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Influence of nitrogen and potassium fertilization on leaf lifespan and allocation of above-ground growth in *Eucalyptus* plantations

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Summary *Eucalyptus grandis* (W. Hill ex Maiden) leaf traits and tree growth were studied over 3 years after the establishment of two adjacent complete randomized block designs in southern Brazil. In a nitrogen (N) input experiment, a treatment with the application of 120 kg N ha^{-1} was compared to a control treatment without N addition, and in a potassium (K) input experiment a control treatment without K addition was compared to a treatment with the application of 116 kg K ha^{-1}. Young leaves were tagged 9 months after planting to estimate the effect of N and K fertilizations on leaf lifespan. Leaf mass, specific leaf area and nutrient concentrations were measured on a composite sample per plot every 28 days until the last tagged leaf fell. Successive inventories, destructive sampling of trees and leaf litter fall collection made it possible to assess the effect of N and K fertilization on the dynamics of biomass accumulation in above-ground tree components. Whilst the effects of N fertilization on tree growth only occurred in the first 24 months after planting, K fertilization increased the above-ground net primary production from 4478 to 8737 g m^{-2} over the first 36 months after planting. The average lifespan of tagged leaves was not modified by N addition but it increased from 111 to 149 days with K fertilization. The peak of leaf production occurred in the second year after planting (about 800 g m^{-2} $year^{-1}$) and was not significantly modified ($P < 0.05$) by N and K fertilizations. By contrast, K addition significantly increased the maximum leaf standing biomass from 292 to 528 g m^{-2}, mainly as a consequence of the increase in leaf lifespan. Potassium fertilization increased the stand biomass mainly through the enhancement in leaf area index (LAI) since growth efficiency (defined as the ratio between woody biomass production and LAI) was not significantly modified. A better understanding of the physiological processes governing the leaf lifespan is necessary to improve process-based models currently used in *Eucalyptus* plantations.

Keywords: biomass, Brazil, eucalypt, fertilizer, leaves, longevity, partitioning.

Introduction

Essential biogeochemical processes in terrestrial ecosystems are driven by leaf canopy dynamics. Plants invest photosynthates and mineral nutrients in the construction of leaves, which in return produce photosynthates over their lifetimes (Hikosaka 2005). Leaf traits have been intensively studied because they influence nutrient requirements and carbohydrate allocation within plant components to a great extent (Hikosaka 2005, Vincent 2006). In natural ecosystems, a meta-analysis spanning 2548 species showed a coordination of key leaf traits that is consistent across major plant functional types, growth forms and biomes (Wright et al. 2004). Maximum assimilation rates are usually negatively correlated to leaf lifespan (Reich et al. 1991, Gower et al. 1993), mainly because a longer leaf lifespan requires a structural reinforcement of the leaf that negatively affects photosynthesis rates (Wright et al. 2004, Niinemets et al. 2007). A general feature in nutrient-limited environments is a long leaf lifespan (Aerts and Chapin 2000), which is an efficient way of increasing nutrient conservation within leaf biomass and nutrient use efficiency (Escudero et al. 1992, Cordell et al. 2001). However, the possibilities for the conservation

of mobile nutrients through a long leaf lifespan are likely to be constrained by the accumulation of non-mobile nutrients in old foliage, which can either immobilize a scarce resource or cause toxicity (Aphalo et al. 2002).

A decrease in leaf lifespan has been observed by physiologists in response to shortages in nutrients, which is contradictory to the overall trend observed in natural ecosystems (e.g., Ono et al. 1996, Hanaoka et al. 2002). Leaf senescence progresses in an age-dependent manner but the symptoms of senescence are also induced by environmental factors such as shading or water shortage (Noodén et al. 1997, Vincent 2006). Expression analysis of the genes that are upregulated during senescence has highlighted the complexity of the processes involved (Yoshida 2003). Source–sink relationships within plants influenced by nutrient availability are likely to affect leaf lifespan considerably (Ono et al. 2001, Hikosaka 2005), even though nutrient deficiencies are not central components of senescence programmes (Noodén et al. 1997). Contradictory effects of fertilizer addition on leaf lifespan have been reported in forest ecosystems. A general trend of reduction in leaf lifespan has been observed after nitrogen (N) fertilization for various tree species (e.g., Ackerly and Bazzaz 1995, Balster and Marshall 2000, Cordell et al. 2001, Amponsah et al. 2005) but an increase in leaf lifespan with nutrient availability was reported in other studies (Kanazawa and Sato 1986, Gholz et al. 1991, Basile et al. 2003).

Concerns about water requirements of fast-growing *Eucalyptus* plantations in various parts of the world led to the development of models to predict the effects of climate variables, nutrient supply and silvicultural management on stand productivity and water use (Whitehead and Beadle 2004). Canopy dynamics are key components of these models based on radiation transfer and physiological processes regulating photosynthesis, transpiration and carbon allocation. The effects of N and phosphorus (P) fertilizer applications on biomass production, photosynthetic parameters and chemical contents of leaves have been extensively studied in *Eucalyptus* forests (Smethurst et al. 2003, Stape et al. 2004, Whitehead and Beadle 2004, Du Toit and Dovey 2005, England and Attiwill 2008), but only few studies have been undertaken on the respective effects of leaf production and leaf lifespan on the increment in leaf area after fertilizer application. Most studies have focused on N and P because those nutrients are involved in basic physiological processes related to photosynthesis and energy transfer within leaves, and they limit plantation productivity in many regions (e.g., Saur et al. 2000, Close et al. 2004). Despite the huge influence of potassium (K) fertilization on *Eucalyptus* growth in tropical plantations, little information is available on the consequences of K addition for foliar dynamics and growth efficiency (GE) (Beadle 1997, Binkley et al. 2004). The aim of this study was to test the hypothesis that N and K fertilizer additions increased leaf lifespan and that this pattern was likely to modify leaf production, leaf turnover rate and tree growth in *Eucalyptus grandis* (W. Hill ex Maiden) plantations.

Materials and methods

Study area

The study was carried out at the Itatinga Experimental Station (University of São Paulo) on a 68 ha experimental watershed (23°02′ S and 48°38′ W) covered with eucalypts. The mean annual rainfall over the 15 years before this study was 1360 mm and the mean annual temperature was 19 °C, with a seasonal cold period from June to September (Figure 1). The relief was typical of the western plateau of São Paulo, with a gentle wavy topography. The experiment was located on a hilltop (slope < 3%) at an altitude of 850 m. The soils were very deep Ferralsols (> 15 m) developed on Cretaceous sandstone, Marília formation, Bauru group, with a clay content ranging from 14% in the A_1 horizon to 23% in deep soil layers. The mineralogy was dominated by quartz, kaolonite and oxyhydroxides, with acidic soil layers (pH between 4.5 and 5) containing very small amounts of available nutrients (sum of base cations < 0.3 $mmol_c\ kg^{-1}$, between the depths of 5 cm and 6 m).

