultural regime, site fertility or genetics. We assume that this result would also apply in the case of the underground compartments of woody vegetation (additional allometric relationships for gorse are presented in Appendix 1). It is noticeable that these relationships for underground compartments were calibrated with sparse stands. StDst could modify the root : shoot ratio of woody plants (Ritson and Sochacki, 2003). Consequently, relationships in Appendix 1 should be used with caution for dense stands. Egunjobi (1969, 1971a) measured in dense gorse stands a root : shoot ratio of 0.16–0.18, whereas it was around 0.20–0.40 in the sparse stands of the present study. We may therefore assume an approximated root : shoot ratio of 0.17 in case of our dense gorse stands.

Using published nutrient concentration values is a possible alternative to field sampling, but the accuracy of the estimates is lower in this case, particularly if the studies cited in the literature are not comparable. In the latter case, estimates could significantly differ from expected values. Another alternative way of estimating the nutrient content of stands is to build direct allometric relationships between the size of the tree and its nutrient content (Thompson *et al.*, 1986; Mann *et al.*, 1988; Laclau *et al.*, 2000). In this approach, no chemical determination is necessary as long as the relationships for the study region are validated in a preliminary study.

We hypothesize that the magnitude of the potential discrepancy between estimated and real values of nutrient content depends on the nature of the tissues and their relative contribution to stand biomass. It is well established that the nutrient concentrations of the foliage tissues are significantly affected by local nutrient bioavailability (e.g. Johansson, 1995). This relationship is commonly used to assess the nutrient status of forest stands (Van den Burg, 1985; Bergmann, 1988; Bonneau, 1988; Van den Burg, 1990; Reuter *et al.*, 1997). On the other hand, nutrient concentrations of the stemwood of adult trees were seen to be quite independent of the site characteristics (Alban, 1979; Augusto *et al.*, 2000). Field trials may be helpful to explain this apparent contradiction. Indeed, when nutrient concentrations of stemwood were measured in adult trees through bulk sampling, they were not significantly modified by NPK fertilization (Heilman and Gessel, 1963; Finer and Kaunisto, 2000; Sicard *et al.*, 2006), liming (Houle *et al.*, 2002) or experimental soil acidification (DeWalle *et al.*, 1999). This reveals a high degree of homeostatic control of stemwood chemistry for most elements (De Visser, 1992; Smith and Shortle, 2001). Conversely, fertilization has often been shown to have a significant effect on the nutrient composition of foliage and sometimes of branches and stem bark (Heilman and Gessel, 1963; Nilsson and Wiklund, 1995; Ingerslev, 1999). Since the soils of our study region are particularly poor (Augusto *et al.*, 2006; Achat *et al.*, 2009), it was not surprising that the measured values of nutrient concentrations in foliage (GT) were lower than most values found in the literature, which were measured in richer ecosystems. Therefore, the more chlorophyllian tissues contribute to the nutrient content of the stand, the greater the potential discrepancy between real nutrient contents and values estimated according to published studies carried out in other contexts.

In conclusion, the way of sampling may have a great influence on the reliability of the allometric relationships commonly used to estimate the above-ground biomass and the nutrient content of a forest. If genericity is a desired property for the biomass equation, it is thus necessary to take all 'between stand' and 'within stand' variability into account (e.g. sylviculture regimes, sites, tree age and so on) when building the equation. Similarly, the accurate determination of the nutrient content of the stand requires correctly stratified sampling of the tree tissues so as to include all possible sources of variability like tree age, tissue composition, tissue dimension, climate, soil chemistry and site management (Bert and Danjon, 2006).

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Conflict of Interest Statement

None declared.

References

Achat, D.L., Bakker, M.R., Augusto, L., Meredieu, C., Saur, E. and Morel, C. 2009 Evaluation of the phosphorus status of highly P-deficient spodosols in temperate pine stands: combining isotopic dilution and extraction methods. *Biogeochemistry*. **92**, 183–200.

Akselsson, C., Westling, O., Sverdrup, H. and Gundersen, P. 2007 Nutrient and carbon budgets in forest soils as decision support in sustainable forest management. *For. Ecol. Manage.* **218**, 167–174.

Alban, D.H. 1979 Biomass and nutrient removal in short rotation intensively cultured plantations. In *Proc. Impact of Intensive Harvesting on Forest Nutrient Cycling*. A.L. Leaf (ed). State University of New York, Syracuse, NY, pp. 152–171.

