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Relationships between forest tree species, stand production and stand nutrient amount

Laurent Augusto[a], Jacques Ranger[a,*], Quentin Ponette[a] and Maurice Rapp[b]

[a] Institut National de la Recherche Agronomique, Centre de Recherches Forestières de Nancy, Équipe Cycles Biogéochimiques, 54280 Champenoux, France
[b] Centre National de la Recherche Scientifique, C.E.F.E.-Montpellier, Route de Mende, BP. 5051, 34033 Montpellier, France

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Abstract – Data from the literature concerning stand aerial biomass, stand nutrient amount (i.e. N, P, K, Ca and Mg) of four major forest tree species of the temperate area were compiled in order to propose simple general relationships to quantify nutrient depletion associated with biomass harvesting. The objectives was to identify the tree species effect on nutrient loss through biomass removal. Mean weighted nutrient concentrations of aerial biomass decreased rapidly until the maximum current annual increment of stands was reached ("adult stands"); the concentration then became more or less constant. For adult stands, linear relations existed between aerial biomass and their nutrient amount. Using total aerial biomass (TAB) or stem biomass including bark (SBB) as references against the corresponding nutrient amount showed: i) that correlation coefficients were higher in the latter case, ii) that nutrient amount per unit of biomass was lower for SBB than for TAB, and iii) that these relations were species-dependent. For a same SBB, species were ranked as follows: mean concentration of N and K, European beech > Douglas fir = Norway spruce = Scots pine; Ca, European beech = Norway spruce ≥ Scots pine ≥ Douglas fir; Mg, European beech ≥ Scots pine ≥ Norway spruce ≥ Douglas fir. For P, no significant difference was found for the tested species. The relationships between biomass and nutrient amount can be easily used by foresters to quantify the nutrient amount exported from a site during both thinning and harvesting operations, as well as the nutrients which remain in the logging residues left on the site and which will slowly yield available elements to the new plantation or the naturally regenerated stand.

biomass / nutrient amount / nutrient content tables / sustainable management / forest tree species

Résumé – **Relations entre les essences forestières, la biomasse et la minéralomasse.** Des données de la littérature concernant les biomasses aériennes et les contenus en N, P, K, Ca, Mg de quatre essences (sapin Douglas, épicéa commun, pin sylvestre, hêtre) ont été compilées. Les concentrations moyennes des parties aériennes en éléments majeurs diminuent avec l'âge jusqu'au stade adulte où elles se stabilisent. Pour les peuplements adultes, il existe des relations linéaires entre la biomasse aérienne et la teneur en éléments de celle-ci. Les coefficients de corrélation sont globalement plus élevés lorsque le seul tronc est considéré. Les tissus du tronc sont moins concentrés en éléments que ceux du houppier. Les relations linéaires entre les biomasses et les minéralomasses sont spécifiques à chacune des quatre essences. Pour une même biomasse de tronc, les essences se différentient selon les quantités d'éléments contenues dans ce compartiment. N et K : hêtre > sapin Douglas, épicéa commun, pin sylvestre. Ca : hêtre, épicéa commun ≥ pin sylvestre ≥ sapin Douglas, pin sylvestre. Mg : hêtre ≥ pin sylvestre ≥ épicéa commun ≥ sapin Douglas. Pour P, il n'existe pas de différence significative entre les espèces. Les relations entre biomasse et contenu minéral peuvent être directement utilisées par les aménagistes pour chiffrer les exportations par les récoltes et les restitutions par les rémanents d'exploitation.

biomasse / minéralomasse / tarif / gestion durable / essence forestière

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* Correspondence and reprints
Tel. 03 83 39 40 68; Fax. 03 83 39 40 69; e-mail: ranger@nancy.inra.fr

1. INTRODUCTION

History of land use shows that the more fertile soils were used for agricultural purposes. Then, lands abandoned by agriculture during the successive depressions were always the poorest, leaving to forests the marginal lands, i.e. those which were chemically poor, hydromorphic, stony, sloped, etc. [26, 30]. Among these different components of soil fertility, chemical fertility, i.e. nutrient availability in the short and long terms, often represents a limiting factor for forest production.