Experimental design

The experiment was set up in a *Eucalyptus saligna* (Sm.) stand conducted as a coppice, without any fertilizer application from 1940 to 1997. Herbicide was applied on the stumps to prevent regrowth and *E. saligna* seedlings were planted in 1998 with a limited fertilizer supply (300 kg ha^{-1} NPK 10:20:10). High levels of nutrient exports with the boles, without fertilization from 1940 to 1998, made the area suitable to expect a eucalypt response to fertilizer inputs.

The *E. saligna* stand was harvested at age of 6 years (February 2004), and herbicide was applied on the stumps. Boles were removed from the site and harvesting residues were uniformly distributed. The *E. grandis* seedlings genetically improved by the Suzano Company (half-sib seeds) were planted in April 2004 between the stumps of the previous rotation, maintaining the same planting density (spacing 2 m × 3 m). Two complete randomized block designs were installed simultaneously in that plot with the same germplasm: one to assess the effect of N fertilization on tree growth and leaf lifetime, and the other to assess the effect of K fertilization on the same parameters. They were adjacent and located in the same topographical position.

N experiment Five treatments were installed in six blocks (100 trees per plot) to study the influence of N inputs on nutrient cycling in *E. grandis* ecosystems, but this study focused only on two treatments:

T_1: Control with no N input (−N).

T_2: 120 kg N ha^{-1} applied (+N) with ammonium sulphate fertilizer. Most Brazilian forest companies

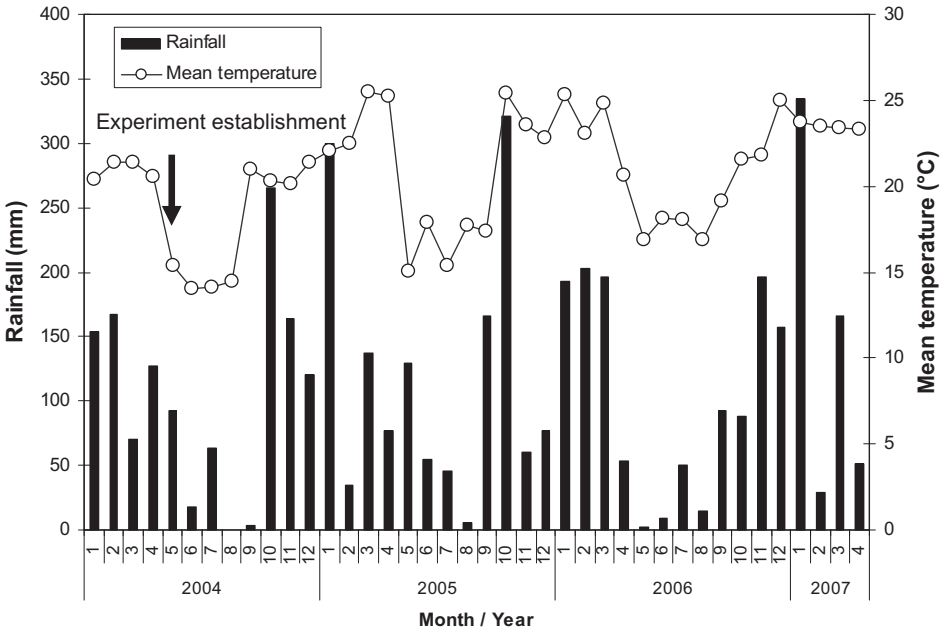

Figure 1. Monthly rainfall and mean air temperature over 3 years after installation of the experimental plantations at the Itatinga experimental station.

apply around 100 kg N ha^{-1} in deep Ferralsols, and N fertilization is usually split into three to four applications. In this study, a quarter of the total amount was applied at planting (buried 20 cm from the seedlings), then at 6 months (broadcast beneath the crowns) and at 12 months and 18 months of age (broadcast over the entire area).

All seedlings received standard commercial-plantation fertilization, which was non-limiting for this soil type (33 kg P ha^{-1}, 100 kg K ha^{-1} and 2 t ha^{-1} of dolomitic lime and micronutrients). Fertilizers were only applied at planting, except KCl which was split in both treatments: a quarter of the total amount was applied at planting, then at 6, 12 and 18 months of age.

K experiment Seven treatments were installed in four blocks (81 trees per plot) to study the influence of K and Na inputs on nutrient cycling in *E. grandis* ecosystems. Our study focused on two treatments:

T_1: Control with no K input (−K).
T_2: 116 kg K ha^{-1} applied (+K) with KCl fertilizer. About 120 kg K ha^{-1} is conventionally applied in the commercial plantations of the region. A third of the total amount was applied at planting (buried 20 cm from the seedlings), then at 6 months (broadcast beneath the crowns) and 12 months of age (broadcast over the entire area).

All seedlings received the same N, P, micronutrient and lime inputs as in treatment T_2 of the N experiment. Fertilizers were only applied at planting, except N which was split in both treatments: a third of the total amount was applied at planting, then at 6 and 12 months of age.

Leaf tagging

Young *E. grandis* leaves were tagged in 12 plots (two treatments × three blocks × two experiments). A short plastic strip was carefully attached at the bottom of the petiole of selected leaves on a subset of 18 trees per plot, 9 months after planting (two buffer rows excluded). Leaves about 1 cm in length were tagged in full-sun positions, at the end of the 17th to the 25th first-order branches (counting from the tree apex). That set of branches was chosen to obtain enough leaves in a full-sun position at the beginning of the experiment. Subsequent observations showed that leaves were tagged on average 4 days after emergence. The number of tagged leaves per branch was counted on the day the tags were installed (t_0 = 9 months after planting), then every 28 days up to when the last tagged leaf fell. All the branches were numbered and two leaves were collected from one branch per tree on each sampling date. Overall sampling was designed to collect the same number of leaves from each position on the branches in the canopy on each date in each plot, except at the end of the sampling period when the number of tagged leaves remaining on the trees was too small. On average, about four leaves per branch were tagged and it was assumed that their removal had no effect on the lifespan of other tagged leaves on the branch. A composite sample per plot of tagged leaves was made upon each observation date (t_0, t_0+28 days, t_0+56 days and so on) to measure leaf mass, specific leaf area (SLA) and nutrient concentrations. Leaves were scanned immediately after collection and dried at 65 °C to constant weight, to assess the SLA of one composite sample per plot. The leaves that died before full-expansion were excluded from the calculation of the mean leaf lifespan. Leaf lifespan was considered as the number of days from leaf emergence

to leaf fall and was assessed for the pool of tagged leaves counted at $t_0 + 28$ days (already fully expanded) in each plot.

Leaf samples were ground to pass through a 2-mm mesh stainless steel screen. Nitrogen was determined using the Kjeldahl method (TE036/1, Tecnal, Brazil), after digestion in sulphuric acid. Phosphorus was determined by colorimetry (U2001, Hitachi Instruments, USA), calcium and magnesium by atomic absorption spectrophotometry (AAnalyst 100, Perkin Elmer, USA) and K by flame emission spectrophotometry (B462, Micronal, Brazil), after digestion in nitric and perchloric acids (Malavolta et al. 1989).

