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Biomass and nutrient cycling of a highly productive Corsican pine stand on former heathland in northern Belgium

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Abstract – Biomass and nutrient cycling were examined in a 62-year-old highly productive Corsican pine stand (*Pinus nigra* Arn. ssp. *laricio* Poiret) growing on a coarse and dry sandy soil with low exchangeable nutrient pools. Total aboveground biomass was estimated at 240 tons dry weight per hectare of which 201 tons concerned boles. The belowground biomass amounted to 46 t ha^{-1} (16 % of total standing biomass). The current annual volume increment was estimated at 20.6 m^3 ha^{-1} $year^{-1}$. Root study emphasized the role of the rooting depth as an important growth factor. Calculated uptake rates for N, P, K, Ca and Mg were respectively 50.5, 1.9, 38.2, 15.6 and 3.3 kg ha^{-1} $year^{-1}$. Despite an abundant nitrogen deposition (46 kg inorg. N ha^{-1} $year^{-1}$) between 23 and 35 % of the nitrogen demand was supplied by internal transfers. Retranslocation of phosphorus fulfilled 64 % of the annual requirement. The root uptake of potassium, calcium and magnesium were better coupled with the tree requirements. The uptake rates of Ca and Mg could be met by atmospheric deposition. The canopy leaching of potassium accounted for 70 % of the root uptake. The low uptake rates of P, Ca and Mg were inconsistent with the vigorous growth of the stand, which could only be maintained by a high nutrient use efficiency. The monitoring of the nutrient status between 1988 and 1995 revealed an obvious decline in the concentrations of Ca, Mg, K and P due to growth dilution. (© Inra/Elsevier, Paris.)

***Pinus nigra* / biomass / nutrient cycling / nitrogen deposition / nutrition**

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Résumé – La biomasse et le cycle des éléments minéraux d'un peuplement de pin *laricio* de Corse de forte production sur un sol sableux. La biomasse et le cycle des éléments minéraux ont été étudiés dans un peuplement de pin *laricio* de Corse (*Pinus nigra* Arn. ssp. *laricio* Poiret) de 62 ans, de forte productivité, sur un sol sableux et sec, aux réserves d'éléments disponibles limitées. La biomasse épigée s'élévait à 240 tonnes de matière sèche par hectare dont 201 tonnes étaient incluses dans les troncs. La biomasse des racines était de 46 tonnes ha^{-1} (16 % de la biomasse totale). L'accroissement courant annuel atteignait 20,6 m^3 ha^{-1} an^{-1}. L'étude des racines a mis en évidence la profondeur de l'enracinement comme facteur de croissance important. Les prélèvements réels de N, P, K, Ca et Mg s'élévaient à respectivement 50,5, 1,9, 38,2, 15,6 et 3,3 kg ha^{-1} an^{-1}. Malgré un apport abondant d'azote (46 kg N inorganique ha^{-1}), entre 23 % et 35 % de la demande azotée était soutenue par le transfert interne. Les transferts internes de phosphore contribuaient pour 64 % à la masse minérale nécessaire pour la formation des tissus nouveaux. Les prélèvements réels de potassium, calcium et magnésium correspondaient mieux à leurs prélèvements apparents. Les prélèvements de Ca et Mg pouvaient être suppléés par des apports atmosphériques. Il ressort que le pluviolessivage de potassium constituait 70 % de l'absorption racinaire. Les prélèvements réels de Ca, Mg et P étaient en opposition avec la forte productivité qui ne pouvait qu'être soutenue par un usage efficace des nutrients. L'évolution de la nutrition foliaire décelait une baisse nette en teneurs de Ca, Mg, K et P engendrée par la discordance entre leurs réserves limitées et la forte croissance du peuplement. (© Inra/Elsevier, Paris.)

***Pinus nigra* / biomasse / cycle des éléments minéraux / azote / nutrition minérale**

1. INTRODUCTION

Over 60 % of the Flemish forest area is located on sandy soils. Because of its low drought sensitivity, the availability of suitable provenances and, especially, its high growth rate, Corsican pine has in recent decades become one of the main tree species on these sandy soils, and occupies around 30 % of these areas.

A decline in Corsican pine vigour was observed during the 1980s as a result of severe frost and infections caused by fungi (*Brunchorstia pinea* and *Sphaeropsis sapinea*), but most Corsican pine stands have recovered well and presently produce considerable amounts of timber. Present volume increments of some stands can even be called excessive compared to the yields found in yield tables from stands belonging to same age and yield class. This increased tree growth is also noted for other tree species and is often associated with chronic nitrogen deposition in forest ecosystems [1, 29, 41].

Today, interest is aroused about the mechanisms that sustained the vigour of the Corsican pine stands growing on these sandy soils with low exchangeable pools. In recent decades, these forest soils were, in addition, liable to high acid loads and were gradually impoverished due to leaching of base cations displaced from exchange sites. Attention was therefore drawn to the changes in nutrient cycling, nutrient soil turnover and stand nutrition of these stands in connection with this vigour.

There are few studies concerning biomass and nutrient cycling of Corsican pine stands growing on nutrient poor soils [16, 25]. The present study was carried out to assess the organic matter and nutrient distribution in a highly productive Corsican pine stand on a former heathland. This research also aimed to calculate stand nutrient uptake and requirement and to compare the uptake rates with the present nutrient pools and the nutrient status.