Arthur, M.A., Hamburg, S.P. and Siccama, T.G. 2001 Validating allometric estimates of aboveground living biomass and nutrient contents of a northern hardwood forest. *Can. J. For. Res.* **31**, 11–17.

Augusto, L. and Bert, D. 2005 Estimating stemwood nutrient concentration with an increment borer: a potential source of error. *Forestry*. **78**, 451–455.

Augusto, L., Ranger, J., Ponette, Q. and Rapp, M. 2000 Relationships between forest tree species, stand production and stand nutrient amount. *Ann. For. Sci.* **57**, 313–324.

Augusto, L., Crampon, N., Saur, E., Bakker, M.R., Jordan-Meille, L. and Pellerin, S. *et al.* 2005 High rates of N_2-fixation of *Ulex* species in the understory of Maritime pine stands (*Pinus pinaster*) and potential effect of P-fertilisation. *Can. J. For. Res.* **35**, 1183–1192.

Augusto, L., Badeau, V., Arrouays, D., Trichet, P., Floc, J.L. and Jolivet, C. *et al.* 2006 Using a meta-analysis approach to characterize the physico-chemistry of soils at the regional scale. Example for the forest soils of the Massif Landais [in French, Abstract, Tables and Figures in English]. *Etude et Gestion des Sols*. **13**, 7–22.

Augusto, L., Meredieu, C., Bert, D., Trichet, P., Porté, A. and Bosc, A. *et al.* 2008 Improving models of forest nutrient export with equations that predict the nutrient concentration of tree compartments. *Ann. For. Sci.* **65**, 808.

Baskerville, G.L. 1972 Use of logarithmic regression in the estimation of plant biomass. *Can. J. For. Res.* **2**, 49–53.

Beier, C., Blanck, K., Bredemeier, M., Lamersdorf, N., Rasmussen, L. and Xu, Y.J. 1998 Field-scale 'clean rain' treatments to two Norway spruce stands within the EXMAN project-effects on soil solution chemistry, foliar nutrition and tree growth. *For. Ecol. Manage.* **101**, 111–123.

Bergmann, W. 1988 Ernährungsstörungen bei Kulturpflanzen. Entstehung, visuelle und analytishe diagnose W. Bergmann (ed). 2nd edn. Gustav Fisher Verlag, Stuttgart, Germany, 762 pp.

Bert, D. and Danjon, F. 2006 Carbon concentration variations in the roots, stem and crown of mature *Pinus pinaster* (Ait.). *For. Ecol. Manage.* **222**, 279–295.

Blanco, J.A., Zavala, M.A., Bosco-Imbert, J. and Castillo, F.J. 2005 Sustainability of forest management practices: evaluation through a simulation model of nutrient cycling. *For. Ecol. Manage.* **213**, 209–228.

Bonneau, M. 1988 The foliar diagnosis [in French]. *Rev. For. Fr.* **40(special volume)**, 19–26.

Cavard, X., Augusto, L., Saur, E. and Trichet, P. 2007 *In situ* effect of P fertilization on N_2 fixation rate of *Ulex europaeus*. *Ann. For. Sci.* **64**, 875–881.

Clements, D.R., Peterson, D. and Prasad, R. 2001 The biology of Canadian weeds – 112 – *Ulex europaeus* L. *Can. J. Plant Sci.* **81**, 325–337.

De Visser, P.H.B. 1992 The relations between chemical composition of oak tree rings, leaf, bark, and soil solution in a partly mixed stand. *Can. J. For. Res.* **22**, 1824–1831.

DeWalle, D.R., Tepp, J.S., Swistock, B.R., Sharpe, W.E. and Edwards, P.J. 1999 Tree-ring cation response to experimental watershed acidification in West Virginia and Maine. *J. Environ. Qual.* **28**, 299–309.

Demounem, R. 1968 Influence of the site class on the growth of the shrub species of the Landes of Gascogny forest [in French]. *C. R. Acad. Sci. Paris*. **266D**, 1501–1504.

Egunjobi, J.K. 1969 Dry matter and nitrogen accumulation in secondary successions involving gorse (*Ulex*

europaeus L.) and associated shrubs and trees. *N. Z. J. Sci.* **12**, 175–193.

