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Tree Growth and Nutrient Dynamics in Pine Plantations in Southern Brazil

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ABSTRACT: For the development of nutrient budget models to recommend lime and fertilizers for agricultural and forestry crops, curves of plant growth and nutrient accumulation are required. Information about how nutrients are partitioned between the different plant organs is also necessary, but still scarce for pine in Brazil. This study evaluated the growth, biomass partitioning, and nutrient dynamics in pine forests in southern Brazil. To this end, we assessed unthinned 2, 4, 6, and 8-year-old stands of *Pinus taeda* L. Three plots of 20 × 30 m per stand were delimited, in which three trees of different classes of diameter at breast height (DBH) were chosen. These trees were measured, felled, and the weight of their fresh components (leaves, branches, bark, and wood) was evaluated. Samples of each tree compartment and from the forest litter were taken to determine dry weight and nutrient content. From trees of the mean DBH class, the roots were also collected and the dry weight and nutrient contents determined. The same sampling procedure was carried out with soil for physical and chemical characterization. Regression models were adjusted to estimate growth, nutrient uptake, and nutrient use efficiency of pine trees, based on data collected in this and previous studies. The equations developed in this research can be used in nutrient budget models as well as in other simulation models, to establish recommendations of lime and fertilizers for *Pinus taeda* stands in southern Brazil.

Keywords: *Pinus taeda*, nutrient content, nutrient partitioning, nutrient use efficiency.

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INTRODUCTION

The most commonly planted pine species in Brazil, *Pinus taeda* and *Pinus elliottii*, are well-adapted to the low availability of soil nutrients (Viera and Schumacher, 2009). In general, the growth rate of these species is not excessively compromised when no liming and fertilization are applied, particularly in the first rotations (Reissmann and Wisniewski, 2000). However, positive responses to fertilization were observed under different managements and in different environments (Muniz et al., 1975; Reissmann and Wisniewski, 2000; Ferreira et al., 2001; Moro et al., 2014; Coyle et al., 2016). Moreover, the nutrients exported by the crops must be replenished (Viera et al., 2011), which is a fundamental practice to reduce the environmental impact of any agricultural or forestry crop. Therefore, fertilizer recommendations have been developed in Brazil (Gonçalves, 1995; Vogel et al., 2005), and their effects on the plant physiology and resource use efficiency were evaluated (Campoe et al., 2013; Ward et al., 2015).

The traditional approach to the establishment of criteria for lime and fertilizer recommendations for agricultural or forestry crops is based on correlation and calibration studies (Alvarez V, 1996). This approach requires the implementation of extensive experimental networks for the elaboration of tables for interpretation of soil analysis results, a condition that can be a strong limitation in the case of poorly studied, long-cycle species, such as pine. An alternative would be the use of models, such as nutrient budget models (Barros et al., 1995; Santos et al., 2008; Silva et al., 2009), as are being used successfully in Brazil for *Eucalyptus*. The assumption behind these models is: there is a close relation between nutrient availability in the soil and tree nutrient accumulation and tree growth.

These models allow a quantification of the nutritional demand of plants, associated to a certain growth rate according to local conditions, and of the capacity of nutrient supply by the soil. Based on the balance between the plant requirements and soil nutrient supply, the application rate of each nutrient and fertilization strategy of the crop are determined.

Underlying the development of these models, curves of plant growth and nutrient accumulation for the crop must be established. This information is still rather scarce for pine in Brazil, but it can be easily obtained in commercial forests.

Here, we present the biomass production and partitioning of nutrients in pine forests in the state of Paraná and equations to estimate plant growth, nutrient contents, and indicators of nutrient use efficiency of *Pinus taeda* L plantations in Brazil.

MATERIALS AND METHODS

The study was carried out in *Pinus taeda* plantations on the Fazenda São Nicolau (24° 11’ S and 49° 58’ W; 733 m a.s.l.), in the district of Arapoti, and on the Fazenda Caetê (24° 2’ S and 50° 27’ W; mean altitude 785 m a.s.l.), in the district of Curiúva (PR).

By the Köppen classification system, the regional climate type is Cfb, defined as mesothermic, humid and superhumid, with no dry season, cool summers, with a mean temperature of the hottest month below 22 °C and severe and frequent frosts. The mean annual rainfall in the growth period of the sampled trees was 1,500 mm.