2. MATERIALS AND METHODS

2.1. Study area

The research was conducted in a 62-year-old Corsican pine (*Pinus nigra* Arn. ssp. *laricio* Poiret) stand located in the Pijnven Forest (51°10' N, 5°20' W), near Hechtel (northeastern Belgium). The forest covers about 800 hectares and is mainly composed of first generation pine stands established on former heathlands and sand dunes. The forest is located at the edge of the High Campine plateau and ranges in elevation from 50 to 58 m. The Campine plateau originates from a mixture of tertiary sands and gravel-rich sands deposited by the Meuse River. During the Pleistocene these sands were covered by aeolian sand deposits.

Mean annual temperature is 9.0 °C with January and July means of 1.5 °C and 16.7 °C, respectively. Mean annual precipitation is 799 mm. Precipitation during the growing season (May–October) averages 430 mm. The prevailing wind direction is southwest. The frost period extends from the end of October until the end of April.

The total stem volume and basal area amounts to 463 m^3 and 39.9 m^2 per hectare, respectively. The crop comprises 460 stems ha^{-1} and attains a mean height of 22.6 m. From 1954 onwards thinnings have been carried out with a frequency of 6 years; data of thinning volumes before 1951 were not available. Between 1951 and 1991, 252 m^2 comprising 3 021 trees (original planting density was 10 000 stems ha^{-1}) were harvested per hectare. The stand is moderately infested by *Sphaeropsis sapinea*.

The coarse sandy soil has a massive, compacted and cemented spodic B horizon and is classified as a Haplic Podzol. The permeability of the Bh1 and Bh2 horizons is particularly low and prevents deep penetration of roots. From 80 cm depth downwards, the parent material is locally enriched by narrow clay and gravel layers. The pH-H_2O and base saturation remain constant and very low throughout the solum to a depth of 90 cm *(table I)*. The biomass of the forest floor is 57.2 tons ha^{-1}. Its C/N ratio is 42, whereas it ranges between 32 and 41 in the surface soil. The C/N ratio of the C horizon (30 to 90 cm depth) is below 25 %.

2.2. Tree selection and sampling

Five sample trees were selected on the basis of the basal area distribution of the trees; three sample trees were representative of the sample median, and the two remaining trees represented the lower and upper quartile of the basal area distribution (see *table II*).

The five trees were felled in 1992. Before felling, however, all branches were harvested individually by means of a tower waggon and were weighed immediately after harvest. In addition, the diameter 3 cm from the branch base and the branch length of every branch were measured in the field. From each whorl, one randomly selected branch was sampled completely; the needles were stripped from the branches and separated according to their age. The branches were chopped into four size classes (diameter: < 1, 1–2, 2–5 and > 5 cm). The fresh weight of every fraction was immediately weighed on the spot. Subsequently, subsamples were taken from every fraction for dry weight determination and chemical analysis.

Each bole was sawn into 1 m long logs; at every 3 m a disc of about 3 cm thickness was removed for laboratory analysis. The disc dimensions, bark thickness and the fresh weights were recorded immediately.

The samples of branches and needles were dried for 48 h at 80 °C and weighed again. The wood and bark pieces were dried at 80 °C to constant weight. The samples were ground in a wood mill before chemical analysis.

The stumps of three of the Corsican pines (one sample median and lower and upper quartile) were excavated over a surface formed by the intersection of the perpendicular lines that pass through the midpoints of the lines connecting the centre of the sample tree to the centre of the nearest neighbouring trees [27]. The roots were cleaned, weighed and subdivided into four diameter classes (0.5–1, 1–2, 2–5 and > 5 cm). The fine rootlets thinner than 0.5 cm were not sampled. The entire sample of rootlets (0.5–2 cm) was taken for analysis, whereas subsamples were taken from the bigger root fractions.

2.3. Estimation of biomass and nutrient contents

The fresh weight data obtained from the selected branches were used to derive regres-

Table I. Soil characteristics of the study site.

Horizon	Depth (cm)	Granulometry < 2 µm (%)	Granulometry 2–50 µm (%)	Granulometry 50–2 000 µm (%)	pH ($H_2$0)	C (%)	N (mg/100 g)	C/N	P (mg/100 g)	CEC (meq/100 g)	Exch. acidity (meq/100 g)	Base saturation (%)
LFH	6				3.8	45.8	1 089.5	42.0	59.7	23.54	6.92	70.60
A	0–5	1.87	7.18	90.95	4.4	2.9	85.5	33.9	14.0	3.90	3.46	11.28
A/E	7–25	0.70	4.30	95.00	3.8	2.4	58.4	41.1	10.4	3.20	2.97	7.19
Bh	25–30	1.36	6.09	92.55	4.0	1.8	55.3	32.5	12.7	4.02	3.85	4.23
C	30–60	2.01	14.44	83.55	4.4	0.5	21.2	23.6	8.7	1.46	1.38	5.48
Cg	60–90	2.62	15.13	82.25	4.3	0.1	12.3	8.1	4.4	1.57	1.48	5.73

Table II. Characteristics of sample trees.

