

Nutrient uptake of a mixed oak/beech forest in Flanders (Belgium)

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Abstract

A 72-year-old mixed oak/beech stand has been studied on the element (N, P, K, Ca and Mg) content in its woody biomass, in the wood increment and in the litter fall. Crown leaching and nutrient uptake have been calculated respectively according to Ulrich (1983) and to Cole & Rapp (1981). Eight oaks and six beeches have been sampled, regression equations between the tree element content and the stem volume have been calculated in order to scale up from the tree to the stand level.

The annual amount of elements taken up is 70 kg N, 4,9 kg P, 69,3 kg K, 43 kg Ca and 6,1 kg Mg per ha. For K, Ca and Mg a large part of the nutrient uptake is due to crown leaching. The amount of N and P in the litter fall constituted the largest part of the uptake of N and P. For the elements K, Ca and Mg, crown leaching is very important in the nutrient cycling : crown leaching amounts respectively 63%, 21% and 43% of the annual return of these elements from the canopy to the forest floor.

Keywords : *nutrient uptake, crown leaching, litter fall, mixed deciduous forest, nutrient cycling*

1. Introduction

Among the functions regulating primary productivity and ecosystem dynamics, nutrient cycling is of critical importance (Duvigneaud & Denaeyer-De Smet 1971, Cole & Rapp 1981). The cycling of elements in forest ecosystems is an integrating process that brings together most other functions of the system. Nutritive elements are obviously essential in physiological processes such as photosynthesis, assimilation and respiration (Cole & Rapp 1981). Particularly N and P influence photosynthetic capacity of leaves and thereby photosynthesis of the canopy (Jose & Gillespie 1996, Foyer & Spencer 1986).

The concentration of nutrients within the ecosystem usually depends upon a functional balance in their intra system cycling (Lodhiyal et al. 1995, Rawat & Singh 1988). Elements taken up by trees become available again for uptake and growth through litter fall, canopy leaching and retranslocation. Nutrient return through litter fall is important in maintaining the fertility of forest ecosystems (Adhikari et al. 1995). However, growth under nutrient limited conditions may be viewed as being completely controlled by the rate at which nutrients become available to plants (Kirschbaum et al. 1994).

The element N can generally be seen as growth limiting in the temperate zone (Lovett 1992). However the deposition of N due to air pollution has increased within the last decades in most parts of the world (Sandvik et al. 1995). Over the past years a lot of hypotheses have been put forward which state that high atmospheric depositions (of inorganic N but also other elements such as S and P) might be detrimental to forest ecosystems (Sandvik et al. 1995, Skeffington 1988). Nutrient imbalances due to increased N depositions and thus increased growth have been discussed for almost two decades (Nilsen & Abrahamsen 1995). High atmospheric N deposition causes i/ high nutrient leaching due to strong acidic precipitation and ii/ increased nutrient demands by trees due to increased tree growth. The Mg deficiencies as experienced in many forest areas esp. in Central Europe is probably partly due to this effect (Nilsen & Abrahamsen 1995, Huettl 1993). Modelling effects of increasing atmospheric deposition could be a useful tool to predict forest behaviour under certain future conditions of Global Change. Within the framework of the Integrated Forest Study (IFS) carried out in the USA, a nutrient model has been developed (Liu et al. 1992). In order to model future forest behaviour, references about the current situation have to be known, which was one of the motives of the current research.

This study aimed i/ to investigate the nutrient content in the above ground woody biomass of an oak/beechn forest, ii/ to quantify the nutrient content in the litter fall and crown leaching of this forest stand and iii/ to calculate nutrient uptake by this stand.

2. Methodology

2.1. Description of the study area

This research was conducted in the Aelmoeseneie forest, a deciduous forest of 28 ha located about 15 km in the South - East of Gent (Belgium). In the Aelmoeseneie forest a scientific zone of 1.83 ha was fenced for intensive scientific monitoring. Two level II plots with a surface of 25 are (European forest monitoring network) and a measuring tower are located within this scientific zone. The level II plot in which this research was carried out is a 72-year-old mixed oak/beechn stand, the other level II plot is an ash stand. The tree species composition of the research site (oak/beechn plot) is shown in Table 1. More details can be found in Samson et al. (1996).