The study site is located in the second plateau region, Ponta Grossa plateau or Paleozoic plateau, with cliffs facing east between 1,100 and 1,200 m a.s.l. The mineralogy of the region consists of paleozoic sediments, containing sandstones, shales, phyllites, carbonaceous and bituminous schists, and limestone (Brasil, 1981). The soil at the sampling site is classified as *Latossolo Vermelho Distrófico típico* (Streck et al., 2008), an Oxisol (Soil Survey Staff, 2014).

The data were collected in four unthinned *P. taeda* stands, with 2, 4, 6, and 8-year-old trees, in November and December 2002 and January 2003. Based on forest inventory data, the management units III (São Caetê) and IV (Faz. São Nicolau) were used, classified according to the dominant height of 20-year-old trees (27.3 and 26 m, respectively). The plant spacing of the 2-year-old stands was 2 × 3 × 4.5 m, and 2 × 3 m in the other stands. The selected areas were not limed or fertilized. In each stand, three 20 × 30 m plots with approximately 105 trees were delimited. Three trees per plot were chosen: one with the mean DBH of the plot; another with the mean DBH of the plot minus one standard deviation; and a third tree with the mean DBH of the plot plus one standard deviation. The purpose of selecting trees based on their diameter was to evaluate possible relationships between plant growth, nutrient use efficiency, and nutrient partitioning. The total height of the selected trees was measured, and then they were felled.

After cutting the trees, the weight of the needles, branches, and trunk with and without bark were determined. The root weight of the mean DBH tree was also determined after extraction by the excavation method, to a depth of 1.50 m. Litter samples were collected at three points per plot, using 0.20 × 0.20 m frames. All samples were taken to the laboratory and weighed on a precision scale. After drying in an oven with air renewal/circulation at 75 °C, for 72 h, the dry matter of each plant and litter component was determined.

Samples of all tree components were chemically analyzed for N, P, K, Ca, and Mg contents. Nitrogen was determined after sulfuric acid digestion, as proposed by Bremner (1965). Nitric-perchloric digestion was used for the other nutrients (Johnson and Ulrich, 1959). The P concentration was determined by molecular absorption spectrophotometry and K by flame emission photometry. The Ca and Mg concentrations were determined by atomic absorption spectrophotometry.

From the nutrient concentrations and dry weight of the components, the nutrient contents in the trees were obtained. The nutrient use efficiency (UE) was calculated as the ratio between the dry matter weight and nutrient content in the evaluated tree component.

Composite samples of the 0.00-0.20 m soil layer were blended from three simple samples, randomly collected per plot. The soil samples were analyzed for their chemical and physical properties (Table 1).

Regression equations were adjusted to estimate nutrient use efficiency, and dry matter and nutrient content in the different plant components. The cylindrical volume and tree age were used as independent variables in the fitting of the equations. The variable UE was included among the independent variables in the equations to estimate nutrient contents in bark, wood, and roots.

To obtain equations with higher extrapolation capacity, the data of Valeri (1988) (*P. taeda*) and Miranda and Barros (1994) (*P. caribaea* var. *hondurensis* and *P. oocarpa*) were used to estimate dry matter production of *Pinus* sp.

Table 1. Soil properties from the 0.00-0.20 m soil layer in the studied stands of different ages

Age	Clay	P	K	Al^{3+}	Ca^{2+}	Mg^{2+}	Cu	Zn	Fe	Mn	Organic matter
years	g kg^{-1}	mg dm^{-3}		cmol$_c$ dm^{-3}			mg dm^{-3}				g kg^{-1}
2	480	4.0	32.0	4.5	1.0	0.3	2.8	0.9	252.1	0.7	34
4	600	4.0	30.0	3.1	0.9	0.3	2.7	0.6	201.8	1.1	43
6	500	3.2	34.0	2.1	1.0	0.3	2.8	1.1	189.8	7.3	37
8	540	4.8	28.0	3.4	0.8	0.3	3.6	0.5	212.5	7.3	42

The analyses were performed according to the methods described by Tedesco et al. (1995).

All models were chosen based on the significance of the coefficients and the values of the determination coefficients (R^2). The model applicability test, recommended by Ahrens (1980), was also performed to minimize the effects of error dispersion and to enable the use of models at locations other than the sampling sites.

RESULTS

In general, there was an increase in the weight of needles and branches with increasing trunk volume (Tables 2 and 3). Aside from the cylindrical tree volume, age was considered as an estimation variable for these components, indicating a relative reduction in the relevance of needles and branches during the stand development. The dry weight values of the trunk and its components were more reliably estimated when the cylindrical volume was used as only independent variable.

