

Fertilization with phosphorus increases soil nitrogen absorption in young plants of *Eucalyptus grandis*

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Abstract

Nitrogen (N) and phosphorus (P) are the nutrients that most commonly limit tree growth. Interactions between fertilization and soil type are well known, and in soils with moderate or low N availability, N-fertilization is frequently recommended to improve tree nutrition. The aim of this paper was to analyze how different doses of P and N applied in three different types of soils affect dry mass and nutrient accumulation and partitioning in *Eucalyptus grandis* young plants, and if fertilization with P may increase N uptake. Fertilization was applied as 1, 2 and 4 g of urea (46% of N) or 6, 12 and 24 g of triple superphosphate (20% of P) per plant. Dry mass and nutrient partitioning were analyzed 44, 72 and 84 days after transplanting (DAT). Interactions between soil type and fertilization were observed. Root:total mass ratio decreased with P-fertilization in all soils. Fertilization with P promoted growth and improved N and S absorption even more than N-fertilization, although some of the soils used have very low N-contents (0.03%). Our data suggest that fertilization with P increased N absorption through a mechanism that was not related to increased N demand by enhanced growth.

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1. Introduction

The nutrients that most frequently limit forest growth are nitrogen (N) and phosphorus (P) (Fisher and Binkley, 2000). Nutrient availability can alter growth rate through changes in dry mass partitioning, in specific leaf area or in the assimilation rate per unit leaf area (Kirschbaum et al., 1992; Madeira et al., 2002; Sands et al., 1992; Xu et al., 2002). The demand for P is high during the first year of growth of *Eucalyptus*, while in later stages the demand decreases due to internal recycling (Fernandez et al., 2000). Interactions between nutrients are important in determining the optimum nutrition for *Eucalyptus grandis* (Dighton et al., 1993). Many experiments with *Eucalyptus* seedlings showed that responses to N applications depend on P-availability, and that growth can be reduced by N-fertilization if P is limiting (Neves et al., 1990). A strong positive response of trees to P-fertilization is frequent because planting is usually done in soils with low natural P-availability (Neves et al., 1990). If the productivity of plantations

increases, the removal of N and P due to harvesting can increase too (Harrison et al., 2000) which has implications for sustainable productivity of forest soils (Fisher and Binkley, 2000).

To determine if fertilization is required, soil chemical properties can be analyzed. However, the efficacy of soil testing to predict fertilizer requirements is usually lower in forest than in agricultural soils, due to the poorer nutrient status of forest soils, the lower rates of P-uptake per unit time by trees, the greater volume of soil explored by tree roots, their greater mycorrhizal colonization and nutrient recycling through litter decomposition (Mc Laughlin, 1996).

Plants tissues have high nutrient concentrations under good growth conditions. With a moderate nutrient shortage, vacuolar nutrient reserves decrease with little effect on plant growth, but at lower tissue nutrient contents, growth and photosynthesis rates decrease (Lambers et al., 1998). However, a higher rate of nutrient absorption after fertilization will not always result in faster growth. Increased growth is achieved with an optimal nutrient balance, expressed mainly by optimal N:P, N:K, N:S, P:K and Ca:Mg ratios (Herbert, 1996).

Fertilization is a common practice in *Eucalyptus* plantations all over the world (Barros et al., 1990; Cromer, 1996; Herbert,

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1996; Knight and Nicholas, 1996). Soil/fertilizer interactions are well known (Judd et al., 1996a,b), and nutrient acquisition by plants depends on the concentration of the ion in the soil solution, the absorbing area of the roots and uptake kinetics (Fisher and Binkley, 2000). In spite of this, the same fertilization schedule (50 kg ha^{-1} of N and 58 kg ha^{-1} of P at planting) is followed in all types of soils planted with *E. grandis* in Argentina (Dalla Tea and Marcó, 1996).

In a previous paper, we showed that fertilization with P increased growth of young *E. grandis* plants more than fertilization with N, even in soils that are relatively poor in N and where N is limiting (Graciano et al., 2005). This effect involved changes in dry mass partitioning, since plants fertilized with P allocated more C to shoot than root growth. These responses to P-fertilization prompted us to determine if addition of P in these type of soils may indirectly enhance uptake of other nutrients, e.g., N. Therefore, the aim of this paper was to analyze how different doses of P and N applied in three different types of soil affect dry mass, and nutrient accumulation and partitioning in young plants of *E. grandis*.

2. Methods and materials

Three-month old *E. grandis* plants were transplanted into 4.5-l pots with soil adhered to their roots, and fertilized either with N or P. Pots were filled with about 6 kg of topsoil matter from three different types of soil used to plant this species in Argentina. These are a deep red sandy soil (Oxic Quartzipsament, “red sand” in this paper), a dark brown loamy sand (Haplumbrept Inceptisols, “loamy sand” in this paper) and a silt clay loam (Argiacuol Vertico, “silty clay loam”). On these soils, wood production for *E. grandis* plantations is 328, 505 and $256 \text{ m}^3/\text{ha}$, respectively, in 10-year old plantations (Dalla Tea and Marcó, 1996; Goya et al., 1997).

Aliquots of each type of soil were analyzed for pH in water 1:2.5 (v/v), electric conductivity in soil paste, P by Bray and Kurtz method, C by Walkley Black method, total N by micro-Kjeldhal, bases and cation exchange capacity (CEC) in ammonium acetate extract (pH 7) by atomic absorption spectrometry (Departamento de Suelos, FAUBA, Universidad de Buenos Aires, Argentina) (Greenberg et al., 1985).