Biomass and litter fall sampling

Leaf biomass and total above-ground biomass were sampled annually at the end of the rainy season. The circumference at breast height and tree height were measured excluding two buffer rows in each plot (36 and 25 trees per plot measured in the N and K experiments, respectively) at ages 4, 6, 9, 12, 18, 24, 30 and 36 months.

Biomass partitioning, including leaf biomass, was estimated by sampling 10 trees distributed over the range of basal areas in both treatments of the N experiment, at 12, 24 and 36 months after planting (60 trees sampled). Eight trees per treatment were sampled at the same ages in the K experiment (48 trees sampled). The trees were separated into components: leaves, living branches, dead branches, stemwood and stembark. The fresh mass of each tree component was measured in the field (± 20 g). The crown of the trees was divided into two parts (upper and lower) in both experiments at ages 12 and 24 months, and into three parts (upper, medium and lower) at age 36 months. Subsamples of each component were dried at 65 °C to constant weight. Thirty leaves randomly selected in each part of the sampled tree foliage were scanned immediately after collection and dried at 65 °C to estimate the biomass and the SLA of the crown part. A specific programme was developed to measure the areas of the sampled leaves and was calibrated for the scanner used. Biomass models were established for each component between the ages of 12 and 36 months and applied to the inventories to estimate biomass on a per square metre basis.

Litter fall was collected every 28 days in 12 plots (two treatments × three blocks × two experiments) up to age 36 months, from five litter-traps (52 cm × 52 cm) systematically located in each plot to representatively sample different distances from the trees (15 traps per treatment). The samples were dried at 65 °C to constant weight. Litter fall exclusively constituted leaves up to age 36 months, because the bark and dead branches remained on the stems.

Leaf production and above-ground net primary production

Leaf biomass production ($P_{i,j,k}$) from age i months to age j months in plot k was calculated using

$$P_{i,j,k} = B_{j,k} - B_{i,k} + L_{i,j,k}, \quad (1)$$

where $B_{i,k}$ and $B_{j,k}$ are the standing leaf biomass at i and j months after planting in plot k, respectively, and $L_{i,j,k}$ is the mass of leaves in litter fall over the same period.

Above-ground net primary production ($\mathrm{ANPP}_{i,j,k}$) was assessed using

$$\mathrm{ANPP}_{i,j,k} = \sum_l I_{l,k} + L_{i,j,k}, \quad (2)$$

where $I_{l,k}$ was the biomass increment from age i months to age j months of component l in plot k, assessed from repeated biomass sampling above-ground.

The contribution of leaf production to $\mathrm{ANPP}_{i,j,k}$ was assessed using

$$A_{i,j,k} = P_{i,j,k}/\mathrm{ANPP}_{i,j,k}, \quad (3)$$

where $A_{i,j,k}$ was the proportion of above-ground dry matter produced from age i months to age j months in plot k allocated to the leaf compartment.

Stand GE was defined as the periodic increment in above-ground woody biomass (mass of the stem wood + bark and branches) per unit leaf area (Waring 1983).

Leaf lifespan and leaf turnover

The lifespan of tagged leaves (S) was estimated using

$$S = (t_S - t_0) + 4 + 14, \quad (4)$$

where t_s was the date of the last observation before leaf shed, t_0 was the date of tagging, 4 was the mean number of days between leaf emergence and leaf tagging and 14 was half of the number of days between two successive leaf counts (28 days).

Leaf turnover was also estimated, between 12 and 36 months after planting, using

$$T_{12,36,k} = \frac{3}{2}\frac{P_{12,36,k}}{(B_{12,k} + B_{24,k} + B_{36,k})}, \quad (5)$$

where $T_{12,36,k}$ was the mean leaf turnover from age 12 months to age 36 months in plot k. The mean leaf lifespan was then estimated as the inverse of the mean turnover rate. This method was not used in the first 12 months after planting because leaf biomass was not measured often enough to estimate the mean value.

Statistical analysis

Differences in tree and stand characteristics between treatments and blocks were tested at each age with SAS using a two-way analysis of variance (ANOVA). Homogeneity of variances was tested at each age by Levene's test and original values were log-transformed when variances were unequal. The probability level used to determine significance was $P < 0.05$; ANOVA was performed on percentage values after data transformation to normalize the distributions.

Biomass equations were of the following form:

$$\text{Linear model: } Y_{m,n} = c_n + b_n X_m + \varepsilon_{m,n}$$

$$\text{Nonlinear model: } Y_{m,n} = c'_n + b'_n X_m^{d'_j} + \varepsilon'_{m,n},$$

where $Y_{m,n}$ was the dry matter of tree m for a given component n; X_m was the independent variable (either D, D^2 or D^2H; D and H were, respectively, the diameter at breast height and the total tree height); c_n, b_n, d_n and c'_n, b'_n, d'_n were the parameters to be estimated; $\varepsilon_{i,j}$ and $\varepsilon'_{i,j}$ were the residual variations not explained by the models. Observations were assumed to be uncorrelated: trees from the same stand were cut as far as possible from each other, and thus had reduced potential competition between them, in the inner buffer row of the K experiment and in two blocks installed especially in the N experiment to perform destructive sampling throughout the rotation. The equations were fitted for each tree component by treatment at each age. Fittings were performed using PROC NLP of the SAS software (SAS Institute 1990) and maximum likelihood estimations were used to select the individual models per treatment and per age or a global model for the two treatments of each experiment at each age (see Sicard et al. 2006, for details). Final models were applied to the stand inventory at each age to assess the biomass of each component.

Results

Influence of fertilization on tree growth

Height growth was significantly enhanced by N application ($P < 0.05$) in the first 24 months after planting (Figure 2A). However, tree response to N fertilization was limited. The difference in mean height between the two treatments was about 0.6 m up to age 24 months, and tree response to N addition was no longer significant from age 24 months onwards. In contrast, a large response to K fertilization was observed (Figure 2B). Potassium addition led to an increment in tree height of 3.7 m at age 36 months.

Nitrogen and K fertilization enhanced the above-ground biomass of the stand 12 months after planting by 50% and 118%, respectively (Table 1). The above-ground biomass was similar in the control treatments of the two experiments at age 12 months (393 and 412 g m^{-2} in the −N and −K treatments, respectively). However, the two fertilizers led to large differences in the subsequent growth of the stands. Whereas the accumulation of above-ground biomass in the control treatment without N addition was no longer significantly different ($P < 0.05$) from the commercial N application at age 36 months, K application led to above-ground biomass accumulation that was twice as high as in the control treatment 24 and 36 months after planting.