Table 1. Tree species composition of the investigated stand (Level II plot A - 1995) (N = number of trees; BA = basal area; V = volume)

Species	N	BA (m ²)	V (m ³)	% BA	% V
<i>Quercus robur</i>	208	16.5	210.6	52.6	53.8
<i>Fagus sylvatica</i>	80	11.2	131.5	35.8	33.6
<i>Larix decidua</i>	28	3.6	49.0	11.4	12.5
<i>Acer pseudoplatanus</i>	12	0.04	0.2	0.1	0.1
<i>Corylus avellana</i>	8	0.02	0.0	0.1	0.0
Total	336	31.36	391.3	100	100

2.2. Element content of the stand and in the yearly increment

In the above described stand (Table 1), 8 sample trees of oak and 6 of beech were felled in order to determine the nutrient content of the aboveground woody part of the forest stand. The diameter distributions of the population of oak and beech were both investigated, the population of oak had a normal distribution. The eight sample trees of oak were selected in accordance with the diameter classes of the trees in the stand. The beech population of the stand showed a bimodal distribution, which represented clearly the presence of the old tree population and a younger generation beneath it. Three sample trees of the old beech population and three sample trees of the young beech population were selected. Two sample trees were representative of the sample mean, while the other sample trees (4) represented the lower and upper quartile of the diameter distribution from each population (Prodan 1965). Table 2 shows the height, circumference, volume and biomass of the model trees of oak and beech.

In order to determine the total nutrient content of each model tree, the boles of the model trees were divided into 1 m logs and weighed. The circumference at the top, in the middle and at the bottom of each 1 m log was measured in order to determine the volume of each log with the formula of Newton. A wood disc was then sawn of each log for dry weight determination and chemical analyses. For the oaks each disc was subdivided into a heartwood, sapwood and bark area. Concerning the beeches, the discs of beech 4 and 5 were divided into wood and bark and the other discs were not divided. All fractions of these discs were dried in a furnace at 80°C to constant weight. Every three meters all fractions (heartwood, sapwood and bark) of the disc were analysed separately on N, P, K, Ca and Mg.

Table 2. Characteristics of the sample trees : height (H), circumference (C), volume (V) and biomass (B)

Model tree	H (m)	C (cm)	V (m ³)	B (kg)
Oak 1	19.4	63	0.33	175.3
Oak 2	23.0	66	0.42	232.8
Oak 3	23.0	84	0.65	426.2
Oak 4	22.7	86	0.70	541.0
Oak 5	25.2	96	0.81	645.5
Oak 6	26.1	107	1.24	865.4
Oak 7	27.4	117	1.44	1034.8
Oak 8	25.6	116	1.40	841.8
Beech 1	8.9	25	0.01	19.8
Beech 2	15.5	38	0.07	72.2
Beech 3	14.0	50	0.14	108.6
Beech 4	22.9	85	0.60	525.0
Beech 5	27.7	147	2.29	1751.0
Beech 6	29.7	176	2.99	2786.0

The concentrations of the discs were then applied to the logs below and above the disc and the total nutrient content of the bole was calculated for each sample tree. A regression equation was then calculated between the bole volume of the sample trees and their nutrient content. By

means of these regression equations the nutrient content of the boles of the sample trees was scaled up to the level of the stand.

The branches of each sample tree were chopped into 4 diameter classes : $<2,5 \text{ cm } \phi$, $2,5 < \phi < 4 \text{ cm}$, $4 < \phi < 7 \text{ cm}$ and $\phi > 7 \text{ cm}$ (ϕ =diameter). For each diameter class the total branch fresh weight was determined and a sample was taken. This sample was dried in a furnace at 80°C to a constant weight. Afterwards the branches were analysed on their N, P, K, Ca and Mg content and the total element content of the crown of each sample tree was calculated. Similar as for the boles, regression equations were calculated between the bole volume and the tree total crown content of the different elements. By means of these regression equations scaling up of the crown content to the level of the stand has been carried out.

In order to assess the quantity of nutrients incorporated into the annual wood increment, the stand nutrient content was calculated for 1995 and 1997 using inventories and the calculated regression equations (more detailed explanation can be found in Bussche 1998).

