ORIGINAL PAPER

Source-driven remobilizations of nutrients within stem wood in *Eucalyptus grandis* plantations

Carlos Roberto Sette Jr. · Jean-Paul Laclau · Mario Tomazello Filho · Rildo M. Moreira · Jean-Pierre Bouillet · Jacques Ranger · Julio Cesar Raposo Almeida

Abstract Nutrient remobilizations in tree ligneous components have been little studied in tropical forests. A complete randomized block design was installed in Brazilian eucalypt plantations to quantify the remobilizations of phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na) within stem wood. Three treatments were studied: control with neither K nor Na addition (C), 3 kmol ha^{-1} K applied (+K), and 3 kmol ha^{-1} Na applied (+Na). Biomass and nutrient contents were measured in the stem wood of eight trees destructively sampled at 1, 2, 3 and 4 years after planting in each treatment and annual rings were localized on discs of wood sampled every 3 m in half of the trees. Chemical analyses and wood density measurements were performed individually for each ring per level and per tree sampled. Nutrient remobilizations in annual rings were calculated through mass balance between two successive ages. Our results show that nutrient remobilizations within stem wood were mainly source-driven. Potassium and Na additions largely increased their concentration in the outer rings as well as the amounts remobilized in the first 2 years after the wood formation. The amount of Na remobilized in annual rings was 15 % higher in +Na than in +K the fourth year after planting despite a 34 % higher production of stem wood in +K leading to a much higher nutrient sink. A partial substitution of K by Na in the remobilizations within stem wood might contribute to enhancing *Eucalyptus grandis* growth in K-depleted soils.

Keywords Resorption · Trunk · Potassium · Sodium · Eucalypt · Retranslocation

C. R. Sette Jr.
Forest Engineer Department, Federal University of Goiás (UFG), Goiânia, GO CEP 74690-900, Brazil

C. R. Sette Jr. · M. Tomazello Filho · R. M. Moreira · J.-P. Bouillet
Forest Science Department, ESALQ, University of São Paulo (USP), Piracicaba, SP CEP 13418-900, Brazil

J.-P. Laclau (✉) · J.-P. Bouillet
Ecologie Fonctionnelle & Biogéochimie des Sols & Agro-écosystèmes, UMR 111, CIRAD, 34060 Montpellier, France
e-mail: laclau@cirad.fr

J.-P. Laclau
Ciência Florestal, Universidade Estadual Paulista (UNESP), Botucatu, SP CEP 18610-307, Brazil

J. Ranger
UR Biogéochimie des Ecosystèmes Forestiers, INRA, 54280 Champenoux, France

J. C. R. Almeida
University of Taubaté, Taubaté, Brazil

Introduction

Reviewing the ecophysiological relevance of nitrogen (N) remobilizations within trees, Millard and Grelet (2010) emphasized the need to cope better with nutrient limitations in the carbon-centric view dominating tree physiology over the past decades. Remobilization processes enable plants to reuse the nutrients and therefore play an important role for maintaining tree growth in infertile soils making them less dependant on current nutrient uptake. The vast majority of studies dealing with nutrient remobilizations in forest have been conducted throughout leaf senescence (Nambiar and Fife 1991; Aerts and Chapin 2000). The

amounts of N, phosphorus (P), and potassium (K) remobilized from the leaves of four evergreen tree species in Australia were strongly positively correlated with their content in fully expanded young leaves (Fife et al. 2008), which was consistent with a general pattern of source-driven N remobilizations within trees (Millard and Grelet 2010). However, remobilizations in tree compartments other than leaves have still been little investigated in the field. Most of the studies on mature trees focused on carbon (C) and N remobilizations using the possibility to track C and N stable isotopes after pulse labelling (Millard and Grelet 2010; El Zein et al. 2011; Epron et al. 2012a). Nitrogen is the most limiting nutrient for tree growth in many forests of the Northern hemisphere (Rennenberg et al. 2009). However, tree growth in highly weathered tropical soils is commonly more limited by P (Vitousek et al. 2010) and K (Laclau et al. 2009; Wright et al. 2011; Santiago et al. 2012) than by N. Studies using stable isotopes other than ^{15}N to gain insight into nutrient remobilizations within ligneous tree components are scarce and, to our knowledge, have only been carried out for seedlings (Proe et al. 2000; Weatherall et al. 2006). The lack of cheap stable isotopes of P, K, calcium (Ca), and magnesium (Mg) for field-use as well as a smaller scientific community in tropical regions than in industrialized countries probably has led to a shortage of information on remobilizations of nutrients others than N within tree compartments in the field.

Remobilizations within stem wood contribute to reducing nutrient concentration in the boles harvested and therefore to balance the input–output of nutrients in forest soils when the length of the rotation increases (Ranger and Turpault 1999; Ranger et al. 2002). A budget approach in annual rings was widely used in the '80s and '90s to estimate nutrient remobilizations within stem wood over forest rotations in temperate and boreal regions. Large remobilizations of N, P, K, and to a lesser extent, Mg, throughout wood ageing have been shown for many tree species (Hingston et al. 1979; Lim and Cousens 1986; Helmisaari and Siltala 1989; Colin-Belgrand et al. 1996). However, nutrient remobilization within stem wood of tropical tree species with continuous growth along the year is poorly known. A chronosequence approach in fast-growing *Eucalyptus* plantations in the Congo showed that the mobility of N, P, K, Ca, and Mg in the stem wood was similar to that in deciduous species (Laclau et al. 2001; Saint-André et al. 2002). However, the seasonal patterns and the influence of soil fertility on nutrient remobilizations within stem wood were not investigated.

Most of tropical *Eucalyptus* plantations are established on highly weathered soils and sustainable yields are largely dependent on fertilization regimes (Laclau et al. 2005; Gonçalves et al. 2008). In Brazil, large amounts of fertilizers applied the first 2 years after planting make it possible

to reach gross primary productivities >4,000 g C m^{-2} year^{-1} (Ryan et al. 2010), among the highest for world forests (Luyssaert et al. 2007). Fertilizer applications are concentrated the first year after planting and remobilization processes play a major role to satisfy the N, P, and K requirements after canopy closure in tropical *Eucalyptus* plantations (Laclau et al. 2003). A recent study has shown that a small supply of NaCl in *Eucalyptus grandis* Hill. ex Maiden stands established on K-depleted soils enhanced the stem wood biomass by 55 % at the harvest relative to control plots without NaCl addition (Epron et al. 2012b). The low cost of NaCl in comparison to purified KCl fertilizers might lead to a large scale application of a mixture between KCl and NaCl in tropical eucalypt plantations (Almeida et al. 2010).

We put forward the hypotheses that: (1) source-driven processes in *Eucalyptus* trees increase the remobilizations of nutrients applied with fertilizers per unit of stem wood biomass produced, and (2) *Eucalyptus* trees remobilize large amounts of Na stored in the stem wood in substitution for K in K-deficient soils when the availability of Na increases. We used a mass balance approach in annual rings to gain insight into the role of the stem wood for the storage of nutrients throughout the development of *Eucalyptus* trees.

Materials and methods

Study area

The study was carried out at the Itatinga Experimental Station (23°10′S and 48°40′W). The mean annual rainfall over the 15 years before our study was 1,360 mm and the mean annual temperature was 20 °C, with a seasonal cold period from June to September. The experiment was located on a hilltop (slope <3 %) at an altitude of 850 m. The soils were very deep Ferralsols (>15 m) developed on Cretaceous sandstone, Marília formation, Bauru group, with a clay content ranging from 14 % in the A1 horizon to 23 % in deep soil layers. The mineralogy was dominated by quartz, kaolinite, and oxyhydroxides, with acidic soil layers (pH between 4.5 and 5) containing very small amounts of available nutrients (sum of base cations <0.3 cmol$_c$ kg^{-1}, between the depths of 5 cm and 6 m) (Laclau et al. 2010).