Five major nutrient fluxes have to be taken into account to quantify the variation in soil fertility of an ecosystem. Among these fluxes, three cannot be regulated by forest managers, i.e. soil mineral weathering, atmospheric deposition and deep drainage losses. As nutrient return to the site by fertilization is not common in forestry where extensive management dominates, it is obvious how important both intensity and methods of thinning and harvesting are to soil fertility maintenance. Nutrient depletion associated with forest biomass harvesting potentially leads to ecosystem impoverishment [43]. Therefore, accurate quantification of exported elements is of uppermost importance. Stem biomass is relatively easy to calculate from stand inventories and yield tables which are most often expressed in volumes [49]. Taking into account the tree crown is not common for current silviculture [45], but will become very important for ecosystem nutrient management purposes. Quantification of nutrients exported from the site during harvesting operations is more difficult, because methodologies necessitate specific, heavy logistics which cannot be applied systematically [e.g. 51]. For this reason it is useful to propose a method capable of estimating the nutrient exportation, but which does not require these type of methodologies which are inappropriate to management purposes.

The objective of this work was to compile data on usual forest stand inventories and yield table applications from the literature in order to identify simple general relations which would directly quantify the nutrients exported during harvesting. If such relations exist, they would be very useful for managers in evaluating i) the nutrients associated to harvested biomass, ii) the nutrients left in the logging residues and which will be restituted to the new stand and iii) the amount of nutrients to be restituted by fertilization in order to preserve the potential of the site and sustain future production.

Table I. Studies about biomass and nutrient content.

references		Douglas	Spruce	Pine	Beech
Alriksson and Eriksson	[3]	.	1	1	.
Belkacem et al.	[4]	.	4	.	.
Bigger and Cole	[5]	2 $^{\cancel{\text{Ca Mg}}}$	.	.	.
Binkley	[6]	3	.	.	.
Bringmark	[8]	.	.	1	.
Cole et al.	[9]	1 $^{\cancel{\text{Mg}}}$	.	.	.
Cole and Rapp	[10]	1	3	.	2
Duvigneaud et al.	[11]	.	1	.	1
Duvigneaud and Denayer	[12]	1	.	.	.
Erikson and Rosén	[13]	.	1	.	.
Feger et al.	[15]	.	1	.	.
Fornes et al.	[16]	.	2	.	.
Heilman	[20]	2 $^{\cancel{\text{Ca Mg}}}$	.	.	.
Helmisaari	[22]	.	.	3	.
Holmen	[23]	.	.	1	.
Kazimirov and Morozova	[24]	.	17	.	.
Kimmins et al.	[25]	12	.	.	.
Krapfenbauer and Buchleitner	[27]	.	3	.	.
Kreutzer	[28]	.	2	2	2
Kubin	[29]	.	1	.	.
Le Goaster et al.	[32]	.	3	.	.
Malkonen	[33]	.	1 $^{\cancel{\text{P Mg}}}$	1 $^{\text{N}}$	.
Malkonen	[34]	.	.	3 $^{\cancel{\text{Mg}}}$	.
Marchenko and Karlov	[35]	.	1	.	.
Meiwes	[36]	.	.	.	1 $^{\cancel{\text{T}}}$
Mitchell et al.	[37]	12	.	.	.
Nihlgard	[38]	.	1	.	1
Nihlgard and Lindgren	[39]	.	.	.	2
Nykvist	[41]	.	1 $^{\cancel{\text{T}}}$	.	.
Nys et al.	[42]	.	1	.	.
Oren et al.	[44]	.	1	.	.
Ovington	[46]	.	.	2	.
Ovington and Madgwick	[47]	.	.	1	.
Ovington	[48]	3	3	1	1
Ponette (in preparation)	[.]	5	.	.	.
Ranger et al.	[50]	.	1	.	.
Ranger et al.	[51]	3	.	.	.
Rodin and Bazilevich	[54]	.	6 $^{\text{N}}$	.	1 $^{\text{N}}$
Rosén	[55]	.	3 $^{\cancel{\text{T}}}$	.	.
Tamm	[61]	.	3 $^{\cancel{\text{Mg}}}$	2 $^{\cancel{\text{Mg}}}$	.
Tamm	[62]	.	1 $^{\cancel{\text{T}}}$	.	.
Tamm and Carbonnier	[63]	.	2	.	.
Turner	[64]	1 $^{\cancel{\text{Ca Mg}}}$	.	.	.
Turner and Singer	[65]	1	.	.	.
Ulrich et al.	[66]	.	.	.	1 $^{\cancel{\text{Mg}}}$
Ulrich et al.	[67]	.	.	.	2
Weaver	[69]	.	1 $^{\cancel{\text{N}}}$	.	.
Webber	[70]	1	.	.	.
Wright and Will	[72]	.	.	3	.

$^{\cancel{\text{T}}}$ = age not indicated; $^{\text{N}}$ = only N analysed; $^{\cancel{\text{N}}, \cancel{\text{P}}, \cancel{\text{Ca}}}$ or $^{\cancel{\text{Mg}}}$ = N, P, Ca or Mg not analysed.