Table 2. Trunk volume and biomass partitioning in *Pinus taeda trees* in southern Brazil

Age	DBH class[1]	Volume	Needles	Branches	Bark	Stem wood	Roots	Total
year		m^3 per tree	kg per tree					
2	M - s	0.001	0.533	0.258	0.109	0.679	*	1.579
2	M - s	0.001	0.929	0.735	0.130	0.929	*	2.723
2	M - s	0.002	1.090	0.598	0.112	2.588	*	4.388
2	M	0.003	0.891	0.602	0.203	1.501	1.350	3.197
2	M	0.003	0.803	0.288	0.197	1.305	0.998	2.592
2	M	0.003	0.958	0.461	0.159	1.491	1.392	3.069
2	M + s	0.004	1.126	0.812	0.164	1.786	*	3.888
2	M + s	0.004	2.077	0.934	0.229	1.938	*	5.178
2	M + s	0.005	2.717	1.835	0.507	2.403	*	7.463
4	M - s	0.038	2.384	3.171	1.340	4.990	*	11.885
4	M - s	0.039	3.782	2.979	0.892	7.388	*	15.041
4	M - s	0.060	5.905	6.264	1.426	9.830	*	23.424
4	M	0.067	9.295	13.803	6.462	11.571	7.334	41.131
4	M	0.078	4.882	5.846	2.782	14.059	7.681	27.569
4	M	0.096	5.563	8.590	3.254	13.325	14.577	30.732
4	M + s	0.103	7.469	7.920	3.808	16.601	*	35.798
4	M + s	0.116	14.164	12.457	2.924	14.252	*	43.797
4	M + s	0.145	19.268	21.685	6.429	25.530	*	72.911
6	M – s	0.109	4.868	5.946	3.594	17.640	*	32.048
6	M – s	0.111	7.419	10.394	4.734	21.734	*	44.281
6	M – s	0.111	4.440	5.544	3.915	14.671	*	28.570
6	M	0.156	7.454	8.500	4.483	22.814	9.298	43.252
6	M	0.161	6.723	10.478	3.057	25.260	9.298	45.518
6	M	0.161	6.694	7.168	1.646	20.107	9.298	35.615
6	M + s	0.237	8.534	14.783	6.749	31.448	*	61.514
6	M + s	0.241	14.143	22.626	6.761	31.945	*	75.476
6	M + s	0.241	7.914	12.781	5.878	31.828	*	58.400
8	M - s	0.232	2.841	10.149	3.960	32.813	*	49.763
8	M - s	0.261	1.705	7.440	4.982	35.854	*	49.980
8	M - s	0.262	3.497	6.544	7.758	34.158	*	51.957
8	M	0.414	9.102	18.468	7.824	56.115	14.624	91.510
8	M	0.436	6.704	21.510	10.264	68.213	11.744	106.691
8	M	0.439	7.552	10.567	14.580	47.082	8.775	79.780
8	M + s	0.605	16.718	37.888	13.233	83.800	*	151.639
8	M + s	0.639	18.262	44.398	17.073	92.525	*	172.258
8	M + s	0.650	12.888	23.513	16.770	79.502	*	132.672

DBH class: diameter at breast height class; M: mean; s: standard deviation. *: Material not collected.

Similar functions were obtained by relating the data of this research with data from previous studies (Table 4). There were no differences in the N, P, K, Ca, and Mg contents between trees of the same age and different DBH classes, although the N, P and K contents in branches, bark, wood, and roots decreased over time with increasing internal nutrient use efficiency (Tables 5 and 6). The Ca and Mg contents in branches and roots increased with age, but did not vary considerably in bark and wood.

The increase in the N, P, K, Ca, and Mg contents was generally followed by an increase in the tree biomass and its components up to the age of 8 years (Figure 1). In the mean, 60 % of the detected total nutrient content was taken up by the trees until the age of 4 years.

Nutrient allocation also shifted over time; nutrient allocation to the woody tree components increased in older plantations (Figure 2). The regression models obtained for estimating the content and use efficiency of N, P, K, Ca, and Mg in the different pine tree components (Tables 6 and 7) fitted well to the obtained data, with determination coefficients equal to or greater than 0.77. It was not possible to fit an equation that could satisfactorily explain the variance in the K litter content.