The experiment was set up in a *Eucalyptus saligna* (Sm.) stand conducted as a coppice, without any fertilizer application from 1940 to 1997. Herbicide was applied on the stumps to prevent regrowth and *E. saligna* seedlings were planted in 1998 with a low fertilizer supply (30 kg N ha^{-1}, 9 kg P ha^{-1}, 8 kg K ha^{-1}). The *E. saligna* stand was harvested at age of 6 years (February 2004) and

the stumps were devitalized using an application of glyphosate. Boles were removed from the site and harvesting residues were uniformly distributed. Concentrations of exchangeable K and Na were 0.02 cmol$_c$ kg^{-1} in the 0–5 cm soil layer at the end of the *E. saligna* rotation and <0.01 cmol$_c$ kg^{-1} below a depth of 5 cm (Maquère 2008). High levels of nutrient exports with the boles, without fertilization from 1940 to 1998, made the area suitable to expect a eucalypt response to fertilizer inputs.

Experimental design

Eucalyptus grandis seedlings were planted in April 2004 between the stumps of the previous rotation (spacing 2 m × 3 m). The seeds were collected on the same mother trees (half-sib family) in an orchard established by the Suzano Company with trees originating from Coffs Harbour (Australia). The seed orchard was established with trees selected for their high growth rate. A complete randomized block design was installed with six treatments and four blocks with individual plots of 9 × 9 trees. A completed description of the experiment is given by Almeida et al. (2010). Our study was carried out in three treatments and three blocks: (1) C, control with no K and no Na input; (2) +K, 3 kmol K ha^{-1} (116 kg K ha^{-1}) applied as KCl fertilizer (a similar amount is applied in commercial plantations of the region); and (3) +Na, 3 kmol Na ha^{-1} (68.5 kg Na ha^{-1}) applied as NaCl fertilizer. A third of the total amount was applied at planting (buried at 20 cm from the seedlings), then at 6 months (broadcast beneath the crowns) and 12 months of age (broadcast over the entire area). All treatments received the same basic fertilization regime (except K and Na), with an addition, the first year after planting, of 120 kg N ha^{-1}, 35 kg P ha^{-1}, micronutrients, and 2 t ha^{-1} of dolomitic lime, not limiting tree growth at the study site (Gonçalves et al. 2008).

Tree sampling

Tree height and circumference at 1.3 m above-ground ($C_{1.3}$) were measured every 12 months in the inner plots (excluding 2 buffer rows) the first 4 years after planting. Destructive samplings of biomass and nutrient contents were carried out at 1, 2, 3, and 4 years after planting in one block of the experiment. At each stand age, the range of basal areas in each treatment was divided in four classes of similar extent and two trees were sampled in each class. Discs of wood were taken at the ground level and every 3 m for each selected tree. Chemical analyses were conducted on a composite sample of stem wood (proportional to the dry matter of wood at all the sampled heights) for the 96 trees sampled (8 trees × 3 treatments × 4 ages) and allometric relationships were established to estimate the

biomass and nutrient contents of stem wood at each age (see Almeida et al. 2010 for a detailed description). For half of the sampled trees (1 tree per basal area class at each age in each treatment), 'virtual' annual rings were positioned on all the discs of wood sampled. The continuous growth throughout the year in tropical eucalypt plantations prevent from distinguishing annual rings. The methodology described by Laclau et al. (2001) to estimate annual remobilizations within stem wood over a full rotation in *Eucalyptus* plantations was adapted here. The first step was to rebuild the cambial growth of a tree from stem profiles.

Taper functions were used for estimating stem profiles under-bark at 1, 2, and 3 years after planting. The circumference of each tree sampled destructively (32 trees per treatment up to 4 years of age) was measured under-bark every metre, up to a diameter of 2 cm. To predict the diameter under-bark (d_z) at height z, models were adjusted (Newnham 1992):

$$\frac{d_z}{d_{1.3}} = \left[\frac{H-z}{H-1.3}\right]^{\left(P_1 + P_2 \times e^{-\left(\frac{P_3 \times z}{P_2 \times H}\right)}\right)} + \varepsilon. \tag{1}$$

where ε follows a normal distribution, $d_{1.3}$ and H are, respectively, the diameter under-bark at 1.3 m above-ground (expressed in centimetres) and the total height of the tree (in metres). The parameters P_1, P_2, and P_3 were adjusted to the measurements of diameter under-bark for each stand age. Root mean square errors of the models were low and residue repartitions were not biased for all the sampled trees.

Annual measurements of $C_{1.3}$ and H for all the sampled trees, combined with treatment-specific taper functions, made it possible to predict the diameter under-bark at 1, 2, and 3 years of age, whatever the height on the stem. Virtual annual rings were thus positioned on each disc of wood sampled. Each annual ring boundary was delineated on the disc using two criteria: (1) the mean radius of the ring (measured in eight directions) was the value predicted by the taper function, and (2) the boundaries were parallel to growth rings visible to the naked eye. Rings are commonly observed in tropical *Eucalyptus* species but the number of rings may be different from tree age (Sette et al. 2010).

Wood density and chemical analyses

The wood of each annual ring was separated in all the discs and dried at 65 °C until constant weight. Half of each sample was used to determine wood density and the other half was ground and homogenized for chemical analyses. Wood density was determined for each annual ring at each tree height sampled from the maximum moisture content method adapted to small wood samples (Smith 1954).

Small wood samples were immersed in water, subjected to a vacuum until saturation, then oven-dried at 103 °C until constant weight. Wood density was determined from the weight of the samples at maximum moisture content and oven-dried. This method is commonly used in studies dealing with wood of *Eucalyptus* tree species (Kibblewhite et al. 2000; Rockwood et al. 2008; Warren et al. 2009).

Chemical analyses were made in Brazil for one composite sample of stem wood per tree for the 96 trees sampled. After digestion in nitric and perchloric acids, Ca and Mg were determined by atomic absorption spectrophotometry (B462, Micronal®, Brazil) and K and Na by flame emission spectrophotometry. For half of the sampled trees, chemical analyses were performed in France individually for each ring per level. Phosphorus, K, Ca, Mg, and Na were determined using an ICP sequential spectrophotometer (JY 24) after digestion by chloridic and hydrofluoric acids and combustion for 2 h at 500 °C. Control quality procedures were used in the two laboratories and samples were analyzed in duplicate for inter-calibration.

Calculations

Dynamics of nutrient accumulation within stem wood

Stem wood biomass and nutrient contents were estimated from the eight trees sampled in each treatment at each age using the model:

$$Y_i = a + b(D_i^2 H_i)^{c_j} + \varepsilon_i$$

where Y_i is the biomass or the nutrient content of the stem wood of tree i, D_i is the diameter at breast height of tree i, H_i is the height of tree i, a, b, and c are the parameters to be estimated and ε_i is the residual error not explained by the model. As age was found to significantly affect this relationship (Saint-André et al. 2005), the equations were fitted by treatment for each age. Fitting was performed using PROC NLP of the SAS software and maximum likelihood estimations. To test treatment effects, comparisons between models were performed using the Akaike information criterion.

Mean nutrient concentration per ring in the four trees per treatment sampled at each age

The area of each annual ring was calculated considering that all the rings were circular:

$$S_{z,[i-1,i]} = \pi \times (r_{z,i}^2 - r_{z,i-1}^2). \tag{2}$$

where $S_{z,[i-1,i]}$ is the area of the ring corresponding to the wood formed between age $(i-1)$ and age i at height z, and where $r_{z,i-1}$ and $r_{z,i}$ are the radius under-bark of the stem at height z predicted by the taper functions (Eq. 1) at age $(i-1)$ and age i, respectively.

