NUTRIENT RELATIONS DURING AN EUCALYPTUS CYCLE AT DIFFERENT POPULATION DENSITIES⁽¹⁾

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SUMMARY

To synchronize nutrient availability with the requirements of eucalyptus during a cultivation cycle, the nutrient flow of this system must be well understood. Essential, for example, is information about nutrient dynamics in eucalyptus plantations throughout a cultivation cycle, as well as impacts on soil nutrient reserves caused by the accumulation and subsequent export of nutrients via biomass. It is also important to quantify the effect of some management practices, such as tree population density (PD) on these fluxes. Some nutrient relations in an experiment with Eucalyptus grandis, grown at different PDs in Santa Barbara, state of Minas Gerais, Brazil, were evaluated for one cultivation cycle. At forest ages of 0.25, 2.5, 4.5, and 6.75 years, evaluations were carried out in the stands at seven different PDs (between 500 and 5,000 trees ha-1) which consisted in chemical analyses of plant tissue sampled from components of the aboveground parts of the tree, from the forest floor and the litterfall. Nutrient contents and allocations of the different biomass components were estimated. In general, there were only small and statistically insignificant effects of PD on the nutrient concentration in trees. With increasing forest age, P, K, Ca and Mg concentrations were reduced in the aboveground components and the forest floor. The magnitud of biochemical nutrient cycling followed the sequence: P > K > N > Mg. At the end of the cycle, the quantities of N, P, Ca and Mg immobilized in the forest floor were higher than in the other components.

Index terms: mineral nutrition, tree spacing, sustainability, fertilization.

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Para compatibilizar a disponibilidade de nutrientes no sistema e a demanda do eucalipto ao longo de seu ciclo de cultivo, é necessário que os fluxos de nutrientes nesse sistema sejam bem entendidos. Para isso, são imprescindíveis informações a respeito da dinâmica nutricional em plantas de eucalipto ao longo de seu ciclo de cultivo e do impacto de acúmulo e de exportação de nutrientes na biomassa sobre o estoque de nutrientes no solo, bem como no que se refere ao efeito de algumas práticas de manejo sobre esses fluxos, como o da densidade populacional (DP) de plantas. Em experimento realizado no município de Santa Bárbara-MG, avaliaramse, ao longo de um ciclo de cultivo, algumas relações nutricionais em plantas de Eucalyptus grandis cultivadas em diferentes densidades populacionais (DP). As avaliações foram feitas em quatro épocas, nas quais a floresta encontrava-se nas idades de 0,25, 2,5, 4,5 e 6,75 anos, cultivada em sete densidades populacionais, de 500 a 5.000 plantas por hectare. Essas avaliações consistiram da análise química de amostras de tecidos vegetais dos componentes da parte aérea, da serapilheira e do folhedo. Caracterizações da fertilidade do solo foram realizadas em amostras de cada parcela. Estimaram-se os conteúdos e a alocação de nutrientes nos diversos componentes da biomassa. Com o envelhecimento da floresta, houve redução nas concentrações de P, K, Ca e Mg dos componentes da parte aérea e da serapilheira. A intensidade da ciclagem bioquímica de nutrientes nos tecidos foliares obedeceu à sequência: P > K > N > Mg. No final do ciclo, a maior quantidade de N, P, Ca e Mg imobilizada entre os componentes da biomassa encontrava-se na serapilheira.

Termos de indexação: nutrição mineral, espaçamento, sustentabilidade, fertilização.

INTRODUCTION

Most eucalyptus forests in Brazil are planted in low fertility soils, frequently resulting in growth limitations due to insufficient nutrient supply (Barros & Novais, 1996; Gonçalves et al., 1997; Leite et al., 1998). As more and more high-yielding materials are planted, this problem becomes more intense due to the close relationship between biomass and its nutrient content (Novais & Barros, 1997; Santana et al., 2002). Knowledge about some nutrient relations in eucalyptus trees throughout a cultivation cycle is therefore imperative for the introduction of nutrient management forms to maintain nutrient contents within limits that ensure the yield sustainability (Gonçalves et al., 2004).

Aside from growth rate and the availability of other production factors, the nutrient demand is also determined by nutrient efficiency. It is known, for example, that the nutrient use efficiency generally increases with increasing forest age due to an increase of the stem wood proportion (low nutrient concentration component) and the reduction of bark, branch, and leaf proportions in the total biomass of the aging tree (Miller, 1984). Besides alterations in the proportions of biomass with different nutrient contents, modifications of nutrient accumulation in different tissues are also observed (Turner & Lambert, 2008). The trunk nutrient content is reduced as the

tree ages, due to the internal cycling during the transformation of sapwood into heartwood in the course of the tree-aging process (Reis & Barros, 1990; Bouillet et al., 2008).