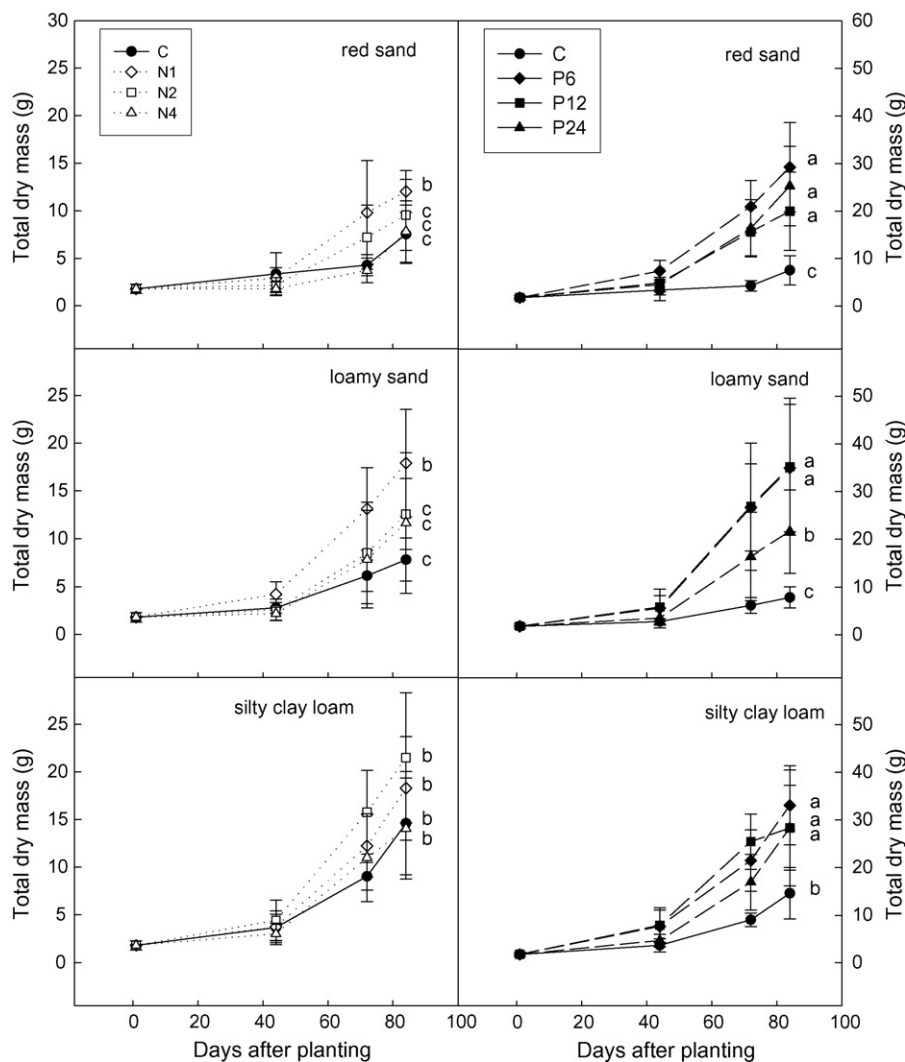


Fig. 1. Total dry mass accumulation of control, N-fertilized and P-fertilized plants during the experiment in each type of soil. Bars indicate standard deviations. In the last date, figures with different letters in each type of soil differ significantly ($P < 0.05$). Note that the y axes are drawn to a different scale in the left and right panels.

Plants (one plant per pot) were grown outdoors in late spring and early summer and watered daily throughout the experiment. A week after transplant, plants were fertilized with N or P. N was applied as 1 g (N1), 2 g (N2) and 4 g (N4) of urea (46% of N) and P was applied as 6 g (P6), 12 g (P12) and 24 g (P24) of triple superphosphate (20% of P) per pot. These rates are within the range of fertilizer applications that increased plant growth in a previous experiment with the same type of soil (Graciano et al., 2005). Plants were randomly allocated to each treatment. Control plants without fertilization (C) were included for each type of soil.

Samples were taken at the beginning of the experiment and 44, 72 and 84 days after transplanting (DAT) to determine dry mass partitioning, total leaf area and tissue nutrient concentration. Ten (44 and 72 DAT) or 20 (0 and 84 DAT) replicate plants were harvested at each sampling date.

For each sampling date, dry mass and tissue nutrient concentration were determined. Plants were divided into roots, stem, branches and leaves. Dry mass was determined after drying plant material in an oven at 70 °C to constant weight. The dried material of each plant part was ground in a Wiley mill, 0.5 mesh, for nutrient concentration analysis (N, P, K, Ca and S). Samples were digested in acid (HNO₃ plus 30% H₂O₂) and analyzed in a Beckman Spectra-Span plasma emission spectrophotometer V in order to determine P, K and Ca-concentrations (Luh Huang and Schulte, 1985). N and S-concentrations were determined by dry

combustion with a LECO CNS-2000 (Tabatabai and Bremner, 1991). N and P-content were determined by multiplying the mean N or P-concentration of each plant part by their respective dry masses.

Data were analyzed using ANOVA ($P < 0.05$) with soil type and doses of fertilization as main factors. When interactions were not significant, each type of soil was analyzed separately. Means were compared by Tukey's test ($P < 0.05$) (Sokal and Rohlf, 1979).

3. Results

3.1. Total dry mass accumulation

Overall, control, non-fertilized plants grew more in the silty clay loam than in the two other types of soil, i.e., the red sand and loamy sand (Fig. 1). No interactions between soil type and fertilization were observed 44 days after transplanting ($P < 0.2257$), but there were significant soil type–fertilization interactions at 72 DAT ($P < 0.0154$) and 84 DAT ($P < 0.0001$). In the last sampling date, 84 DAT, control plants had grown more on the silty clay loam than in the other two soils. All rates of P-fertilization, as well as N1, promoted growth in the red sand and the loamy sand. In the red sand all applications of P increased growth to the same extent but more than N1. In the loamy sand, P6 and P12 had a higher effect than