The amount of mineral M, $M_{z,[i-1,i]}$, contained in the wood formed between age $(i-1)$ and age i at height z, in a disc of thickness 1 cm, was calculated using the equation:

$$M_{z,[i-1,1]} = C_{z,[i-1,i]} \times S_{z,[i-1,i]} \times d_{z,[i-1,i]} \tag{3}$$

where $C_{z,[i-1,i]}$ and $d_{z,[i-1,i]}$ are the mineral concentration and the density of the wood formed between age $(i-1)$ and age i at height z, respectively.

The mean nutrient concentration (C_{tree}) within ring i in a given sampled tree was calculated using the equation:

$$(C_{\text{tree}})_i = \frac{\sum_{z=0}^{n} M_{z,[i-1,1]}}{\sum_{z=0}^{z=n} S_{z,[i-1,i]} \times d_{z,[i-1,i]}}. \tag{4}$$

where ring i was the ring formed between age $(i-1)$ years and age i years, and n the number of heights sampled in the tree.

Estimation of nutrient contents in annual rings for the whole stand

Mean wood density in ring i for the whole stand was estimated at each age from the equation:

$$d_i = \sum_{p=0}^{4} \alpha_p \times \frac{\sum_{z=0}^{n} S_{i,z,p} \times d_{i,z,p}}{\sum_{z=0}^{n} S_{i,z,p}} \tag{5}$$

where $S_{i,p,z}$ and $d_{i,p,z}$ are the area and the wood density of ring i at height z for tree p, and α_p is the proportion of total stand basal area represented by the basal area class of tree p.

Wood biomass in each annual ring was estimated for the whole stand using Eq. (6) for internal rings and Eq. (7) for the external ring of the trunk.

For an internal ring i in a stand of age a > i

$$B_{i,a} = B_{i,0} \times \frac{d_{i,a}}{d_{i,0}} \tag{6}$$

where $B_{i,0}$ is the biomass of ring i the year of its formation, $d_{i,a}$ and $d_{i,0}$ are the mean wood densities in ring i estimated from Eq. (5), at a years after planting and the year of wood formation, respectively.

For the external ring i in a tree of age a (a = i), we used the equation

$$B_{i,a} = B_{\text{tot},a} - \sum_{k=1}^{k=i-1} B_{k,a} \tag{7}$$

where $B_{\text{tot},a}$ is the total stem wood biomass of the stand at age a estimated applying allometric equations to the inventory, and $B_{k,a}$ is the biomass of ring k calculated with Eq. (6).

The mean nutrient concentration within ring i in the stand $(C_{\text{stand}})_i$ was estimated using the equation:

$$(C_{\text{stand}})_i = \sum_{p=1}^{4} \alpha_p (C_{\text{tree}})_{p,i}. \tag{8}$$

where $(C_{\text{tree}})_{p,i}$ is the mean nutrient concentration within ring i in the tree p.

Nutrient contents in a given ring per hectare (N_i) were thus estimated multiplying the wood mass of the ring estimated with Eqs. (6) and (7) by the mean concentrations in the ring estimated with Eq. (8). The equation used was:

$$N_i = \frac{(C_{\text{stand}})_i \times \sum_{l=1}^{v} B_{i,a,l}}{A} \tag{9}$$

where $B_{i,a,l}$ is the mass of ring i in a tree l of age a, v is the number of trees inventoried and A the area of the studied plot.

Nutrient remobilizations at the stand level

Annual remobilizations were calculated stepwise between two successive ages. Nutrient remobilizations into the i ring from $(a-1)$ to a years after planting, $(R_{i,[a-1,a]})$ were calculated with the equation:

$$R_{i[a-1,a]} = N_{i,a-1} - N_{i,a} \tag{10}$$

Total remobilization in stem wood between the successive ages $(a-1)$ and a ($R_{\text{tot}[a-1,a]}$) was calculated by adding the nutrient remobilizations in all the rings initiated before age $(a-1)$ with the equation:

$$R_{\text{tot},[a-1,a]} = \sum_{i=1}^{a-1} R_{i,[a-1,a]}. \tag{11}$$

Nutrient remobilization efficiency

Nutrient remobilization efficiency was assessed for the wood produced the first 2 years after planting because heartwood stands only in the two first rings in 4-year-old trees. The equation used was:

$$E_{N,i,t} = 100 \times \frac{C_{i,i} - C_{i,4} \times (d_{i,4}/d_{i,i})}{C_{i,i}} \tag{12}$$

where $E_{N,i,t}$ is the remobilization efficiency of nutrient N in the ring produced the ith year after planting ($i = 1$ or 2) in tree t, $C_{i,4}$ is the concentration of nutrient N in ring i of tree t at age 4 years, and $d_{i,4}$ is the wood density in ring i of tree t at age 4 years. Equation (12) was used for the four trees sampled at age 4 years in each treatment for annual ring determinations. We considered that $C_{i,i}$ and $d_{i,i}$ were the nutrient concentration and the wood density, respectively, in ring i of the tree sampled at age i years in the same treatment for the same basal area class.

Statistical analyses

Differences in nutrient concentrations between tree ages, tree social status (basal area class), and treatments were tested using the MIXED procedure of the SAS software. Ring cambial age (number of years since ring formation), tree social status and treatment were considered as fixed factors. Annual rings were considered as random factor. Observations were assumed to be uncorrelated among the sampled trees because they were cut far from each other. The probability level used to determine significance was $P < 0.05$. When differences were significant, the means were compared with the Tukey–Kramer multiple comparison tests using the Lsmeans/Pdiff option. Two-way ANOVAs were used to test the effects of treatments and tree social status on the remobilization efficiencies of each nutrient in an individual ring. The GLM procedure of the SAS 9.2 software package was used (SAS Inc., Cary, NC, USA). A residual analysis was performed to check whether the residuals met the assumptions of the ANOVA and, if necessary, raw data were log- or sqrt-transformed so that residuals were homoscedastic and normally distributed. When significant differences were detected between treatment levels, the Tukey multiple range test was used to compare treatment means.

Results

Dynamics of biomass and nutrient accumulation in stem wood

Potassium and Na additions significantly increased the stem wood biomass the first 4 years after planting (Fig. 1). At 4 years of age, it was higher by 116 and 51 % in treatments +K and +Na, respectively, than in the C treatment. The biomass of the rings produced the first, second, third, and fourth years after planting amounted to 2–3, 24–28, 32–34, and 36–41 % of the stem wood biomass at age 4 years in the three treatments. Nutrient contents within stem wood were driven by both biomass accumulation and changes in nutrient concentrations throughout the study period. A low tree growth in the C treatment led to a lower accumulation of P, K, Ca, Mg, and Na in stem wood than in treatments +Na and +K. Whilst P, Ca, and Mg contents within stem wood were mainly driven by the accumulation of biomass in the three treatments, K and Na additions the first year after planting largely influenced their content within stem wood up to 4 years of age. A similar K accumulation in treatments C and +Na, despite a stem wood biomass in +Na 51 % larger than in C at 4 years after planting, suggested that the enhancement in tree growth after Na addition was not due