2. MATERIALS AND METHODS

This paper is based on numerous studies of biomass and nutrient inventories in stands of following species: Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco);

Norway spruce (*Picea abies* Karsten); Scots pine (*Pinus sylvestris* L.); European Beech (*Fagus sylvatica* L.).

No selective criterion was retained about site localization, in order to obtain conclusions applicable to a large geographical area. Only stands presenting exceptional characteristics were eliminated, e.g. very old stands [1], declining stands [44], unevenaged stands, multispecies stands, or coppice with standards stands.

Main variables retained were stand age, total aerial biomass (TAB), stem biomass with bark (SBB) and the nutrient amount of TAB and SBB compartments.

Table I presents the references of the literature used in the present work. Some studies did not give all the variables selected: some of them only presented TAB or SBB, some did not consider all the nutrients (Mg was mostly absent). Data found were 48 for Douglas fir, 65 for Norway spruce, 21 for Scots pine and 14 for European beech (*table I*).

The mostly used methodology for quantifying stand biomass consisted in a destructive sampling of at least ten trees, stratified by diameter classes. From these samples, predictive and unbiased mathematical relations were established between an easy to measure dendrometrical parameter (e.g. circumference at breast height; height) and biomass or nutrient amount of the sampled tree. This is the so-called regression technique for forest-tree biomass quantification [56]. A limited amount of data concerned unpublished information (Ponette et al., in preparation). In this case the methodology used is described in Ranger et al. [51].

Analysed nutrient amounts were nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg). N was determined by variants of the Kjeldahl method. For the other nutrients, analysis were performed on ash residue obtained by dry combustion or after wet acid digestion followed by various methods of identification. The most recent studies used ICP spectrophotometry for all nutrients. Older studies usually used colorimetry for P, flame photometry for K and atomic absorption spectrophotometry for Ca and Mg.

Stands were considered as adults stands when their age was higher than the approximate age of maximum current increment. The age of maximum current increment was determined according to yield tables for volume production for France presented by Vannière [68]: Douglas fir (30 years); Scots pine (40 years); Norway spruce (50 years); European beech (80 years). Statistical analyses were made using SAS (SAS Inst., USA).

3. RESULTS

Figure 1 showed that mean nutrient concentrations (i.e. nutrient amount: biomass ratio) strongly decreased after the young stages and then stabilized. This evolution has been observed for the four species of the present study. The results showed that the mean nutrient concentration was fairly constant for adults stands (Douglas fir > 30 years; Scots pine > 40 years; Norway spruce > 50 years; European beech > 80 years). This result suggested that for a given tree species soil fertility had only marginal influence on this parameter. Data from works which compared stands of the same age with different conditions of soil fertility seem to confirm the hypothesis that soil fertility do not greatly influence the mean nutrient concentration (*table II*). However, a certain variability was observed and the constancy of the concentration is not absolute.

Linear correlation coefficients were calculated between nutrient amount and TAB or SBB for the four species and the five nutrient elements (*table III*). In order to obtain linear relationships, calculations were made only on stands older than the age limit fixed above. The majority of regressions were significant ($p < 0.05$), including species for which the number of stands was low (*figure 2*). SBB regressions had always lower *p*-values

Table II. Nutrient concentration in three tree species according to soil fertility.

tree species	reference	fertility	age yrs	TAB $t\ ha^{-1}$	N $kg\ ha^{-1}$	P $kg\ ha^{-1}$	K $kg\ ha^{-1}$	Ca $kg\ ha^{-1}$	Mg $kg\ ha^{-1}$	N/TAB $kg\ t^{-1}$	P/TAB $kg\ t^{-1}$	K/TAB $kg\ t^{-1}$	Ca/TAB $kg\ t^{-1}$	Mg/TAB $kg\ t^{-1}$
Picea abies	[48]	poor	47	140	331	37	161	212	39	2.4	0.26	1.2	1.5	0.3
Picea abies	[48]	rich	47	263	705	82	226	507	85	2.7	0.31	0.9	1.9	0.3
Platanus occidentalis	[71]	poor	3	9.2	52	10	21	46	17	5.7	1.09	2.3	5.0	1.9
Platanus occidentalis	[71]	rich	3	13.7	90	21	53	53	24	6.6	1.53	3.9	3.9	1.8
Pseudotsuga menziesii	[5]	poor	53	164.8	325	55.8	141	.	.	2.0	0.17	2.5	.	.
Pseudotsuga menziesii	[5]	rich	53	318.1	728	95	326	.	.	2.3	0.13	3.4	.	.