Different growth stages of the forest are reflected in processes of change that contribute to the control of nutrient demand, storage, and distribution in trees. In the beginning the gross productivity proportion of the forest is highest in the crown (leaves and branches), with high nutrient concentrations. Redistribution of nutrients linked to leaf senescence is small during this period, and great amounts of nutrients are absorbed from the soil. This stage is characterized by increased nutrient accumulation rates, which peak during the crown closing phase (Attiwill, 1981; Grove et al., 1996). Growth may be restricted by a limited soil nutrient supply due to the high demand and small root volume during this period. The second stage includes crown closing when leaf biomass is stable or slightly decreasing and the heartwood generates most of the primary gross production. The heartwood nutrient content is low and this leads to a decrease in the nutrient accumulation rate of the tree. This is the phase of maximum soil exploitation by the fine roots and cycling processes are very intense. During the third growth stage of the tree, the greatest part of gross primary productivity is associated to the maintenance of the produced biomass (Miller, 1984; Grove et al., 1996).

Population density (PD) modifies the availability of production factors such as water (Leite et al., 1999) and, therefore, certainly affects nutrient dynamics during the forest growth cycle, determining distinct management forms for the control of nutrient availability. Initially, an increase in PD normally causes an increase in biomass production (Leles et al., 2001), and consequently the exportation of a greater nutrient amount from the site (Reis & Barros, 1990; Bernardo et al., 1998; Leite et al., 1998). At high PDs, the production capacity of the site is soon affected, before the forest system can reach a nutrient balance (Reis & Barros, 1990). Forests with lower PDs, on the other hand, tend to catch up with the biomass and nutrient quantities of stands with higher densities later in the growth cycle (Miller, 1995).

In the present study, some nutrient relations were evaluated in plantations with varying population densities during a complete cultivation cycle with a view to an improved nutrient management of planted eucalyptus forests.

MATERIALS AND METHODS

The experiment was carried out in the county of Santa Barbara, state of Minas Gerais, Brazil, in a Typic Hapludox. According to Köppen's classification the climate of this region is a Cwa rainy-mesothermic type. *Eucalyptus grandis* (Coff's Harbour provenance) was planted in December 1991 at several population densities (PD). Fertilization during the cultivation cycle was applied at rates of: 100 g NPK (5-25-10) per seedling at planting, and 167 kg ha⁻¹ NPK (15-05-15) 12 and 24 months after planting.

The different PDs (500, 625, 833, 1,250, 1,666, 2,500, and 5,000 trees ha⁻¹) in their corresponding spacing (4 x5, 4 x 4, 4 x 3, 4 x 2, 3 x 2, 2 x 2, and 2 x 1 m, respectively) were arranged in a randomized complete block design with three replications. Each plot covered an area of 500 m².

An average tree in diameter and height was chosen in each plot for the quantification of aboveground biomass components four times during the study (February 1992, July 1994, July 1996, and September 1998). This average tree was cut and the components weighed and sampled to determine dry matter weight and the N, P, K, Ca, and Mg concentrations. In the samples of 1996 and 1998, concentrations of Zn, Fe, Mn, Cu, and B were also measured. The forest floor was evaluated three times, based on five simple samples per plot in grids of 0.16 m².

Material gathered in leaf litter collectors (three of 0.72 m²) that had been installed around the average tree of every plot was also analyzed for P, K, Ca, and Mg every two months, for one year, one sequence beginning in July 1994 and the other in July 1996 at

PDs of 500, 833, 1,666, and 5,000 trees ha⁻¹. Two samples of this material, one from the whole litterfall (leaves, branches, bark and fruits) and another only from litterfall leaves were analyzed for their concentrations of N, P, K, Ca, Mg, Zn, Fe, Mn, Cu, and B. In July 1996, 12 litter bags with plant material for decomposition evaluation were placed on some plots (those with PDs of 500, 833, 1.666, and 5,000 trees ha⁻¹). The bags contained 70.0 g of forest litterfall from the respective plot, covering 0.075 m² of the soil surface. Every two months, two litter bags were recollected from each plot, the decomposing material was weighed, and samples were taken to determine N, P, K, Ca, Mg, Zn, Fe, Mn, Cu, and B. Tissue samples of the aboveground biomass, twigs, leaf litter, and the leaves in the leaf litter were airdried to constant weight, ground and acid-digested. Phosphorus was determined by the ascorbic acid method (Braga & Defelipo, 1974) in extracts of nitricperchloric digestion, K by flame emission photometry, and Ca, Mg, Zn, Mn, and Cu by atomic absorption spectrophotometry. After mineralization of the material with sulfuric acid and heating, N was determined by the Kjeldahl method (Embrapa, 1997). For the determination of B, curcumin was used as indicator in the colorimetric method after mineralizing the samples by calcination and their dissolution in 0.1 mol L-1 HCl (Vitti et al., 1997).

Five soil samples were taken from each plot from the 0-5 and 5-10 cm layers, in 1986 and in 1998, the 10-30 cm layer was also sampled. All soil samples were analyzed for pH, Ca, Mg, exchangeable Al (1 mol $\rm L^{-1}$ KCl extractable), P, K, Zn, Fe, Cu, Mn (Mehlich-1), B (Hot water extractable), H + Al (1 mol $\rm L^{-1}$ NH₄OAc extractable) and organic carbon (Walkley and Black) (Embrapa, 1997).

