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Review

Mineral nutrient concentrations in sapwood and heartwood: a literature review

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Abstract – Patterns in mineral nutrient concentrations in sapwood and heartwood are investigated from published data for N, P, K, Ca and Mg in 22 species of Gymnosperms and 71 species of Angiosperms. The average value of heartwood/sapwood concentration ratio is element-specific, increasing in the following order: P (0.36) < N (0.76) < K (0.78) < Mg (1.20) = Ca (1.25). Concentrations of P, N and K are mostly lower in heartwood compared to sapwood. Large variation exists in the concentration pattern of Ca and Mg, whose functional significance is unclear. A phylogenetic pattern is confirmed, Gymnosperms having lower mineral nutrient concentrations in wood compared to Angiosperms, most strikingly so for N, K and Mg in sapwood. Heartwood and sapwood concentrations are positively correlated across species, and species with nutrient-poor sapwood have disproportionately poorer heartwood. The results are discussed in relation to the hypothesis that mineral nutrients are recycled from senescing sapwood.

wood / mineral nutrient concentration / translocation / resorption efficiency / Gymnosperms / Angiosperms

Résumé – Concentrations en éléments minéraux dans le bois de cœur et l'aubier : une revue de la littérature. Les patrons de variation des concentrations en N, P, K, Ca et Mg dans le bois de cœur et l'aubier sont analysés à partir de données de la littérature se rapportant à 22 espèces de Gymnospermes et 71 espèces d'Angiospermes. Le bois de cœur est le plus souvent plus pauvre en N, P et K que l'aubier. Les rapports de concentration cœur/aubier varient selon l'élément, dans l'ordre suivant : P (0,36) < N (0,76) < K (0,78) < Mg (1,20) = Ca (1,25). De grandes variations existent dans le patron de concentration en Ca et Mg, dont la signification fonctionnelle n'est pas claire. Un patron phylogénétique est confirmé : le bois des Gymnospermes est plus pauvre en éléments minéraux, particulièrement pour N, Mg et K dans l'aubier. Les concentrations dans le cœur et dans l'aubier sont corrélées positivement, et les espèces à aubier pauvre tendent à avoir un cœur appauvri de façon disproportionnée. La discussion examine la cohérence des résultats avec l'hypothèse selon laquelle des éléments minéraux sont résorbés au moment de la formation du bois de cœur.

bois / concentration en éléments minéraux / translocation / efficacité de résorption / Gymnospermes / Angiospermes

1. INTRODUCTION

Mineral nutrients are limiting resources to plants and the allocation and translocation of mineral nutrients among different organs are important mechanisms enhancing nutrient use efficiency in plants [3, 25, 37, 55, 65]. It is commonplace that different plant organs have vastly different mineral element concentrations. In trees, wood usually has the lowest mineral nutrient concentration of all organs [24, 26, 70, 74]. However, wood itself is not necessarily homogeneous with respect to mineral element concentrations [14, 32, 54]. Daube (1883) cited in [9] was the first to report higher mineral nutrient concentrations in sapwood compared to heartwood. Computations of mineral element budgets and fluxes in forest stands need to allow for differences in mineral nutrient content between sapwood and heartwood [6, 7, 15, 16, 19, 62, 71].

In woody organs, the outermost wood layers that contain living cells are referred to as sapwood. In most if not all, tree species, inner sapwood rings are eventually converted into heartwood. Heartwood no longer contains living cells, often has vessels blocked with tyloses and can accumulate

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secondary compounds [9, 27, 32, 60, 67, 77]. The cause and function of heartwood formation are disputed. It is now generally admitted that heartwood formation is a developmentally controlled process, functioning as a regulator of the amount of sapwood in the trunk [8, 9]. During the conversion of sapwood into heartwood, extensive translocation of chemical compounds occurs. Secondary compounds tend to accumulate in heartwood, while storage products (starch), soluble sugars, amino-acids and mineral elements are removed from senescing sapwood rings [9, 10, 15, 16, 32, 50, 76].

The assumption that heartwood has lower concentrations of all mineral nutrients compared to sapwood mostly derives from the widely cited papers by Bamber [8] and Lambert [38] both of which being based almost exclusively on Eucalypts. In the last 20 years, however, the emergence of dendrochemistry has yielded a large amount of new data on mineral element concentrations in heartwood and sapwood [17, 66]. The picture emerging from these new data might be more complex than previously thought. In particular, higher concentrations of specific mineral elements in heartwood compared to sapwood have been reported [52, 63]. Furthermore, the difference in concentration between heartwood and sapwood may depend on element, species and life-form (Gymnosperms vs. Angiosperms) [13, 54, 56, 57], making generalisations difficult. Clearly, our knowledge of nutrient resorption from senescing wood lags far behind that of nutrient resorption from leaves [15, 25, 37]. Improved knowledge of mineral nutrient economy of trees is crucial to the understanding of the response of forest ecosystems to environmental stress [48].