TAB = Total Aerial Biomass.

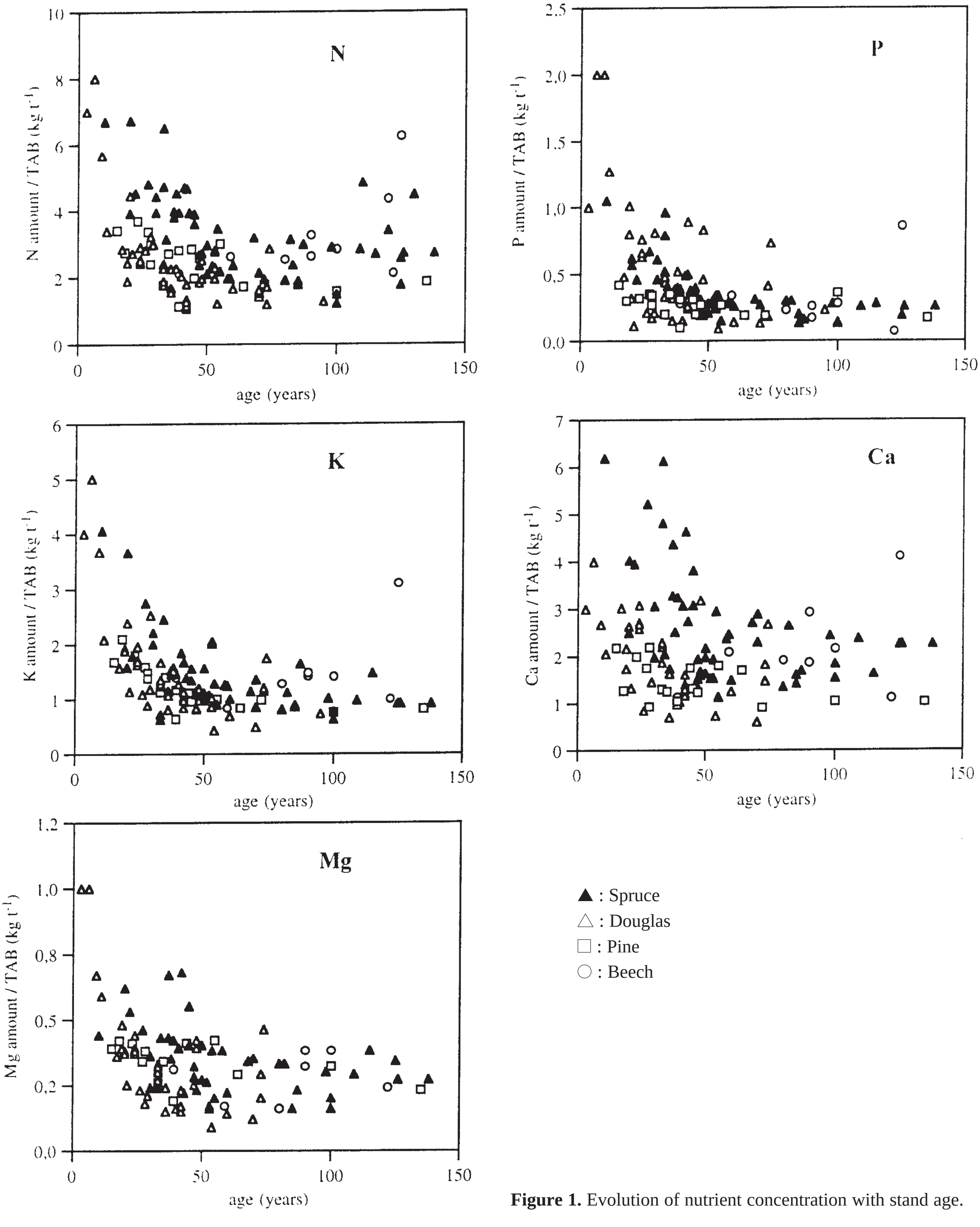

Figure 1. Evolution of nutrient concentration with stand age.