Adjusted regression equations were used to describe the relations between the accumulated nutrients, PD, and forest age. The chosen models were based on the significance of the coefficients of the equations and the values of adjusted determination coefficient. The effects of PD and age on the concentrations were evaluated by variance analysis.

RESULTS AND DISCUSSION

Nutrient concentrations

The statistical analysis considered only information obtained in the forest at ages of 2.5, 4.5, and 6.75 year, where the PD effect on nutrient concentrations in the leaves was significant only in the case of K in 2.5 year-old (p < 0.05) and 4.5 year-old trees (p < 0.1). It was also significant for Mg in 4.4 year-old trees (p < 0.01). From these results it was decided to discuss the findings based on the mean PD.

Examining the nutrient status of the forest during the growth cycle, based on the values of leaf concentrations, it is evident that some restriction occurred in P and Ca supply with increasing age (from 2.5 to 6.75 years) (Table 1). These values decreased gradually below those considered adequate (Barros et al., 1990; Herbert, 1996; Raij et al., 1996). The concentrations of Mg, Zn, and B were also clearly below the critical levels, though without decreases over the course of time.

The decreasing concentrations of Ca and Mg in the bark with increasing tree age may indicate a reduced availability of these nutrients for plants due to exhaustion of their exchangeable forms in the soil, as well as retranslocation of nutrients from this tissue as trees grew older. The reduction of K, Ca, and Mg concentrations in the stem wood, however, may have been caused by stronger supply restrictions by the soil, just as much as by higher internal cycling rates stimulated by higher heartwood production rates with increasing age (Reis & Barros, 1990).

Nutrient remobilization (on a mass base) from the bark and stem wood has the greatest contribution to the biochemical cycle in eucalyptus trees (Grove et al., 1996). The non-mobile nutrients in the phloem, similarly to Ca in the trunk, are retransferred outward during heartwood formation, or from the outer bark to tissues in growth process. This process is not observed in leaves, where Ca is retained in the aging tissues (Grove et al., 1996). Near the cambium,

nutrient concentration is high and there is a strong decreasing gradient from the external to the internal core. On the contrary, the gradient from the outer to the inner bark is not always remarkably significant. Turner & Lambert (1983) found lower concentrations of N, P, K, and Ca (37, 80, 86, and 26 %, respectively) in heartwood tissues in relation to sapwood in 27 yearold *E. grandis*. Calcium remobilization in trunk and branches seems to be the greatest Ca source in many species with marked differences of Ca concentrations between heart- and sapwood, or between inner and outer bark, particularly when Ca absorption by the roots is limited. These mechanisms of Ca retention and remobilization in the stem wood are not yet well understood, despite their relevance (Grove et al., 1996).

Low concentrations of K, Ca, Mg, and P in bark and stem wood indicate a reduced exportation of these nutrients from the system at older cutting ages (which is not true for N) (Table 1). In the stem wood the variation of the population density did not alter the concentrations of N, P, and Ca significantly. The increase in PD, however, may contribute to a greater exhaustion of nutrients because of the higher quantity of wood produced and exported per unit of planted area (Table 2).

The observed reduction in the P, K, Ca, and Mg concentrations in the forest floor with increasing forest age (Table 1) can be explained by an intensification of the biochemical nutrient cycling with forest age.

Table 1. Nutrient concentration of the aboveground components, the forest floor, and the forest litterfall at different ages (mean values of stands cultivated at different population densities)

Component	Age	N	P	K	Ca	Mg	Zn	Cu	\mathbf{Fe}	$\mathbf{M}\mathbf{n}$	В
	yr			_ g kg ⁻¹ .					_ mg kg ⁻¹ _		
Leaves	0.25	14.0	2.80	14.5	7.8	3.90	101.7	14.7	583.7	774.0	28.3
	2.50	19.0	1.10	7.9	5.6	1.90	-	-	-	-	-
	4.50	21.0	1.10	13.5	5.0	1.80	9.2	6.1	593.6	419.7	9.6
	6.75	20.0	1.00	10.6	4.3	1.90	9.7	9.9	251.8	431.7	23.2
Branches	0.25	11.0	1.30	12.4	3.9	0.60	45.0	7.0	195.0	127.0	20.0
	2.50	3.0	0.40	3.2	3.6	0.60	-	-	-	-	-
	4.50	4.6	0.50	8.8	3.9	0.90	5.6	4.4	105.0	292.5	13.1
	6.75	4.7	0.40	5.2	3.2	0.70	5.7	17.2	75.6	269.4	19.1
Bark	0.25	6.4	5.50	17.1	17.2	2.00	122.0	8.0	468.0	379.0	30.6
	2.50	3.1	0.40	5.2	10.9	1.80	-	-	=	-	-
	4.50	3.2	0.50	11.1	9.9	1.70	5.04	3.5	103.3	445.6	24.5
	6.75	3.4	0.40	9.0	5.6	1.50	3.13	3.9	53.7	353.0	17.7
Stem wood	0.25	3.4	0.40	12.6	2.6	0.50	56.0	11.0	68.0	164.0	7.0
	2.50	0.6	0.10	1.3	1.0	0.17	-	-	-	-	-
	4.50	1.0	0.05	1.2	0.5	0.07	4.8	2.2	31.6	9.8	6.4
	6.75	1.0	0.05	0.7	0.3	0.06	12.2	1.0	65.1	23.5	2.6
Forest floor	2.50	8.0	0.34	2.0	13.2	2.10	-	-	-	-	-
	4.50	8.0	0.30	2.3	7.7	1.30	8.8	1.6	1744.0	504.0	37.7
	6.75	8.0	0.27	1.0	4.6	0.90	11.2	10.2	2473.0	429.3	23.8
Forest litterfall	2.50	-	0.40	3.4	6.2	1.50	-	-	-	-	-
	4.50	9.50	0.40	5.4	5.2	1.10	9.4	2.5	557.0	504.0	25.5