Tree number	DBH (cm)	Basal area (cm^2)	Height (m)	Bole volume (m^3)	Bark proportion in bole volume (%)	Bole dry weight (kg)	Aboveground tree biomass (kg dry weight)	Root weight (kg)	Maximum root depth in soil (cm)
1	28.0	616.2	21.0	0.64	27.4	293	345	54	95
2	32.5	827.9	24.4	1.07	24.9	423	482	—	—
3	31.9	795.8	22.2	0.97	20.7	424	503	116	220
4	31.9	795.8	22.1	0.91	24.1	394	465	—	—
5	35.8	1 007.2	23.6	1.41	22.7	635	806	129	240

DBH, diameter at breast height.

sions relating fresh weight of needles (three age classes) and branch wood weight (total wood weight of the branch and wood weight of the four size classes) to branch diameter, branch length, whorl position and fresh weight of the branch (i.e. including needles). Fresh weights of the separate crown tree parts from every sample tree could then be calculated. The fresh weights of the branch wood thicker than 5 cm were calculated by subtracting the wood weight of branches < 5 cm from the total branch wood weight. The regressions that relate the fresh weights of different branch and needle fractions to independent variables are listed in *table III*. The regression equations were all highly significant ($P < 0.001$).

The dead branches and the cones from each sample tree were pooled together, weighed and a subsample was taken to determine fresh weight, dry weight and chemical analysis.

The dry branch wood and needle weight of every tree was estimated by reducing the calculated fresh weight by the average moisture content measured on the sampled branches and needles.

The nutrient content of every tree part was calculated from its dry weight multiplied by its nutrient concentration measured at the respective sampling height.

The biomass of the stand was estimated by multiplying the sample tree biomass by the ratio of stand basal area to sample tree basal area [2]. A second method consisted of determining the ratio of stand volume to sample tree bole volume. The nutrient contents of the different tree components were calculated in the same way. It was concluded that the method involving bole volume was more accurate for the estimation of total stand biomass, as its coefficient of variance was much lower than the tree basal area proportion method (6 % vs. 12 %). Further calculations of weights and nutrient contents of the 14 component parts were performed using the sample tree bole volume.

2.4. Nutrient fluxes

Nutrient uptake was calculated as the quantity of nutrients incorporated into the annual wood increment plus litterfall, plus canopy leaching. Requirement was calculated as the sum of the annual elemental wood increment and the current foliage production [7]. An indication of the extent of the internal recycling of elements was obtained by subtracting uptake from requirement.

Current nutrient accumulation in the wood increment was calculated by subtracting the nutrient contents of the boles and branches (four size classes) of 1988 from those of 1995, assuming no temporal variation in woody tissue concentrations. Litter was collected using litter traps. Canopy leaching was calculated from detailed measurements of precipitation and throughfall fluxes.

Bolewood increments were calculated from annual measurements of height and girth increments in a permanent sample 0.25 ha plot in which throughfall and litterfall measurements were also performed. The girth measurements started in 1988 and have continued until 1995 with the exceptions of 1993 and 1994. The heights of the trees were measured with a Blume-leiss altimeter in 1988, 1992 and 1995. The height increments between 1988 and 1992 were obtained by measuring the interwhorl lengths from felled trees. The bole volumes were calculated according to the cubing method of Berben [4]. Biomasses of the boles were estimated from bole volumes assuming that the relationship between bole volume and biomass found in 1992 was also valid for the preceding years. Branch wood increments were assumed to follow the measured proportionality with bole volume.

Litterfall (foliage, branches and cones) measurements for 1988–1992 were provided by Muys [20]. Litter was collected at a height of 1 m using five randomly located 0.28 m^2 litter traps equipped with nylon bags at 2-week intervals.

Bulk precipitation (BP) and throughfall (TF) were measured from February 1992 to January 1993. Throughfall and the bulk precipitation (measured on a nearby clearcutting) were sampled with each four randomly distributed bulk collectors. They consisted of a polyethylene funnel (15 cm diameter) which was connected to a 2 L polyethylene bottle. A nylon mesh was placed in the funnel to avoid contamination by large particles. The collectors were sampled and replaced by distilled water rinsed collectors on a monthly basis. Net throughfall (TF-BP) of base cations was adjusted for the contribution of particle interception deposition by the canopy exchange model of Ulrich [33]. In this model Na is assumed not to be influenced by

Table III. Regressions for fresh weight of needles and branch wood weight (y in grams) on branch diameter, branch length, branch fresh weight and whorl position.

Dependent variable (y)	Regression form	a	b	c	d	e	R^2	Significance level
Branch wood weight	$y = aBD + bBD^2$	–308.65	236.05	—	—	—	0.982	< 0.001
Needle weight	$y = aBW^b$	2.1053	0.7336	—	—	—	0.920	< 0.001
Weight of								
First year's needles	$y = a + bWP + cWP^2 + dBW + eBW^2$	–2682.06	259.53	–6.077	0.205	–0.000016	0.650	< 0.001
Second year's needles	$y = aWP + bBW$	1.7968	0.07980	—	—	—	0.853	< 0.001
Third year's needles	$y = aBW$	0.03268	—	—	—	—	0.612	< 0.001
Weight of twigs	$y = aWP + bBW + cBL$	–3.5064	0.1559	70.365	—	—	0.972	< 0.001
Weight of branch wood section 1–2 cm	$y = aWP + bBW^2 + cBL$	2.4326	$6.109.10^{-6}$	—	55.742	—	0.911	< 0.001
Weight of branch wood section 2–5 cm	$y = aBD + bBD^2 + cBW + dBW^2$	–313.035	134.816	0.3205	–0.000041	—	0.970	< 0.001

Independent variables: BD, branch diameter (cm); WP, whorl position (m); BW, branch fresh weight (kg); BL, branch length (m).

canopy exchange and Ca-, Mg- and K-bearing particles are assumed to have the same mass median diameter as Na- containing particles [9]. The particle interception deposition (DD) of Ca, Mg and K were estimated by multipying the bulk deposition with the calculated dry deposition factor (TF_{Na}-BP_{Na})/BP_{Na}. The canopy exchange rates of the base cations were obtained by subtracting the estimated dry deposition amounts from the net throughfall (TF-BP-DD). Canopy leaching of Ca, Mg and K minus canopy leaching of Ca, Mg and K associated with foliar excretion of weak acids was further assumed to equal uptake of H and NH_4 [9, 10]. Canopy leaching of P was assumed to be zero.