Traits of leaves produced on 9-month-old trees

The mean leaf lifespan for the commercial fertilizer inputs (+N and +K) was about 140–150 days in both

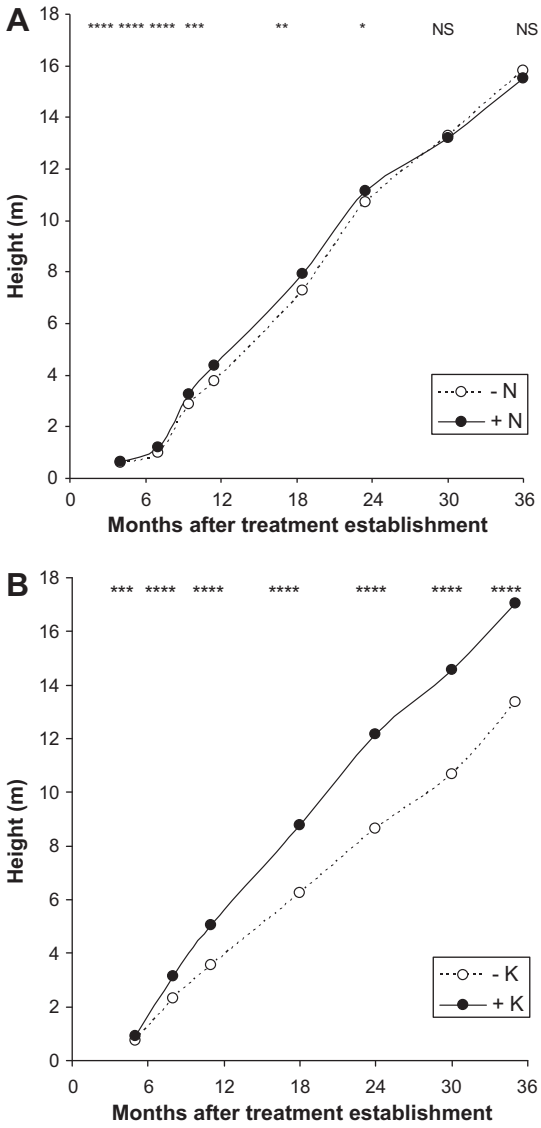

Figure 2. Tree growth over 3 years after the establishment of the N experiment (A) and the K experiment (B). Significant differences at each age are indicated by $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, $****P < 0.0001$. NS, differences were not significant at $P < 0.05$.

experiments (Figure 3). However, a broad lifespan range was observed and the last tagged leaves were shed about 250 days after emergence. Nitrogen fertilization had little effect on leaf mortality over the study period. By contrast, K application was found to have a significant effect, with a reduction in the mean leaf lifespan of 38 days in the absence of K. A steady leaf shed rate of about 25% every 50 days of ageing was observed from 50 to 250 days after emergence with K fertilization, whereas about 50% of tagged leaves were shed between 50 and 100 days after emergence without K input.

Leaf dry mass was not modified by N addition, whatever be the sampling age, and remained stable at around 0.35 g $leaf^{-1}$, up to leaf senescence (Figure 4A). Small

Table 1. Influence of N and K fertilization on the accumulation of above-ground biomass, annual litter fall, ANPP, GE and average leaf lifespan over the first 3 years of growth. Above-ground biomass and ANPP are given in g m^{-2} $year^{-1}$, litter fall in g m^{-2} $year^{-1}$ and GE in g m^{-2} $year^{-1}$ LAI^{-1}. Standard deviations between blocks are indicated ($n = 3$). Different letters in the same row within the same experiment indicate significant differences ($P < 0.05$).

	N experiment		K experiment	
	−N	+N	−K	+K
First year after planting: biomass at age 12 months				
Leaf	137 ± 18 a	197 ± 7 b	97 ± 17 a	212 ± 8 b
Branch	141 ± 24 a	230 ± 11 b	209 ± 21 a	362 ± 8 b
Stem	116 ± 21 a	195 ± 10 b	109 ± 24 a	324 ± 12 b
Total above-ground	393 ± 63 a	622 ± 28 b	412 ± 61 a	898 ± 28 b
Litter fall	91 ± 33 a	134 ± 21 a	70 ± 4 a	115 ± 8 b
ANPP	484 ± 95 a	755 ± 32 b	486 ± 65 a	1012 ± 35 b
LAI	2.2 ± 0.2 a	2.7 ± 0.1 b	1.4 ± 0.2 a	3.1 ± 0.1 b
Second year after planting: biomass at age 24 months				
Leaf	473 ± 32 a	474 ± 35 a	292 ± 28 a	528 ± 26 b
Branch	636 ± 41 a	743 ± 49 b	610 ± 53 a	808 ± 33 b
Stem	1806 ± 131 a	2628 ± 188 b	1118 ± 101 a	2763 ± 131 b
Total above-ground	2917 ± 201 a	3844 ± 272 b	2049 ± 182 a	4099 ± 190 b
Litter fall	446 ± 40 a	539 ± 42 a	592 ± 56 a	524 ± 25 a
ANPP	2969 ± 184 a	3744 ± 243 b	2197 ± 155 a	3726 ± 200 b
LAI	4.5 ± 0.3 a	4.7 ± 0.3 a	2.7 ± 0.3 a	5.3 ± 0.3 b
GE	660 ± 12 a	793 ± 17 b	677 ± 38 a	683 ± 28 a
Third year after planting: biomass at age 36 months				
Leaf	325 ± 5 a	335 ± 17 a	215 ± 22 a	518 ± 46 b
Branch	648 ± 13 a	748 ± 38 a	627 ± 64 a	1330 ± 119 b
Stem	3982 ± 69 a	4118 ± 226 a	2359 ± 239 a	5602 ± 501 b
Total above-ground	4955 ± 87 a	5202 ± 281 a	3265 ± 324 a	7450 ± 666 b
Litter fall	671 ± 10 a	699 ± 18 a	551 ± 58 a	648 ± 43 a
ANPP	2730 ± 220 a	2043 ± 160 b	1732 ± 102 a	3999 ± 461 b
LAI	3.0 ± 0.0 a	3.1 ± 0.1 a	2.4 ± 0.2 a	5.5 ± 0.5 b
GE	585 ± 72 a	385 ± 49 b	490 ± 31 a	622 ± 50 a

variations in mean leaf mass among the sampling ages were probably a consequence of the small number of leaves sampled (20–30 leaves per plot at each age except for the last sampling dates, where the number of leaves per plot was ≈ 10). A trend was found for lower leaf mass in the –K treatment than in the +K treatment at most of the sampling ages, but the differences were only significant 32 days after emergence (Figure 4B). Nitrogen application did not significantly modify N contents in the leaves, except at 88 days after leaf emergence (Figure 4C–F), whereas K fertilization led to a significant increase in leaf K contents. Potassium dynamics in the leaves were consistent in all the plots where K fertilizer was applied (+K, −N and +N), with a large increase in K content over the period of leaf expansion, then a decrease in the second month after leaf emergence. The lower accumulation of K in the leaves of the −K treatment was a result of both the lower mass of individual leaves and lower K concentrations.