Age	PD	Leaves	Bark	Branches	Stem wood	Forest floor
yr	trees ha ⁻¹			t ha	a ⁻¹	
2,5	5,000	4.0	7.6	5.5	45.2	7.4
2,5	2,500	4.7	6.3	5.8	46.6	8.1
2,5	1,666	4.0	6.6	5.0	32.4	6.5
2,5	1,250	4.2	5.6	3.3	27.5	6.5
2,5	833	3.8	4.1	3.7	25.6	5.9
2,5	625	2.8	3.6	2.8	19.2	4.3
2,5	500	2.6	4.0	1.9	13.2	3.7
4,5	5,000	1.9	13.0	3.2	76.6	15.4
4,5	2,500	3.0	11.2	3.7	83.0	16.8
4,5	1,666	3.5	8.4	3.7	68.5	15.5
4,5	1,250	3.0	11.2	4.1	56.8	13.6
4,5	833	2.9	9.4	5.5	65.3	14.6
4,5	625	2.8	7.7	3.8	50.9	15.5
4,5	500	3.3	7.3	3.7	51.7	10.5
6,75	5,000	3.9	12.5	6.3	125.8	20.9
6,75	2,500	2.9	10.6	4.1	110.8	21.4
6,75	1,666	2.7	10.2	4.8	103.9	19.8
6,75	1,250	3.5	11.4	4.7	115.8	19.3
6,75	833	2.1	10.7	4.3	98.8	17.4
6,75	625	2.2	8.3	3.7	88.7	16.2
6,75	500	2.1	10.7	4.7	73.4	13.5

Table 2. Dry weight of the aboveground components (and the forest floor) of trees cultivated at different population densities (PD), at three ages

Significant release of K (49-6 %), Ca (18-20 %) and Mg (27-39 %) was observed by Costa et al. (2005) in $E.\ grandis$ litter while P was immobilized (-20 to -40 %).

Another possibility would be that after a certain time, the concentrations of these nutrients in the materials that make up the litter decrease, due to the nutrient availability reduction in soil during the growth cycle; a fact that is validated for K and Ca in leaves, and K and Mg in branches (Table 1). Alternatively, the proportion of components with higher nutrient concentrations in the forest floor composition could decrease with age. Nitrogen concentrations were constant in forest floor as well as in leaves and branches, the main components of this material. Moreover, this constancy indicates no alterations in biogeochemical N cycling rates since there was no reduction in content of this nutrient in the forest floor with increasing tree ages (Table 1).

After one year, evaluation of mineralization of the forest floor components using litter bags indicated that there was a 30.4 % reduction in the K concentration compared to the initial values, while the concentration of other nutrients did not vary significantly during the evaluated period (Table 3). Several authors have reported a marked reduction of K in eucalyptus litter (Guo & Sims, 2002; Zaia & Gama-Rodrigues, 2004; Costa et al., 2005).

Besides K made available by the mineralization of decomposed materials, K leaching from the forest floor must also have taken place before its decomposition,

making it available more quickly than the others that are released as the forest floor is decomposed (Shammas et al., 2003).

The variations in nutrient concentration of the litterfall samples (consisting of leaves, bark, branches, and fruits) collected throughout the year were not significant either (Table 3). The same was observed for leaves dropped from the tree (litterfall leaves) (Table 3). This indicates that the seasonal climatic effect, which is rather strong in this region (cold dry period from May to September, and warm rainy period, from October to April), did not influence the nutrient concentrations in leaves dropped from the trees. Biochemical cycling rates would therefore have been similar all year long, in spite of the likely differences in the absorption rates due to the variation of water availability in the soil (Leite et al., 1999).