2.5. Nutrient status

Nutrient status was measured by sampling needles from five to ten dominant to codominant trees in the plot during October and November. The sample trees were representative of the mean defoliation level of the plot [3]. The needles were taken from the upper third of the crown (between the 5th and 9th whorl). The sampling was carried out in such a way that all orientations of the crown were included.

2.6. Chemical analysis

2.6.1. Tree component

Nitrogen was determined by the Kjeldahl method, using Se as catalyst. Ashes were extracted with a 1 N HNO_3 solution. Magnesium was determined by atomic absorption spectrophotometry. Calcium, potassium and sodium were measured by flame emission spectrometry. Phosphorus contents were measured colorimetrically using vanadomolybdate reagent.

2.6.2. Soil and forest floor

Total N of the soil and the forest floor samples was determined by Kjeldahl digestion. Total P was measured after total destruction in $HClO_4$ (13 %) by ICP. The exchangeable Ca, Mg and K of the soil were measured by ICP (by 0.1 N $BaCl_2$ extraction). Ashes of the forest floor were extracted with Aqua Regia reagens. Total concentrations of Ca, Mg and K were measured by ICP.

2.6.3. Rain and throughfall

Calcium, magnesium and potassium in the rainwater were measured by atomic absorption spectrophotometry. Nitrogen (NH_4 and NO_3) and phosphorus were determined colorimetrically.

3. RESULTS

3.1. Stand increment and biomass

Between 1988 and 1995 the current annual volume increment was estimated at 20.6 m^3 ha^{-1}. The mean height and girth increment averaged, respectively, 0.35 m and 1.6 cm $year^{-1}$. Radial increment was subject to strong year-to-year variation with maximum girth increment occurring in 1991–1992.

The bark accounted on average for 24 % of the total bole volume, although at the stem base bark proportions as large as 35 % were observed.

Stemwood accounted for on average 60 % of the total tree biomass and 71 % of aboveground stand biomass *(table IV)*. The woody part represented 85 % of the bole dry weight. Roots, bark and branches were 16, 10.8 and 8.1 %, respectively, of the total stand biomass. Foliage and dead branches were little less than 3 % each.

The first and second year's needles were, respectively, 53 and 36 % of the foliage (total = 8 265 kg ha^{-1}). Branches with thicknesses ranging between 2 and 5 cm and twigs < 1 cm accounted for 50 and 28 % of the total branch weight, respectively. The mass of thicker branches (> 5 cm) was very small (< 1 %).

Coarse roots (> 5 cm) constituted the largest part of the total root biomass of the tree (80 %). Roots with diameter rang-

Table IV. Distribution of organic matter over tree components.

	Dry weight (kg ha^{-1})	% total	% aboveground
Needles			
Age class 1	4 343	1.5	1.8
Age class 2	3 006	1.1	1.3
Age class 3	916	0.3	0.4
Total needles	8 265	2.9	3.4
Branches			
Twigs	6 317	2.2	2.6
Ø 1–2 cm	3 883	1.4	1.6
Ø 2–5 cm	11 460	4.0	4.8
Ø > 5 cm	1 469	0.5	0.6
Total branches	23 129	8.1	9.6
Boles			
Wood	170 459	59.7	71.0
Bark	30 759	10.8	12.8
Wood + bark	201 219	70.4	83.8
Dead branches	7 443	2.6	3.1
Total aboveground parts	240 055	84.0	100.0
Roots			
Ø 0.5–1 cm	703	0.2	
Ø 1–2 cm	1 129	0.4	
Ø 2–5 cm	7 073	2.5	
Ø > 5 cm	36 660	12.8	
Total belowground parts	45 565	16.0	
Total biomass	285 620	100.0	

ing from 2 to 5 cm represented 16 % of the total weight of the root system, whereas fine roots (0.5–2 cm) represented only appromixately 4 % of the belowground biomass. The weights and the shapes of the root systems from the excavated trees varied according to the permeability of the subsoil. The smallest sample tree had developed a compact surface root system (rooting depth only 95 cm), on top of a cemented spodic horizon, with a total biomass of 54 kg *(table II)*. The two other root systems (from the median and 3rd quartile) were more vigorous and their dry weights amounted to 116 and 129 kg, respectively. A shallow tap root was developed with well-formed closely linked lateral roots penetrating the compacted subsoil along cracks up to a depth of 240 cm. Lateral roots and rootlets were interweaved to form dense vertical root mats.