In this paper, we explore patterns in macronutrient concentrations (N, P, K, Ca, Mg) in heartwood and sapwood based on literature data. Our specific objectives are as follows: (i) to assess variation ranges and mean values of mineral nutrient concentrations in heartwood and sapwood; (ii) to test whether mineral nutrient concentrations are systematically lower in heartwood compared to sapwood; (iii) to test whether the heartwood/sapwood concentration ratio varies depending on element; (iv) to test whether Gymnosperms and Angiosperms have contrasting patterns and (v) to investigate correlations among different elements.

In the discussion it is examined whether the results are consistent with the hypothesis that mineral nutrients are resorbed from senescing wood.

2. MATERIALS AND METHODS

The database consists of literature values of macronutrient concentrations (N, P, K, Ca, Mg) in the heartwood and the sapwood of a total of 93 tree species (22 Gymnosperms and 71 Angiosperms). The data were compiled from papers published between 1957 and 1999 (Appendix). The data set is unbalanced, with the number of observations for N, P, K, Ca and Mg being 56, 64, 80, 92 and 76, respectively. The original data were reported either as average sapwood and heartwood concentration or as radial concentration profiles. In the latter case, data were extracted as follows. For heartwood concentrations, the median value was used, except in a few cases where there existed a steep, outwardly decreasing concentration gradient in the heartwood, followed by a sharp concentration increase at the heartwood/sapwood boundary. In such cases, sapwood should be compared with the outermost heartwood ring to obtain a reliable picture of translocation processes that may be occurring at the heartwood-sapwood transition zone [5]. Sapwood concentrations were median values, except when outwardly increasing concentration gradients existed within the sapwood. In these cases, the outermost ring group or the penultimate annual growth ring was used; the outermost ring was discarded, due to possible contamination by the mineral-rich bark and cambium. When the original paper reported concentrations from several individuals, sites or trunk heights, the oldest individual was retained and the data were taken from 1.3 m (or the nearest height sampled); cross-sites averages were computed as necessary. Dendroanalytical studies explicitly aimed to monitor environmental pollution were not retained, except when an unpolluted site was included as a control. Data not expressed in concentration units per unit wood mass were not included. In some cases, data had to be tabulated from figures, and this was performed with the best possible approximation. In the case of the large data set of Lambert [38] on 38 species of *Eucalyptus*, a subsample of six species was included (the first two species in alphabetic order in each of the three subgenera *Corymbia*, *Monocalyptus* and *Symphyomyrtus*), using the sites for which nitrogen concentrations were reported. The four other species of *Eucalyptus* included in the data set are from [10].

The data were statistically analysed with SYSTAT. Cross-species means, standard deviations, minimum and maximum values for sapwood and heartwood concentrations were calculated separately for Gymnosperms and Angiosperms and for both groups pooled. Concentration ratios of mineral nutrients in heartwood and sapwood were calculated. The values were compared between Angiosperms and Gymnosperms by means of Mann-Whitney U-test. For each element, sapwood and heartwood concentrations were compared by means of Wilcoxon signed rank test. Correlations between heartwood/sapwood concentration ratios of different elements were assessed by means of Spearman rank correlation coefficient. An allometric approach was applied to analyse correlation patterns between heartwood and sapwood concentrations of each element. To that end, the allometric regression line of heartwood vs. sapwood concentration was calculated as the reduced major axis of the bi-plot of log-transformed values of heartwood (Y) and sapwood (X) concentrations. The allometric model used was $Y = b X^a$. In this model, an allometric coefficient (a) equal to unity indicates that heartwood and sapwood concentrations vary in a 1:1 ratio or, in other words, that the heartwood/sapwood concentration ratio does not vary systematically with sapwood concentration. $a < 1$ indicates that heartwood concentration increases less rapidly than sapwood concentrations, or, in other words, that the heartwood/sapwood concentration ratio decreases with increasing sapwood concentrations. Finally, $a > 1$ points to an increase in heartwood/sapwood concentration ratio with increasing sapwood concentration. Conformity tests for allometric coefficients were performed after [18].

3. RESULTS

Heartwood concentrations were lower than sapwood concentrations in 42 of 56 cases for N (Wilcoxon signed rank test: $Z = 4.61$, $P < 0.001$), in 59 of 64 cases for P ($Z = 5.59$, $P < 0.001$),

Table I. Mineral element concentrations in heartwood and sapwood and heartwood/sapwood concentration ratio: mean values ± standard deviation for Angiosperms and Gymnosperms.

	n	Heartwood % dry matter	Sapwood % dry matter	Heartwood/sapwood concentration ratio
Angiosperms				
N	47	0.117 ± 0.050	0.174 ± 0.078	0.76 ± 0.42
P	50	0.005 ± 0.012	0.013 ± 0.011	0.38 ± 0.43
K	59	0.087 ± 0.088	0.127 ± 0.062	0.69 ± 0.70
Ca	66	0.154 ± 0.200	0.157 ± 0.236	1.33 ± 1.43
Mg	51	0.037 ± 0.058	0.032 ± 0.028	1.03 ± 1.07
Gymnosperms				
N	9	0.080 ± 0.050	0.103 ± 0.042	0.77 ± 0.26
P	14	0.002 ± 0.002	0.009 ± 0.007	0.28 ± 0.28
K	21	0.080 ± 0.120	0.077 ± 0.059	1.05 ± 1.11
Ca	26	0.097 ± 0.101	0.090 ± 0.070	1.05 ± 0.40
Mg	25	0.019 ± 0.012	0.014 ± 0.009	1.54 ± 1.14