DISCUSSION

The growth and biomass allocation patterns described in this study differed from those in previous studies, especially from those developed under temperate conditions, for which more information about pine cultivation is available. For example, the dry matter yield of 2-year-old medium-sized trees was lower than that observed by Adegbidi et al. (2002) for intensely managed P. taeda trees (treated with weeding and fertilized with 120 kg ha^{-1} N, 58 kg ha^{-1} P, 40 kg ha^{-1} K, and 1.5 kg ha^{-1} B), grown in sandy and low-fertility soils in Georgia, USA. However, in 4-year-old trees, the values observed in this study were almost twice as high as those reported in the previous study.

Table 3. Regression equations to estimate the dry weight (DW) of needles, branches, bark, stem wood, roots, and litter in *P. taeda* stands in Arapoti (PR)

Component	Equation	R^2
	kg per tree	
Needles (N)	ln NDW = 5.819 + 0.8482 ln Vol - 0.39384 y	0.87
Branches (Br)	ln BrDW = 5.393 + 0.92662 ln Vol - 0.22748 y	0.93
Bark (Ba)	BaDW = 0.515 + 24.0231 Vol	0.90
Wood (W)	WDW = 1.732 + 131.035 Vol	0.98
Root (R)	ln RDW = 5.90 + 0.85834 ln Vol - 0.320731 y	0.94
	Mg ha^{-1}	
Litter (L)	LDL = 0.0823631 + 0.363112 shootDW	0.83

ln: natural logarithm; DW: dry weight; Vol: cylinder volume (m^3 per ha); y: years (tree age).

Table 4. Regression equations to estimate the dry weight of needles, branches, bark, and stem wood in *P. taeda* stands

Components	Equation	R^2
	kg per tree	
Needles (N)	ln NDW = -0.415102 + 1.03584 ln Vol - 0.484914 y	0.87
Branches (Br)	ln BrDW = -1.34278 + 1.13669 ln Vol - 0.364137 y	0.93
Bark (Ba)	ln BaDW = -2.51787 + 0.896257 ln Vol - 0.102595 y	0.90
Stem wood (W)	ln WDW = -0.622394 + 0.933288 ln Vol - 0.134741 y	0.98
Trunk (Tr)	ln TDW = -0.465464 + 0.933076 ln Vol - 0.136027 y	0.94

ln: natural logarithm; Vol: cylinder volume (m^3 per ha); y: years (tree age); NDW: needle dry weight; BrDW: branch dry weight; BaDW: bark dry weight; WDW: wood dry weight; TDW: trunk dry weight (kg per tree).