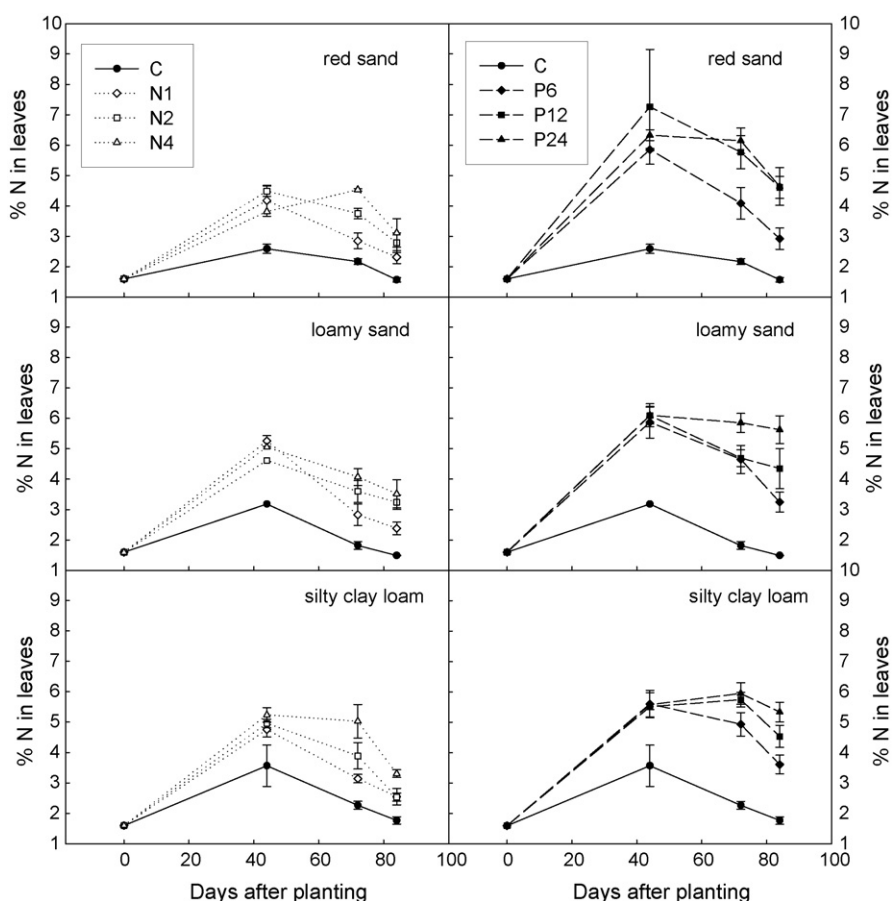


Fig. 2. Changes in mean N-concentration (%) in leaves in control and N or P-fertilized plants in three soils. Bars indicate standard deviations.

P24 and N1. In the silty clay loam, all rates of N application had small, but non-significant, growth-promoting effects, whereas all rates of P increased growth significantly, to a similar extent (Fig. 1). Therefore, strong fertilization/soil type interactions were observed, with a general positive response to P-applications across all soil types, and growth promotion by some N doses in the more coarse-textured soils.

Dry mass partitioning was altered by fertilization. The leaf:total plant mass ratio was not modified by any fertilization treatment in any soil type (data not shown). In the red sand and the loamy sand, the root:total plant mass ratio was decreased by all fertilization treatments, whereas in the silty clay loam only P-fertilization decreased this ratio. P-fertilization had a larger and more consistent effect reducing dry mass allocation to roots than N-fertilization treatments (data not shown).

3.2. Nutrient concentration and nutrient content

N-concentration in leaves, branches and stems peaked at 44 DAT in most treatments (Fig. 2). Tissue N-concentrations changed through time with a similar pattern in control and fertilized plants in all soils, but plants fertilized with N or P exhibited higher N-concentrations than control plants. Surprisingly, N-concentrations were generally higher in P-fertilized plants than in N-fertilized plants, in all plant parts and irrespective of soil type.

P-concentrations in leaves, branches, stem and roots were higher in P-fertilized plants than in control and N-fertilized plants (Fig. 3). P-concentration in leaves, branches and stem of P-fertilized plants were highest at 44 DAT and then declined, whereas P-concentration in roots continued to increase up to the last sampling date at 84 DAT.

In the last sampling date, N-concentrations in leaves were similar in all non-fertilized plants, although N-content was different in the three soils (Table 2). N-concentration in leaves increased significantly with P-fertilization in all soils, while N-fertilization caused a significant increase only at the higher doses. Regardless of soil type, and soil N-content, the highest concentrations of N were always measured in plants fertilized with P, rather than N. P-concentration in leaves increased only with P-fertilization, although for some doses differences were not significant. K-concentration was higher in the silty clay loam than in the loamy sand, and the lowest in the red sand. For all soil types, fertilization did not alter K-concentrations. In all soils, P-fertilization increased S-concentration in leaves, whereas N-fertilization had no effect. Ca-concentration was higher in the loamy sand and lower in the silty clay loam, but fertilization did not alter Ca-concentrations in any of the soil types tested.

Total plant N-content was higher in P-fertilized treatments in all soils (Fig. 4). Although the pattern of response of plant N-content to P-fertilization was the same in all soils, total