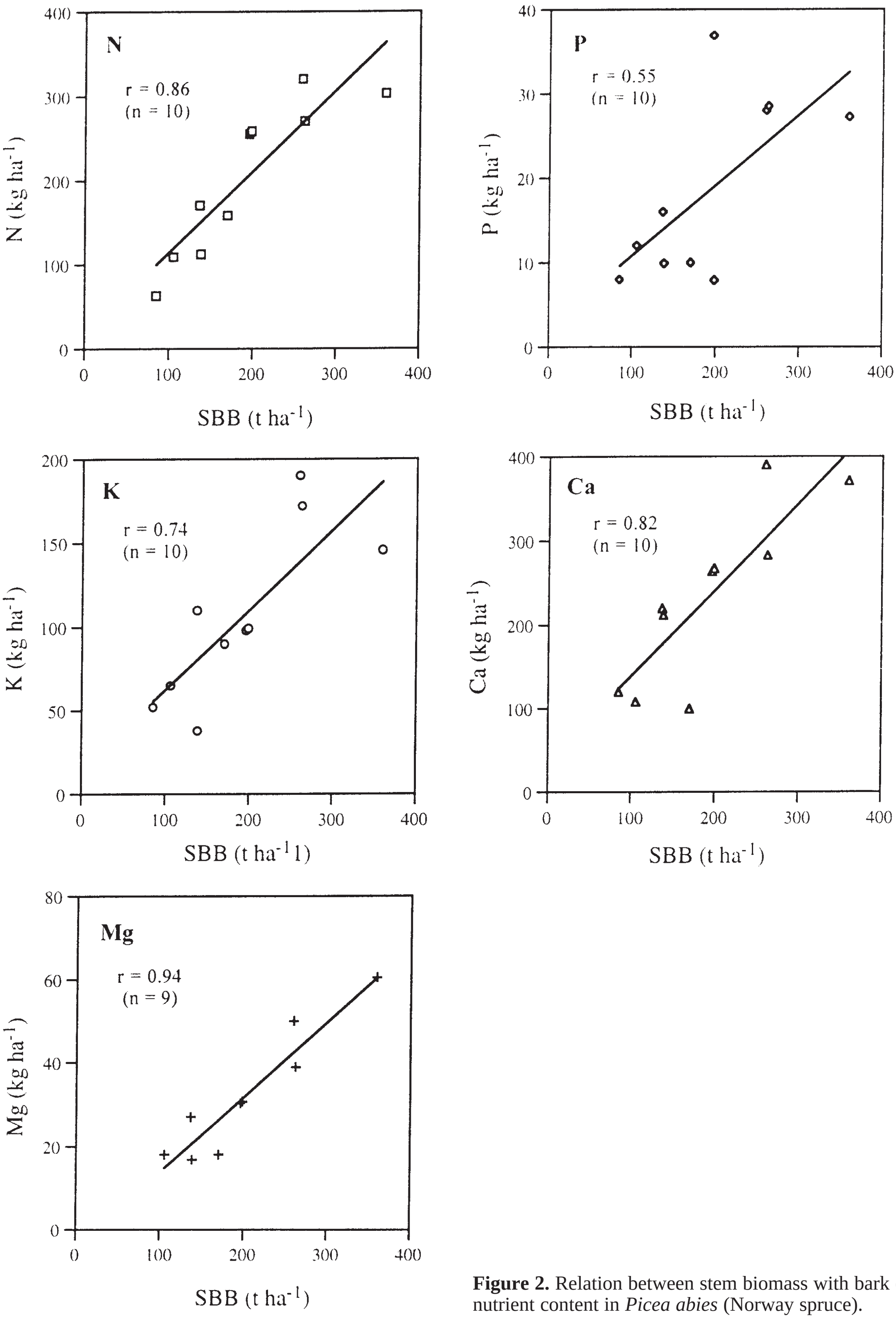

Figure 2. Relation between stem biomass with bark (SBB) and nutrient content in *Picea abies* (Norway spruce).

Table III. Relation between biomass and nutrient amount.

Table IIIa. Douglas fir

NUTRIENT (kg ha^{-1})	Total Aerial Biomass (TAB) (t ha^{-1})					Stem Biomass including Bark (SBB) (t ha^{-1})				
	a	*b*	*r*	*p*	*n*	*a*	*b*	*r*	*p*	*n*
N	1.456	+ 46.0	0.90	< 0.001	26	1.237	– 35.4	0.87	< 0.001	20
P	0.135	+ 34.5	0.40	0.07	26	0.175	– 4.9	0.67	< 0.01	20
K	0.680	+ 63.0	0.74	< 0.001	26	0.615	+ 3.8	0.79	< 0.001	20
Ca	0.952	+ 96.1	0.71	< 0.001	22	0.983	– 34.6	0.76	< 0.001	18
Mg	0.168	+ 10.2	0.65	< 0.01	21	0.138	– 4.2	0.76	< 0.001	17