3.2. Nutrient concentrations, contents and nutrient distribution

The average nutrient concentrations of the different tree parts are listed in *table V*. Needles, twigs, smaller branches and rootlets contained the highest nutrient levels. Concentrations of all nutrients were

Table V. Mean concentration and standard error of nutrient elements in the different components of the sample trees (in g kg^{-1}).

	n	N	P	K	Ca	Mg
Needles						
1 year	53	14.123 (0.345)	1.033 (0.024)	6.056 (0.189)	1.221 (0.065)	0.539 (0.024)
2 year	48	13.257 (0.460)	0.916 (0.019)	5.457 (0.189)	1.911 (0.108)	0.501 (0.029)
3 year	16	13.264 (0.443)	0.876 (0.018)	5.416 (0.176)	2.451 (0.195)	0.435 (0.037)
Twigs Ø < 1 cm	21	8.289 (0.402)	0.498 (0.038)	2.238 (0.259)	2.254 (0.197)	0.455 (0.029)
Branches						
Ø 1–2 cm	15	4.699 (0.496)	0.386 (0.058)	2.067 (0.333)	1.853 (0.124)	0.418 (0.062)
Ø 2–5 cm	13	3.786 (0.633)	0.312 (0.056)	1.653 (0.378)	1.489 (0.127)	0.360 (0.047)
Wood	42	1.319 (0.058)	0.070 (0.009)	0.300 (0.047)	0.530 (0.018)	0.120 (0.005)
Bark	36	4.137 (0.227)	0.185 (0.016)	1.096 (0.120)	1.301 (0.081)	0.253 (0.032)
Roots						
Ø 0.5–1 cm	6	6.316 (0.687)	0.208 (0.021)	2.049 (0.204)	0.880 (0.124)	0.354 (0.072)
Ø 1–2 cm	7	4.352 (0.409)	0.155 (0.035)	1.324 (0.249)	0.671 (0.063)	0.254 (0.033)
Ø 2–5 cm	7	3.337 (0.569)	0.111 (0.015)	1.081 (0.318)	0.603 (0.079)	0.170 (0.044)
Ø > 5 cm	6	1.817 (0.212)	0.076 (0.021)	0.445 (0.143)	0.423 (0.029)	0.102 (0.011)
Dead branches	9	3.230 (0.655)	0.121 (0.032)	0.231 (0.051)	2.118 (0.461)	0.167 (0.041)
Cones	2	9.377 (1.770)	0.420 (0.097)	1.823 (0.202)	0.503 (0.043)	0.270 (0.055)

lowest in the woody parts and the coarse roots.

Per hectare, 659 kg N, 36 kg P, 188 kg K, 220 kg Ca and 49 kg Mg were stored in the stand biomass *(table VI)*. Although comprising only 11 % of the total biomass, branches and needles were important pools for K *(table VII)*. Almost 45 % of the total K content of the trees was located in the crown. Phosphorus was equally apportioned to the boles and the crown (43 % each). Stem boles constituted a major sink for Ca, Mg and N with, respectively, 57, 52 and 49 % of their respective tree nutrient content. The proportion of elements in the roots ranged between 9 and 15 % of the total stand nutrient content.

3.3. Nutrient pools versus nutrient fluxes

The nutrient capital of K, Ca and Mg in the trees represented, respectively, 46, 36 and 46 % of the ecosystem total (with mineral pools defined to a soil depth of 90 cm) *(table VIII)*. The amounts of total N and P sequestered in the stand are small compared to the total contents stored in the mineral soil and the forest floor.

Table VI. Nutrient contents of the different stand components (kg ha^{-1}).

	N	P	K	Ca	Mg
Needles					
Age class 1	58.4	4.4	25.9	5.8	2.3
Age class 2	38.4	2.8	16.7	6.4	1.5
Age class 3	12.2	0.8	4.8	2.3	0.4
Total needles	108.9	7.9	47.4	14.5	4.2
Branches					
Twigs	45.2	2.6	12.8	16.0	2.3
Ø 1–2 cm	16.6	1.3	6.7	7.6	1.4
Ø 2–5 cm	38.5	3.1	14.6	17.0	3.4
Ø > 5 cm	5.6	0.5	2.4	2.2	5.7
Total branches	105.9	7.4	36.6	42.8	12.8
Boles					
Wood	211.7	11.2	48.7	88.9	19.6
Bark	108.4	4.7	26.9	36.9	6.0
Wood + bark	320.1	15.9	75.6	125.8	25.6
Dead branches	24.0	0.9	1.7	15.8	1.2
Total aboveground parts	558.9	32.1	161.2	198.9	43.9
Roots					
Ø 0.5–1 cm	4.4	0.2	1.4	0.6	0.3
Ø 1–2 cm	4.9	0.2	1.5	0.8	0.3
Ø 2–5 cm	23.6	0.8	7.6	4.2	1.2
Ø > 5 cm	66.6	2.8	16.2	15.5	3.7
Total roots	99.6	4.0	26.8	21.1	5.5
Total biomass	658.5	36.1	188.0	220.0	49.4

Canopy leaching was only important for K (27.0 kg ha^{-1}). The presence of Ca and Mg in the net throughfall may be ascribed to interception deposition of Ca- and Mg-bearing particles. The contribution of this dry deposition was up to 25 % of the throughfall fluxes. Total inorganic N in throughfall amounted to 45.8 kg ha^{-1}, which was subdivided into 17.7 kg NO_3–N and 28.1 kg NH_4–N. The net throughfall of inorganic N (27.2 kg) was mainly composed of ammonium, which can be explained by the high gaseous or particle interception of NH_x. The dry deposition of N might have been underestimated due to uptake of NH_x. Additions of P by rain-

Table VII. Distribution of nutrients over tree parts (% of total).