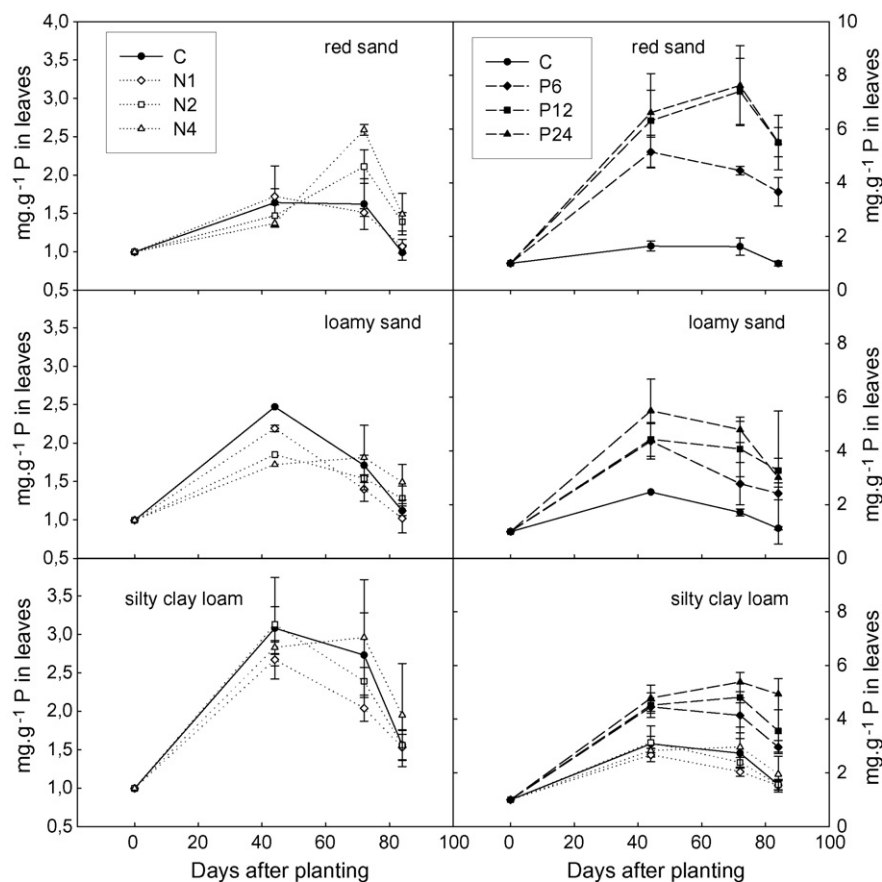


Fig. 3. Mean P-concentration (mg g^{-1}) in leaves of control and plants fertilized with N or P in three soils. Bars indicate standard deviations. Note that the y axes are drawn to a different scale in the left and right panels.

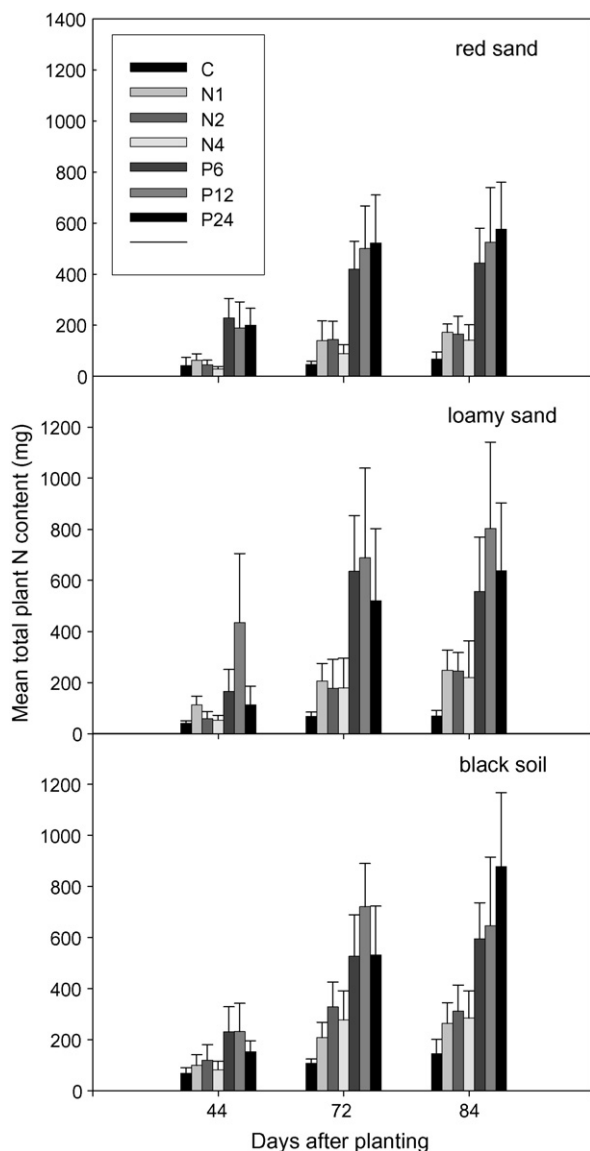


Fig. 4. Changes in total N-content (mg) per plant in control and fertilized with N or P plants in three soils. Bars indicate standard deviation.

N-content was lower in the red sand and higher in the silty clay loam. Total P-content increased only with P-fertilization in all soils (Fig. 5). Total K-content was higher in P-fertilized plants in all soils, but in general K-content was higher in the silty clay loam and lower in the red sand (Fig. 6).

4. Discussion

4.1. Total dry mass accumulation

The fertilizers and doses applied in each type of soil produced different effects on growth of young *E. grandis* plants. In general, P-applications had larger effects on dry mass accumulation than N-applications, in spite of the fact that some of the soils studied have low amounts of N (Table 1). The results of this experiment are similar to our previously reported data (Graciano et al., 2005) showing that P-fertilization generally

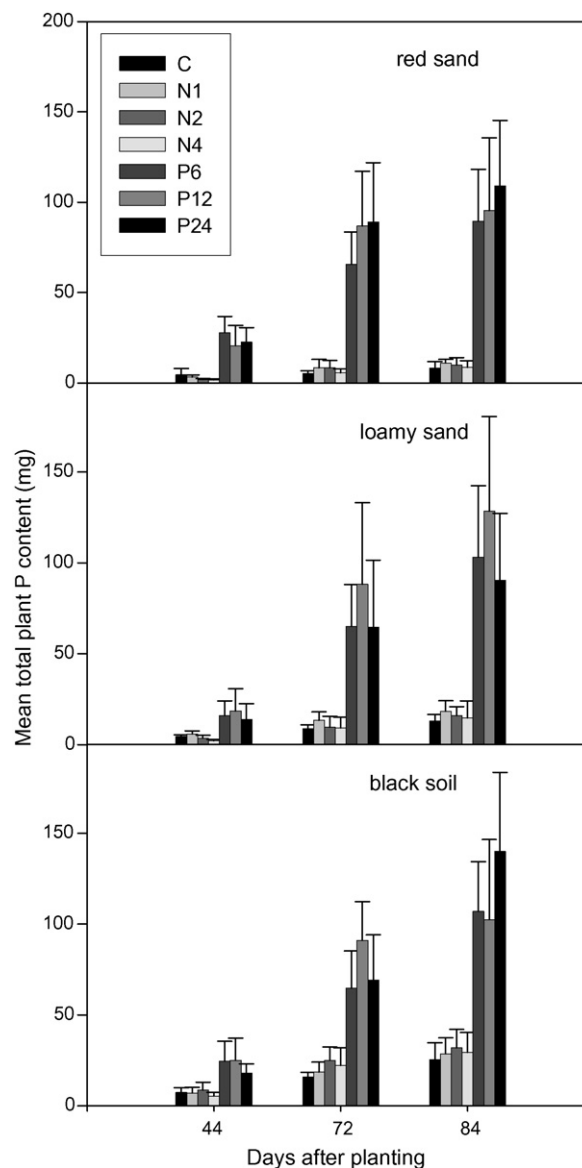


Fig. 5. Changes in total P-content (mg) in each plant in control and fertilized with N or P plants in three soils. Bars indicate standard deviation.