The concentrations in the physiologically active leaves (Table 1) and litterfall leaves (Table 3) differed after 4.5 years, indicating the magnitude of biochemical nutrient cycling that occurs during the process of leaf senescence. Values of -43.8, -63.6, -53.3, +24.0, -22.2 % were found for N, P, K, Ca, and Mg, respectively, showing the release sequence: P > K > N > Mg and the absence of Ca mobility. The same sequence was observed for leaves and leaf litter (consisting mainly of leaves) after 2.5 years, (-62.9, -56.7, +10.6, and -18.0 % for P, K, Ca, and Mg, respectively) (Leite et al., 1998). For *E. diversicolor* and *E. marginata*, the nutrient percentage retranslocated from senescent to younger leaves was -56.0, -71.1,

Table 3. Nutrient concentration in the forest floor material (sampled July 1996) of a 4.5 year-old eucalyptus
stand in litter bags containing material of forest floor, litterfall, and litterfall leaves sampled every two
months (mean values of stands at different population densities)

75				Sa	ampling dat	e		
Material	Nutrient	Jul./96	Sept./96	Nov./96	Jan./97	Mar./97	May/97	Jul./97
					g kg-1			
Forest floor	N	8.3	10.0	10.0	10.9	9.3	11.7	10.9
	P	0.3	0.4	0.3	0.4	0.3	0.4	0.4
	K	2.3	1.9	1.2	1.1	1.6	0.8	0.7
	Ca	7.7	7.5	7.3	7.4	5.9	7.9	7.0
	${ m Mg}$	1.3	1.2	1.1	1.0	1.3	1.1	1.0
Litterfall	N	-	9.5	8.6	9.0	9.5	8.4	-
	P	-	0.4	0.3	0.3	0.4	0.2	-
	K	-	5.4	2.5	1.6	0.6	2.7	-
	Ca	-	5.2	4.6	4.7	6.3	6.6	-
	${ m Mg}$	-	1.1	1.0	1.1	1.0	1.4	-
Litterfall leaves	N	-	11.8	10.3	11.5	11.1	8.3	-
	P	-	0.4	0.3	0.4	0.4	0.2	-
	K	-	6.3	3.1	2.2	0.7	2.5	-
	Ca	-	6.2	5.3	6.3	7.4	6.6	-
	$_{ m Mg}$	-	1.4	1.1	1.3	1.2	1.4	-

-63.0, +30.0, and -4.0 % for N, P, K, Ca, and Mg, respectively (Grove et al., 1996). Attiwill (1981) reports that the remobilized N and P quantities of senescent eucalyptus leaves are greater than in other annual or woody species. Relative retransfer is higher in low-fertility than in more fertile soils (Grove et al., 1996).

Nutrient accumulation in tree parts and litter

The nutrient quantities accumulated in the aboveground tree parts (leaves, branches, bark, and stem wood) (AG) summed with that in the litter (FF), i.e., AG + FF, throughout a full cultivation cycle, represents an estimate of the entire forest nutrient demand. This estimate would be more accurate if nutrient accumulation in the root system had also been recorded. In another study carried out near the present experiment (unpublished data) the quantity of N, P, K, Ca, and Mg accumulated in the root system of seven year-old *E. grandis* forest accounted for 12.1, 8.6, 8.9, 10.0, and 9.9 % of the nutrients immobilized in AG + FF. From information on accumulated quantities in AG + FF at different ages, the dynamics of nutrient demand can be estimated for the full cycle. This knowledge is fundamental to determine the most appropriate moments for fertilization, that is, periods that precede demand peaks.

Nitrogen accumulation in AG + FF was linear in relation to tree age (Table 4), while P, K, Ca, and Mg accumulation followed quadratic models at intermediate and high PDs, and linear models (except

for Ca) at lower PDs (Table 4). The quadratic relation between these two variables may indicate a trend of soil nutrient exhaustion at older ages. At higher PDs, other developments such as intensified cycling processes, higher tree mortality and increased allocation of photoassimilates to the root system probably also occurred.

If growth and, consequently, nutrient accumulation had mainly been limited by nutrient availability in the system, the observed accumulation dynamics could be indicating that the available N was not limiting for forest growth at any of the evaluated PDs. Phosphorus, K, and Mg were also not restrictive at lower PDs, while Ca could have been limiting, even at low PDs. Besides the natural growth rate of the forest, the low level of available nutrients in the soil (Table 5) could have contributed to the accumulation dynamics as observed for P, K, Ca, and Mg.

Older trees still have a significant N demand; averaged 9.2 % between the sixth and seventh year (Figure 1), although the peaks are in the first and second year. This shows that N fertilization restricted to the first and second year of forest growth is not adjusted to the dynamics of the stand demand. This can explain the explicit lack of eucalyptus response to nitrogen fertilizers (Novais et al., 1990), which is aggravated by the high volatilization and leaching losses of most N fertilizers.

Annual P demand is highest in the first year and reaches 51.7 % of the maximum accumulation after two years, as indicated by P accumulation in AG + FF (Figure 1). This demand drops drastically in the last

Table 4. Regression equations of N, P, K, Ca, and Mg accumulated (kg ha⁻¹) in the total aboveground biomass plus forest floor (AG + FF) according to the stand age (SA) and population densities (PD)