Table IIIb. Norway spruce

NUTRIENT (kg ha^{-1})	Total Aerial Biomass (TAB) (t ha^{-1})					Stem Biomass including Bark (SBB) (t ha^{-1})				
	a	*b*	*r*	*p*	*n*	*a*	*b*	*r*	*p*	*n*
N	2.341	+ 28.9	0.60	< 0.01	34	0.802	+ 61.2	0.86	< 0.01	10
P	0.197	+ 7.4	0.76	< 0.001	28	0.073	+ 5.4	0.55	0.15	10
K	0.718	+ 93.0	0.60	< 0.01	29	0.400	+ 37.0	0.74	< 0.05	10
Ca	1.386	+ 118.4	0.76	< 0.001	29	1.080	+ 22.6	0.82	< 0.05	10
Mg	0.293	– 5.1	0.79	< 0.001	25	0.174	– 2.4	0.94	< 0.001	9

Table IIIc. Scots pine

NUTRIENT (kg ha^{-1})	Total Aerial Biomass (TAB) (t ha^{-1})					Stem Biomass including Bark (SBB) (t ha^{-1})				
	a	*b*	*r*	*p*	*n*	*a*	*b*	*r*	*p*	*n*
N	2.521	– 32.5	0.83	0.08	9	1.249	– 17.9	0.93	< 0.01	8
P	0.293	– 2.8	0.87	0.06	8	0.138	– 2.3	0.89	< 0.05	8
K	0.890	– 0.2	0.96	< 0.05	8	0.826	– 18.5	0.92	< 0.01	8
Ca	1.743	– 24.9	0.90	< 0.05	8	1.560	– 23.8	0.94	< 0.01	8
Mg	0.408	– 6.7	0.93	< 0.05	5	0.258	– 2.7	0.98	< 0.001	6

Table IIId. European beech

NUTRIENT (kg ha^{-1})	Total Aerial Biomass (TAB) (t ha^{-1})					Stem Biomass including Bark (SBB) (t ha^{-1})				
	a	*b*	*r*	*p*	*n*	*a*	*b*	*r*	*p*	*n*
N	3.225	– 133.5	0.88	< 0.05	9	1.936	– 95.3	0.98	< 0.001	9
P	.	.	0.45	0.45	8	0.204	– 16.3	0.74	< 0.05	9
K	1.507	– 47.3	0.89	< 0.05	8	0.904	+ 22.0	0.94	< 0.001	9
Ca	.	.	0.68	0.21	8	1.470	– 34.0	0.82	< 0.05	9
Mg	0.477	– 42.9	0.89	< 0.05	7	0.260	– 3.3	0.93	< 0.001	8

a and *b* from the equation: (nutrient amount) = (a × biomass) + b.

Table IV. Tree species nutrient concentration.

TREE SPECIES	NUTRIENT CONCENTRATION (kg t^{-1})					
	N / TAB $p < 0.001$			N / SBB $p < 0.05$		
	mean	std err		mean	std err	
Douglas fir	1.80	0.10	a	1.09	0.09	a
Norway spruce	2.59	0.16	a b	1.08	0.07	a
Scots pine	2.09	0.19	a	1.01	0.08	a
European beech	3.43	0.48	b	1.39	0.08	b
	P / TAB $p < 0.05$			P / SBB $p = 0.10$		
	mean	std err		mean	std err	
Douglas fir	0.36	0.04	n.s.	0.16	0.02	n.s.
Norway spruce	0.24	0.02	n.s.	0.10	0.01	n.s.
Scots pine	0.25	0.02	n.s.	0.11	0.01	n.s.
European beech	0.31	0.10	n.s.	0.12	0.02	n.s.
	K / TAB $p < 0.01$			K / SBB $p < 0.001$		
	mean	std err		mean	std err	
Douglas fir	1.06	0.07	a	0.67	0.05	a
Norway spruce	1.20	0.09	a b	0.59	0.05	a
Scots pine	0.95	0.04	a	0.56	0.07	a
European beech	1.61	0.26	b	0.97	0.06	b
	Ca / TAB $p < 0.01$			Ca / SBB $p < 0.05$		
	mean	std err	meanstd err			
Douglas fir	1.59	0.14	a	0.84	0.12	a
Norway spruce	2.04	0.15	a b	1.22	0.10	b
Scots pine	1.35	0.13	a	1.17	0.13	a b
European beech	2.35	0.46	b	1.24	0.13	b
	Mg / TAB $p = 0.15$			Mg / SBB $p < 0.001$		
	mean	std err	meanstd err			
Douglas fir	0.24	0.02	n.s.	0.12	0.01	a
Norway spruce	0.27	0.02	n.s.	0.16	0.01	a b
Scots pine	0.33	0.04	n.s.	0.22	0.02	b c
European beech	0.30	0.03	n.s.	0.24	0.02	c

Species followed by different letters differ significantly.
TAB = Total Aerial Biomass; SBB = Stem Biomass with Bark.

than TAB. Correlations between biomass and nutrient amount for European beech were the least significant. Slopes of the regression lines “Stand nutrient amount” = $a \times$ (TAB) were significantly higher ($p < 0.01$) than “Stand nutrient amount” = $a' \times$ (SBB).