increased dry mass accumulation more than N application in these soils. The effects of P were probably not due to indirect effects on soil N mineralization, since the concentrations of ammonium and nitrate were quite similar in the loamy sand after fertilization with P6 (14.2 mg kg^{-1} versus 12.6 mg kg^{-1} of nitrate-N and 0.33 mg kg^{-1} versus 0.88 mg kg^{-1} of ammonium-N at 33 DAT, and 7.3 mg kg^{-1} versus 8.6 mg kg^{-1} of nitrate-N and 0.02 mg kg^{-1} versus 0.44 mg kg^{-1} of ammonium-N at 52 DAT, in control and P-fertilized pots, respectively). In soils with moderate organic matter, responses to N and P are not surprising (Herbert, 1990). However, lack of response to N-applications without an adequate supply of P has been widely reported, and even depressive effects on growth have been observed (Neves et al., 1990). No effect or a depressive effect of P-fertilization might be expected when N status in the soil is very low because P-uptake is strongly influenced by N supply (Herbert, 1990). Increases in total

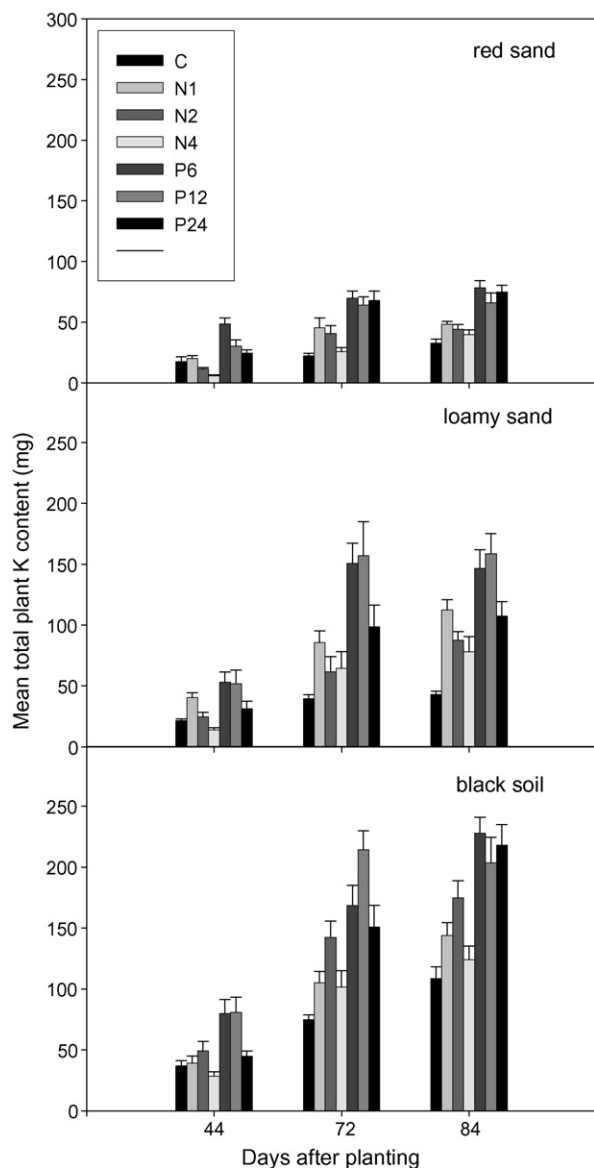


Fig. 6. Changes in total K content (mg) in each plant in control and fertilized with N or P plants in three soils. Bars indicate standard deviation.

height due to P-fertilization were observed 3 months after planting in soils with an adequate N supply (Xu et al., 2002), and positive responses of growth to P-fertilization have been observed in *E. grandis* in soils with even higher P-concentrations than those of the soils used in this experiment (Herbert, 1983).

High productivity is clearly dependent on the maintenance of a high leaf area to intercept a high proportion of available solar radiation (Cromer et al., 1993). However, under N-deficit plants allocate carbon preferentially to roots and develop leaves with less area per unit mass (Cromer and Jarvis, 1990), whereas with a higher nutrient status plants have a greater proportion of dry matter allocated to stem and foliage than to roots (Sands et al., 1992). The root:total plant mass ratio was decreased by fertilization in the two poorer soils (data not shown). In low nutrient environments, absorption of nutrients is determined by root density because in most soils diffusion of nutrients is the

Table 1

Soil properties of the three soils used in the experiment

	Red sand	Loamy sand	Silty clay loam
US classification	Oxic Quartzipsamment	Fluventic Haplumbrept	Argiudolic Pelludert
pH	6.44	6.3	6.92
Electrical conductivity (dS/m)	0.08	0.08	0.9
P (ppm)	3.74	5.84	7.99
C (mg g ⁻¹)	4.5	4.1	16.7
Total N (mg g ⁻¹)	0.3	0.3	1.5
Ca (meq/100 g)	1.78	2.14	18.12
Mg (meq/100 g)	0.46	0.87	1.65
Na (meq/100 g)	0.23	0.56	0.33
K (meq/100 g)	0.31	0.35	1.14
CEC (meq/100 g)	6.95	8.25	23.14
Clay (%)	7.5	12.5	42.5
Silt (%)	5	10.0	27.5
Sand (%)	87.5	77.5	30
Soil texture	Sand	Loamy sand	Silt clay loam

Methods used for determinations were: pH in water 1:2.5, electric conductivity in soil paste, P by the Kurtz and Bray method, carbon by the Walkely Black method, N by micro-Kjeldhal and calcium, magnesium, sodium, potassium and cation exchange capacity (CEC) in ammonium acetate (pH 7) by atomic absorption.

primary factor limiting absorption, therefore, increased root growth might enable plants to explore the soil for additional nutrients and lessen any growth limitation imposed by nutrients (Kirschbaum et al., 1992).