Table 5. Nutrient content in *P. taeda in* Southern Brazil

Age	Tree[1]	Plant components	N	P	K	Ca	Mg
year					g kg^{-1}		
2	M - s	Needles	14.74	1.30	7.30	1.91	0.59
2	M - s	Branches	5.62	0.59	5.49	1.39	0.62
2	M - s	Bark	2.58	0.21	2.10	0.93	0.24
2	M - s	Stem wood	2.07	0.24	2.34	0.38	0.29
2	M	Needles	15.89	1.28	6.73	2.04	0.55
2	M	Branches	6.25	0.67	6.12	1.75	0.64
2	M	Bark	2.75	0.16	1.30	1.47	0.29
2	M	Stem wood	1.89	0.21	1.81	0.41	0.28
2	M	Root	9.81	0.91	3.82	1.34	0.70
2	M	Fine roots	4.99	0.3	2.00	0.54	0.41
2	M + s	Needles	15.03	1.21	7.08	2.71	0.63
2	M + s	Branches	4.42	0.49	4.75	1.79	0.68
2	M + s	Bark	2.35	0.16	1.24	0.62	0.27
2	M + s	Stem wood	1.89	0.20	1.85	0.70	0.32
4	M - s	Needles	15.54	1.21	7.30	1.91	0.59
4	M - s	Branches	3.56	0.40	5.49	1.39	0.62
4	M - s	Bark	1.89	0.10	2.10	0.93	0.24
4	M - s	Stem wood	1.26	0.06	2.34	0.38	0.29
4	M	Needles	15.94	1.17	6.73	2.04	0.55
4	M	Branches	2.92	0.39	6.12	1.75	0.64
4	M	Bark	2.64	0.08	1.30	1.47	0.29
4	M	Stem wood	0.78	0.06	1.81	0.41	0.28
4	M	Root	5.68	0.35	3.82	1.34	0.70
4	M	Fine roots	7.46	0.45	2.00	0.54	0.41
4	M + s	Needles	13.88	1.01	7.08	2.71	0.63
4	M + s	Branches	3.44	0.50	4.75	1.79	0.68
4	M + s	Bark	1.72	0.08	1.24	0.62	0.27
4	M + s	Stem wood	0.98	0.07	1.85	0.70	0.32
6	M - s	Needles	15.83	0.99	3.99	2.46	0.75
6	M - s	Branches	3.27	0.32	1.57	1.96	0.61
6	M - s	Bark	1.84	0.07	0.32	0.74	0.14
6	M - s	Stem wood	0.69	0.04	0.49	0.38	0.24
6	M	Needles	16.97	1.09	4.44	3.51	0.98
6	M	Branches	4.76	0.49	2.72	2.54	0.85
6	M	Bark	1.66	0.09	0.44	1.14	0.16
6	M	Stem wood	0.63	0.04	0.37	0.45	0.24
6	M	Root	7.91	0.41	2.30	2.33	0.50
6	M	Fine roots	8.26	0.47	1.95	2.10	0.76
6	M + s	Needles	18.12	1.18	4.59	2.52	0.65
6	M + s	Branches	4.53	0.43	2.17	1.56	0.65
6	M + s	Bark	1.72	0.06	0.34	0.63	0.10
6	M + s	Stem wood	0.40	0.04	0.42	0.35	0.22
8	M - s	Needles	15.54	1.23	5.83	3.32	1.08
8	M - s	Branches	4.13	0.44	2.62	2.24	0.60
8	M - s	Bark	1.89	0.13	0.70	1.13	0.21
8	M - s	Stem wood	0.60	0.05	0.63	0.43	0.21
8	M	Needles	16.46	1.30	5.57	2.03	0.88
8	M	Branches	3.96	0.43	2.63	2.67	0.86
8	M	Bark	2.01	0.14	0.57	1.32	0.21
8	M	Stem wood	0.63	0.03	0.42	0.42	0.19
8	M	Root	6.48	0.26	1.82	3.46	0.74
8	M	Fine roots	6.65	0.31	1.71	2.46	0.70
8	M + s	Needles	16.52	1.13	4.85	2.74	1.18
8	M + s	Branches	3.67	0.42	2.52	2.59	0.79
8	M + s	Bark	2.18	0.13	0.44	0.58	0.16
8	M + s	Stem wood	0.60	0.04	0.46	0.52	0.20

(1) M: mean. s: standard deviation.

Table 6. Equations to estimate the nutrient use efficiency in the trunk of *P. taeda* trees in southern Brazil

Nutrient	Equation	R^2
N	$\ln N = 5.279 + 0.6145 y - 0.03884 y^2 - 0.108746 \ln TDW$	0.86
P	$\ln P = 6.71312 + 1.0200 y - 0.084058 y^2 + 0.090069 \ln TDW$	0.87
K	$\ln K = 4.4449 + 0.96715 y - 0.087483 y^2 + 0.2278 \ln TDW$	0.80
Ca	$\ln Ca = 7.2246 + 0.213232 y - 0.020843 y^2 - 0.0096606 \ln TDW$	0.77
Mg	$\ln Mg = 7.8883 + 0.09738 y - 0.013220 y^2 + 0.157726 \ln TDW$	0.84

Ln: natural logarithm; TDW: Trunk Dry weight (kg per tree); y: years (tree age).

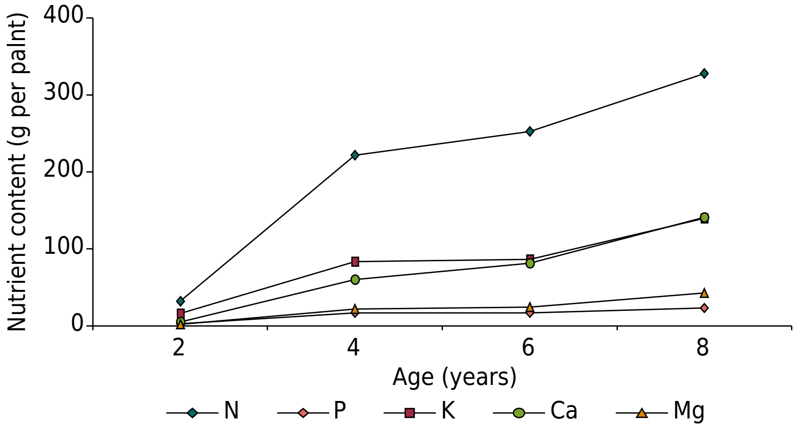

Figure 1. Nutrient content in *Pinus taeda* trees in southern Brazil.