Fig. 1 Dynamics of biomass, phosphorus (P), potassium (K), sodium (Na), calcium (Ca), and magnesium (Mg) accumulation within stem wood the first 4 years after planting, estimated sampling eight trees per treatment at each age. Least significant differences between treatments ($P < 0.05$) are indicated at each age
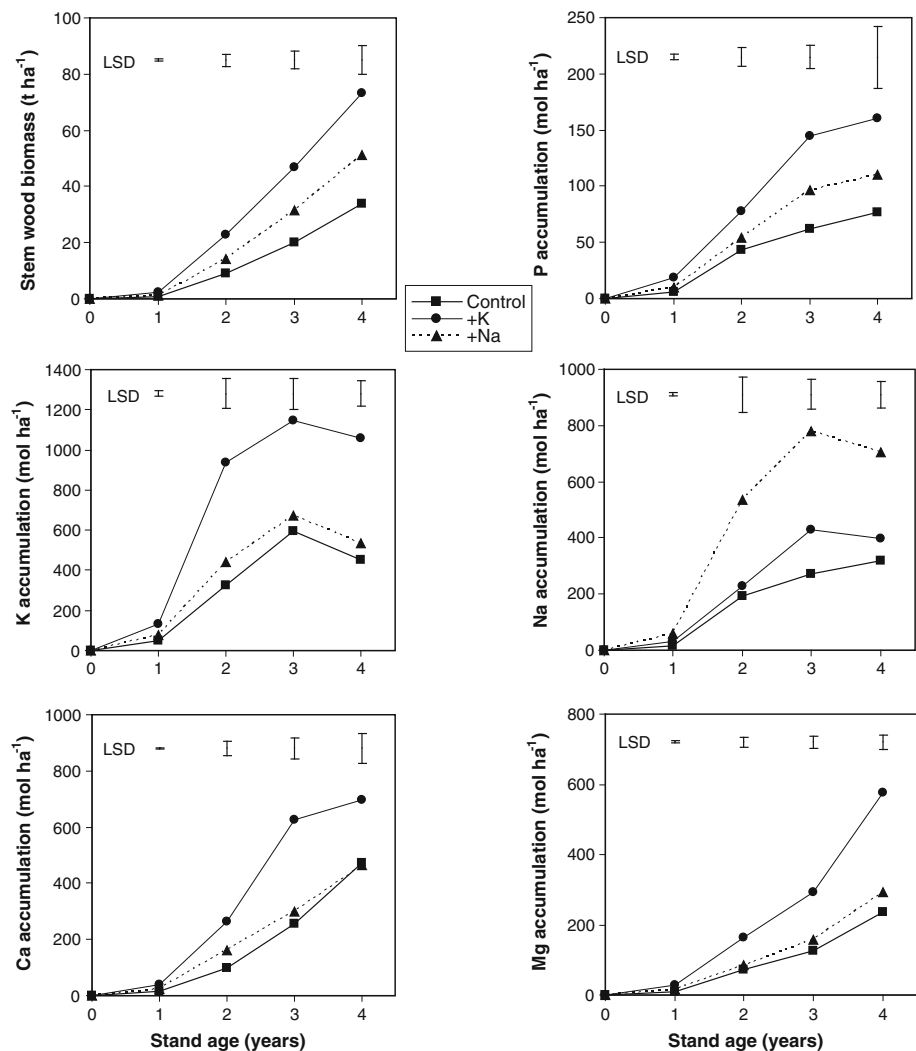

to a higher K uptake in the soil. Sodium addition the first year after planting led to an accumulation of Na within stem wood about twice as high in treatment +Na, as in the C and +K treatments at 4 years of age. The amounts of K and Na within stem wood decreased by 8–24 %, from 3 to 4 years after planting in the three treatments (except for Na in treatment C), although the biomass of this compartment increased by about 50 %. This result suggested intense remobilizations of those nutrients in the stem wood at the end of the study period.

Concentrations of K, Na, P, Ca, and Mg within annual rings

A general pattern of decrease in concentrations of K, Na, and P from the outer to the inner rings, whatever the tree age, showed that these nutrients were found in the most physiologically active tissues (Fig. 2). Nutrient withdrawals were higher the first 2 years after the formation of the ring than thereafter. Potassium and Na additions

significantly increased the concentrations of those elements within annual rings (Table 1; Fig. 2). The concentrations of Ca and Mg in annual rings were also significantly influenced, with higher concentrations at most ring cambial ages in the C treatment than in treatments +K and +Na. The interaction between ring cambial age and treatment was significant for the concentrations of K, Na, and Ca. This pattern for K and Na resulted from a sharper decrease in concentration with ring ageing for the trees fertilized with these elements than in the other treatments (Fig. 2). In the case of Ca, the interaction resulted from a slight decrease in concentrations after ring formation in treatments +K and +Na whereas the concentrations of this element changed little throughout ring ageing in the C treatment (a trend towards an accumulation was found in the ring produced the first year after planting).

The concentration of Na in the outer ring was about twice as low in the +K treatment as in treatment C, whatever the tree age, and the decrease in concentrations of Na throughout ring ageing was less pronounced in the +K treatment than in
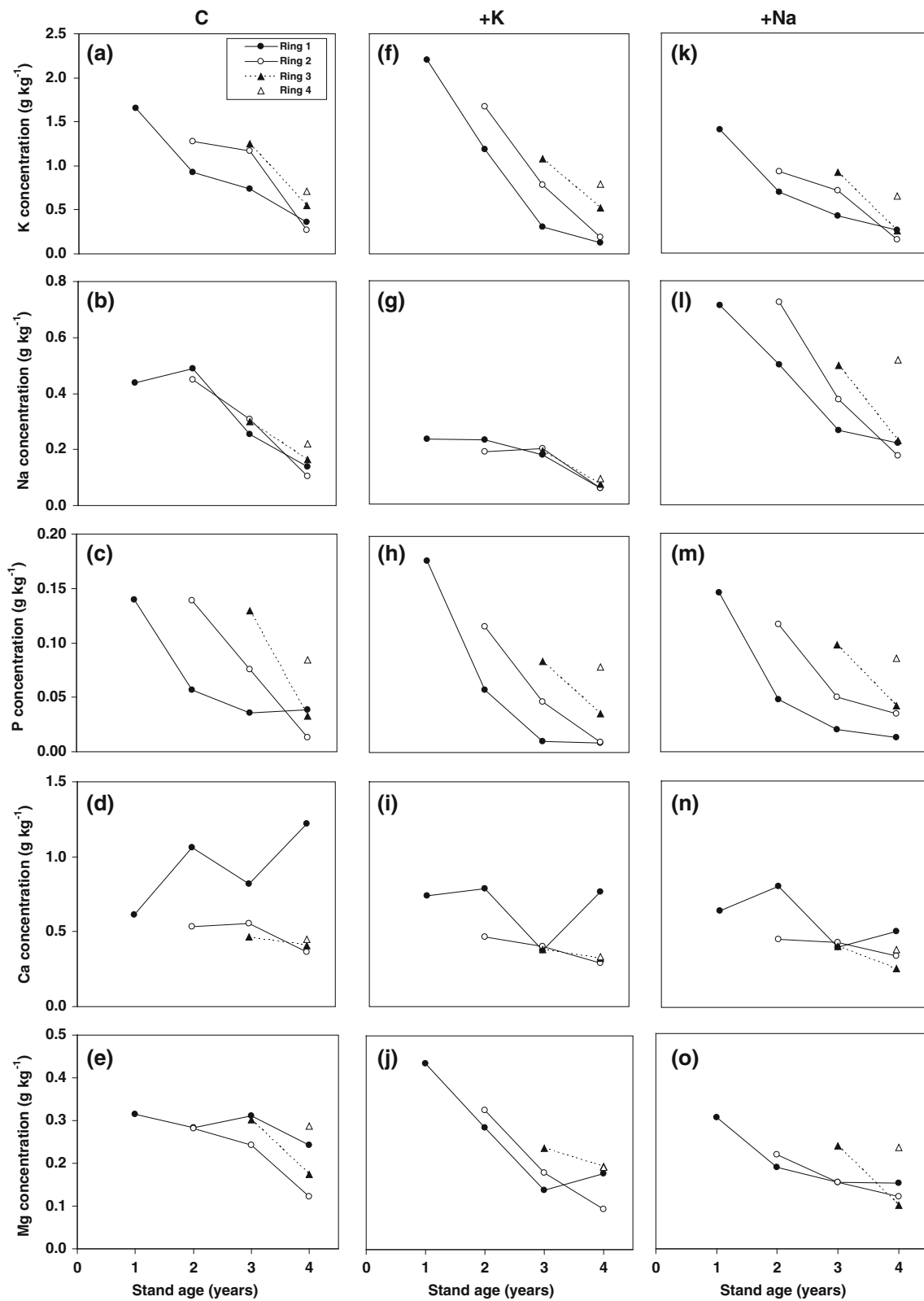
Fig. 2 Changes in concentrations of K, Na, P, Ca, and Mg within annual rings over the first 4 years after planting in treatments C (**a–e**, respectively), +K (**f–j**, respectively), and +Na (**k–o**, respectively)