4.2. Nutrient concentration

Nutrient availability, due to soil nutrient concentration or fertilization, affects nutrient distribution in plant tissues (Grove et al., 1996). In all treatments, N and P-concentrations ranked in the order leaves > branches > stem > roots (data not shown). In young *Eucalyptus* seedlings, leaves contain the highest N and P proportion of aboveground plant part, although the stem can store a high proportion of P in species that have lignotuber (Grove et al., 1996). N and P-concentrations, specially in leaves, branches and stem (Figs. 2 and 3) increased immediately after fertilization, and before any effect on growth could be detected (Fig. 1). When growth rate increased in fertilized plants after 44 DAT, tissue N-concentrations decreased in most cases (Figs. 1 and 2). Use of limiting nutrients is optimized in *Eucalyptus* through nutrient storage in excess of actual requirements, and the subsequent translocation to young tissues (Grove et al., 1996). Nevertheless, new growth after 44 DAT relied only partially on stored N, since total plant N-content continued to increase with time in all soil and fertilization treatments (Fig. 5). Evergreen plants have high nutrient and carbohydrate storage capacity, that allows leaf expansion in spite of short term carbon and nutrient shortages (Lambers et al., 1998).

Fertilization altered leaf N and P-concentrations, but the natural content of N and P of each soil was not reflected in leaf nutrient concentrations in control plants. Leaf N and P-concentration at the end of the experiment increased in all soils

Table 2

Leaf nutrient concentration at the end of the experiment (84 DAT) in control (C) and plants fertilized with N and P in three types of soil

	N (mg g ⁻¹)	P (mg g ⁻¹)	Ca (mg g ⁻¹)	S (mg g ⁻¹)
Red sand				
C	15.7 ± 0.7c	0.99 ± 0.10c	6.43 ± 0.26ab	1.8 ± 0.01c
N1	23.1 ± 2.0bc	1.07 ± 0.09c	5.95 ± 0.86b	1.3 ± 0.01c
N2	27.9 ± 3.2b	1.39 ± 0.12c	7.55 ± 0.60ab	1.4 ± 0.01c
N4	31.1 ± 4.7b	1.49 ± 0.27c	8.22 ± 0.63a	2.1 ± 0.04c
P6	29.2 ± 3.5b	3.66 ± 0.53b	7.45 ± 1.42ab	4.1 ± 0.04b
P12	46.1 ± 3.6a	5.50 ± 1.02a	6.18 ± 0.49b	6.3 ± 0.05a
P24	46.4 ± 6.2a	5.51 ± 0.55a	6.68 ± 0.29ab	6.3 ± 0.09a
Loamy sand				
C	14.9 ± 0.1e	1.12 ± 0.06d	5.90 ± 0.15a	1.6 ± 0.00c
N1	23.8 ± 2.1de	1.02 ± 0.19d	6.45 ± 1.23a	1.3 ± 0.01c
N2	32.4 ± 2.4cd	1.28 ± 0.16d	6.53 ± 1.38a	1.5 ± 0.01c
N4	35.2 ± 4.6bc	1.49 ± 0.23cd	6.32 ± 0.67a	2.3 ± 0.04c
P6	32.5 ± 3.3bcd	2.42 ± 0.23bc	5.51 ± 0.35a	3.9 ± 0.04b
P12	43.5 ± 6.6b	3.27 ± 0.46ab	4.54 ± 0.72a	5.0 ± 0.06b
P24	56.3 ± 4.6a	4.34 ± 1.21a	4.63 ± 1.16a	6.6 ± 0.09a
Silty clay loam				
C	17.7 ± 1.2e	1.56 ± 0.19d	12.63 ± 0.69a	2.0 ± 0.02c
N1	25.5 ± 2.7d	1.53 ± 0.17d	12.70 ± 1.59a	1.7 ± 0.03c
N2	25.4 ± 1.3d	1.56 ± 0.20d	13.29 ± 2.24a	1.5 ± 0.02c
N4	33.1 ± 1.3c	1.95 ± 0.67cd	11.66 ± 4.02a	1.6 ± 0.03c
P6	36.1 ± 3.0c	2.96 ± 0.25bc	11.44 ± 0.77a	3.8 ± 0.03b
P12	45.4 ± 3.6b	3.56 ± 0.79b	10.34 ± 1.80a	4.6 ± 0.03a
P24	53.4 ± 3.2a	4.93 ± 0.58a	9.88 ± 0.96a	5.4 ± 0.05a

Values are means ± standard deviations. Different letters (a–d) indicate significant differences ($P < 0.05$) for each nutrient in each type of soil.

with P-fertilization whereas N-fertilization only improved N-concentration in leaves (Table 2). P-concentration in some treatments was higher than would be expected according to an aeroponic experiment in which the highest rate of P applied produced a P-concentration of 3.49 mg g⁻¹ in mature leaves (Kirschbaum et al., 1992). However, our highest leaf P-concentrations were similar to those found in *E. grandis* growing with high P-availability (Dighton et al., 1993) and in seedling leaves (Judd et al., 1996a,b).

Foliar N and P-concentrations exhibit a relatively constant relationship among plant species, around 8:1–10:1 (Lambers et al., 1998). A deviation from a 10:1 N:P ratio in terrestrial plants, may indicate a nutritional imbalance caused by a reduced uptake of the limiting nutrient (Koerselman and Meuleman, 1996), sometimes combined with luxury consumption of nutrients that do not limit growth (Lambers et al., 1998). However, taking into account the optimum leaf nutrient concentrations reported for plantations in different countries, the N:P ratio for *E. grandis* is somewhat higher than for most species (11–18:1). If the N:P ratio is lower than the species optimum, defined between 11:1 and 18:1 for *E. grandis*, a positive response to N-fertilization is expected. On the other hand, if the N:P ratio is higher than optimum, a positive response to P addition is likely to occur (Herbert, 1990).