Egunjobi, J.K. 1971a Ecosystem processes in a stand of *Ulex europaeus* L. I – dry matter production, litter fall and efficiency of solar energy utilization. *J. Ecol.* **59**, 31–38.

Egunjobi, J.K. 1971b Ecosystem processes in a stand of *Ulex europaeus* L. II – the cycling of chemical elements in the ecosystem. *J. Ecol.* **59**, 669–678.

Fahey, T.J., Hill, M.O., Stevens, P.A., Hornung, M. and Rowland, P. 1991 Nutrient accumulation in vegetation following conventional and whole-tree harvest of Sitka spruce plantations in North Wales. *Forestry*. **64**, 271–288.

Finer, L. and Kaunisto, S. 2000 Variation in stemwood nutrient concentrations in Scots pine growing on peatland. *Scand. J. For. Res.* **15**, 424–432.

Forgeard, F. 1977 *The heathland ecosystem in Paimpont region – study of the organic matter and nutrients cycle [in French]*. Ph.D. thesis. University of Lille II, France, 220 pp.

Fox, T.R. 2000 Sustained productivity in intensively managed forest plantations. *For. Ecol. Manage.* **138**, 187–202.

Gehu-Franck, J. 1974 Contribution to the autoecological and the synecological study of European gorse (*Ulex europaeus* L.) [in French] Ph.D. thesis, University of Lille II, France, 372 pp.

Harms, W.R. and Langdom, O.G. 1976 Development of Loblolly pine in dense stands. *For. Sci.* **22**, 331–337.

Heilman, P.E. and Gessel, S.P. 1963 The effect of nitrogen fertilization on the concentration and weight of nitrogen, phosphorus, and potassium in Douglas fir trees. *Soil Sci. Soc. Am. Proc.* **27**, 102–105.

Hely, C. and Forgeard, F. 1998 Heterogeneity of an *Ulex europaeus* heathland in relation with fire spread [in French]. *Can. J. Bot.* **76**, 804–817.

Horneck, D.A. and Miller, R.O. 1998 Determination of total nitrogen in plant tissue. In *Handbook of Reference Methods for Plant Analysis*. Y.P. Kalra (ed). CRC Press, Boca Raton, FL, pp. 75–83.

Houle, D., Duchesne, L., Moore, J.D., Laflèche, M.R. and Ouimet, R. 2002 Soil and tree-ring chemistry response to liming in a sugar maple stand. *J. Environ. Qual.* **31**, 1993–2000.

Hunter, I. and Schuck, A. 2002 Increasing forest growth in Europe – possible causes and implications for sustainable forest management. *Plant Biosyst.* **136**, 133–141.

Ingerslev, M. 1999 Aboveground biomass and nutrient distribution in a limed and fertilized Norway spruce (*Picea abies*) plantation. Part I – nutrients concentrations. *For. Ecol. Manage.* **119**, 13–20.

Johansson, M.B. 1995 The chemical composition of needle and leaf litter from Scots pine, Norway spruce and White birch in Scandinavian forest. *Forestry*. **68**, 49–62.

Kimmins, J.P. 1974 Sustained yield, timber mining, and the concept of ecological rotation, a British Columbian view. *For. Chron.* 27–31.

Laclau, J.P., Bouillet, J.P. and Ranger, J. 2000 Dynamics of biomass and nutrient accumulation in a clonal plantation of Eucalyptus in Congo. *For. Ecol. Manage.* **128**, 181–196.

Laclau, J.P., Ranger, J., Deleporte, P., Nouvellon, Y., Saint-André, L. and Marlet, S. *et al.* 2005 Nutrient cycling in a clonal stand of Eucalyptus and an adjacent savanna ecosystem in Congo. 3-Input-ouput budgets and consequences for the sustainability of the plantations. *For. Ecol. Manage.* **210**, 375–391.

Lambert, M.G., Jung, C.A., Harpster, H.W. and Lee, J. 1989 Forage shrubs in North Island hill country. 4-Chemical composition and conclusions. *N. Z. J. Exp. Agric.* **32**, 499–506.

Lee, W.G., Allen, R.B. and Johnson, P.N. 1986 Succession and dynamics of gorse (*Ulex europaeus* L.) communities in the Dunedin ecological district south island, New Zealand. *N. Z. J. Bot.* **24**, 279–292.

Lopez-Serrano, F.R., Garcia-Morote, A., Andres-Abellan, M., Tendero, A. and Del Cerro, A. 2005 Site and weather effects in allometries: a simple approach to climate change effect on pines. *For. Ecol. Manage.* **215**, 251–270.