Table 1 Influence of ring cambial age, treatment, social status of sampled trees and their interactions on the concentrations of K, Na, P, Ca, and Mg in annual stem wood rings produced the first 4 years after planting in *Eucalyptus grandis* stands

Fixed factors	df	Nutrient									
		K		Na		P		Ca		Mg	
		F	P	F	P	F	P	F	P	F	P
Ring cambial age	3	149.5	**<0.0001**	67.1	**<0.0001**	102.7	**<0.0001**	12.3	**<0.0001**	43.6	**<0.0001**
Treatment	2	5.9	**0.004**	57.6	**<0.0001**	2.6	0.077	18.6	**<0.0001**	11.0	**<0.0001**
Social status	3	0.7	0.544	1.2	0.302	0.2	0.905	2.2	0.088	1.7	0.176
Cambial age × treatment	6	3.8	**0.002**	6.8	**<0.0001**	0.3	0.939	4.2	**0.009**	1.6	0.164
Cambial age × social status	6	0.3	0.934	1.1	0.378	0.6	0.721	0.4	0.902	1.1	0.345
Treatment × social status	9	1.2	0.325	0.5	0.899	0.4	0.949	0.9	0.492	0.4	0.946

Significant values ($P < 0.05$) are indicated in bold

treatments C and +Na (Fig. 2). A sharp decrease in K concentrations with ring ageing irrespective of the treatment suggested that K was strongly remobilized in our K-deficient soil, even when the availability of Na rose. The social status of the trees (dominated or dominant in the stand) did not significantly influence the concentrations of K, Na, P, Ca, and Mg in annual rings over the study period (Table 1). Interactions between the social status and the ring cambial age were not significant as well as interactions between tree social status and treatment, whatever the nutrient.

Nutrient contents and remobilizations in annual rings

The amounts of nutrients in annual rings were largely driven by the mass of the ring (Fig. 3). Even though large changes in nutrient concentrations were found in the wood produced the first year after planting, the contribution of this ring in annual remobilizations within stem wood was minor from 2 years after planting onwards. The highest mineral contents were found in the outer rings at each age. Outer rings had both the largest biomass and the highest nutrient concentrations (except for Ca). Even though changes in Na concentrations throughout ring ageing in treatment +K were low in comparison with the C treatment, the much larger stem wood biomass in +K led to similar amounts of Na in annual rings as in the control treatment throughout the study period. The amounts of K in annual rings were little influenced by Na application over the first 4 years after planting. The highest accumulation of K and Na in the stem wood of the +K and +Na treatments, respectively, was mainly a result of high K and Na contents in the two outer rings (Fig. 1). The highest accumulation of P, Ca, and Mg in the stem wood of the +K treatment at each age was also mainly localized in the two outer rings.

Remobilization efficiencies in the rings produced the first 2 years after planting were not significantly different between treatments, except for P in the inner ring (Table 2). The effects of tree social status on remobilization efficiencies were not significant whatever the nutrient and the annual ring. Mean remobilization efficiencies across treatments in the two inner rings were 83, 72, 87, 4, and 51 % for K, Na, P, Ca, and Mg, respectively.
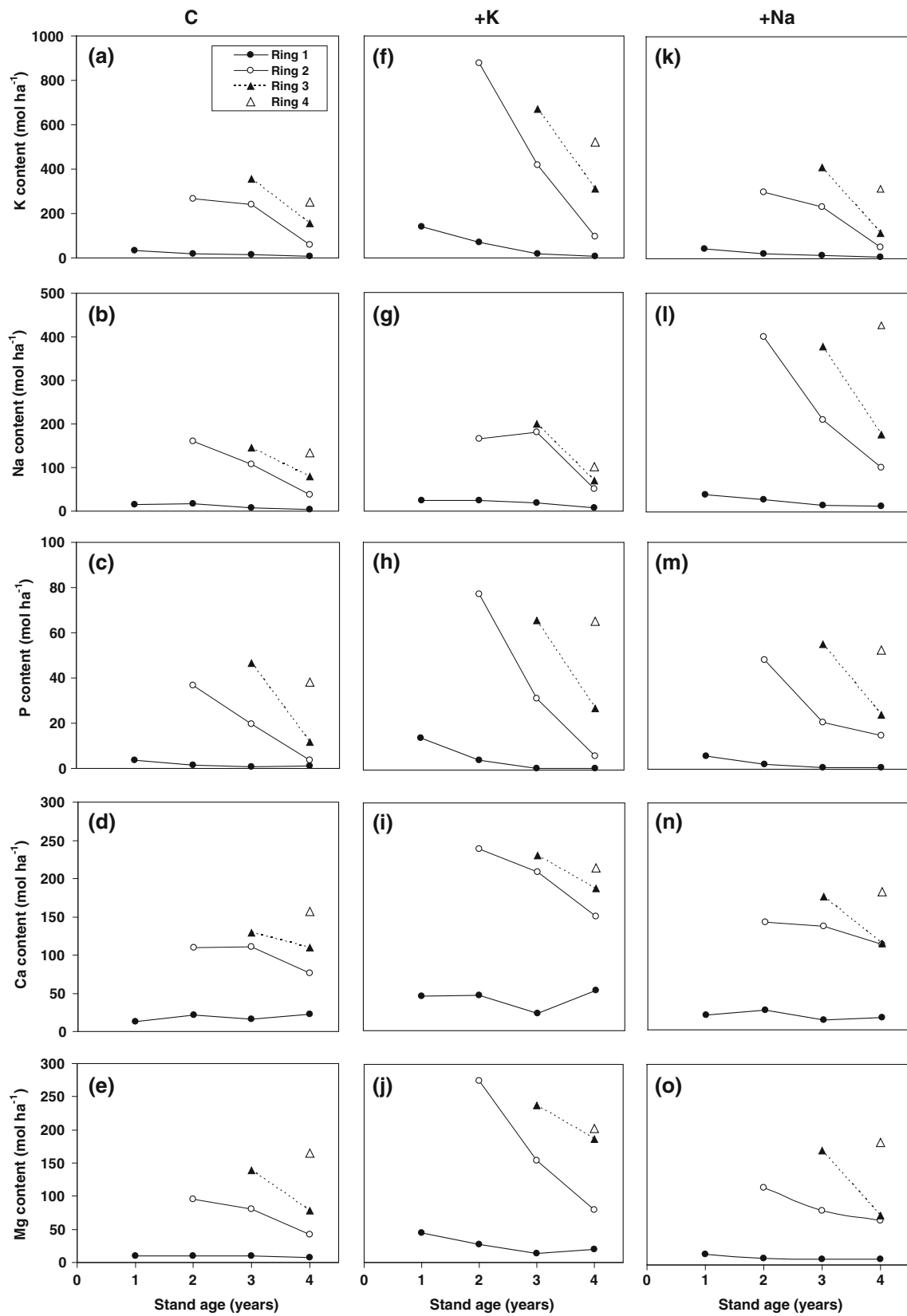
Annual remobilizations of K, Na, P, Ca, and Mg within stem wood increased throughout stand development, irrespective of the treatment (except for Mg in treatment +K). Among the studied nutrients, the highest remobilizations occurred for K (Table 3). The annual amounts of K remobilized in the stem wood were 4.5, 15.7, and 1.7 times higher for trees in the +K treatments than in treatment C, the second, third and fourth year after planting (1, 2, and 3 years after fertilizer addition), respectively, for a stem wood biomass production about twofold larger. Annual K remobilizations over the study period were of the same order of magnitude in the C treatment and in Na-fertilized trees. Whilst Na was not remobilized in well K-supplied trees the second and the third years after planting, high remobilizations occurred in treatment +Na. Annual Na remobilizations from 1 to 4 years after planting in treatment +Na were two to three times higher than in the C treatment. The amount of Na remobilized in annual rings was 15 % higher in +Na than in +K the fourth year after planting despite a 34 % smaller stem wood biomass production. In the +Na treatment, the amounts of K and Na remobilized within the stem wood were of the same order of magnitude up to 4 years after planting. Although stem wood biomass at age 4 years was 2.3-fold larger in +K than in C, the annual remobilizations of P, Ca, Mg the fourth year after planting were only higher in +K by 25, 49, and 17 %, respectively.