2.3. Canopy leaching and litter fall

Canopy leaching can be defined as the movement of substances derived exclusively from plant tissues to an aqueous solution in direct contact with the vegetation. Leaching may represent the largest transfer pathway from the canopy to the forest floor for mobile elements (Potter & al. 1991, Parker 1983). Especially the elements K, Ca and Mg are prone to leaching during the growing season or during autumn.

In this study the canopy leaching of K, Ca, and Mg has been calculated according to Ulrich (1983). Ulrich defined the throughfall of a certain element (TF_x) as the sum of the bulk deposition (BD_x), the interception deposition (gaseous and particles) (ID_x) and the crown leaching (Q_x) of that element. Net throughfall (NTF_x) is defined as TF_x minus BD_x . In that way the crown leaching Q_x can be calculated as the net throughfall minus the interception deposition. As the elements K, Ca and Mg do not occur in the gaseous phase, their interception deposition is calculated by means of the dry deposition factor of Na. Na is not involved in the processes concerning crown leaching, in that way crown leaching is assumed to be zero.

Concerning Na this means :

$$TF_{Na} - BD_{Na} = ID_{Na}$$

or

$$NTF_{Na} = ID_{Na}$$

According to Ulrich (1983), Ivens (1990) and Beier (1991) the particle interception deposition of other, non gaseous elements such as Ca, K and Mg, can be calculated with the throughfall factor (= dry deposition factor) of Na which is :

$$(TF_{Na} - BD_{Na}) / BD_{Na}$$

The particle interception of the other elements is then calculated as :

$$ID_{\text{element}} = \text{dry deposition factor Na} \times BD_{\text{element}}$$

The crown leaching Q_x of a certain element x can be found as follows :

$$Q_x = NTF_x - ID_x$$

In order to calculate crown leaching of K, Ca and Mg, measurements of bulk deposition, throughfall water and stem flow water have been made during 1997 as described in De Schrijver (1998) and Bussche (1998).

Litter fall has been collected in order to determine its element content. In the test stand 30 litter traps were installed randomly as described in Mussche (1997). The litter in these traps was collected in the period October 1997 - January 1998. Six of these traps were selected in order to separate the leaves of oak, beech, the branches and the fruits. Fresh and dry weight of these fractions was determined. Total fresh and dry weight was determined for all traps. Leaves of oak and beech were analysed separately; fruits and branches were not analysed but results from a previous work were used (Muys 1993). A more detailed description of methodology can be found in Bussche (1998).

2.4. Nutrient uptake

Nutrient uptake has been calculated according to Cole and Rapp (1981) :

$$\begin{aligned} \text{nutrient uptake} &= \text{nutrient content in the yearly wood increment} \\ &+ \text{yearly nutrient content in litter fall} \\ &+ \text{crown leaching} \end{aligned}$$

Completely correct measurements of the nutrient uptake are impossible to make, as it is very difficult to determine crown leaching and aboveground turnover. However, the values calculated according to the above formula are a good estimate, especially for elements such as N and P which almost have no crown leaching.

2.5. Analyses

With exception of P, the samples of wood and leaves were analysed in the same way for each element. For N the Kjeldahl method was used : 200 mg of plant material was destructed in the Tecator Digestion System 20; a distillation was carried out with the Tecator 1026 Distilling Unit; finally the N concentration was determined by titration with 0.01 N HCl.

K, Ca and Mg were determined by AAS (Flame) after extracting ashes with 6 N HNO₃.

P was determined by photospectrometry for both leaves and wood samples. The destruction of the leaves was carried out in the same way as the destruction for the AAS (ashing). Destruction of the wood samples was carried with the Tecator Digestion System 20. More information can be found in Bussche (1998).

3. Results and discussion

3.1. Nutrient concentration of the aboveground woody parts

Table 3 shows the measured average element concentrations together with the 95% confidence interval.