	N	P	K	Ca	Mg
Needles	16.5	22.0	25.2	6.6	8.6
Branches	16.1	20.5	19.5	19.5	26.0
Wood	32.1	30.9	25.9	40.4	39.6
Bark	16.5	13.1	14.3	16.8	12.2
Dead branches	3.7	2.5	0.9	7.2	2.5
Roots	15.1	11.1	14.2	9.6	11.1

Table VIII. Nutrient pools (kg ha^{-1}) and nutrient fluxes (kg ha^{-1} year^{-1}).

	N	P	K	Ca	Mg
Nutrient pools (kg ha^{-1})					
Standing crop	658.5	36.2	188.0	220.0	49.4
Forest floor (total contents)	623.2	34.1	46.3	118.4	25.7
Mineral soil (0–90 cm)[a]	4 171.5	1 134.0	173.0	280.0	33.0
Ecosystem total	5 453.2	1 204.3	407.3	618.4	108.1
Atmospheric deposition (kg ha^{-1} year^{-1})					
Bulk precipitation	18.6	< 0.5	4.0	14.4	3.1
Throughfall	45.8	< 0.5	32.4	19.8	4.9
Net throughfall	27.2	< 0.5	28.4	5.4	1.8
Dry deposition[b]	-	< 0.5	1.4	4.9	1.1
Canopy losses	-	-	27.0	0.5	0.7
Uptake and requirement (kg ha^{-1} year^{-1})					
Immobilization in boles	14.2	0.7	3.4	5.6	1.1
Immobilization in branches	5.5	0.3	1.6	2.5	0.4
Litterfall	30.8	0.9	6.2	7.0	1.1
Canopy leaching	-	-	27.0	0.5	0.7
Uptake[c]	50.5	1.9	38.2	15.6	3.3
Requirement[d]	78.1	5.3	30.9	13.9	3.8
% Nutrient capital stand/ecosystem total	12.1	3.0	46.2	35.6	45.7
% Uptake/nutrient pools LFH + soil	1.4	0.2	16.3	3.9	5.6

[a] Mineral pools represent extractable contents for K, Ca and Mg; [b] dry deposition factor = 0.34; [c] annual elemental increment of bole and branch wood + litterfall + canopy leaching; [d] annual elemental increment of bole and branch wood + new foliage.

fall were mostly below the detection limit and did not exceed 0.5 kg ha^{-1}.

Annual litterfall was estimated at 3 067 kg ha^{-1}, of which 72 % was foliage, and contained 30.8 kg N ha^{-1}. Calculation of annual N immobilization in the boles (NPP = 8 949 kg ha^{-1}) and branches (NPP = 1 076 kg ha^{-1}) yielded a value of 19.7 kg ha^{-1}. Annual uptake rates of K were estimated at 38.2 kg ha^{-1}. Canopy losses accounted for 70 % of total root uptake of K. The amounts of P, Ca, K and Mg returned in litter were of similar magnitude to the amounts which were accumulated in the wood.

The requirements for N and P exceeded their uptake rates, indicating the presence of internal transfers. Retranslocation of P fulfilled approximately 64 % of the annual requirement. The internal transfer of P constituted 77 % of the content sequestered in the current foliage. For nitrogen 28 kg N (35 % of annual requirement) was recovered from older tissues to support growth in younger needles. This amount might have been overestimated since no allowance was made for a possible uptake of NH_x by the crown. However, if NH_x was taken up and exchanged for base cations, only potassium would have been involved in this exchange, as canopy losses of Ca and Mg were negligible. Canopy losses of K (27.0 kg or 0.69 keq) can be apportioned to excretion or exchange for NH_4 and H (canopy uptake of NH_4 and H must balance canopy leaching of K). If we assume that only NH_4 uptake accounted for the potassium losses, maximum 9.6 kg NH_4–N would have been absorbed by the canopy. This would imply that still at least 18 kg N was involved in retranslocation.

The uptake of K, Ca and Mg was better coupled with the tree requirements, although root uptake of K exceeded the potassium demand by 24 %.

The elemental uptake rate was expressed as proportion of mineral and LFH nutrient pool to obtain a crude insight in percent soil turnover rate irrespective of atmospheric inputs and leaching losses. This ratio was especially high in the case of K, Mg and Ca in decreasing order of importance.

3.4. Nutrition

Monitoring of the nutrient status between 1988 and 1995 clearly revealed an obvious decline in nutrient concentrations of P, K, Ca and Mg *(table IX)*. In the current year's foliage this decrease had ceased during the last years but the steady decline continued in the second year's needles for P, Ca and Mg. Nitrogen levels remained constant with the exception of the second year's needles for which a slight increase was noted. According to the criteria of Van den Burgh [34, 35], nutrient concentrations of P, Ca and Mg shifted from a sufficient to an insufficient level. The levels for K dropped from an optimum to a sufficient range. Nitrogen levels were maintained in a sufficient range.

These shifts were also observed for the element ratios with highest values occurring in 1992. Evaluation of nutrient ratios marked a possible nutrient imbalance between N and P in 1992 and 1995.