Discussion

Nutrient concentrations in annual rings

Although annual rings cannot be detected visually in tropical *E. grandis* trees, our method combining annual

Fig. 3 Changes in K, Na, P, Ca, and Mg contents within annual rings over the first 4 years after planting in treatments C (**a–e**, respectively), +K (**f–j**, respectively), and +Na (**k–o**, respectively)

Table 2 Remobilization efficiency (%) within the wood produced the first 2 years after planting in 4-year-old trees

Nutrient	Treatment		
	C	+K	+Na
K			
Ring 1	80.7 ± 10.3	92.5 ± 3.8	78.8 ± 4.2
Ring 2	80.6 ± 7.1	87.3 ± 3.2	76.2 ± 21.8
Na			
Ring 1	70.2 ± 8.1	66.1 ± 22.2	71.0 ± 5.3
Ring 2	78.2 ± 5.9	70.1 ± 3.5	73.8 ± 12.9
P			
Ring 1	76.5 ± 13.5 a	94.2 ± 1.4 b	92.8 ± 1.3 b
Ring 2	91.0 ± 3.0	91.5 ± 2.3	75.0 ± 19.3
Ca			
Ring 1	−78.8 ± 53.5	−18.4 ± 28.2	13.2 ± 10.6
Ring 2	33.0 ± 12.2	43.3 ± 16.1	30.8 ± 16.1
Mg			
Ring 1	30.6 ± 6.1	42.6 ± 28.6	49.3 ± 15.9
Ring 2	58.2 ± 10.7	72.2 ± 8.4	52.2 ± 10.4

Different letters in the same row indicate significant differences between treatments ($P < 0.05$)

C: no K and Na addition; +K: application of 3.0 kmol K ha^{-1}; +Na: application of 3.0 kmol Na ha^{-1}

inventories with stem profile equations and intensive sampling of discs along the trunk in four trees per treatment and per age provided estimates of nutrient contents in the stands of the same magnitude as sampling eight trees per age in each treatment. Consistent changes in concentrations of mobile nutrients within annual rings throughout stand development in each treatment confirmed that the boundaries of each ring were correctly delimited. The non-significant influence of the tree social status on nutrient concentrations in annual rings supported our simple up-scaling approach to estimate mean nutrient concentrations in annual rings for the whole stand. Budgets of nutrients in tree compartments are, however, dependent on the timing of sampling and this method is usually considered less accurate than isotopic approaches to estimate nutrient remobilizations (Millard and Grelet 2010). Total remobilizations might have been underestimated in our study since the continuous growth of tropical *Eucalyptus* trees might have led to several storage/remobilization phases within annual rings along the year. We acknowledge that nutrient remobilizations within stem wood were probably estimated with high uncertainty and our approach did not make it possible to quantify the magnitude of the uncertainty. However, nutrient budgets are commonly used to quantify the remobilizations of nutrients in ligneous tree components in the field when stable isotopes cannot be used (Milla et al. 2005). Nutrient concentrations within tree rings were so different between treatments in our study that the budgets clearly showed a strong effect of K and Na additions on nutrient remobilizations. Further studies based on intensive sampling of xylem sap would be useful to gain insight into the amounts and the types of compounds translocated seasonally from the stem and the roots in plantation forests (Pfautsch et al. 2009).

Whilst tree response to KCl and NaCl additions was mainly attributed to K and Na in our study, Cl might also have an effect on wood formation. A specific effect of Cl cannot be excluded since we did not determine Cl concentrations within stem wood. However, KCl and K_2SO_4 additions did not lead to significantly different tree growth in basal area and height the first 4 years after planting in our experiment (Almeida et al. 2010). The much higher positive effects on tree growth of KCl and NaCl additions (relative to the C treatment) than Cl addition (comparing KCl- and K_2SO_4-supplied plots) suggest that tree response in treatments +K and +Na resulted much more from the addition of K and Na than of Cl.

The dynamics of nutrient concentrations in annual rings commonly described for tree species were not modified by fertilizer addition in our study. Whilst, the concentrations of P and K decreased sharply over ring ageing, the mobility of Ca was low and Mg was intermediate, as reported for other *Eucalyptus* species (Turner and Lambert 1983; Grove et al. 1996; Laclau et al. 2001; Saint-André et al. 2002). A similar pattern was found in *Picea abies* (Dambrine et al. 1991), *Castanea sativa* (Colin-Belgrand et al. 1996), *Pinus sylvestris* L. (Helmisaari and Siltala 1989; Finér and Kaunisto 2000), *Quercus robur* L. (Penninckx et al. 2001), and *Pinus pinaster* (Augusto et al. 2008). Although radial variations in wood mineral concentrations are highly species- and element-specific (Penninckx et al. 2001), the concentrations of N, P, and K are, in general, higher in the sapwood than in inner rings as a result of their metabolic role in living cells (Meerts 2002). Microscopic, molecular, and biophysical techniques showed that K is mainly required for cell expansion in cambial cells, whereas Ca seems to be essential for cell division and cell wall strengthening (Fromm 2010). Changes in radial concentrations of K, Na, P, Ca, and Mg throughout stem growth seem, therefore, to reflect both the role of these elements in cambial activity and their mobility in xylem cells.

Source-driven remobilizations within stem wood

Nutrient remobilizations in senescent leaves have been extensively studied and their adaptive significance is well documented (Aerts and Chapin 2000). Remobilization processes enable plants to reuse the nutrients and therefore play an important role for maintaining tree growth in infertile soils making them less dependant on current

Table 3 Net remobilizations (expressed in mol ha^{-1}) of K, Na, P, Ca, and Mg in annual rings of *Eucalyptus grandis* trees the first 4 years after planting

Stand age (years)	Treatment											
	C				+K				+Na			
	1–2	2–3	3–4	1–4	1–2	2–3	3–4	1–4	1–2	2–3	3–4	1–4
K												
Ring 1	15	5	8	28	68	54	9	131	22	9	5	36
Ring 2		28	183	211		457	322	778		68	179	248
Ring 3			203	203			358	358			296	296
Total K remobilized	15	33	394		68	510	689		22	77	480	
Na												
Ring 1	−2	9	4	11	1	5	11	18	11	13	2	26
Ring 2		54	69	123		−15	131	115		191	109	301
Ring 3			66	66			129	129			201	201
Total Na remobilized	−2	62	140		1	−10	271		11	205	312	
P												
Ring 1	2	1	0	3	10	4	0	13	4	1	0	5
Ring 2		17	16	33		46	25	71		27	6	33
Ring 3			35	35			39	39			31	31
Total P remobilized	2	18	51		10	49	64		4	29	37	
Ca												
Ring 1	−9	6	−7	−10	−1	24	−31	−8	−6	13	−4	3
Ring 2		−2	35	33		30	58	88		6	24	30
Ring 3			19	19			43	43			62	62
Total Ca remobilized	−9	4	47		−1	54	70		−6	19	82	
Mg												
Ring 1	1	0	2	3	17	14	−7	24	6	2	0	7
Ring 2		15	38	53		121	74	195		34	15	49
Ring 3			61	61			51	51			97	97
Total Mg remobilized	1	15	101		17	135	118		6	36	112	