Nutrient	Component	PD	Equation	Pt. max	\mathbb{R}^2
		trees ha-1		yr	
N	AG + FF $AG + FF$ $AG + FF$	5,000 1,667 500	$\hat{y} = 9.0134 + 64.3500 \text{ SA}$ $\hat{y} = 7.9072 + 58.011 \text{ SA}$ $\hat{y} = -7.517 + 48.834 \text{ SA}$	$6.75^{(1)} \ 6.75^{(1)} \ 6.75^{(1)}$	0.971 0.957 0.981
P	AG + FF AG + FF AG + FF	5,000 1,667 500	$\hat{y} = -0.5718 + 7.7218 \text{ SA} - 0.5886 \text{ SA}^2$ $\hat{y} = -0.7539 + 6.9146 \text{ SA} - 0.6148 \text{ SA}^2$ $\hat{y} = -0.40909 + 2.5185 \text{ SA}$	6.56 5.62 6.75 (1)	0.977 0.955 0.981
K	AG + FF $AG + FF$ $AG + FF$	5,000 1,667 500	$\hat{y} = -16.1964 + 108.832 \text{ SA} - 8.4821 \text{ SA}^2$ $\hat{y} = -17.1780 + 95.000 \text{ SA} - 8.033 \text{ SA}^2$ $\hat{y} = 0.5995 + 34.881 \text{ SA}$	6.41 5.91 6.75 ⁽¹⁾	0.982 0.936 0.858
Ca	AG + FF $AG + FF$ $AG + FF$	5,000 1,667 500	$ \hat{y} = -19.345 + 144.369 \text{ SA} \cdot 15.4417 \text{ SA}^2 $ $ \hat{y} = -15.662 + 117.179 \text{ SA} \cdot 12.9418 \text{ SA}^2 $ $ \hat{y} = -11.138 + 84.960 \text{ SA} \cdot 8.0880 \text{ SA}^2 $	4.67 4.53 5.25	0.984 0.983 0.990
Mg	AG + FF AG + FF AG + FF	5,000 1,667 500	$\hat{y} = -1.3628 + 19.7052 \text{ SA} - 1.6102 \text{ SA}^2$ $\hat{y} = -2.3958 + 20.718 \text{ SA} - 2.0245 \text{ SA}^2$ $\hat{y} = 1.46279 + 6.9808 \text{ SA}$	6.12 5.12 $6.75^{(1)}$	0.968 0.995 0.937

⁽¹⁾ Estimated age of maximum.

Table 5. Chemical properties of soil sampled at different depths and times under eucalyptus stands (mean values of soil samples from plantations with different population densities)

Depth	$\mathbf{Age}^{ ext{ iny (1)}}$	pН	OM	P	K	Ca	Mg	Al	H + Al
cm	yr		$\mathrm{g}\;\mathrm{kg}^{\text{-}1}$	mg	dm ⁻³ ——		mm	ol _c dm ⁻³ —	
0-5	2.50	4.9	30.0	1.75	26.4	2.0	1.0	14.0	72.0
	4.50	4.6	22.0	0.94	14.9	1.4	0.7	15.0	59.0
	6.75	4.5	22.0	1.46	31.9	1.4	0.9	16.0	74.0
5-10	2.50	4.9	28.0	1.69	18.2	1.7	0.7	14.0	74.0
	4.50	4.5	20.0	0.94	12.1	0.9	0.5	16.0	62.0
	6.75	4.5	20.0	1.23	27.4	0.8	0.7	16.0	73.0
10-30	4.50	4.5	16.0	0.73	9.6	0.4	0.3	14.0	55.0
	6.75	4.5	16.0	0.72	19.9	0.6	0.5	14.0	63.0

⁽¹⁾ Forest age at the time of soil sampling.

three years. The same trend was observed for K, suggesting that fertilization in the first two years is more adequate, since more than 50 % of P and K neededy for the complete cycle have already been absorbed.

The Ca and Mg accumulation observed in AG + FF followed the trend of P and K. The demand of the first two years (64 % for Ca and 56.1 % for Mg) (Figure 1) was even more evident than those observed for P and K. These nutrients must therefore be supplied within the first two years, possibly before planting.

Nutrient accumulation in the trunk as a variable of PD at 2.5 years, and for N and K, at 4.5 years, was better expressed by quadratic equations; for P and

Ca, by linear equations (Table 6). At the age of 6.75 years, it was found that the quantities of exported P and K would vary according to PD. However, for N, Ca and Mg accumulated in the trunk there was no clear trend as a function of distinct PDs. This shows that modifying PD would not change the amount of these nutrients exported from the site in the harvested trunk at this age.

The PD effect on Ca demand by the AG + FF after 2.5 years, on K and Mg after 2.5 and 4.5 years, and on N and P at all ages is well expressed by quadratic models (Table 6). Best adjustments for K, Ca, and Mg at the age of 6.75 years were linear (Table 6). This demonstrates that the greater individual growth of trees at lower PDs, at this age, was still insufficient

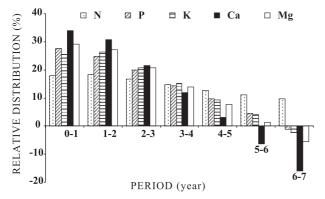


Figure 1. Relative distribution of nutrients accumulated in the forest biomass throughout the cultivation cycle, estimated by regression equations adjusted for nutrient content values of the aboveground biomass and the forest floor, according to the forest age (mean values of seven population densities).

to immobilize equivalent amounts of nutrients per area in comparison to trees cultivated at higher PDs.