In the red sand and in the loamy sand, the N:P ratio increased with N-fertilization, indicating that P became the limiting nutrient (Table 3). In contrast, the N:P ratio was between the optimum ranges in these soils when plants were fertilized with

Table 3

Nutrient concentration ratios for leaves of *Eucalyptus grandis* in control plants (C) and plants fertilized with N or P in three types of soil

	Red sand			Loamy sand			Silty clay loam		
	C	N1	P6	C	N1	P12	C	N2	P6
N:P	16	22	8	13	24	13	11	16	12
N:K	3.9	5.7	8.9	2.8	3.9	11.5	2.4	3.0	6.1
N:S	8.8	17.8	7.1	9.5	18.1	8.7	8.9	16.6	9.5
P:K	0.25	0.26	1.13	0.21	0.16	0.86	0.21	0.18	0.50
Ca:Mg	2.62	2.46	2.81	2.37	2.48	2.06	6.52	6.69	5.95

Ratios derive from data reported in Table 2. Treatments are control plants and the doses of N and P in which the highest growth was obtained in each type of soil.

P, therefore N was not limiting growth in P-fertilized plants. Besides N and P, other nutrients might become limiting in fertilized plants.

In general P-fertilization ameliorated leaf nutrient status and presumably photosynthetic capacity (Kirschbaum and Tompkins, 1990; Kirschbaum et al., 1992; Sheriff and Nambiar, 1991). Our results show that P-fertilization improved leaf nutrient status more than N-fertilization, which can explain the higher effect on growth of P-fertilization. P-fertilization allowed plants to take up more nutrients (e.g., N and S) from the soil. Therefore, it improved growth not only through a higher P-concentration, but also a better N and S nutrition.

4.3. Nutrient content

Total N-content was higher in N-fertilized plants than in control plants (Fig. 4). However, even at 84 days after planting N-fertilized plants had not taken up all the N applied with the fertilizer. Total P-content in plants increased in P-fertilized plants, due to both a higher tissue concentration and a higher dry mass accumulation (Fig. 5). It is interesting to note that N-content was higher with P-fertilization than with N-fertilization. As P-treatments increased N-concentration and also plant dry mass, P-fertilization increased total N-content (Fig. 3) and therefore N uptake, even in soils, like the red sand and loamy sand, which are very low in N-content (Table 1). Therefore, although they were not supplied with N, plants fertilized with P were able to extract more N from the soil than even plants fertilized with N. Increased uptake of soil N in P-fertilized plants was probably not due to indirect effects of P on soil N mineralization, since soil contents of nitrate and ammonium were quite similar in the soil solution of the loamy sand with or without P-fertilization. Furthermore, increased N absorption was not due to higher soil exploration or higher leaf demand, because the largest increase in leaf nutrients was at 44 DAT, before the increase in growth of both leaves and roots that occurred 72 DAT.

In *E. grandis* × *E. urophylla* plantations fertilization with P did not increase N-concentration in leaves but increased N-accumulation per hectare four-fold because of increased growth (Xu et al., 2002). The greater N-uptake with the application of only P is a factor to be considered in silvicultural plans. The effects of fertilization at planting may continue to harvest (Schönaue, 1977), therefore, if the uptake of higher amounts of

N in P-fertilized stands continues through time, this could reduce soil N stocks (Laclau et al., 2000). The higher N extraction at harvest could affect the sustainability of forest soil productivity (Fisher and Binkley, 2000). Thus, it is necessary to carry out longer term experiments in order to study the changes in soil nutrient stocks as affected by fertilization with P.

5. Conclusions

N and P-fertilization affect growth to different extents depending on soil characteristics. However, the chemical analysis of soils alone does not allow prediction of the effects of fertilization. This is because interactions are complex and when a nutrient is supplied, luxury consumption of some elements can make other elements limiting.

P-fertilization increased growth more than N-fertilization in the three soils used, in spite of the low natural N-concentration of the red sand and the loamy sand. In the three soils, the extraction of N from the soil increased substantially in P-fertilized plants, which accumulated more N even than plants fertilized with N.