Neither N nor K fertilization regimes significantly modified the SLAs, irrespective of leaf age. The SLA values decreased from about 15 m^2 kg^{-1} at 4 days after emergence to about 10 m^2 kg^{-1} before leaf shed (data not shown).

Foliage dynamics on a stand level

Foliage biomass Even though N fertilization did not change the main traits (mass, SLA and nutrient contents) of tagged leaves produced on 9-month-old trees, N fertilization increased the standing leaf biomass by 32% at age 12 months (Figure 5A). However, the response to N fertilization was no longer significant from age 24 months onwards.

Potassium fertilization increased the standing leaf biomass by a factor of about two over the study period (Figure 5B). The decrease in fertilization effect on leaf biomass over time observed for N did not occur for K. Canopy closure occurred in the second year after planting and the maximum standing leaf biomass was found 24 months after planting, irrespective of the treatment. A decrease in leaf biomass of about 30% occurred in the third year after planting whatever the treatment in the N experiment, and a decrease in leaf biomass of about 25% occurred in the control treatment of the K experiment. This decrease was only 4% in the +K treatment of the K experiment, although the sampling date was identical in the two experiments at each age.

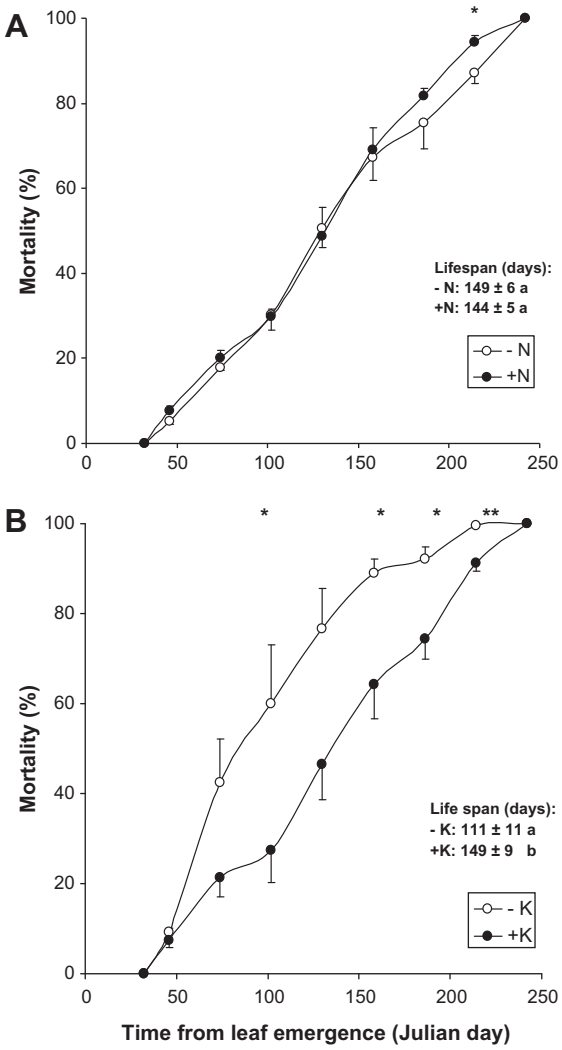

Figure 3. Cumulative mortality of leaves marked at emergence as a function of time since emergence in two treatments of the N experiment (A) and the K experiment (B). Bars represent standard errors between blocks on each observation date ($n = 3$). Significant differences between the cumulated mortalities on each date are indicated by $*P < 0.05$ and $**P < 0.01$. Mean leaf lifespan and standard errors between blocks are indicated for each treatment. Different letters indicate significant differences ($P < 0.05$).

Leaf litter fall Leaf litter fall was not significantly influenced by N fertilization over the study period, except on one date (Figure 6A). The variability between collection months was low in the first 24 months after planting and it increased sharply in the third year of growth. The coefficients of variation for the mass of leaf litter fall between the collection months were about 40% up to 24 months of age and 70% in the third year of growth in both treatments. A sharp increase in leaf litter fall occurred in the middle of the summer in the third year after planting.

A similar pattern of increased variability between collection months with stand age was observed in the K experiment (Figure 6B). The coefficients of variation for the mass of leaf litter fall were 43% up to age 24 months and 88% in the third year of growth in the +K treatment. The lack of K fertilization led to much higher coefficients of variation between the collection months: 72% and 123% up to age 24 months and in the third year of growth, respectively. Significant differences in leaf litter biomass between the two treatments of the K experiment were found for 5 collection months over the study period.

Despite large differences in the time course of leaf litter fall between treatments, the cumulated amounts of leaf litter fall ranged from 12.1 to 12.9 Mg ha^{-1} over 36 months after planting and were less modified by K and N fertilizations (Table 1).

Foliage production and leaf lifespan Nitrogen fertilization did not significantly modify foliage production (Eq. (1)) over the study period, but leaf production was significantly enhanced by K addition in the first and the third years of growth (Figure 5C and D). However, K fertilization increased the standing leaf biomass much more than leaf production. Leaf biomass production was only enhanced by 13% and 29% in the second and the third years after planting, respectively, whereas standing leaf biomass was doubled by K fertilization. The area of leaf produced was enhanced in the same proportion as leaf biomass by K addition (SLA not significantly modified).

Leaf lifespan assessed from repeated sampling of foliage biomass and litter fall monitoring was consistent with the results obtained from the leaves tagged 9 months after planting: K fertilization increased leaf lifespan significantly, but N addition did not influence leaf lifespan (Table 2). The mean leaf lifespan in the −K treatment was 117 days between 12 and 36 months after planting and about 78% longer in the +K treatment (208 days). Leaf turnover was about 2 $year^{-1}$ with K fertilization and 3 $year^{-1}$ in the –K treatment.

ANPP and GEs

Nitrogen and K fertilization enhanced ANPP significantly ($P < 0.05$) in the first 12 months after planting (Table 1). Even though K fertilization no longer had a significant effect on litter fall from age 12 months onwards, the increment in above-ground biomass, which was about twice as high in the +K treatment as in the –K treatment, led to a significant effect of K fertilization on ANPP over the study period. By contrast, the large decrease in biomass increment in the third year after planting in the +N treatment led to a significantly lower ANPP than that in the –N treatment.