Nutrient allocation

The relative participation of N, P, K, Ca, and Mg immobilized in leaves and branches compared to the total amount immobilized in the biomass (AG + FF) dropped drastically with increasing forest ages (Table 7). In the bark, this proportion increased until the age of 4.5 years and remained constant from then on, except for K, which continued to increase until 6.75 years. In the stem wood, only N percentage increased, whereas the other nutrients remained constant at all three ages (2.5, 4.5, and 6.75 years). The relative participation of K, Ca, and Mg in the litter was also stable along the time.

The highest accumulation of N and P was verified in leaves after $2.5~\rm years$ and after $4.5~\rm years$ in the forest floor. In turn, K accumulation was highest in

Table 6. Regression equations of accumulated amounts of N, P, K, Ca, and Mg (kg ha^{-1}) in the trunk and the total aboveground biomass plus forest floor (AG + FF) according to the population density (PD) (evaluated at three ages)

Nutrient	Component	Age	Equation	Pt. max.	R
		yr		trees ha-1	
N	AG + FF	2.5	$\hat{y} = 71.076 + 0.0908 \text{ PD} - 0.00001186 \text{ PD}^2$	3,828	0.924
	AG + FF	4.5	$\hat{y} = 228.076 + 0.0748 \text{ PD} - 0.00001204 \text{ PD}^2$	3,106	0.814
	AG + FF	6.75	$\hat{y} = 285.133 + 0.0731 \text{ PD} - 0.00000909 \text{ PD}^2$	4,021	0.670
P	AG + FF	2.5	$\hat{y} = 5.248 + 0.00687 \text{ PD} - 0.000000874 \text{ PD}^2$	3,930	0.96
	AG + FF	4.5	$\hat{y} = 14.138 + 0.00318 \text{ PD} - 0.000000399 \text{ PD}^2$	3,978	0.75'
	AG + FF	6.75	$\hat{y} = 13.161 + 0.00513 \text{ PD} - 0.000000539 \text{ PD}^2$	4,759	0.770
K	AG + FF	2.5	$\hat{y} = 37.922 + 0.0735 \text{ PD} - 0.00000888 \text{ PD}^2$	4,138	0.98
	AG + FF	4.5	$\hat{y} = 185.952 + 0.1115 \text{ PD} - 0.00001642 \text{ PD}^2$	3,395	0.87°
	AG + FF	6.75	$\hat{y} = 192.20 + 0.0271 \text{ PD}$	$5,000^{(1)}$	0.77
Ca	AG + FF	2.5	$\hat{y} = 110.291 + 0.0734 \text{ PD} - 0.00000981 \text{ PD}^2$	3,741	0.85
	AG + FF	4.5	$\hat{y} = 228.286 + 0.023399 \text{ PD}$	$5,000^{(1)}$	0.91
	AG + FF	6.75	$\hat{y} = 182.11 + 0.0134 \text{ PD}$	$5,000^{(1)}$	0.55
$_{ m Mg}$	AG + FF	2.5	$\hat{y} = 14.738 + 0.0202 \text{ PD} - 0.0000028 \text{ PD}^2$	3,607	0.93
	AG + FF	4.5	$\hat{y} = 35.014 + 0.0137 \text{ PD} - 0.00000221 \text{ PD}^2$	3,099	0.92
	AG + FF	6.75	$\hat{y} = 41.374 + 0.00371 \text{ PD}$	$5,000^{(1)}$	0.79
N	Trunk	2.5	$\hat{y} = -1.729 + 0.0320 \text{ PD} - 0.000004397 \text{ PD}^2$	3,639	0.97
	Trunk	4.5	$\hat{y} = 65.077 + 0.0267 \text{ PD} - 0.000002831 \text{ PD}^2$	4,714	0.90
	Trunk	6.75	$\hat{y} = \overline{y} = 142.5$	-	ns
P	Trunk	2.5	$\hat{y} = 1.070 + 0.0034 \text{ PD} - 0.000000460 \text{ PD}^2$	3,695	0.95
	Trunk	4.5	$\hat{y} = 6.607 + 0.00097 \text{ PD}$	$5,000^{(1)}$	0.78
	Tru nk	6.75	$\hat{y} = 5.578 + 0.00353 \text{ PD} - 0.000000437 \text{ PD}^2$	4,039	0.77
K	Trunk	2.5	$\hat{y} = 10.499 + 0.0469 \text{ PD} - 0.000006066 \text{ PD}^2$	3,865	0.96
	Trunk	4.5	$\hat{y} = 10.127 + 0.0822 \text{ PD} - 0.00001081 \text{ PD}^2$	3,802	0.88
	Trunk	6.75	$\hat{y} = 136.00 + 0.01759 \text{ PD}$	$5,000^{(1)}$	0.72
Ca	Trunk	2.5	$\hat{y} = 39.710 + 0.0269 \text{ PD} - 0.000003139 \text{ PD}^2$	4,284	0.71
	Trunk	4.5	$\hat{y} = 92.0114 - 0.022109 \text{ PD}$	$5,000^{(1)}$	0.94
	Trunk	6.75	$\hat{y} = \overline{y} = 95.75$	-	ns
$_{ m Mg}$	Trunk	2.5	$\hat{y} = 4.297 + 0.0072 \text{ PD} - 0.000000951 \text{ PD}^2$	3,785	0.87
-	Trunk	4.5	$\hat{\mathbf{y}} = \overline{\mathbf{y}} = 21.0$	-	ns
	Trunk	6.75	$\hat{\mathbf{y}} = \overline{\mathbf{y}} = 22.1$	-	ns

⁽¹⁾ Maximum estimated population density.