Also in Georgia, Samuelson et al. (2014) obtained lower values in the treatments with the best results in that study (with fertilization and without exclusion of rainwater). Minor differences were observed in comparison with previous experiments performed in Brazil (Valeri, 1988). These findings show the high production capacity of the sites where *P. taeda* is grown in Brazil, compared to other producing countries, such as the United States.

Aside from the climatic differences, it is important to consider that differences between the cited studies are probably also associated to the properties of each forest site, e.g., the low content of clay in the soil used by Adegbidi et al. (2002) and of organic matter in the study of Samuelson et al. (2014).

Nutrient concentrations and content in plants

The reduction in N, P and K content in branches, bark, wood, and roots of the plants over time was already expected and can basically be explained by the intensification of internal cycling of these nutrients that have a higher phloem mobility. On the other hand, the greater stability or increase in calcium content in the different plant organs is a result of its lower mobility in the phloem. Thus, the Ca content tends to remain stable or increase in the tissues throughout the rotation. These allocation patterns were expected, although it is important to consider the environmental influence on the internal nutrient cycling in the trees (Turner and Lambert, 2015), mainly in the recyclable components, e.g., the needles.

The macronutrient contents considered adequate in *Pinus* sp. needles ranged from 1.1 to 1.3 dag kg^{-1} for N; 0.08 to 0.12 dag kg^{-1} for P; 0.6 to 1.0 dag kg^{-1} for K; 0.3 to 0.5 dag kg^{-1} for Ca; and 0.13 to 0.20 dag kg^{-1} for Mg (Gonçalves et al., 1996). The contents of P, K, Ca, and Mg observed in this study were higher than the reference values mentioned above, indicating a higher availability of these nutrients at the studied site. Moreover, the data sampling for the cited study started in November (spring), and was completed by the end of January (summer), a period during which water availability is greater, associated with a greater nutrient supply of the plants.