The proportion of ANPP allocated to foliage production decreased from 32% in the first year after planting to 16% in the third year of growth in the +K treatment (Figure 5F). In the +N treatment, the low growth observed in the third year after planting was accompanied by a slight increase in the proportion of above-ground biomass allocated to produce leaves. Potassium fertilization significantly reduced the proportion of above-ground biomass allocated to produce leaves in the first 2 years after planting and the

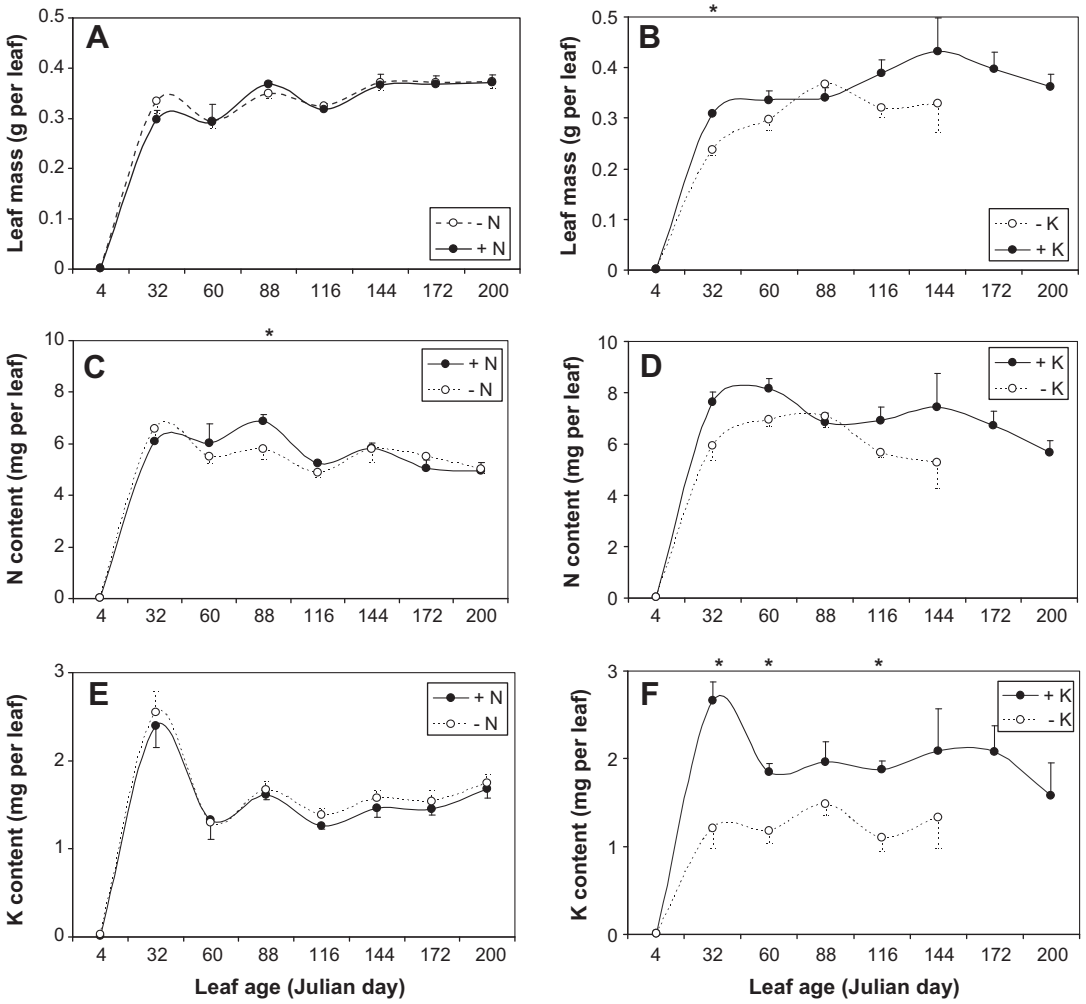

Figure 4. Changes in leaf mass (A), N content (C) and K content (E) with leaf ageing in the N experiment, and changes in leaf mass (B), N content (D) and K content (F) in the K experiment. Bars indicate standard errors ($n = 3$). Significant differences at each age are indicated by $*P < 0.05$.

trend remained unchanged in the third year, even though the differences between treatments were no longer significant. A general upward trend in the proportion of ANPP allocated to foliage production when the growth rate decreased was observed in both experiments.

Growth efficiency ranged from 660 to 793 g m^{-2} $year^{-1}$ LAI^{-1} in the second year after planting and was significantly enhanced by N fertilization (Table 1). However, a sharp decline in GE in the third year of growth in the +N treatment led to a significantly lower GE than that in the –N treatment. Despite a huge effect of K addition on LAI, GE was not significantly affected.

Discussion

Leaf traits

A broad range of leaf lifespans was observed for leaves tagged on 9-month-old trees. Ackerly (1999) showed on saplings of three species of tropical pioneer trees that leaf senescence was primarily a function of the position of a leaf within the canopy, rather than its chronological age. Leaves were tagged at a period of maximum height growth, and self-shading led to a fast upward movement of the bottom of the canopy, which started about 1 year after planting. The LAI dynamics suggest that self-shading among leaves was considerable in these stands, and this had a major influence on leaf senescence (Ackerly and Bazzaz 1995). The influence of the position of tagged leaves on self-shading might, therefore, account for the large variability in leaf lifespan observed.

Mean leaf lifespan values estimated from repeated sampling and litter fall quantification were slightly higher than the estimations from tagged leaves (Table 2; Figure 3). Leaf lifespan in Table 2 might be slightly over-estimated since the mean foliage biomass over each year of growth was probably lower than the estimates used in Eq. (5), calculated from trees sampled every year at the end of the rainy season. In a review on physiological regulation of