in 60 of 80 cases for K (Z = 4.13, $P < 0.001$), in 49 of 92 cases for Ca (Z = 0.14, ns) and in 38 of 76 cases for Mg (Z = 0.98, ns) (Appendix). These results were not qualitatively different between Gymnosperms and Angiosperms, even though the proportion of observations with lower concentrations in heartwood compared to sapwood is lower in Gymnosperms in the case of Ca (11 of 26 cases in Gymnosperms; 38 of 66 cases in Angiosperms) and Mg (8 of 23 cases in Gymnosperms; 30 of 53 cases in Angiosperms).

Compared to Gymnosperms (G), Angiosperms (A) had higher concentrations of all elements in the sapwood (*table I*). The difference was significant for N (A: 0.174%, G: 0.103%, Mann-Whitney U-test = 83.5, $P < 0.01$), K (A: 0.127%, G: 0.077%, U = 220.5, $P < 0.001$) and Mg (A: 0.032%, G: 0.014%, U = 258, $P < 0.001$). Heartwood concentrations were also higher in Angiosperms compared to Gymnosperms for all elements, but the difference was significant for N only (A: 0.117%, G: 0.080%, U = 110, $P < 0.05$).

Nutrient concentrations in heartwood span two (N) to three (all other elements) orders of magnitude across species. The lowest absolute concentrations in heartwood decreased in the following order: N (A: 0.038%; G: 0.040%) > Ca (A: 0.003%, G: 0.020%) > Mg (A: 0%, G: 0.004%) > K (A: 0.001%, G: 0%) > P (A: 0.00%, G: 0.00%).

Heartwood/sapwood concentration ratios increased in the following order: P (0.36) < N (0.76) < K (0.78) < Mg (1.20) = Ca (1.25) (Angiosperms and Gymnosperms pooled) (*table I*); all pairwise comparisons between elements were significant except between Ca and Mg. There was no significant difference between Angiosperms and Gymnosperms in the heartwood/sapwood concentration ratio except for Mg (A: 1.03, G: 1.54, U = 389, $P < 0.01$). Thus, on average, Mg was more markedly accumulated in the heartwood in Gymnosperms.

Table II. Spearman rank correlation coefficients between heartwood/sapwood concentration ratio of different elements. * $P < 0.05$; *** $P < 0.001$.

	N	P	K	Ca
P	0.566 (34) ***			
K	0.390 (35) *	0.414 (63) ***		
Ca	0.246 (35)	0.204 (65)	0.201 (79)	
Mg	0.264 (34)	0.341 (50) *	0.508 (65) ***	0.568 (75) ***

Table III. Allometric relationships between heartwood and sapwood concentrations for five elements. $Y = b X^a$ or $\log Y = b + a \log X$, where Y = heartwood concentration; X = sapwood concentration; a > 1 indicates that heartwood concentration increases more rapidly than sapwood concentration, i.e. increasing heartwood/sapwood concentration ratio with increasing sapwood concentration; conformity test of the allometric coefficient (H_0: a = 1). NS $P > 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	n	r^2	a	t
N	56	0.247	1.07	0.62 NS
P	64	0.197	1.75	6.60 ***
K	80	0.284	2.44	12.52 ***
Ca	92	0.554	1.19	3.72 **
Mg	76	0.339	1.75	7.67 ***

There were significant, positive correlations between heartwood/sapwood concentration ratios for four element pairs, namely N and P, P and K, K and Mg, Ca and Mg; the other pairwise correlations were all positive, but not significantly so (*table II*).

Cross-species correlations between concentration in sapwood and heartwood were highly significant for all elements (*table III; figure 1*). The slope of the heartwood-sapwood allometric regression line was superior to unity for all elements, significantly so for P, K, Ca and Mg (*table III*). Thus, for these elements, concentrations vary within narrower limits in sapwood than in heartwood or, in other words, species with low concentrations in sapwood tend to have disproportionately lower concentrations in heartwood.

4. DISCUSSION

4.1. Do the results fit in with a scenario of mineral element resorption from senescing wood?

Much attention has been paid to foliar nutrient resorption as a mechanism increasing mean residence time of nutrients within the plant, a component of nutrient use efficiency [2, 3, 25, 36, 37, 55, 65]. The similarity, from a functional point of view, between heartwood formation and leaf senescence has often been postulated [7, 9, 37–39, 71, 72, 74]. Since the pioneering works of Merrill and Cowling [50] and Ziegler