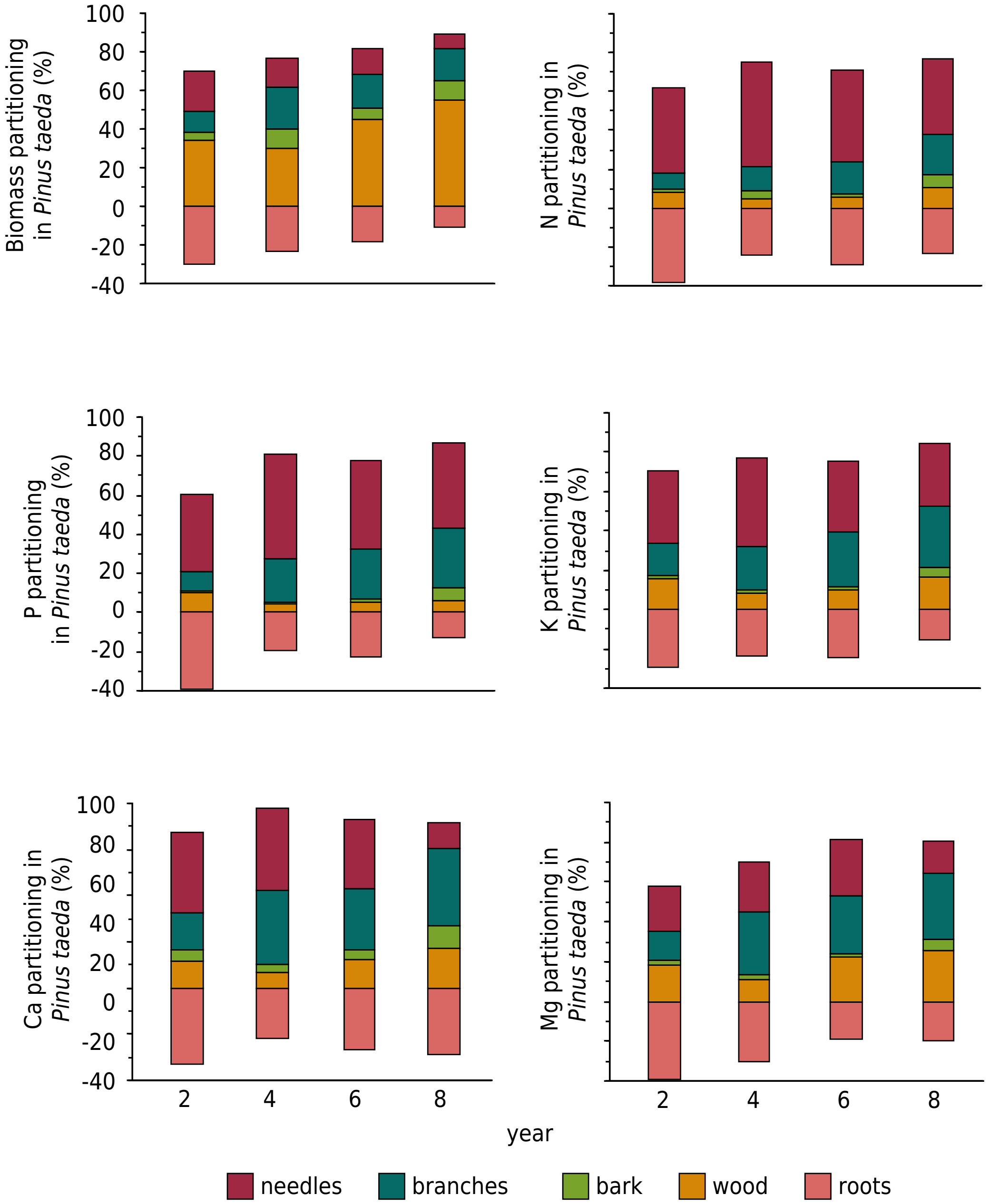

Figure 2. Biomass and nutrient partitioning in *Pinus taeda* trees in southern Brazil.

The rapid nutrient accumulation by the trees up to the age of 4 years (Figure 1) strongly indicated that fertilization, if required, should be applied before the stands reach that age. This information is corroborated by the data reported by Miranda and Barros (1994) since, in a fertilization experiment of *Pinus caribaea* var. *caribaea*, greater volume increase was obtained in the treatment in which fertilization was applied until the age of 3 years. The treatment effect was more pronounced in younger trees. The gain in relation to the control was 13.6 %, corresponding to 42 m^3 of wood per ha.

A comparison showed that the nutrient content reported by Adegbidi et al. (2002) for 2-year-old trees in the United States was higher than that found in our research. Similar to biomass accumulation in 4- year-old trees, nutrient contents in the trees and their components were higher in this study.

For *Eucalyptus* plantations, considering a cutting cycle of 6.5 years at the normal spacings used in Brazil, about 70 % of the demand for each nutrient is required in the first 4.5 years of stand growth (Santana et al., 2008), as similarly found by Miranda and Barros (1994) and in this study.

Table 7. Equations to estimate nutrient accumulation in *Pinus taeda* stands in Southern Brazil

Components	Equation		R^2
		g per tree	
Needles	$\ln N =$	$2.37838 + 1.76662 \ln TDW - 0.612868 y$	0.86
	$\ln P =$	$-0.095414 + 1.66829 \ln TDW - 0.584454 y$	0.87
	$\ln K =$	$1.6573 + 1.51461 \ln TDW - 0.547946 y$	0.80
	$\ln Ca =$	$0.5138 + 1.77146 \ln TDW - 0.605546 y$	0.77
	$\ln Mg =$	$-0.9937 + 1.611807 \ln TDW - 0.463626 y$	0.84
Branches	$\ln N =$	$0.3302 + 1.66555 \ln TDW - 0.381933 y$	0.92
	$\ln P =$	$-1.8408 + 1.82145 \ln TDW - 0.473748 y$	0.93
	$\ln K =$	$0.36516 + 1.61461 \ln TDW - 0.438423 y$	0.90
	$\ln Ca =$	$-0.8562 + 1.93987 \ln TDW - 0.434144 y$	0.90
	$\ln Mg =$	$-1.7735 + 2.02725 \ln TDW - 0.515048 y$	0.92
Bark	$\ln N =$	$-1.6018 + 1.37031 \ln TDW - 0.0007253 NUE N$	0.90
	$\ln P =$	$- 4.5362 + 1.32448 \ln TDW - 0.00003907 NUE P$	0.94
	$\ln K =$	$-2.2111 + 1.05021 \ln TDW - 0.0002710 NUE K$	0.88
	$\ln Ca =$	$-4.6661 + 1.16892 \ln TDW + 0.00092484 NUE Ca$	0.87
	$\ln Mg =$	$-5.05684 + 1.01382 \ln TDW + 0.0002609 NUE Mg$	0.90
Stem wood	$\ln N =$	$0.6210 + 0.941434 \ln TDW - 0.0008812 NUE N$	0.74
	$\ln P =$	$-1.7646 + 0.78398 \ln TDW - 0.00004159 NUE P$	0.78
	$\ln K =$	$0.33746 + 0.893684 \ln TDW - 0.0004188 NUE K$	0.87
	$\ln Ca =$	$-1.56828 + 1.10363 \ln TDW + 0.00007164 NUE Ca$	0.93
	$\ln Mg =$	$-2.8845 + 0.8897 \ln TDW + 0.0003124 NUE Mg$	0.96
Roots	$N =$	$-69.0908 - 1.11323 TDW + 0.158283 NUE N$	0.91
	$\ln P =$	$-0.2289 - 0.195538 \ln TDW + 0.0001127 NUE P$	0.93
	$\ln K =$	$1.0028 + 0.047893 \ln TDW + 0.0009609 NUE K$	0.89
	$\ln Ca =$	$-4.0748 + 1.0011 \ln TDW + 0.0018485 NUE Ca$	0.97
	$\ln Mg =$	$-4.3093 + 0.27679 \ln TDW + 0.0010928 NUE Mg$	0.97
		Mg ha^{-1}	
Litter	$N =$	$0.0496 + 10.8783 LDW$	0.95
	$P =$	$0.4254 + 0.6077 LDW$	0.82
	$K =$	$0.7731 + 0.9860 NDW$	0.50
	$Ca =$	$-5.5556 + 1.8970 CDW$	0.80
	$Mg =$	$-0.9017 + 0.2934 BDW$	0.85