Table 3. Average element concentrations (ppm) and 95% confidence interval of oak and beech samples (A=0-2,5 cm ; B = 2,5-4 cm ; C= 4-7 cm and D = >7 cm diameter)

Species	Fraction	N	P	Ca	K	Mg	
Oak	Heartwood (1)	1197.4 ± 55.8	145.1 ± 17.8	240.8 ± 37.9	296.3 ± 41.2	78.2 ± 46.2	
	Sapwood (2)	2146.2 ± 152.1	117.9 ± 15.9	480.3 ± 98.3	1202.1 ± 101.4	185.0 ± 34.5	
	Bark (3)	6213.1 ± 154.2	92.8 ± 14.02	13251.8 ± 2638.4	1978.1 ± 332.0	590.0 ± 53.8	
	Weighted average 1,2,3	2006.6 ± 116.5	129.0 ± 13.0	1634.6 ± 220.9	715.7 ± 61.4	163.5 ± 36.3	
	Branches A	8236.7 ± 479.2	296.7 ± 30.7	4003.5 ± 301.3	2117.8 ± 169.0	673.7 ± 58.9	
	Branches B	5199.0 ± 205.5	215.8 ± 30.3	3339.2 ± 321.4	1727.6 ± 157.3	433.6 ± 65.5	
	Branches C	4210.3 ± 274.4	164.8 ± 22.7	2919.5 ± 226.3	1640.8 ± 131.2	410.1 ± 53.3	
	Branches D	3463.9 ± 279.2	154.0 ± 24.2	2994.9 ± 447.3	1494.8 ± 208.1	287.8 ± 36.5	
	Beech	Wood (1)	1693.6 ± 505.7	51.4 ± 33.5	1402.6 ± 993.7	1089.5 ± 216.4	211.9 ± 61.4
		Bark (2)	7651.2 ± 532.9	197.6 ± 52.8	8375.2 ± 2323.7	1667.5 ± 181.5	390.8 ± 52.8
		Weighted average 1,2	2054.5 ± 337.6	54.7 ± 16.4	1953.0 ± 574.4	1078.1 ± 109.0	188.2 ± 30.3
		Branches A	8029.0 ± 1533.2	356.5 ± 136.7	3409.3 ± 1313.5	2103.7 ± 362.6	377.1 ± 50.5
		Branches B	3118.0 ± 764.3	249.6 ± 75.5	1995.3 ± 823.5	1222.9 ± 363.3	218.6 ± 32.8
Branches C		2904.7 ± 468.8	175.9 ± 83.2	1493.3 ± 679.0	1131.9 ± 281.2	230.4 ± 28.6	
Branches D		2412.9 ± 1540.5	170.7 ± 180.8	1446.7 ± 1068.5	1043.6 ± 661.5	219.2 ± 109.9	

For oak average concentrations of eight trees have been calculated. Concerning beech only the weighed average concentration takes into account 6 trees, the other parameters are calculated on basis of beech 4 and 5. Heartwood accounted for on average 65% of the bole dry weight, followed by sapwood and bark (respectively 25% and 10%)

As most of the data appeared not to have a normal distribution, no t-tests for comparison of means were carried out. The 95% confidence interval gives an idea of the significance of the differences among the means.

Apparently, the concentrations of the bark are as well for oak as for beech, significantly higher than those of the heartwood and the sapwood, with exception of P. The concentrations of all elements decrease with increasing branch diameter. Remarkable are the high concentrations of Ca, especially in the bark.

In comparison with nutrient analyses for Corsican pine (Neiryck et al. 1998) the N, K and Ca concentrations in the bark of oak and beech appear to be higher. The high Ca concentrations in the bark of oak are neither found for Corsican pine, nor for beech. The concentrations of P and Mg found in the bark of Corsican pine are higher than those found in the bark of oak and beech.

3.2. Regression equations

The regression equations calculated in order to scale up from the level of the tree to the stand are shown in Table 4. Linear regression equations are all very significant.

Table 4. Regressions equations calculated for scaling up from the leaf level to the level of the tree (* significant $p < 0.05$; ** significant $p < 0.01$; *** significant $p < 0.001$; R^2 = determination coefficient; X = tree volume in m^3 ; Y = stem element content in g)