Lovenstein, H.M. and Berliner, P.R. 1993 Biometric relationships for non-destructive above ground biomass estimations in young plantations of *Acacia salicina* Lindl. and *Eucalyptus occidentalis* Endl. *New For.* **7**, 255–273.

Mann, L.K., Johnson, D.W., West, D.C., Cole, D.W., Hornbeck, J.W. and Martin, C.W. *et al.* 1988 Effects of whole-tree and stem-only clearcutting on postharvest hydrologic losses, nutrient capital, and regrowth. *For. Sci.* **34**, 412–428.

Masson, P. and Esvan, J.M. 1995 Simultaneous determination by emission spectrometry with inductively coupled plasma of N, P, K, Ca, Cu, Mg, Fe, Mn and Zn in plants, from a single digestion [in French]. *Analusis*. **23**, 437–440.

Mayer, D.G. and Butler, D.G. 1993 Statistical validation. *Ecol. Model.* **68**, 21–32.

McMurtrie, R.E. and Dewar, R.C. 1997 Sustainable forestry: a model of the effects of nitrogen removals

in wood harvesting and fire on the nitrogen balance of regrowth eucalypt stands. *Aust. J. Ecol.* **22**, 243–255.

Medhurst, J.L. and Beadle, C.L. 2002 Sapwood hydraulic conductivity and leaf area – sapwood area relationships following thinning of a *Eucalyptus nitens* plantation. *Plant Cell Environ.* **25**, 1011–1019.

Mitchell, R.J., Auld, M.H.D., Hughes, J.M. and Marrs, R.H. 2000 Estimates of nutrient removal during heathland restoration on successional sites in Dorset, southern England. *Biol. Conserv.* **95**, 233–246.

Morataya, R., Galloway, G., Berninger, F. and Kanninen, M. 1999 Foliage biomass – sapwood (area and volume) relationships of *Tectona grandis* L.F. and *Gmelina arborea* Roxb.: silvicultural implications. *For. Ecol. Manage.* **113**, 231–239.

Nilsson, L.O. and Wiklund, K. 1995 Nutrient balance and P, K, Ca, Mg, S and B accumulation in a Norway spruce stand following ammonium sulphate application, fertilization, irrigation, drought and N-free fertilisation. *Plant Soil*. **168–169**, 437–446.

Nunez-Regueira, L., Rodriguez-Anon, J.A., Proupin, J., Mourinon, B. and Artiaga-Diaz, R. 2005 Energic study of residual forest biomass using calorimetry and thermal analysis. *J. Therm. Anal. Calorim.* **80**, 457–464.

Oleksyn, J., Reich, P.B., Karolewski, P., Tjoelker, M.G. and Chalupka, W. 1999 Nutritional status of pollen and needles of diverse *Pinus sylvestris* populations grown at sites with contrasting pollution. *Water Air Soil Pollut.* **110**, 195–212.

Piñeiro, G., Perelman, S., Guerschman, J.P. and Paruelo, J.M. 2008 How to evaluate models: observed vs. predicted or predicted vs. observed? *Ecol. Model.* **216**, 316–322.

Pinta, M. 1971 In *Spectrométrie d'absorption atomique – Applications à l'analyse chimique*. Tome II Masson (ed). Paris, France, pp. 466–539.

Puentes, A. and Basanta, M. 2002 Architecture of *Ulex europaeus*: changes in the vertical distribution of organs in relation to plant height and season. *J. Veg. Sci.* **13**, 793–802.

Rameau, J.C., Mansion, D., Dume, G., Timbal, J., Lecointe, A. and Dupont, P. *et al.* 1989 *French Forest Flora – 1 Plains and Hills [in French]*. IDF, DERF Ministère de l'Agriculture et de la Forêt, ENGREF, Nancy, France, 1785 pp.

Ranger, J. and Turpault, M.P. 1999 Input-output nutrient budgets as a diagnostic tool for sustainable forest management. *For. Ecol. Manage.* **122**, 139–154.

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

Ranger, J., Allié, S., Gelhaye, D., Pollier, B., Turpault, M.P. and Granier, A. 2002 Nutrient budgets for a rotation of a Douglas-fir plantation in the Beaujolais (France) based on a chronosequence study. *For. Ecol. Manage.* **171**, 3–16.