In the case of Douglas fir, for which the data set was the most complete (17 stands), stem biomass with bark (SBB) represented 81 ± 1% of the total tree biomass (TAB) whereas their corresponding nutrient amount were only between 39 ± 3% for Mg and 50 ± 3% for K. This result is an effect of the higher nutrient concentration in the crown than in the stem.

Considering the relative constancy of the biomass: nutrient amount ratio, variance analysis was used to compare the tree species effect on individual nutrient amount for TAB and SBB (*table IV*). Results showed that differences between species were more significant for nutrient: SBB ratios than for nutrient: TAB ones. Differences concerning P: biomass ratios were not significant. Concerning the nutrient: SBB ratio, European beech presented values greater than those of the three coniferous species for N and K. European beech and Norway spruce presented a Ca: SBB ratio greater than that of Douglas fir. For the Mg : SBB ratio, the tree species order was as follows: European beech ≥ Scots pine ≥ Norway spruce ≥ Douglas fir.

4. DISCUSSION

The mean chemical composition of a cross section of stem depends on the proportion of its different components. In the juvenile stages of tree development, the proportion of nutrient rich parts (e.g. bark, sapwood and, to a lesser extent, pith [52, 53]), is important. Thereafter, most stem biomass is made up of heartwood, which has a low nutrient concentration. The mean concentration of major nutrients rapidly decreases with increasing stem age until the adult stage is reached (heartwood biomass: stem biomass ratio tends towards 1) [19, 31]. At the adult stage, the mean concentration depends mainly on general wood chemistry. In fertilization trials, Heilman and Gessel [21] and Nilsson and Wiklund [40] showed that fertilization induced modifications in nutrient concentrations which were high for needles, moderate for bark and branches, but nil for heartwood. Alban [2] also observed that nutrient concentrations for heartwood were fairly constant for a given species. Their results indicate that environmental conditions, and especially conditions affecting nutrition, influence the various tree components differently. The secondary wood (xylema), which constitutes the major part of the stemwood of an adult tree, has a low mean level of physiological activity because only a few rings near the cambium contain significant amounts of living cells [59]. Heartwood represents a tissue whose nutrient composition is stabilized and residual, resulting from opposite processes (nutrient absorption and nutrient retranslocation from aged to young tissues [52]). This situation could explain the relative independence of heartwood composition from environmental conditions. Given that this wood represents the largest part of the stem biomass of an adult tree, the relative independency of wood chemistry from site conditions applied to the whole stem becomes coherent. The age limit when mean nutrient concentration becomes more or less constant depends on the tree species and corresponds quite well to the approximate age of maximum current increment. At this age, biomass increment seems to occur with no significant changes to mean nutrient composition: the relative weight of components with high nutrient concentrations becomes progressively smaller and heartwood tissues are no longer physiologically active.

For an adult stand of a given species, a linear relation exists between aerial biomass and its corresponding nutrient amount. This relation indicates that the nutrient amount were far more correlated to biomass production than to soil fertility. Nevertheless, the fact that relationships concerning TAB and nutrients were less significant than those concerning SBB and its nutrient amount indicates that the high nutrient amount of tree crowns is not only species-dependent. The nutrients of tree crown components are also strongly internally (translocation) and externally (litterfall) recycled. These processes of recycling strongly participate in the global efficiency of perennial vegetation to produce rather large amounts of biomass on soil with limited nutrient reserves. The physiological activity of the tree crown makes it sensitive to environmental constraints (climate, soil fertility). As such leaves (or needles) are used for diagnosing tree nutritional status [7]. Another important factor affecting the nutrient amount = f(TAB) relation is the stand structure, which is dependent on both tree age and silviculture. The denser the stand, the stronger the light extinction in the canopy and the smaller the living part of the tree crown. Considering the large difference in chemical composition between the stem and the crown, the variation of the crown biomass: tree biomass ratio can lead to a change in the mean TAB concentration in comparison of stands of the same biomass. This kind of variability may decrease the statistical significance of the relationships between TAB and its nutrient amount. The different methodologies used in the literature are another source of variability, but it is impossible to quantifify the specific weight of this parameter.