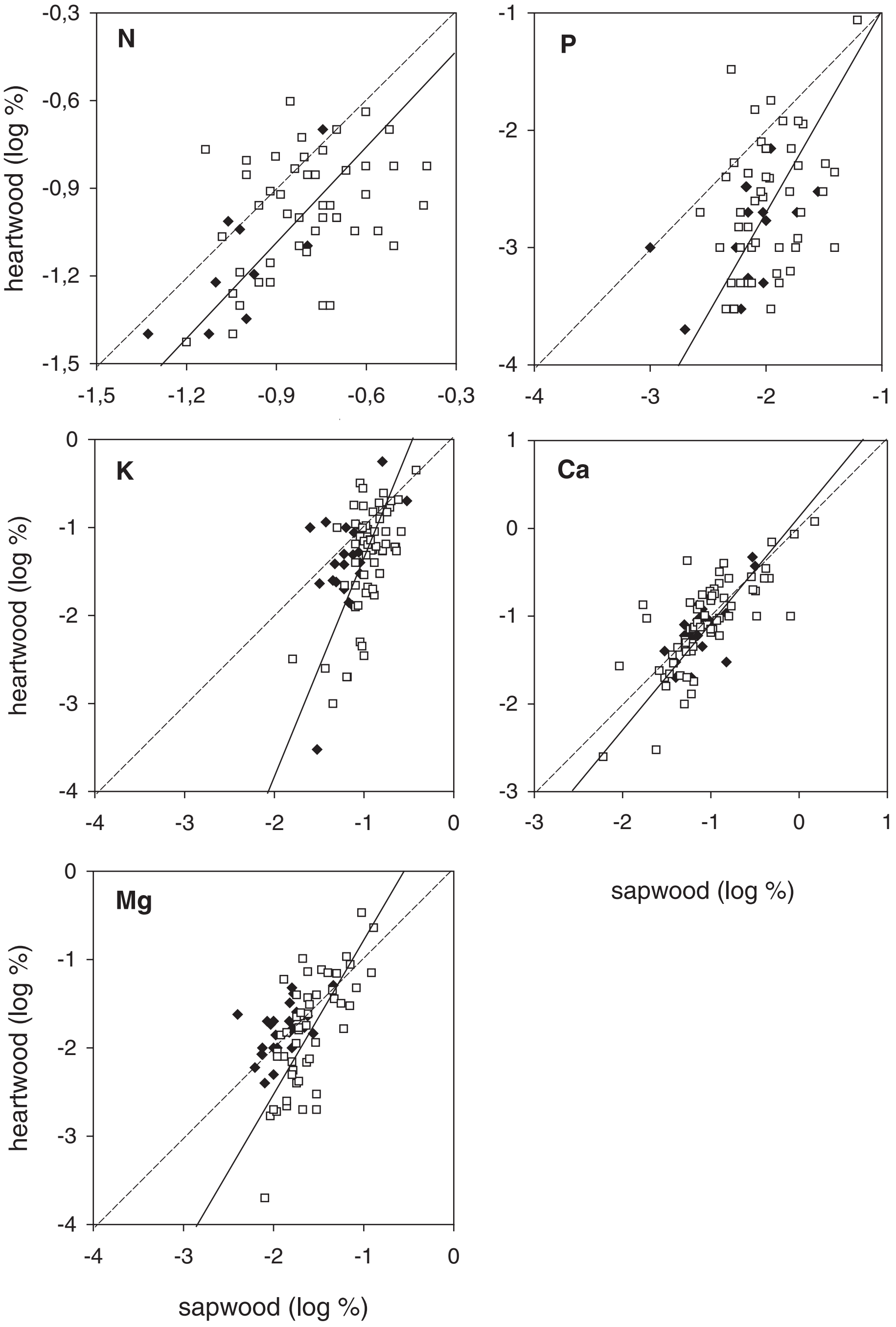

Figure 1. Allometric regression lines between heartwood and sapwood concentrations of N, P, K, Ca and Mg. □ Angiosperms, ◆ Gymnosperms; the stippled line denotes equal concentration in sapwood and heartwood.

[76], it is generally assumed that N- and P-compounds are actively hydrolysed and retrieved from senescing sapwood rings. However, the observation of differences in mineral nutrient concentrations between heartwood and sapwood does not in itself prove that translocations are involved. First, wood structure and chemical composition change with cambial age [12, 33, 60]. For instance, wood cation binding capacity generally decreases from pith to cambium [11, 52]. Secondly, accumulation of secondary metabolites and formation of tyloses might alter mineral element concentrations at the time of heartwood formation, without any translocation of mineral elements being involved. Fungal infection can also alter the mineral element content of heartwood [59].

In a recent review of nutrient conservation strategies in plants Eckstein et al. [25] stated that "There is probably no resorption from woody stems [...]". The skepticism surrounding this issue may be rooted in the fact that "Information about movements of water and mineral nutrients in rays is mostly derived from indirect evidence" [77]. Admittedly, comparing average nutrient concentrations in sapwood and heartwood at a single height in trunk does not allow to discuss the complex dynamics of mineral nutrient translocations in woody stems [15, 16]. Another limitation of the database is that nutrient content (i.e. concentrations weighed by the biomass of sapwood and heartwood) is not available. In the very few studies that have carefully examined the dynamics of mineral element translocations in woody stems, Colin-Belgrand et al. [15, 16] have convincingly demonstrated that mineral nutrients are indeed removed from senescing sapwood, although a substantial proportion of mineral nutrient fluxes may actually occur in the vertical direction.