4. DISCUSSION

Total standing biomass of the 62-year-old Corsican pine stand amounted to 286 tons dry weight per hectare, of which 16 % is in the belowground portions. Total aboveground biomass of the Pijnven stand was estimated at 240 tons ha^{-1}. The total biomass of 58-year-old Corsican pine stands growing on blown sands at Culbin Forest in Scotland extended from 155 (control) to 221 tons ha^{-1} (highest level of N dressing) [23], whereas Ovington

Table IX. Nutrient concentrations and element ratios of needles from upper crown in 1988, 1992 and 1995 (in g kg^{-1}).

	First year's needles			Second year's needles		
	1988	1992	1995	1988	1992	1995
N	14.000	14.346	14.045	11.900	14.581	15.028
P	1.456	0.980	1.041	1.067	0.972	0.834
K	8.485	5.750	5.963	8.735	5.038	4.923
Ca	1.350	0.935	0.915	2.115	1.406	1.311
Mg	0.816	0.499	0.543	0.553	0.425	0.327
N/P	9.6	14.6	13.5			
N/K	1.6	2.5	2.4			
N/Mg	17.2	28.7	25.9			

Criteria of Van den Burgh for half year's needles:
N sufficient: 13.0–18.0, optimum: 18.0–25.0
P insufficient: 1.0–1.3, sufficient: 1.3–1.6
K sufficient: 5.0–7.0, optimum: > 7.0
Ca insufficient: 0.5–1.0, sufficient: 1.0–1.5
Mg insufficient: 0.3–0.6, sufficient: 0.6–1.0
Balanced nutrition for N/P = 6–12, N/K = 1–3 and N/Mg = 8–30.

[22] estimated the aboveground biomass of a 48-year-old Corsican pine plantation in the United Kingdom at 242 tons ha^{-1}. Miller and Cooper [15] and Proe et al. [23] reported root proportions of 19 % and 12 % in Corsican pine stands (*Pinus nigra* ssp. *maritima*) growing on blown sands (Culbin Forest) at an age of 39 and 58 years, respectively. Minderman [18] reported root proportions of 16.6 % in 22-year-old pole-stage crops of *Pinus nigra* var. *austrica*.

Stemwood accounted for on average 71 % of the aboveground biomass. Bark comprised 24 % of the bole volume and 15 % of the total bole weight. Similar bark proportions were reported by Tomanic [31].

The foliage of the Pijnven stand amounted to nearly 8 300 kg ha^{-1} and constituted 3.4 % of the aboveground biomass. Other studies reported foliage masses ranging from 5.6 [24, 40] to 21 tons ha^{-1} [25].

The current annual increment of the stand amounted to 20.6 m^3 ha^{-1} year^{-1}. According to the yield tables of Berben [4], an increment of 15–17 m^3 ha^{-1} year^{-1} was more likely to be expected for stands belonging to same age and yield class. The high productivity of the stand may be due to the development of deep rooting lateral roots penetrating the compacted subsoil along friable cracks up to a depth of 240 cm. The root study clearly stressed the presence of a compacted to cemented B horizon as a severe impediment to stem and height growth. Toth and Turrel [32], Timbal et al. [30] and Heinze et al. [13] pointed out that Corsican pine tree growth was determined to a large extent by the available root space, which ensured a more favourable water balance.

The vigorous increments might also be ascribed to the abundant airborne deposition of nitrogen (46 kg inorg. N ha^{-1} year^{-1} in throughfall). Since N was an important growth-limiting factor in the past, it is conceivable that relief from N deficiency by atmospheric deposition favours current growth. Miller and colleagues [15, 16] reported large increases in basal area and volume increments after application of nitrogen in a severely nitrogen deficient pole-stage crop of Corsican pine on blown sands at Culbin Forest. Maximum volume increment occurred when nitrogen concentrations in the needles of top-whorl foliage rose to 2 %. In the same stands Proe et al. [23] observed a long-term N fertilizer growth response, achieved through internal transfers of nitrogen. Blok et al. [6] and Goor [38] noted only small responses in height growth on nitrogen dressings in young Austrian and Corsican pine stands in the Netherlands. Nys et al. [21] came to similar conclusions in fertilization experiments in Sologne (France).

Nitrogen fertilization in Scots pine stands do not always entail a sustainable or even a transient improvement of growth, even when nitrogen is growth limiting. Initially they result in growth increases but they are, however, often followed by a phase of growth suppression due to depletion of nutrients that are not provided by the fertilizer [11]. Nitrogen deposition can stimulate growth beyond the capacity of the soil to supply other limiting nutrients [28]. The results of this study indicate that other elements like phosphorus and magnesium have become more growth limiting than nitrogen and therefore a lower growth rate was perhaps more likely to be expected.

Boles and stumps contained about 65 % of the total Ca, Mg and N content. This proportion is expected to continue to rise with increasing age. The high allocation of nitrogen to the boles and roots can also be explained by an alteration of nitrogen allocation patterns inflicted by the high nitrogen deposition. An abundant external nitrogen supply by fertilizer may result in a higher retention of nitrogen in the tree [36], but can also provoke a shift in nitrogen storage towards the stem bole and roots. Proe et al. [23] observed marked nitrogen content increases by 44 % and a concomitant shift in distribution of nitrogen between components in 58-year-old Corsican pine stands, 22 years after nitrogen fertilizer application. Proportions of nitrogen in boles and stumps of fertilized Corsican pine plots increased to 55 % compared with 45 % in the untreated plots. This occurred at the expense of twigs and foliage, which share dropped by 6–7 %.