Nevertheless, relationships between biomass and nutrient amount were often statistically significant. The relations which were not significant concerned P or the part of the table where the quantity of data was very limited. Even in these cases, four of the relations tend to be linear (*table III*). All but one of the relations between SBB and nutrients were significant.

For a given species, the nutrient content: TAB ratio was systematically higher than the nutrient amount: SBB ratio because nutrient concentrations were higher in the tree crown than in stemwood. This situation has been described numerous times in the literature [14, 28, 58, 73].

Tree species was a parameter which directly influenced the amount of nutrients exported during stem harvesting [2]. Globally, European beech has higher nutrient concentrations than Douglas fir, Norway spruce and Scots pine. This was the case for N and K in our study. For Ca and Mg, however, the situation of beech compared to other species was not as clear as the case described above for N and K. The species effect on P was not significant enough to be discussed. It is necessary to specify that the higher nutrient concentrations of beech do not indicate greater soil impoverishment linked to beech harvesting. Indeed, nutrient amounts exported from a site depend not only on nutrient concentrations of biomass, but also on biomass production, harvest frequency and intensity of biomass removal. For a same fertility class, Douglas fir or Norway spruce have far higher biomass production levels than European beech or Scots pine [68]. The rotation length of European beech is longer than those of coniferous species, due to its lower rate of increment. If a rotation length index is used in weighting nutrient removal, species effect can be completely altered.

As soil fertility can decrease with nutrient deep drainage and biomass removals, it is obvious how important both intensity and methods of thinning and harvesting are to soil fertility maintenance. The correct estimate of biomass and nutrient removal must take into account several parameters such as: i) species which composed the stand throughout its development. ii) forest management (rotation length [27, 60], intensity and selectivity of biomass removal [14, 28, 52, 58, 73], method of stand harvesting and regeneration). iii) site fertility, as it influences both production and nutrient removal and because it indicates the potential impact of nutrient depletion.

Any forest management aiming at preserving site capacity for production of ecosystems must consider these parameters. Forest managers can easily estimate major nutrient (i.e. N, P, K, Ca, Mg) exportation associated with thinning and harvesting operations for the four species studied herein. Stand inventory and yield tables are used classically to quantify standing volume. To transform stand volume into biomass one must dispose of mean wood density, data must be known: general values of specific wood infradensity for air dried wood are: 0.51 to 0.58 for Douglas fir, 0.43 to 0.47 for Norway spruce, 0.51 to 0.55 for Scots pine, 0.70 to 0.79 for European beech [57]. The data collected herein gives valid information for Douglas fir because the number of cases which have been studied is sufficient and the geographical dispersion of sites allows extrapolation. More information is needed for Norway-spruce, Scots pine or European beech before extrapolation.

Trying to quantify the nutrients exported by thinning and harvesting operations of forest stands from simple dendrometrical information is not new (see [53] for a short review); e.g., it has already been proposed by Freedman et al. [18] and by Rochon et al. [53]. Nevertheless, the models proposed by these authors were established only on small geographical areas (central Nova Scotia [18]; Duparquet Lake forest, Québec, Canada [53]). The general relations proposed in this study, which refer to a geographically dispersed data set, are proposed to be applied to sites under non-extreme conditions, located in temperate to cold temperate areas.

5. CONCLUSION

Forest tree species and silvicultural approaches can noticeably influence the soil bioelement status. In order to give a tool for sustainable management of forest stands, a compilation of existing data was made to find simple and applicable general relationships between biomass harvesting intensity and nutrient depletion of forest sites.

Examples presented in this study show that reliable relationships between harvested biomass and nutrient drain can be proposed for four important forest species: Douglas fir, Norway spruce, Scots pine and European beech. The validity of the relations depends mainly on the number of case-studies found in the literature. For Norway spruce, Scots pine or European beech, more measurements are necessary to increase the reliability of models.

The objective for the mid-term is to simulate stand development and nutrient incorporation in stand compartments. Such a goal necessitate to associate i) stand development models, giving the dynamics of wood volume increment and tree-crown development during forest rotation, ii) wood quality models giving the dynamics of distribution of wood density in the forest stands and iii) nutrient models, giving the dynamics of nutrient incorporation in the stand components during the forest rotation. This kind of model would be useful both for ecosystem function and for management purposes. Such models will serve as a basis for a realistic sustainable management of forest ecosystems based on ecologically sound management models.

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