Reuter, D.J., Robinson, J.B. and Dutkiewicz, C. 1997 *Plant Analysis: An Interpretation Manual*. CSIRO Publishing, Collingwood, Australia, 572 pp.

Rhen, C. 2004 Chemical composition and gross calorific value of the above-ground biomass components of young *Picea abies*. *Scand. J. For. Res.* **19**, 72–81.

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

Shinozaki, K., Yoda, K., Hozumi, K. and Kira, T. 1964 A quantitative analysis of plant form – the pipe model theory. I – basic analyses. *Jpn. J. Ecol.* **14**, 97–105.

Sicard, C., Saint-André, L., Gelhaye, D. and Ranger, J. 2006 Effect of initial fertilisation on biomass, nutrient content and nutrient-use efficiency of even-aged Norway spruce and Douglas-fir stands planted under the same ecological conditions. *Trees*. **20**, 229–246.

Smith, K.T. and Shortle, W.C. 2001 Conservation of element concentration in xylem sap of red spruce. *Trees*. **15**, 148–153.

Son, Y. and Gower, S.T. 1992 Nitrogen and phosphorus distribution for five plantation species in southwestern Wisconsin. *For. Ecol. Manage.* **53**, 175–193.

Soto, B., Basanta, R. and Diaz-Fierros, F. 1997 Effects of burning on nutrient balance in an area of gorse (*Ulex europaeus* L.) scrub. *Sci. Total Environ.* **204**, 271–281.

Sverdrup, H., Thelin, G., Robles, M., Stjernquist, I. and Sorensen, J. 2006 Assessing nutrient sustainability of forest production for different tree species considering Ca, Mg, K, N, and P at Bjornstorp estate, Sweden. *Biogeochemistry*. **81**, 219–238.

Thompson, T.D., Morris, L.A., Lee, A.H. and Wells, C.G. 1986 Estimates of nutrient removal, displacement and loss resulting from harvest and site preparation of a *Pinus taeda* plantation in the Piedmont of North Carolina. *For. Ecol. Manage.* **15**, 257–267.

Toman, M.A. and Ashton, P.M.S. 1995 Sustainable forest ecosystems and management: a review article. *For. Sci.* **42**, 366–377.

Trichet, P., Jolivet, C., Arrouays, D., Loustau, D., Bert, D. and Ranger, J. 1999 Soil sustainable management for the maritime pine sylviculture in southwest France [in French]. *Etude et Gestion des Sols*. **6**, 197–214.

Van den Burg, J. 1985 *Foliar Analysis for Determination of Tree Nutrient Status: A Compilation of Literature Data [in Dutch]*. Rijksinstituut voor onderzoek in de bos en landschapsbouw "De Dorschkamp", Wageningen, The Netherlands.

Van den Burg, J. 1990 *Foliar Analysis for Determination of Tree Nutrient Status: A Compilation of Literature Data 2. Literature 1985–1989 [in Dutch]*. "De Dorschkamp" Institute for forestry and urban ecology, Wageningen, The Netherlands.

Wallach, D. and Goffinet, B. 1987 Mean squared error of prediction in models for studying ecological and agronomic systems. *Biometrics*. **43**, 561–573.

Yanai, R.D. 1998 The effect of whole-tree harvest on phosphorus cycling in the northern hardwood forest. *For. Ecol. Manage.* **104**, 281–295.

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Appendix 1

Allometric relationships for underground biomass of *Ulex europaeus*

Predicted variable	Equation	r^2
FR	$\mathrm{FR} = 0.029 \times \mathrm{SB}_{10}$	0.86
CR	$\mathrm{CR} = 0.326 \times \mathrm{SB}_{10}$	0.79
RP	$\mathrm{RP} = \frac{((-0.1808 \times D_{10}) + 19.5097)}{(D_{10} + 39.2885)}$	0.60
RS	$\mathrm{RS} = \frac{((-0.5599 \times D_{10}) + 33.4285)}{(D_{10} + 34.7066)}$	0.57

CR, coarse roots (g); FR, fine roots (g); RP, proportion of roots = (CR + FR)/(PAB + CR + FR); RS, root : shoot ratio = (CR + FR)/PAB; D_{10}, stem diameter (mm) measured 10 cm from its base; SB_{10}, stem basal area (mm^2) at 10 cm from its base and number of studied plants $n = 35$.