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References

- Barros, N.F., Novais, R.F., Neves, J.C.L., 1990. Fertilização e correção do solo para o plantio de eucalipto. In: Barros, N.F., Novais, R.F. (Eds.), *Relação solo-eucalipto*. Editora Folha de Viçosa, pp. 106–127.
- Cromer, R.N., 1996. Silviculture of eucalypt plantations in Australia. In: Attiwill, P.M., Adams, M.A. (Eds.), *Nutrition of Eucalypts*. CSIRO Publishing, pp. 259–273.
- Cromer, R.N., Jarvis, P.G., 1990. Growth and biomass partitioning in *Eucalyptus grandis* seedlings in response to nitrogen supply. *Aust. J. Plant Physiol.* 17, 503–515.
- Cromer, R.N., Cameron, D.M., Rance, S.J., Ryan, P.A., Brown, M., 1993. Response to nutrients in *Eucalyptus grandis*. 1: Biomass accumulation. *Forest Ecol. Manage.* 62, 211–230.
- Dalla Tea, F., Marcó, M., 1996. Fertilizers and eucalypt plantations in Argentina. In: Attiwill, P., Adams, M. (Eds.), *Nutrition of Eucalypts*. CSIRO Publishing, pp. 327–333.
- Dighton, J., Jones, H.E., Poskitt, J.M., 1993. The use of nutrient bioassays to assess the response of *Eucalyptus grandis* to fertilizer application. 1: Interaction between nitrogen, phosphorus and potassium in seedling nutrition. *Can. J. Forest Res.* 23, 1–6.
- Fernandez, J.Q.P., Dias, L.E., Barros, N.F., Novais, R.F., Moraes, E.J., 2000. Productivity of *Eucalyptus camaldulensis* affected by rate and placement of two phosphorus fertilizers to a Brazilian Oxisol. *Forest Ecol. Manage.* 127, 93–102.
- Fisher, R., Binkley, D., 2000. *Ecology and Management of Forest Soils*. John Wiley and Sons Inc., 489 pp.
- Goya, J.F., Frangi, J.L., Dalla Tea, F., 1997. Relación entre biomasa aérea, área foliar y tipos de suelos en plantaciones de *Eucalyptus grandis* del NE de Entre Ríos, Argentina. *Revista de la Facultad de Agronomía, La Plata* 102, 11–21.
- Graciano, C., Guimet, J.J., Goya, J.F., 2005. Impact of nitrogen and phosphorus fertilization on drought responses in *Eucalyptus grandis* seedlings. *Forest Ecol. Manage.* 212, 40–49.
- Greenberg, A.E., Trussell, R.R., Clesceri, L.S. (Eds.), 1985. *Standard Methods. For the Examination of Water and Wastewater*, American Public Health Association, American Water Works Association and Water Pollution Control Federation.
- Grove, T.S., Thomson, B.D., Malajczuk, N., 1996. Nutritional physiology of Eucalypts: uptake, distribution and utilization. In: Attiwill, P.M., Adams, M.A. (Eds.), *Nutrition of Eucalypts*. CSIRO Publishing, pp. 77–108.
- Harrison, R.B., Reis, G.G., Reis, M.D.G.F., Bernardo, A.L., Firme, D.J., 2000. Effect of spacing and age on nitrogen and phosphorus distribution in biomass of *Eucalyptus camaldulensis*, *Eucalyptus pellita* and *Eucalyptus urophylla* plantations in southeastern Brazil. *Forest Ecol. Manage.* 133, 167–177.
- Herbert, M.A., 1983. The response of *Eucalyptus grandis* to fertilising with nitrogen, phosphorus, potassium and dolomitic lime on a Mispah soil series. *Suid-Afrikaanse Bosbouydskif* 124, 4–12.
- Herbert, M.A., 1990. Fertilizer/site interactions on the growth and foliar nutrient levels of *Eucalyptus grandis*. *Forest Ecol. Manage.* 30, 247–257.
- Herbert, M.A., 1996. Fertilizer and eucalypt plantations in South Africa. In: Attiwill, P.M., Adams, M. (Eds.), *Nutrition of Eucalypts*. CSIRO Publishing, pp. 303–325.
- Judd, T.S., Attiwill, P.M., Adams, M., 1996a. Nutrient concentrations in *Eucalyptus*: a synthesis in relation to differences between taxa, sites and components. In: Attiwill, P.M., Adams, M. (Eds.), *Nutrition of Eucalypts*. CSIRO Publishing, pp. 123–153.
- Judd, T.S., Bennett, L.T., Weston, C.J., Attiwill, P.M., Whiteman, P.H., 1996b. The response of growth and foliar nutrients to fertilizers in young *Eucalyptus globulus* (Labill.) plantations in Gippsland, southeastern Australia. *Forest Ecol. Manage.* 82, 87–101.
- Kirschbaum, M.U.F., Tompkins, D., 1990. Photosynthetic responses to phosphorus nutrition in *Eucalyptus grandis* seedlings. *Aust. J. Plant Physiol.* 17, 527–535.
- Kirschbaum, M.U.F., Bellingham, D.W., Cromer, R.N., 1992. Growth analysis of the effect of phosphorous nutrition on seedlings of *Eucalyptus grandis*. *Aust. J. Plant Physiol.* 55–66.
- Knight, P.J., Nicholas, I.D., 1996. Eucalypt nutrition: New Zealand experience. In: Attiwill, P.M., Adams, M.A. (Eds.), *Nutrition of Eucalypts*. CSIRO Publishing, pp. 275–302.
- Koerselman, W., Meuleman, A.F.M., 1996. The vegetation N:P ratio: a new tool to detect the nature of nutrient limitation. *J. Appl. Ecol.* 33, 1441–1450.
- Laclau, J.-P., Bouillet, J.-P., Ranger, J., 2000. Dynamics of biomass and nutrient accumulation in a clonal plantation of *Eucalyptus* in Congo. *Forest Ecol. Manage.* 128, 181–196.
- Lambers, H., Chapin III, F.S., Pons, Y.L., 1998. *Plant Physiological Ecology*. Springer-Verlag, 540 pp.
- Luh Huang, C., Schulte, E., 1985. Digestion of plant tissue for analysis by ICP emission spectroscopy. *Commun. Soil Sci. Plant Anal.* 16, 943–958.
- Madeira, M.V., Fabiao, A., Pereira, J.S., Araújo, M.C., Ribeiro, C., 2002. Changes in carbon stocks in *Eucalyptus globulus* Labill. plantations induced by different water and nutrient availability. *Forest Ecol. Manage.* 171, 75–85.
- Mc Laughlin, M.J., 1996. Phosphorous in Australian forest soil. In: Attiwill, P.M., Adams, M.A. (Eds.), *Nutrition of Eucalypts*. CSIRO Publishing, pp. 1–30.
- Neves, J.C.L., Gomes, J.M., Novais, R.F., 1990. Fertilização mineral de mudas de Eucalipto. In: Barros, N.F., Novais, R.F. (Eds.), *Relação solo-eucalipto*. Editora Folha de Viçosa, pp. 99–126.
- Sands, P.J., Cromer, R.N., Kirschbaum, M.U.F., 1992. A model of nutrient response in *Eucalyptus grandis* seedlings. *Aust. J. Plant Physiol.* 459–470.

- Schönau, A.P.G., 1977. Initial responses to fertilizing *Eucalyptus grandis* at planting are sustained until harvesting. Suid-Afrikaanse Bosbouydskif 100, 72–80.
- Sheriff, D.W., Nambiar, E.K.S., 1991. Nitrogen nutrition, growth and gas exchange in *Eucalyptus globulus* Labill. seedlings. Aust. J. Plant Physiol. 18, 37–52.
- Sokal, R., Rohlf, F., 1979. In: Blume, H. (Ed.), Biometria. Primera edición español ed.
- Tabatabai, M., Bremner, J., 1991. Automated instruments for determination of total carbon, nitrogen and sulfur in soils by combustion techniques. In: Soil Analysis, Modern Instrumental Techniques, second ed. Marcel Dekker Inc., pp. 261–286.
- Xu, D., Dell, B., Malajczuk, N., Gong, M., 2002. Effects of P fertilisation on productivity and nutrient accumulation in a *Eucalyptus grandis* × *E. urophylla* plantation in southern China. Forest Ecol. Manage. 161, 89–100.