Elements	Equation	A	B	R^2	Significance p
Oak Stem					
N	$Y = A + B \cdot X$	102.54	880.20	0.95	$p < 0.001$ ***
P	$Y = A + B \cdot X$	-16.56	101.57	0.71	$p < 0.01$ **
K	$Y = A + B \cdot X$	31.92	317.41	0.91	$p < 0.001$ ***
Ca	$Y = B \cdot X$		805.54	0.89	$p < 0.001$ ***
Mg	$Y = B \cdot X$		78.14	0.78	$p < 0.01$ **
Beech stem					
N	$Y = B \cdot X$		1200.89	0.86	$p < 0.01$ **
P	$Y = B \cdot X$		24.37	0.86	$p < 0.01$ **
K	$Y = B \cdot X$		627.37	0.997	$p < 0.001$ ***
Ca	$Y = B \cdot X$		1192.13	0.76	$p = 0.01$ **
Mg	$Y = B \cdot X$		115.54	0.93	$p = 0.001$ ***
Oak branches					
N	$Y = B \cdot X$		666.37	0.88	$p < 0.001$ ***
P	$Y = B \cdot X$		25.68	0.84	$p = 0.001$ ***
K	$Y = B \cdot X$		210.14	0.85	$p < 0.001$ ***
Ca	$Y = B \cdot X$		416.00	0.81	$p = 0.001$ ***
Mg	$Y = B \cdot X$		57.10	0.93	$p < 0.001$ ***

Table 5. Volumetric branch nutrient content of beech, calculated for model trees 4 and 5

	N (g/m^3)	P (g/m^3)	K (g/m^3)	Ca (g/m^3)	Mg (g/m^3)
Beech 4	919.9	61.5	390.5	411.9	75.5
Beech 5	793.5	45.1	208.6	445.4	41.1
Average	856.7	53.3	299.6	428.7	58.3

Since the results of only two trees (beech 4 and 5) are available for the branches of beech, another scaling up method was used. The branch nutrient content of both trees was divided by its bole volume, this volumetric branch nutrient content was then averaged over both trees.

Results are shown in Table 5. This average branch nutrient content was multiplied by the total stand volume of beech.

3.3. Biomass and nutrient content

Table 6 shows the biomass and element content of the stand in 1995 and 1997 as well as the element content in the annual wood increment of the stand. Table 7 shows literature data (Cole & Rapp 1981) representing biomass and nutrient content of the aboveground woody parts (W) and upper storey litter fall (LF) of some deciduous forest stands. When comparing Tables 6 and 7 it becomes clear that the examined stand has a high amount of biomass in the woody compartment (W) compared to its stand age. The amount of biomass present in a 122-year-old beech stand and a 115 à 160 year old oak stand on a calcareous brown soil varies between 270,8 and 288,3 ton per ha (Table 7). The examined, 72-year-old mixed oak/beech stand has an amount of biomass of 246,1 ton per ha, which approximates to these literature data.

Table 6. Biomass (dry matter) and element content of the stand (1995 and 1997) and of the annual increment

Year	Species	Biomass (Ton/ha)	N (kg/ha)	P (kg/ha)	K (kg/ha)	Ca (kg/ha)	Mg (kg/ha)
1995	Quercus r.	128.8	312.4	21.1	106.0	231.8	25.7
	Fagus s.	107.8	253.7	9.6	114.3	199.9	21.4
	Sum	236.5	566.1	30.7	220.3	431.7	47.1
1997	Quercus r.	134.8	325.5	22.2	110.5	242.2	26.8
	Fagus s.	111.3	263.2	9.8	118.1	206.4	22.1
	Sum	246.1	588.7	32.0	228.5	448.6	49.0
Increment (kg.ha ⁻¹ .y ⁻¹)		4790	11.3	0.7	4.1	8.5	0.9

Concerning the element content, rather large variations can be found in literature (Table 7). The examined stand can be considered to have element contents in between the values of the 115 à 160 year old oak stand and the 122 year old beech stand. In literature a remarkable difference between the relative element content of oak and beech can be seen (Table 7). Beech has a much lower relative element content. In this research however such a lower element content of beech has not been found, except for P. The mixed oak stand examined by Duvigneaud & Denayer-De Smet shows an extremely high Ca content, which is not found in this study. The total N and P contents of the examined stand are in agreement with the N and P content of the mixed oak stand. However, the relative K and Mg content of the examined stand are rather low compared with the mixed oak and the beech stand.