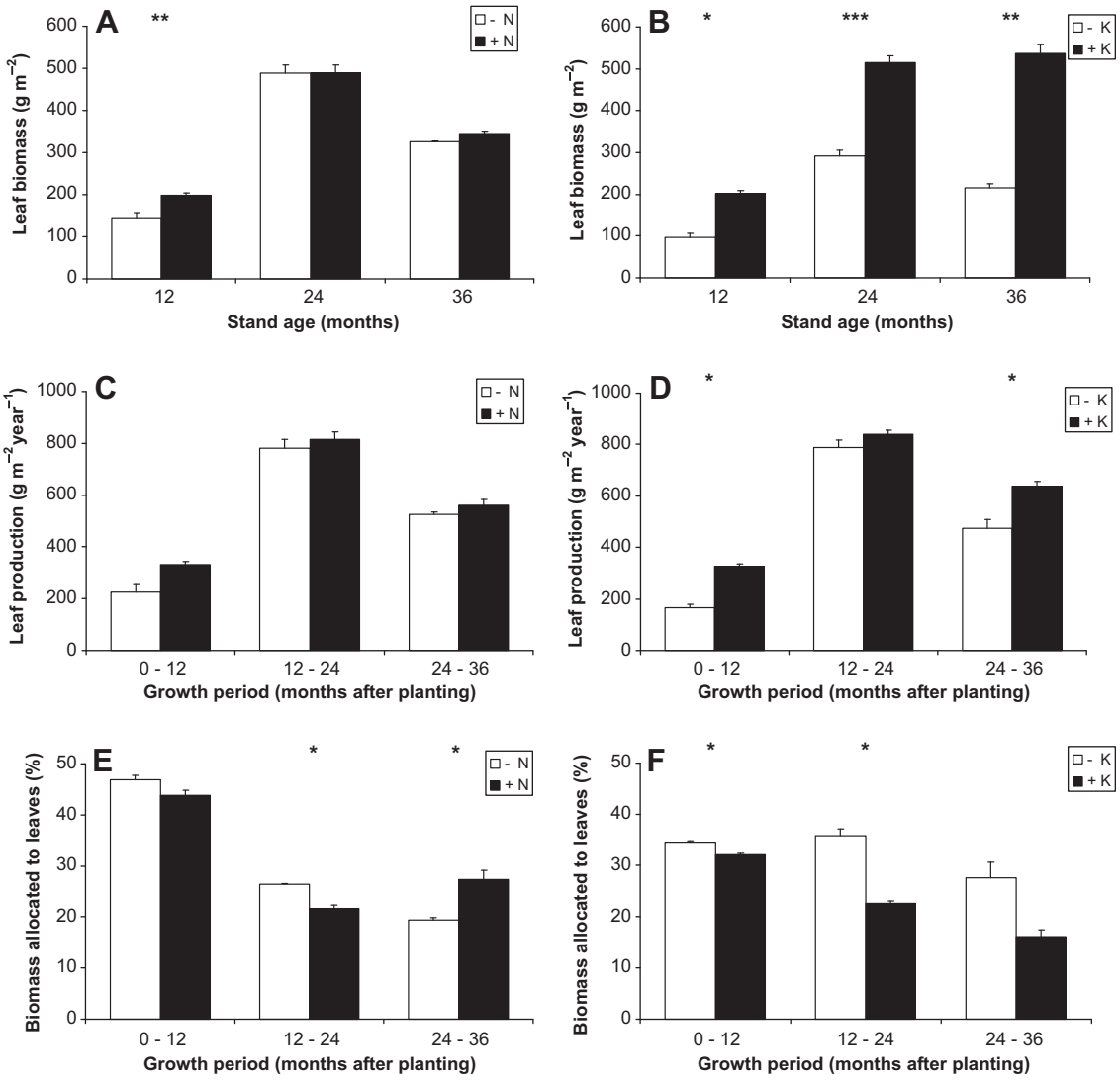

Figure 5. Dynamics of leaf biomass, leaf production and percentage of the above-ground biomass production allocated to leaf production in the N experiment (A, C and E, respectively) and in the K experiment (B, D and F, respectively). Significant differences at each age are indicated by $*P < 0.05$, $**P < 0.01$ and $***P < 0.001$. Bars indicate standard errors between the blocks ($n = 4$ for leaf biomass and $n = 3$ for leaf production and allocation of above-ground biomass to leaf production).

productivity in *Eucalyptus*, Whitehead and Beadle (2004) reported a broad leaf lifespan range, from < 1 up to 3 years. The lifespan of foliage in *Eucalyptus* stands averaged 1.0 year at the end of the rotation in northern Brazil (Stape et al. 2008). A large range of litter fall rates (monthly leaf litter fall divided by foliage biomass) was used to parameterize the 3-PG process-based growth model in commercial *Eucalyptus* plantations (Sands and Landsberg 2002, Dye et al. 2004, Fontes et al. 2006). Mean leaf lifespan calculated as the inverse of the litter fall rate of the 3-PG model was 0.6 year in Brazilian *E. grandis* plantations (Almeida et al. 2004), close to the mean values obtained for fertilization regimes representative of commercial plantations in this study (+N and +K treatments).

The lack of influence of N addition on leaf traits in the present study differs from the results of other studies that showed that nutrient addition on N-poor soil reduced leaf lifespan (Ackerly and Bazzaz 1995, Balster and Marshall 2000, Cordell et al. 2001, Amponsah et al. 2005, Oikawa et al. 2006). This pattern might be explained by a low N deficiency in the present study since N concentrations were less influenced by N fertilization (Figure 4C). Nitrogen fertilization enhanced LAI and above-ground biomass 1 year after planting but the differences between the –N and +N treatments were no longer significant at age 3 years (Table 1). Leaf lifespan was reported, in other studies, to increase with nutrient availability. The mean leaf lifespan of *Leucena leucocephala* (Lam.) in the Philippines varied from 1.7 to 3.5 months for three stands of the same age and the highest leaf lifespan was found at the site with the highest fertility (Kanazawa and Sato 1986). In banana crops, K fertilization has been used for a long time to increase leaf lifespan