C: no K and Na addition; +K: application of 3.0 kmol K ha^{-1}; +Na: application of 3.0 kmol Na ha^{-1}

nutrient uptake. Large ranges of remobilization rates from senescent leaves have been reported for N and P, with median values around 50 % for plant species in natural ecosystems (Aerts and Chapin 2000). Remobilization efficiencies of K, Na, and P within stem wood in our study were at the upper range of values reported throughout leaf senescence in tree species (Saur et al. 2000; Kozovits et al. 2007; Fife et al. 2008). Even though N remobilizations are seasonally programmed in temperate and boreal tree species (Millard and Grelet 2010), the continuous growth along the year of *E. grandis* trees did not prevent it from large remobilizations of K, Na, and P in the stem wood. The highest nutrient availability in the soils under fast-growing *Eucalyptus* plantations occur the first year after planting as a result of large fertilizer inputs combined with a high amount of nutrients released via organic matter decomposition and a relatively low nutrient uptake by trees the first months after planting (Laclau et al. 2010). The

sharp decrease in K, P, and Mg concentrations in the outer ring from 1 to 3 years after planting in the +K treatment (Fig. 2) suggests that the sapwood in *E. grandis* trees has a capacity to accumulate nutrients when their availability is high, far beyond the necessity required for cambial activity and xylem cell development. The capacity of *Eucalyptus* trees to store nutrients within stem wood for a further use when the demand for growth is much higher is likely to contribute to preventing nutrient losses by deep drainage in forests established on sandy soils with high hydraulic conductivities.

In agreement with our first hypothesis, the dynamics of nutrient concentrations within stem wood showed that remobilizations were mainly source-driven. This feature was particularly clear for Na. Remobilizations of Na were estimated at 11, 205, and 312 mol ha^{-1} in treatment +Na the second, third, and fourth year after planting, respectively, whereas they only amounted to 1, −10, and 271 mol ha^{-1} in

treatment +K (Table 3). The 43 % larger stem wood biomass in treatment +K than in +Na at age 4 years even led to a much stronger nutrient sink in K-supplied trees. The amounts of K remobilized in annual rings of K-deficient trees were close in the +Na and C treatments in our study despite a 51 % larger stem wood biomass at age 4 years in +Na, leading to a much stronger K sink. Our results suggest that K and Na remobilizations in stem wood follow the general tendency found for N in both coniferous and deciduous species whose remobilizations depend upon the amount of nutrients in store, not the amount of new growth or current uptake rate (Carswell et al. 2003; Millard and Grelet 2010). However, information for nutrients other than N is scarce and suggests that the effect of nutrient supply on remobilizations may not always be the same for all the nutrients. Remobilizations of K and Mg were, like that of N, independent of current nutrient supply in *Picea sitchensis* (Bong.) Carr. seedlings labelled with ^{15}N, ^{41}K, and ^{26}Mg (Weatherall et al. 2006). Nevertheless, another study using the same isotopes in *P. sylvestris* L. seedlings showed a different behaviour between those nutrients: whilst current nutrient supply had no significant effect on the amount of N or Mg remobilized to new tissues, K remobilization was lower in seedlings growing on sand culture with a reduced nutrient supply (Proe et al. 2000).

Remobilizations of Na within stem wood

In agreement with our second hypothesis, large amounts of Na were remobilized in the stem wood of Na-supplied trees in our K-depleted soil. Epron et al. (2012b) showed that the addition of 4.5 kmol ha^{-1} of NaCl increased the stem wood biomass of *E. grandis* trees by 55 % at harvest in our experiment. A growing body of evidence led Subbarao et al. (2003) to consider Na as a functional nutrient that can be important in the physiology of numerous glycophyte species under K starvation conditions. Similar dynamics within annual rings for Na, as for K in our study, as well a strong response to NaCl addition in biomass production, suggest a substitution of K by Na in living wood cells for certain physiological functions. Potassium remobilizations in the branches of evergreen Mediterranean species appeared to be related to osmotic requirements (Milla et al. 2005). The osmotic role of K for the expansion of xylem cell is well established (Fromm 2010) and further studies are needed to assess whether this function can be fulfilled by Na, as shown for the maintenance of osmotic potential and cell turgor in leaves of K-starved *E. grandis* trees (unpublished data). To our knowledge, a positive effect of NaCl addition on tree growth in field experiments has only been demonstrated at our study site (Almeida et al. 2010; Epron et al. 2012b) and the physiological mechanisms are still poorly understood.

In conclusion, the annual remobilizations of nutrients within the stem wood of *E. grandis* trees were mainly source-driven the first 4 years after planting. High remobilizations of Na on a K-depleted soil were likely to contribute to the enhancement of stem wood production by about 50 %, via a reduction in K requirements for the development of the trees. Further studies are needed to gain insight into the physiological mechanisms responsible for the positive effects of low NaCl additions on the growth of *Eucalyptus* trees in highly weathered soils. The function of Na in the biological cycle of forest ecosystems would deserve further attention, since the availability of this element might contribute to driving tree growth in K-depleted tropical soils subjected to high marine aerosol input.

References

Aerts R, Chapin FS III (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv Ecol Res 30:1–67

Almeida JCR, Laclau J-P, Gonçalves JLM, Ranger J, Saint-André L (2010) A positive growth response to NaCl applications in Eucalyptus plantations established on K-deficient soils. For Ecol Manag 259:1786–1795

Augusto L, Meredieu C, Bert D, Trichet P, Porté A, Bosc A, Lagane F, Loustau D, Pellerin S, Danjon F, Ranger J, Gelpe J (2008) Improving models of forest nutrient export with equations that predict the nutrient concentration of tree compartments. Ann For Sci 65:808

Carswell FE, Millard P, Rogers GND, Whitehead D (2003) Influence of nitrogen and phosphorus supply on foliage growth and internal recycling of nitrogen in conifer seedlings (*Prumnopitys ferruginea*). Funct Plant Biol 30:49–55

Colin-Belgrand M, Ranger J, Bouchon J (1996) Internal nutrient translocation in chestnut tree stem wood: III. Dynamics across an age series of *Castanea sativa* (Miller). Ann Bot 78:729–740

Dambrine ELE, Goaster S, Ranger J (1991) Croissance et nutrition minerale d'un peuplement d'épicea sur sol pauvre. II—Prélèvement racinaire et translocation d'elements mineraux au cours de la croissance. Oecologia 12:791–808

El Zein R, Bréda N, Gérant D, Zeller B, Maillard P (2011) Nitrogen sources for current-year shoot growth in 50-year-old sessile oak trees: an in situ ^{15}N labeling approach. Tree Physiol 31:1390–1400

Epron D, Bahn M, Derrien D, Lattanzi FA, Pumpanen J, Gessler A, Högberg P, Maillard P, Dannoura M, Gérant D, Buchmann N (2012a) Pulse-labelling trees to study carbon allocation dynamics: a review of methods, current knowledge and future prospects. Tree Physiol 32:776–798

Epron D, Laclau J-P, Almeida JCR, Gonçalves JLM, Ponton S, Sette CRJR, Delgado-Rojas JS, Bouillet J-P, Nouvellon Y (2012b) Do changes in carbon allocation account for the growth response to potassium and sodium applications in tropical *Eucalyptus* plantations? Tree Physiol 31:1–13

Fife DN, Nambiar EKS, Saur E (2008) Remobilization of foliar nutrients in evergreen tree species planted in a Mediterranean environment. Tree Physiol 28:187–196

Finér L, Kaunisto S (2000) Variation in stemwood nutrient concentrations in scots pine growing on peatland. Scand J For Res 15:424–432

Fromm J (2010) Wood formation of trees in relation to potassium and calcium nutrition. Tree Physiol 30:1140–1147