Table 7. Biomass (dry matter) and nutrient content (kg/ha) of the aboveground woody parts (W) and upper storey litter fall (LF) of some deciduous forest stands as found in literature (Cole & Rapp 1981)

Species Location	Age (y)		Biomass	N	P	K	Ca	Mg	Investigator
Mixed oak (<i>Quercus</i> r.) Virelles, Belgium	115à 160	W	288350	645	40	358	1108	85	Duvigneaud & Denaeyer-De Smet
		LF	5600	59	3.4	28	66	9.7	
Mixed oak (<i>Quercus</i> r.) Virelles, Belgium	80	W	-	-	-	-	-	-	Duvigneaud & Denaeyer-De Smet
		LF	5287	50	2.4	21	110	5.6	
Beech (<i>Fagus</i> s.) Solling project, Germany	80	W	155470	308.6	30.3	171.1	285.2	23.6	Ulrich & Ellenberg
		LF	4046	54.3	4.3	17.5	17.8	1.6	
Beech (<i>Fagus</i> s.) Solling project, Germany	122	W	270880	496.6	15.3	248.2	291.9	64.7	Ulrich & Ellenberg
		LF	3783	49.4	4.0	15.9	16.2	1.4	
Fagus, Acer, Betula Hubbard Brook, USA	60	W	130820	297.1	27.2	123.7	382.5	32.7	Whittaker & Likens
		LF	5860	54.2	4.0	18.3	40.7	5.9	
Quercus, Betula Meathop, UK	80	W	109560	192.4	12.1	174.7	438.4	16.5	Satchell
		LF	3697	63.5	2.6	19	83.3	9.7	
Mixed oak-beech Gontrode, Belgium	72	W	246120	588.7	32.0	228.5	448.6	49.0	Mussche et al.
		LF	4152	58.7	4.3	24.2	27.4	2.9	

3.4. Canopy leaching and litter fall

The total litter biomass of the examined stand amounts to 4,15 tons per ha (Table 8). The large share of the fruits and branches in the total amount of litter is remarkable.

Table 8. Biomass (dry matter) and element content in the litter fall

Fraction	Biomass (kg/ha)	N (kg/ha)	P (kg/ha)	K (kg/ha)	Ca (kg/ha)	Mg (kg/ha)
Leaf fall						
Quercus r.	1919.3	30.4	2.2	10.3	19.1	1.7
Fagus s.	874.2	11.4	0.6	3.8	5.0	0.4
Sum	2793.5	41.8	2.9	14.1	24.2	2.1
Branch fall	816.8	9.9	0.8	6.3	2.0	0.5
Fruit fall	541.3	7.0	0.6	3.8	1.3	0.4
TOTAL	4151.6	58.7	4.3	24.2	27.4	2.9

As Table 7 shows, biomass and element content of different forest stands are very variable. The amount of litter of the examined stand is a lot lower than the amounts found in literature for both mixed oak stands. Taking in consideration both beech stands in Table 7, it was concluded that litter fall biomass lies between literature data for a mixed oak and a beech stand. However, the N, P and K content of the litter fall of the examined stand are very comparable with the content of the 115 à 160 year old mixed oak stand. Only the Ca and Mg content of the examined stand are, analogously to the biomass, much lower than the content found in literature for the mixed oak stand (Tables 7 and 8).

Table 9 shows the canopy leaching calculated according to Ulrich (1983). It is obvious that K has a very high amount of canopy leaching. As stated by Lovett & Schaefer (1992) leaching of Ca^{2+} , Mg^{2+} and K^+ from forest canopies into throughfall and stem flow solutions constitutes an important part of the nutrient cycle of these elements. Canopy leaching can account for 10 to 80% of the total annual return of these elements from the canopy to the forest floor, the remainder occurs as litter fall (Cole & Rapp 1981, Johnson et al. 1985, Waring & Schlesinger 1985).

Table 9. Canopy leaching (1997) calculated according to Ulrich (1983) (abbreviations : see methodology; CF = through fall; SF = stem flow)

	K ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$)	Ca ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$)	Mg ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$)	Na ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$)
BD _x	3.8	7	1.8	17.1
CF _x	43.4	15.1	4.2	20.8
SF _x	3.1	2.1	0.6	3.8
NTF _x	42.7	10.2	3	7.5
ID _x	1.7	3.1	0.8	7.5
Q_x	41.0	7.1	2.2	0

In this study indeed, the K, Ca and Mg content in crown leaching amount to respectively 63%, 21% and 43% of the annual return from the canopy to the forest floor (Table 9).