In spite of the abovementioned limitations, our results appear to be consistent with the hypothesis that specific mineral nutrients are removed from senescing sapwood. First, heartwood/sapwood concentration ratio was highly element-specific. This result would be difficult to explain by a "dilution effect" through accumulation of secondary metabolites in the heartwood. Secondly, the differences among elements and the correlation pattern among them (N-P on the one hand and Ca-Mg on the other hand) are consistent with the well-known differences in mobility and chemical form of these elements in the xylem. Thus, a high proportion of N, P and K is located in the symplast of parenchyma ray cells [50, 64, 72] which is thought to be withdrawn during sapwood senescence [27, 66, 76]. In contrast, a substantial proportion of Ca and Mg in wood is located in the cell wall either adsorbed on negatively charged exchange sites or incorporated in the form of pectates or in the lignin matrix [17, 44, 48]. Ca and Mg are thus less mobile than N, P and K in the xylem [17, 44]. It is worth noticing, however, that specific genera (e.g. *Eucalyptus* and *Quercus*) consistently exhibit lower concentrations of Ca and Mg in the heartwood compared to the sapwood, suggesting that resorption of these elements is not physiologically impossible.

4.2. Lower concentrations of N, P and K in the heartwood

Heartwood generally has lower concentrations of P, N and K compared to sapwood (92%, 75% and 75% of records, respectively). The few outliers for P and N are mostly from a single study concerning a mountain rainforest in New Guinea [28], and it is possible that the corresponding trees did not possess typical heartwood. Lambert & Turner [39] suggest that tropical rainforest trees might be less efficient at resorbing nutrients from senescing wood, this being compensated for by a more efficient foliar resorption. This hypothesis cannot be validly tested here due to the limited number of data for tropical species.

In leaves, the intensity of elemental transfers during senescence usually decreases in the following order: $N \approx P > K > Mg > Ca$ [45, 66]. The similarities in the pattern of nutrient resorption from leaves and from wood are striking, considering the vast differences in chemical composition of wood and leaf tissues.

Heartwood/sapwood concentration ratio was markedly lower for P compared to N (N: 0.76, P: 0.36, $t^{118} = 5.43$, $P < 0.001$). This ratio was lower for P than for N in 27 of 33 studies where both elements were analysed (Appendix). These findings are surprising, considering that N and P have similar average foliar resorption efficiency (ca. 50%) [3]. P may thus be the main target of resorption from senescing wood. In line with these results, P in sapwood is in the form of adenine nucleotides which are massively translocated during conversion to heartwood [42]. Analytical difficulties may be suspected in a few cases, where extremely low P concentrations were reported in heartwood.

4.3. Complex patterns of divalent cations

Compared to N and P, the pattern of Ca and Mg is much more variable among species, ranging from markedly lower concentrations in heartwood to accumulation into heartwood, with a majority of species showing similar concentrations in either tissue. In specific cases, higher concentration of Ca in heartwood reflects accumulation of this element in the form of crystals [32–34]. In contrast, all species of *Quercus* and *Eucalyptus* in the database had markedly lower concentrations of Ca and Mg in heartwood compared to sapwood, suggesting that the radial distribution pattern of these elements in wood is subject to strong phylogenetic constraints.

Okada et al. [56, 57] stated that Gymnosperms generally had outwardly decreasing concentrations of cations in stemwood, while Angiosperms would not show the same trend. Our results reveal a rather more complex pattern, with large variation within both groups. In Gymnosperms, the outwardly decreasing profile seems to hold true for Mg only. Outwardly decreasing concentrations of alkaline earth elements in coniferous stemwood have been ascribed to decreasing wood cation binding capacity (CBC) from pith to bark, possibly due to a similar decrease in the proportion of pectic materials [11, 49, 52]. CBC might also increase with wood ageing and Mg would then migrate centripetally and adsorb on the acquired binding sites [11, 52]. The lower mobility of Ca in xylem might explain why this element is less markedly accumulated in heartwood in Gymnosperms.

Phylogenetic constraints on cation distribution patterns in wood are not that strong, since one of the most striking cases of Ca and Mg resorption from senescing wood was documented in the Gymnosperm *Chamaecyparis thyoides* [4, 5]. In this species, both Ca and Mg have outwardly decreasing concentrations in the heartwood, followed by a sharp concentration increase in the sapwood. A comprehensive interpretation of cation distribution patterns in stemwood will not be possible until extensive measurements of radial variation of wood CBC become available.

4.4. Are there differences between Gymnosperms and Angiosperms?

Gymnosperms apparently have lower concentrations of all mineral nutrients in the sapwood compared to Angiosperms, although the limited number of data (especially for N and P in Gymnosperm sapwood) precludes from drawing definitive conclusions. This result could be due to a direct environmental effect, since evergreen coniferous species often occupy nutrient-poorer sites than broad-leaved, deciduous trees [1, 37, 65]. In line with our results, lower wood concentrations of N and K for Gymnosperms compared to Angiosperms have already been reported (e.g. [70]). The lower mineral element concentrations in Gymnosperm sapwood may well be constitutive, since N concentration in wood is correlated to the proportion of living parenchyma cells [50], which is lower in Gymnosperm sapwood compared to Angiosperms [32]. It is well known that evergreen species, including Conifers, have intrinsically lower concentrations of N in leaves (on a mass basis) compared to deciduous species and such low foliar concentrations are regarded as a key component of the nutrient conservation strategy of evergreens [1–3, 37]. Our results suggest that, for Conifers, this conclusion could be extended to wood.