The calculated annual uptake of nitrogen matched the average value reported by Cole and Rapp [7] for temperate coniferous forests *(table X)*. Higher uptake values of nitrogen were reported by Ranger [25] and Miller et al. [17] for nitrogen-fertilized Corsican pine plots. Despite the abundant external supply of nitrogen, between 23 and 35 % of the nitrogen requirement (between 18 and 27.6 kg) was

Table X. Annual production and nutrient uptake for Corsican pine stands and temperate coniferous forests (kg ha^{-1}year^{-1}).

	Present study	Temperate coniferous average
Aboveground biomass (kg ha^{-1})	240 000	307 000
Aboveground production (kg ha^{-1} year^{-1})[a]	14 368	8 354
Nitrogen uptake (kg ha^{-1} year^{-1})	50.5	47
Phosphorus uptake (kg ha^{-1} year^{-1})	1.9	5
Potassium uptake (kg ha^{-1} year^{-1})	38.2	32.6
Calcium uptake (kg ha^{-1} year^{-1})	15.6	44.6
Magnesium uptake (kg ha^{-1} year^{-1})	3.3	7.1

[a] Aboveground production = increment bole and branches + biomass current foliage.

satisfied by internal transfers. This is surprising, although other nitrogen experiments confirm that the N status of the tree does not affect the efficiency of N cycling or the amount of N translocated [8, 14, 19]. Moreover, the withdrawal of mobile nitrogen compounds from the abundant storage sites requires less energy expenditure than uptake of nitrate from the soil [5]. Soil solution analysis by suction tension lysimeters yielded nitrate concentrations averaging 17.6 mg·L^{-1} NO_3–N in the parent material, which indicated that the uptake capacity of the ecosystem was finite.

On the basis of the large phosphorus soil pool, the uptake rates were unexpectedly low *(table X)*. Soil solution analysis in the surface soil and the subsoil did not detect any dissolved inorganic or organic phosphorus. Its absence could be largely attributed to the strong biological retention within surface soils and the high geochemical control over phosphorus movements in the subsoil contributing to a tight cycling of phosphorus within the ecosystem [39]. Moreover, the high aluminium concentrations in the soil solution (concentrations of which averaged 8 mg·L^{-1} in the B and 19 mg·L^{-1} in the C horizon) might have decreased its availability by provoking precipitation of P as Al-phosphates. At low pH values these poorly soluble phosphate salts are known to regulate P availability [5]. The decreasing P levels of the litter can, in addition, trigger a stronger biological retention in the future. The low P availability may be the reason for the high retranslocation of phosphorus (64 % of requirement) within the trees.

The uptake of basic cations was obviously limited by the low available mineral soil and forest floor nutrient pools. For potassium, annual uptake amounted to 16 % of the available nutrient pools. The high potassium uptake was especially attributable to the severe canopy losses, since this element is very subject to leaching. The uptake of ammonium and its exchange for potassium as shown by field investigations and ecophysiological experiments [26] could have reinforced these losses. The uptake rates of Ca and Mg, expressed as a proportion of the available mineral soil and LFH pools, were lower. In contrast with potassium their elemental inputs by bulk precipitation and dry deposition satisfy to a great extent the requirements of the trees. The deposition of atmospheric base cations in Europe is, however, following a declining trend in recent decades [12].

The uptake values for P, Ca and Mg represented less than a half of the listed average values for temperate coniferous forests *(table X)*. The calculated nutrient use efficiency (above ground production/unit of nutrient uptake) for those elements is far above those found in a variety of forest ecosystems [7]. It is unclear whether a future decrease in their availability will be met by a further increase in nutrient use efficiency (more retranslocation or higher production per unit of nutrient consumed) or whether the response will be a decline in growth.

Monitoring of the nutrient status revealed a decrease in concentrations of Ca, Mg and P that was especially marked in the second year's needles. Applying the criteria to evaluate the nutrition of half year's needles given by Van den Burg [34, 35], the nutrient status of P, Ca and Mg was shifting from a suboptimal to an insufficient range. Nitrogen levels remained constant in current foliage but increased in the older needles. They did not attain excessive values, which are to be expected in the surroundings of pig farms. Van Dijk et al. [37] recorded higher nitrogen levels (2.2 %) in Corsican pine stands, which were heavily affected by *Sphaeropsis sapinea* in the southern part of the Netherlands. A drastic increase of nitrogen in the needles as a consequence of the chronic nitrogen deposition has perhaps been offset by a shift towards the woody parts or a gradual increase in foliar biomass. Aber et al. [1] suggested that in the initial stages of the development of nitrogen saturation, constant additions from chronic deposition would not lead to a detectable increase in foliar nitrogen concentration, but rather to a gradual increase in foliar biomass with a constant nitrogen concentration.

Moreover, the nutrient ratios exhibited a decline indicating the development of a nutrient imbalance. It is, however, doubtful whether this decline was due to a competitive inhibition by NH_4 in the soil or an ammonium–cation exchange. The moderate nitrogen levels found in the needles (1.4 %) do not, however, support the presence of a strong competition between ammonium and the other nutrients. We suggest therefore that the steady decrease in Ca, Mg and P and their element ratios was more related to the mismatch between the low available nutrient pools and the vigorous growth of the stand which led to a dilution of nutrients.

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