ln: natural logarithm; TDW: trunk dry weight (kg per tree); y: years (tree age); NUE: nutrient use efficiency; LDW: estimated litter dry weight; NDW: needle dry weight; CDW: crown dry weight; and BDW: branch dry weight.

Table 8. Conversion of mean nutrient content in the biomass of 8-year-old *Pinus taeda* trees in soil nutrient contents in two soil layers

Soil Layer	P	K	Ca^{2+}	Mg^{2+}
	mg dm^{-3}		$cmol_c$ dm^{-3}	
0.00-0.20 m	2.61	66.57	0.32	0.17
0.20-0.40 m	1.12	30.82	0.14	0.07

Note: we assumed that 70 % of the total nutrient content in plants was extracted from the 0.00-0.20 m soil layer and 30 % from the 0.20-0.40 m soil layer. The P and K contents were determined by Mehlich-1; and exchangeable Ca and Mg extracted by 1 mol L^{-1} KCl . The recovery rates of extractants for P and K were based on Prezotti (2001) and for Ca and Mg were based on Freire (2001).

The regression equations fitted in this study to estimate nutrient contents in pine trees can be used in models for fertilization recommendations for the crop. These equations are useful in these models to calculate nutrient extraction and export from pine stands. However, it is noteworthy that the scarcity of information about nutrient dynamics in pine plantations in Brazil is still a great obstacle for the generation of models with greater extrapolation capacity. Thus, studies such as this, carried out under other growth conditions, are necessary for the formation of more robust databases, to promote pine management in the tropics.

Based on the mean nutrient content accumulated in 8-year-old trees, the nutrient concentrations extracted from the soil to support *Pinus taeda* tree growth under the experimental conditions could also be estimated (Table 8). These values can be used as reference for pine fertilization.

Nutrient use efficiency

Several indices show the nutritional efficiency of forest species or forest stands (Vitousek, 1982; Shaver and Melillo, 1984; Hiremath, 1999; Turner and Lambert, 2015), one of which is represented by the ratio of the plant dry matter by its nutrient content (Shaver and Melillo, 1984). Apart from their importance for the understanding of plant nutrient dynamics, these indices are also used in simulation models, including nutrient budget models (Barros et al., 1995; Comerford et al., 2006).

In this analysis, we established UE-estimation equations for the trunk (Table 6). The resulting equations represent, basically, the increase of UE over time, reflecting the intensification of biochemical cycling processes during forest growth and development. Despite the importance of the effect of age on the nutrient use efficiency of forest species, other factors may also be associated to improve plant nutrient use. In this study, the input of the produced biomass improved the fit of the models.

CONCLUSIONS

The equations developed in this study to estimate biomass, nutrient use efficiency, and nutrient contents in the trees can be used in nutrient budget as well as other simulation models, for nutrient management in *Pinus taeda* stands.

The rapid nutrient accumulation by trees up to the age of four years is a strong indication that fertilization should be applied before the stands reach this age.

The high nutrient allocation in *Pinus taeda* branches and needles up to the age of eight years reinforces the recommendations for the maintenance of these residues at the forest site at the time of thinning and/or debranching in the stands.

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