4.5. Heartwood-sapwood correlation

The positive correlation between sapwood and heartwood concentrations for all elements is a striking pattern emerging from this study. In this respect, wood resorption is similar to foliar resorption, because species with nutrient-rich leaves also tend to have higher nutrient concentrations in senesced leaves [2, 65].

The slope of the heartwood/sapwood allometric regression line was significantly superior to 1 for all elements except N. In other words, species with nutrient-poor sapwood tend to have disproportionately poorer heartwood. Assuming that sapwood mineral element concentrations reflect the tree's nutritional status [22] this result might point to a nutritional control on wood resorption. However, this control is relatively weak since there exist species with nutrient-rich sapwood which have low heartwood/sapwood concentration and vice versa. The possibility that nutrient resorption efficiency is enhanced in conditions of low nutrient availability has received much attention, because it might represent an adaptation to nutrient-poor habitats [1–3]. This hypothesis has been rarely tested for wood. In *Chamaecyparis thyoides*, wood resorption of K, Ca and Mg was more complete, i.e. heartwood concentrations were lower, in sites with lower availability of these elements in the soil, pointing to a direct environmental control on wood resorption [5]. In the present study, it is not possible to discriminate between species-specific differences and direct environmental effects, because different species were sampled from sites with different mineral element availability.

5. CONCLUSIONS

The distribution pattern of mineral element concentrations in sapwood and heartwood provides circumstantial support to the hypothesis that N, P and K are generally translocated from senescing sapwood. In view of its low heartwood/sapwood concentration ratio, P would appear to be the main target of the resorption process in wood.

In contrast, large variation exists in the concentration patterns of divalent cations, whose functional significance needs further investigation, particularly in the broader context of alkaline earth depletion of forest soil through atmospheric pollution. Extensive measurements of radial profiles of cation binding capacity of wood are required to address this interesting issue.

Gymnosperms have lower concentrations of mineral nutrients in the wood compared to Angiosperms, a feature which may contribute to their higher nutrient use efficiency.

Future work should be directed to investigating the functional relationships between foliar and wood resorption, in relation to life form (evergreen vs. deciduous), taxonomic group (Gymnosperms vs. Angiosperms) and climate (tropical vs. non tropical) and to testing the hypothesis of a nutritional control on mineral nutrient resorption from senescing wood.

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Appendix. Concentrations of N, P, K, Ca and Mg in the sapwood (s) and the heartwood (h), and heartwood/sapwood concentration ratio in Gymnosperms (taxon = 1) and Angiosperms (taxon = 2).