The annual loss from the canopies resulting from canopy leaching often represents from 20% to 30% (for Ca^{2+} and Mg^{2+}) and as much as 50% (for K) of the midsummer canopy content of the element (Lovett & Schaefer 1992). Binkley (1986) states that K is the most mobile element and that about half of the K in the leaves leaches prior to litter fall.

3.5. Nutrient uptake

Nutrient uptake (Table 10) has been calculated according to Cole and Rapp (1981) as described above. Measuring nutrient pools and fluxes, and especially calculation of crown leaching involves usually a wide array of assumptions, approximations and simplifications (Binkley 1986). Calculating nutrient uptake gives a better approximation for N and P, the elements for which crown leaching is assumed to be zero.

Table 11 shows some literature data for aboveground production and element uptake for deciduous forest (Cole & Rapp 1981). Generally, N uptake is low compared to literature data, as

well as P, Ca and Mg uptake. In contrast, the K uptake is very high compared to literature; this might be due to the very high canopy leaching of K (represents to 60% of the K uptake).

Table 10. Biomass increment and nutrient uptake ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) calculated according to Cole and Rapp (1981)

	Biomass	N	P	K	Ca	Mg
Wood increment	4790	11.3	0.6	4.1	8.5	0.9
Litter fall	4152	58.7	4.3	24.2	27.4	3.0
Crown leaching		/	/	41.0	7.1	2.2
Nutrient uptake		70.0	4.9	69.3	43.0	6.1

Table 11. Aboveground production ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$) and element uptake ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{y}^{-1}$) for some deciduous forests as found in literature (Cole & Rapp 1981)

Species Location	Age (y)	Total above- ground prod. Biomass	N Uptake	P Uptake	K Uptake	Ca Uptake	Mg Uptake
Mixed oak (<i>Quercus r.</i>) Virelles, Belgium	80	14775	80	4.6	48.8	169.4	16.4
Mixed oak (<i>Quercus r.</i>) Virelles, Belgium	115 à 160	7980	86.4	5.4	51.0	91.0	19.7
Beech (<i>Fagus s.</i>) Solling project, Germany	80	9648	87.6	5.7	46.7	55.0	6.4
Beech (<i>Fagus s.</i>) Solling project, Germany	122	10352	75.6	6.5	45.0	50.2	7.0
Average temperate Deciduous forest		10050	75.4	5.6	50.7	85.0	13.2
Oak-beech Gontrode, Belgium	72	8942	70.0	4.9	69.3	43.0	6.1

4. Conclusions

The element content in the aboveground woody biomass of the examined oak/beech stand amounts to 588,7 kg N/ha, 32 kg P/ha, 228,5 kg K/ha, 448,6 kg Ca/h and 49 kg Mg/ha. After comparison with some literature data, it was concluded that the examined stand has a high biomass and element content related to its age. However, it is also clear that literature data are not conform and that biomass, element content and litter fall can vary considerably depending on site.

The annual wood increment of the examined stand amounts to 4,8 ton dry matter, 11 kg N, 0,6 kg P, 4,1 kg K, 8,5 kg Ca and 0,9 kg Mg per ha. Calculated in volumes, the increment amounts to 6,3 $\text{m}^3\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, which is rather low. The amount of litter fall (4,15 ton dry matter per ha) is low

compared with some literature data for mixed oak stands on one hand. Compared to some beech stands on the other hand the amount of litter fall is rather similar. The share of fruits and branches in the total litter fall is very high, analyses of fruits and branches will be carried out in future research.

Crown leaching was calculated according to Ulrich (1983) and appeared to play a significant role in the cycling of Ca, Mg and especially K : K, Ca and Mg in crown leaching amount respectively 63%, 21% and 43% of the annual return from the canopy to the forest floor.

Finally, element uptake has been calculated according to Cole and Rapp (1981). It appears that uptake of all elements, except of K, is low compared to literature data for oak and beech stands. The uptake of K is very high, which might be explained by the high amount of crown leaching for this element. Generally it is concluded that for the elements N, P and Ca litter fall plays the major role in nutrient uptake. For the elements K and Mg crown leaching contributes to a large extent to the element uptake.

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