Gonçalves JLM, Stape JL, Laclau J-P, Bouillet J-P, Ranger J (2008) Assessing the effects of early silvicultural management on long-term site productivity of fast-growing eucalypt plantations: the Brazilian experience. South For 70:105–118

Grove TS, Thomson BD, Malajczuk N (1996) Nutritional physiology of eucalypts: uptake, distribution and utilization. In: Attiwill PM, Adams MA (eds) Nutrition of eucalypts. CSIRO, Australia, pp 77–108

Helmisaari HS, Siltala T (1989) Variation in nutrient concentrations of *Pinus sylvestris* stems. Scand J For Res 4:443–451

Hingston FJ, Turton AG, Dimmock GM (1979) Nutrient distribution in Karri (*Eucalyptus diversicolor* F. Muell) ecosystems in Southwest Western Australia. For Ecol Manag 2:133–158

Kibblewhite RP, Johnson BI, Shelbourne CJA (2000) Kraft pulp qualities of *Eucalyptus nitens*, *E. globulus*, and *E. maidenii*, at ages 8 and 11 years. N Z J For Sci 30:447–457

Kozovits AR, Bustamante MMC, Garofalo CR, Bucci S, Franco AC, Goldstein G, Meinzer FC (2007) Nutrient resorption and patterns of litter production and decomposition in a Neotropical Savanna. Funct Ecol 21:1034–1043

Laclau J-P, Bouillet J-P, Ranger J, Joffre R, Gouma R, Saya A (2001) Dynamics of nutrient translocation in stem wood across an age series of a *Eucalyptus*. Ann Bot 88:1079–1092

Laclau J-P, Deleporte P, Ranger J, Bouillet J-P, Kazotti G (2003) Nutrient dynamics throughout the rotation of *Eucalyptus* clonal stands in Congo. Ann Bot 91:879–892

Laclau J-P, Ranger J, Deleporte P, Nouvellon Y, Saint-André L, Marlet S, Bouillet J-P (2005) Nutrient cycling in a clonal stand of *Eucalyptus* and an adjacent savanna ecosystem in Congo: input–output budgets and consequences for the sustainability of the plantations. For Ecol Manag 210:375–391

Laclau J-P, Almeida JCR, Gonçalves JLM, Saint-André L, Ventura M, Ranger J, Moreira MR, Nouvellon Y (2009) Influence of nitrogen and potassium fertilization on leaf lifespan and allocation of above-ground growth in *Eucalyptus* plantations. Tree Physiol 29:111–124

Laclau J-P, Ranger J, Gonçalves JLM, Maquère V, Krusche AV, M'Bou AT, Nouvellon Y, Saint-André L, Bouillet J-P, Piccolo MC, Deleporte P (2010) Biogeochemical cycles of nutrients in tropical *Eucalyptus* plantations: main features shown by intensive monitoring in Congo and Brazil. For Ecol Manag 259:1771–1785

Lim MT, Cousens JE (1986) The internal transfer of nutrients in a Scots pine stand. 2. The patterns of transfer and the effects of nitrogen availability. Forestry 59:17–27

Luyssaert S et al (2007) CO₂ balance of boreal, temperate, and tropical forests derived from a global database. Glob Change Biol 13:2509–2537

Maquère V (2008) Dynamics of mineral elements under a fast-growing *Eucalyptus* plantation in Brazil. Implication for soil sustainability. PhD thesis, AgroParisTech, Paris, p 369

Meerts P (2002) Mineral nutrient concentrations in sapwood and heartwood: a literature review. Ann For Sci 59:713–722

Milla R, Castro-Díez P, Maestro-Martínez M, Montserrat-Martí G (2005) Relationships between phenology and the remobilization of nitrogen, phosphorus and potassium in branches of eight Mediterranean evergreens. New Phytol 168:167–178

Millard P, Grelet GA (2010) Nitrogen storage and remobilization by trees: ecophysiological relevance in a changing world. Tree Physiol 30:1083–1095

Nambiar EKS, Fife DN (1991) Nutrient remobilization in temperate conifers. Tree Physiol 9:185–207

Newnham RM (1992) Variable-form taper functions for four Alberta tree species. Can J For Res 22:210–223

Penninckx V, Glineur S, Gruber W, Herbauts J, Meerts P (2001) Radial variations in wood mineral element concentrations: a comparison of beech and pedunculate oak from the Belgian Ardennes. Ann For Sci 58:253–260

Pfautsch SA, Gessler MAA, Rennenberg H (2009) Using amino-nitrogen pools and fluxes to identify contributions of understory Acacia spp. to overstory *Eucalyptus regnans* and stand nitrogen uptake in temperate Australia. New Phytol 183:1097–1113

Proe MF, Midwood AJ, Craig J (2000) Use of stable isotopes to quantify nitrogen, potassium and magnesium dynamics in young Scots pine (*Pinus sylvestris*). New Phytol 146:461–469

Ranger J, Turpault M-P (1999) Input–output nutrient budgets as a diagnostic tool for sustainable forest management. For Ecol Manag 122:139–154

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

Rennenberg H, Dannenmann M, Gessler A, Kreuzwieser J, Simon J, Papen H (2009) Nitrogen balance in forests: nutritional limitation of plants under climate change stresses. Plant Biol 11:S4–S23

Rockwood DL, Rudie AW, Ralph SA, Zhu JY, Winandy JE (2008) Energy product options for *Eucalyptus* species grown as short rotation woody crops. Int J Mol Sci 9:1361–1378

Ryan MG et al (2010) Factors controlling *Eucalyptus* productivity: how water availability and stand structure alter production and carbon allocation. For Ecol Manag 259:1695–1703

Saint-André L, Laclau J-P, Deleporte P, Ranger J, Gouma R, Saya A, Joffre R (2002) A generic model to describe the dynamics of nutrient concentrations within stemwood across an age series of a Eucalyptus hybrid. Ann Bot 90:65–76

Saint-André L, Thongo M'Bou A, Mabiala A, Mouvondy W, Jourdan C, Roupsard O, Deleporte P, Hamel O, Nouvellon Y (2005) Age-related equations for above- and below-ground biomass of a Eucalyptus hybrid in Congo. For Ecol Manag 205:199–214

Santiago LS, Wright SJ, Harms KE, Yavitt JB, Korine C, Garcia MN, Turner BL (2012) Tropical tree seedling growth responses to nitrogen, phosphorus and potassium addition. J Ecol 100:309–316

Saur E, Nambiar EKS, Fife DN (2000) Foliar nutrient retranslocation in *Eucalyptus globulus*. Tree Physiol 20:1105–1112

Sette CR Jr, Tomazello FM, Dias CTS, Laclau J-P (2010) Crescimento em diâmetro do tronco das árvores de *Eucalyptus grandis* W. Hill. EX. Maiden e relação com as variáveis climáticas e fertilização mineral. Revista Árvore 34:979–990

Smith DM (1954) Maximum moisture content method for determining specific gravity of small wood samples. U.S. Forest Products Laboratory Report 2014, pp 1–8

Subbarao G, Ito O, Berry W, Wheeler R (2003) Sodium: a functional plant nutrient. Plant Sci 22:391–416

Turner J, Lambert MJ (1983) Nutrient cycling within a 27-year-old *Eucalyptus grandis* plantation in New South Wales. For Ecol Manag 6:155–168

Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial P limitation: mechanisms, implications, and N–P interactions. Ecol Appl 20:5–15

Warren E, Smith RGB, Apiolaza LA, Walker JCF (2009) Effect of stocking on juvenile wood stiffness for three *Eucalyptus* species. New For 37:241–250

Weatherall A, Proe MF, Craig J, Cameron AD, Midwood AJ (2006) Internal cycling of nitrogen, potassium and magnesium in young Sitka spruce. Tree Physiol 26:673–680

Wright SJ et al (2011) Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. Ecology 92:1616–1625