		Concentrations in sapwood (s) and heartwood (h) (mg kg^{-1})										Heartwood/sapwood					
Species	Taxon	N_s	N_h	P_s	P_h	K_s	K_h	Ca_s	Ca_h	Mg_s	Mg_h	N	P	K	Ca	Mg	Reference
Abies firma	1					3000	2000			110	100			0.67		0.91	[56]
Abies firma	1			20	2	250	1000	300	400	100	100		0.10	4.00	1.33	1.00	[68]
Abies sacchalinensis	1					630	1000	800	1200	150	200			1.59	1.50	1.33	[56]
Callitris columellaris	1			10	10	320	230	3170	3710	460	510		1.00	0.72	1.17	1.11	[38]
Callitris hugelii	1			55	10	600	380	2960	4710	160	480		0.18	0.63	1.59	3.00	[38]
Cedrus deodara	1							1500	300						0.20		[56]
Chamaecyparis obtusa	1					600	500	400	300	75	100			0.83	0.75	1.33	[56]
Chamaecyparis thyoides	1							600	200	80	40				0.33	0.50	[5]
Cryptomeria japonica	1							606	562	93	184				0.93	1.98	[69]
Cryptomeria japonica	1					1600	5600	1000	800	100	200			3.50	0.80	2.00	[56]
Cryptomeria japonica	1			70	5.5	375	1150	950	900	85	200		0.08	3.07	0.95	2.35	[53]
Larix decidua	1			280	30	678	140	709	600	164	167		0.11	0.21	0.85	1.02	[54]
Larix laricina	1			185	20	754	490	559	652	151	323		0.11	0.65	1.17	2.14	[54]
Larix leptolepis	1					600	200	400	200	100	50			0.33	0.50	0.50	[56]
Metasequoia glyptostroboides	1							800	450	160	100				0.56	0.63	[56]
Picea abies	1	1600	800	95	5	900	300	600	700			0.50	0.05	0.33	1.17		[19]
Picea rubens	1					873	522	936	810	166	412			0.60	0.87	2.48	[47]
Picea rubens	1							500	800	62	60				1.60	0.97	[11]
Picea rubens	1			67	33	776	875	597	673	74	85		0.49	1.13	1.13	1.15	[53]
Pinus densiflora	1					450	250	700	900	100	200			0.56	1.29	2.00	[56]
Pinus nigra	1	950	910	94	20	900	400	570	660	180	255	0.96	0.21	0.44	1.16	1.42	[75]
Pinus rigida	1	870	970	70	20	490	240	810	1040	275	146	1.11	0.29	0.49	1.28	0.53	[74]
Pinus strobus	1	1000	450									0.45					[50]
Pinus sylvestris	1	1060	640	100	17	740	130	580	710	240	230	0.60	0.17	0.18	1.22	0.96	[75]
Pinus sylvestris	1	790	600	68	33	473	385	796	969	106	140	0.76	0.49	0.81	1.22	1.32	[30]
Pinus sylvestris	1	470	400	61	3	300	3	500	600	150	150	0.85	0.05	0.01	1.20	1.00	[31]
Podocarpus archboldii	1	1800	2000	110	70	840	1080	1480	1080	220	170	1.11	0.64	1.29	0.73	0.77	[28]
Thuyopsis dolobrata	1							706	1330	40	239				1.88	5.98	[69]
Tsuga diversifolia	1	750	400									0.53					[58]
Acer rubrum	2	900	400									0.44					[45]
Acer saccharum	2					1260	1502	2874	2812	643	1084			1.19	0.98	1.69	[47]
Acer saccharum	2			80	25			8000	1000				0.31		0.13		[73]
Ackama paniculata	2			53	53	1100	210	610	490				1.00	0.19	0.80		[10]
Aesculus turbinata	2					500	1000	1250	3200	500	700			2.00	2.56	1.40	[56]
Ardisia sp.	2	1250	1620	90	30	860	130	420	440	160	70	1.30	0.33	0.15	1.05	0.44	[28]
Banksia serratifolia	2			58	15	1300	170	580	710				0.26	0.13	1.22		[10]
Betula lenta	2	950	500									0.53					[45]
Carya sp.	2	2500	1500									0.60					[45]
Castanea crenata	2							366	363	210	20.1				0.99	0.10	[69]
Castanea crenata	2					1250	560	300	200	300	20			0.45	0.67	0.07	[57]
Castanea sativa	2	1588	762	124	6	607	220	377	291	292	115	0.48	0.05	0.36	0.77	0.39	[16]
Casuarina cristata	2			70	43	770	1800	8800	8600				0.61	2.34	0.98		[10]
Casuarina torulosa	2			40	10	450	10	630	720	120	140		0.25	0.02	1.14	1.17	[38]
Cedrela tonduzii	2	1200	600									0.50					[50]
Ceiba pentendra	2	3900	1100									0.28					[50]
Ceratopetalum apetalum	2			209	113	1940	1695	187	944				0.54	0.87	5.05		[10]
Ceratopetalum apetalum	2	1700	1400	45	40	800	1100	3210	1930	240	370	0.82	0.89	1.38	0.60	1.54	[38]
Cornus florida	2	2000	2000									1.00					[45]
Cryptocarya sp.	2	1000	1570	140	120	960	990	700	1200	950	3400	1.57	0.86	1.03	1.71	3.58	[28]
Dryadodaphne crassa	2	1370	1030	60	10	2300	540	540	4300	1220	710	0.75	0.17	0.23	7.96	0.58	[28]
Elaeocarpus ptilanthus	2	1200	1230	100	40	1180	720	1030	1700	210	1030	1.03	0.40	0.61	1.65	4.90	[28]
Eucalyptus cameronii	2			53	3	370	25	240	30				0.06	0.07	0.13		[10]
Eucalyptus campanulata	2			53	3	160	32	60	25				0.06	0.20	0.42		[10]
Eucalyptus dalrympleana	2	2000	1000	615	870	2250	600	580	1430	470	360	0.50	1.41	0.27	2.47	0.77	[38]