Table 7. Percentage participation of nutrients in aboveground biomass (AG) and forest floor (FF) in relation to total immobilized (AG + FF) throughout an eucalyptus cultivation cycle (mean values of seven population densities)

Nutrient	\mathbf{Age}	Leaves	Branches	Bark	Stem wood	Forest floor
	yr			%		
N	0.25	77.3	5.1	9.8	7.8	0.0
	2.50	42.8	9.8	7.3	10.6	29.5
	4.50	20.9	6.1	10.5	22.2	40.3
	6.75	14.8	6.0	9.8	29.2	40.2
P	0.25	60.0	2.4	33.6	4.0	0.0
	2.50	32.2	16.0	12.3	23.3	16.2
	4.50	18.1	10.3	27.0	19.8	24.7
	6.75	14.7	10.3	23.3	25.6	26.1
K	0.25	57.0	4.1	18.5	20.5	0.0
	2.50	24.9	14.9	17.2	32.8	10.2
	4.50	13.5	11.5	36.0	27.4	11.6
	6.75	12.2	10.1	40.0	29.7	8.0
Ca	0.25	55.6	2.4	34.3	7.8	0.0
	2.50	11.0	10.3	22.2	15.0	41.5
	4.50	5.5	5.2	36.2	11.8	41.3
	6.75	5.8	7.3	30.0	16.5	40.5
$_{ m Mg}$	0.25	82.9	1.1	11.7	4.4	0.0
	2.50	20.6	9.3	20.0	13.8	36.4
	4.50	10.6	6.5	34.0	10.1	38.5
	6.75	10.5	7.0	33.8	12.7	35.9
Zn	4.50	5.3	4.0	9.1	57.1	24.4
	6.75	1.7	1.7	2.2	81.3	13.2
Cu	4.50	7.9	7.4	14.8	60.1	9.8
	6.75	6.5	18.9	9.6	22.5	42.4
Fe	4.50	5.8	1.3	3.9	6.4	82.5
	6.75	1.3	0.6	1.1	12.3	84.7
Mn	4.50	8.4	7.4	29.4	4.4	50.5
	6.75	7.1	7.6	23.2	14.5	47.6
В	4.50	2.3	3.9	18.9	31.8	43.0
	6.75	5.8	8.9	18.9	24.8	41.7

the stem wood after 2.5 years and after 6.75 years in the bark. Calcium and Mg accumulations were more prominent in the litter between 2.5 and 6.75 years.

At the end of the cycle, the concentrations of N, P, Ca, and Mg were highest in the forest floor (Table 7). Burning this material will lead to losses by volatilization (of some nutrients) as the ashes are carried away by the wind, besides making way for leaching of soluble nutrients and P fixation, and consequently, help accelerate the nutrient exhaustion in these systems.

Nutrient distribution observed among the biomass components may be a consequence of a dystrophic system, since in environments with more fertile soils, as on the coastal plateaus in the State of Espírito Santo, for example, results obtained so far differ from those reported here. In nine year-old eucalyptus stands the forest floor was not the main accumulation component of any macronutrient (Neves, 2000).

After forest floor, the trunk was the second component with most immobilized nutrients at the end of the cycle (Table 7). Thus, the exported quantities are substantial and must be adequately replaced to maintain the potential productivity of the system for the following cultivation cycles. Debarking on site will minimize exportation especially of P, K, Ca and Mg.

CONCLUSIONS

- 1. The dynamics of Ca demand by eucalyptus plantations were similar to those of Mg, P and K, with larger requirements in the first couple of years of the rotation, while the N differed significantly, with a substantial demand up to the $7^{\rm th}$ year.
- 2. Extending the forest cutting age could be a strategy to reduce the quantities of P, K, Ca, and Mg exported from the system per harvested wood unit.

- 3. Since N, P, Ca, and Mg are mainly stored in the forest floor by the end of the cycle, their maintenance at the site and the synchronization of their mineralization with the forest nutrient demand are essential steps towards an optimized nutrient use in forest systems.
- 4. In low-fertility soils the forest floor represents the main nutrient reservoir of eucalyptus plantations.
- 5. At the age of 6.75 years there were no substantial differences in the quantity of nutrient absorbed per area unit by trees planted at different population densities.
- 6. Sustainability of eucalyptus production at sites similar to those presented here depends on the mantainance of forest floor and harvest residue, besides the adequate replacement of exported nutrients.

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