Eucalyptus dives	2	1200	700	75	10	1050	180	640	180	180	40	0.58	0.13	0.17	0.28	0.22	[38]
Eucalyptus grandis	2	3100	1500	130	5	1250	200	650	750	200	230	0.48	0.04	0.16	1.15	1.15	[38]
Eucalyptus gummifera	2			60	5	900	50	310	160	110	90		0.08	0.06	0.52	0.82	[38]
Eucalyptus laevopinea	2	1900	1100	70	15	650	20	260	240	130	80	0.58	0.21	0.03	0.92	0.62	[38]
Eucalyptus maculata	2	1800	1000	50	5	800	220	1240	2370	340	770	0.56	0.10	0.28	1.91	2.26	[38]
Eucalyptus oleosa	2			45	3	1600	540	1600	2700				0.07	0.34	1.69		[10]
Eucalyptus saligna	2			110	3	1000	35	500	100				0.03	0.04	0.20		[10]
Fagus sylvatica	2	1500	800	165	70	1100	950	700	850	180	225	0.53	0.42	0.86	1.21	1.25	[61]
Flindersia maculosa	2			70	43	900	790	4200	3500				0.61	0.88	0.83		[10]
Flindersia pimenteliana	2	730	1710	60	20	640	20	170	1350	190	170	2.34	0.33	0.03	7.94	0.89	[28]
Fraxinus americana	2	1700	900									0.53					[50]
Galbulimima belgraveana	2	1450	1470	50	330	2410	2070	1170	890	830	480	1.01	6.60	0.86	0.76	0.58	[28]
Geijera parviflora	2			190	120	900	3200	15000	12000				0.63	3.56	0.80		[10]
Hovenia dulcis	2					2000	2000	1000	1600	450	450			1.00	1.60	1.00	[57]
Jacaranda copaia	2	1600	1400									0.88					[50]
Kalopanax pictus	2							1090	2050	241	243				1.88	1.01	[69]
Kalopanax pictus	2					1500	1250	1000	1600	250	310			0.83	1.60	1.24	[57]
Licaria cayennensis	2	1100	1100									1.00					[50]
Liriodendron tulipifera	2	1500	1000									0.67					[45]
Maclura pomifera	2			390	10			4600	2700	700	300		0.03		0.59	0.43	[29]
Magnolia obovata	2					800	125	450	210	80	2			0.16	0.47	0.03	[57]
Nothofagus truncata	2	630	375			1200	550	1000	650	200	250	0.60		0.46	0.65	1.25	[51]
Ochroma lagopus	2	1800	500									0.28					[50]
Orites excelsa	2			94	27	1300	400	92	270				0.29	0.31	2.93		[10]
Orvenia acidula	2			81	11	1000	290	4900	7000				0.14	0.29	1.43		[10]
Oxydendron arboreum	2	2500	2300									0.92					[45]
Phellodendron amurense	2					1500	300	910	800		200			0.20	0.88		[57]
Planchonella firma	2	1400	2500	100	70	1470	1900	750	1350	400	710	1.79	0.70	1.29	1.80	1.78	[28]
Populus robusta	2			390	44	980	1760	1400	4000	240	730		0.11	1.80	2.86	3.04	[34]
Populus trichocarpa	2			107	39	970	2800	980	1920	180	400		0.36	2.89	1.96	2.22	[14]
Prunus sargentii	2							510	532	233	68.5				1.04	0.29	[69]
Prunus avium	2	1100	600	130	10	800	400	1100	1800	230	180	0.55	0.08	0.50	1.64	0.78	[20]
Quercus alba	2			115		1311	900	1050	708	92	17		0.00	0.69	0.67	0.18	[72]
Quercus alba	2	1530	1880	190	50	1160	730	850	1020	178	113	1.23	0.26	0.63	1.20	0.63	[74]
Quercus alba	2			188	12	1609	548	994	713	108	19		0.06	0.34	0.72	0.18	[41]
Quercus alba	2	900	550	100	70	1000	700	3300	1000	140	150	0.61	0.70	0.70	0.30	1.07	[43]
Quercus alba	2	4000	1500									0.38					[45]
Quercus coccinea	2	1000	1400	27	20	1360	610	520	500	165	56	1.40	0.74	0.45	0.96	0.34	[74]
Quercus coccinea	2			162	6.3	1056	485	532	201	140	22		0.04	0.46	0.38	0.16	[35]
Quercus coccinea	2	3000	2000									0.67					[45]
Quercus petraea	2					1100	640	3000	2000	140	25			0.58	0.67	0.18	[46]
Quercus prinus	2	2000	1000									0.50					[45]
Quercus robur	2	2500	1200	200	20	2200	600	600	400	300	30	0.48	0.10	0.27	0.67	0.10	[23]
Quercus robur	2	2150	1450	160	30	1750	900	1250	950	600	165	0.67	0.19	0.51	0.76	0.28	[24]
Quercus robur	2	1800	1100	325	52	1750	650	525	395	190	42	0.61	0.16	0.37	0.75	0.22	[40]
Quercus robur	2	2750	900	180	10	1500	300	340	220	160	50	0.33	0.06	0.20	0.65	0.31	[21]
Quercus rubra	2	3100	800									0.26					[50]
Quercus rubra	2	950	650	100	70	800	650	1250	600	110	80	0.68	0.70	0.81	0.48	0.73	[43]
Quercus rubra	2	2300	900									0.39					[45]
Quercus serrata	2					1600	1600	630	450	100	20			1.00	0.71	0.20	[57]
Robinia pseudoacacia	2			310	30	1800	1500	1700	1300	190	160		0.10	0.83	0.76	0.84	[29]
Sloanea pulleniana	2	830	860	80	150	1650	2460	4040	2700	710	880	1.04	1.88	1.49	0.67	1.24	[28]
Sorbus alnifolia	2							1000	1500	300	400				1.50	1.33	[57]
Sphenostemon papuanum	2	1560	1610	110	180	3800	4500	1410	1610	1290	2300	1.03	1.64	1.18	1.14	1.78	[28]
Symphonia globulifera	2	1900	500									0.26					[50]
Syncarpia glomulifera	2			70	5	950	45	600	130	250	75		0.07	0.05	0.22	0.30	[38]
Tarretia actinophylla	2			91	80	2600	900	760	750				0.88	0.35	0.99		[10]
Tristania conferta	2	1800	1700	75	5	1050	1050	800	1750	130	600	0.94	0.07	1.00	2.19	4.62	[38]
Vouacapoua americana	2	1300	1200									0.92					[50]
Zelkova serrata	2							1600	1000	560	320				0.63	0.57	[57]