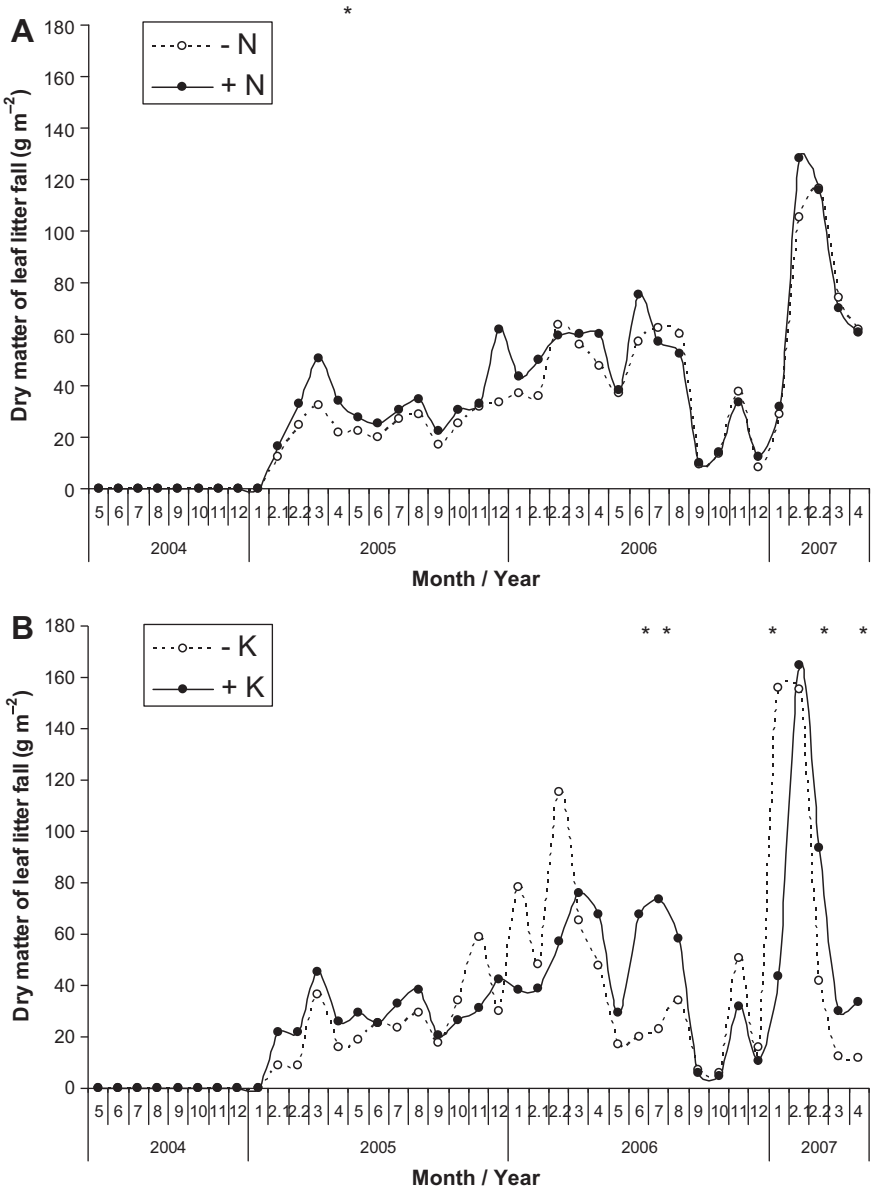

Figure 6. Time course of leaf litter fall since treatment establishment in April 2004 in the N experiment (A) and the K experiment (B). Months 2.1 and 2.2 are indicated because the collection of litter fall every 28 days led to 13 measurement periods per year. Significant differences between treatments ($P < 0.05$) are indicated by *.

Table 2. Influence of N and K fertilization on leaf turnover and mean leaf lifespan from 1 to 3 years after planting. Leaf turnover is given in year^{-1} and leaf lifespan in year. Standard deviations between blocks are indicated ($n = 3$). Different letters in the same row within the same experiment indicate significant differences ($P < 0.05$).

	N experiment		K experiment	
	−N	+N	−K	+K
Leaf turnover	2.10 ± 0.06 a	2.06 ± 0.16 a	3.16 ± 0.41 a	1.77 ± 0.09 b
Leaf lifespan	0.48 ± 0.01 a	0.49 ± 0.04 a	0.32 ± 0.04 a	0.57 ± 0.03 b

but the underlying processes have not been investigated (Teixeira et al. 2001). A positive effect of K fertilization on the leaf lifespan of field-grown almond trees (Basile et al. 2003) and root lifespan of *Hibiscus rosa-sinensis* cv. Leprechaun (Egilla et al. 2001) was also reported. This study showed a positive effect of K addition on *E. grandis* leaf lifespan in highly deficient soils, despite the increase in self-shading resulting from the shift in LAI. One hypothesis to explain this pattern might be that the decline in photosynthetic capacity with leaf age, which drives leaf senescence to maintain the leaves with the highest C gain (Kitajima et al. 2002, Escudero and Mediavilla

2003, Oikawa et al. 2006), was slowed by K addition. Basile et al. (2003) showed a significant increase in photosynthesis rate with K availability for almond trees. The differences in photosynthesis rate between K-deficient and K-fertilized trees greatly increased as the season progressed, suggesting that the effects of K supply on photosynthesis increased with leaf ageing in this deciduous species. They concluded that the major influence of K on leaf photosynthesis may be attributed to a biochemical limitation rather than to stomatal limitation. In our study, conservative values of GE were observed across treatments, whereas a decrease in GE was expected in the +K treatment as a result of a large increase in self-shading. This pattern suggests that K addition enhanced light conversion efficiency to wood production, which might result partly from an improvement in leaf photosynthetic capacity and partly from an increase in the proportion of dry matter allocated to wood production. However, a second hypothesis might be that the low leaf lifespan observed in highly K-deficient soils is a result of stomatal control deterioration. Benlloch-González et al. (2008) showed in olive trees and sunflower plants that moderate K deficiency inhibited water stress-induced stomatal closure. Little information is available in the literature on how K deficiency affects the stomatal control mechanisms, and contradictory results have been found for different species (Cakmak 2005, Benlloch-González et al. 2008). In this study, K deficiency might have damaged stomatal control mechanisms and an increase in the amount of water transpired per unit leaf area would increase tree susceptibility to water stress, leading to a decrease in leaf lifespan and foliage area. Further physiological studies are required to improve our understanding on the effects of K fertilization on leaf lifespan and functioning in *Eucalyptus* plantations.

Nutrient concentrations in fully expanded young leaves have been intensively studied in *Eucalyptus* trees and leaf analyses are currently used to detect deficiencies in commercial *Eucalyptus* plantations (Herbert 1996, Wadt 2004). However, quantitative data on the patterns of nutrient accumulation during leaf development are scarce for *Eucalyptus* trees. Leaves reached full expansion about 1 month after emergence in this study, whereas 3–4 months were reported for other *Eucalyptus* species in Australia (Saur et al. 2000, England and Attiwill 2008, Fife et al. 2008). Changes in the concentrations and the contents of nutrients throughout leaf ageing were similar to the pattern indicated for the other species, except for K (data not shown for P, Ca and Mg). The large decrease in K content observed between the first and the second months after leaf emergence in the +K treatment was not found in the previous studies (Figure 4F). High K concentrations in 1-month-old leaves might increase leaf growth, through enhanced turgor pressure and cell-wall elasticity (Jordan-Meille and Pellerin 2008). Concentrations of K and leaf mass were significantly lower in the –K treatment than in the +K treatment 1 month after emergence, but the large inter-leaf variability led to nonsignificant differences in leaf mass from that age onwards. The peak in K content 1 month after leaf emergence shows the difficulty in using leaf analysis to guide fertilization in *Eucalyptus* plantations, since K concentrations are highly dependent on the age of the sampled leaves. The similar pattern with N content in tagged leaves (Figure 4E), despite 50% more above-ground biomass 12 months after planting in the +N treatment than in the –N treatment, also shows the limits of leaf analyses for *E. grandis* trees.

Leaf litter fall

A singular pattern of leaf litter fall was observed in the two experiments, with a large increase in inter-month variability in the third year after planting which was not a consequence of specific climatic conditions. Monitoring of the soil water content in the N experiment over 4 years down to a depth of 3 m and the installation of probes down to a depth of 10 m at age 3.5 years suggested that the amount of water stored in deep soil layers acted as a buffer in the first 2 years after planting, supplying water requirements during dry periods (unpublished data). The shortage in available water in deep soil layers in the third year after planting might account for the higher variability in leaf litter fall observed. Leaf litter fall might have been used to reduce tree transpiration during the periods when stomatal conductance regulation was not sufficient to match soil water uptake to atmospheric demand (e.g., Pook 1986). Damaged stomatal control mechanisms in the −K treatment might account for the high variability in leaf litter fall observed.

The large amounts of leaf litter fall observed despite a rainfall of 328 mm in January 2007 in the –K treatment showed that factors other than water stress controlled the leaf litter fall in highly K-deficient soils (Figure 1). A similar pattern of high leaf litter fall simultaneously with or following a rapid shoot growth in the spring was also observed on *Eucalyptus maculata* (Hook) trees (Pook 1984). Large amounts of leaf litter fall in the –K treatment after flushes of leaf production might have contributed to keep the limited pool of K in a low biomass of leaves with the highest assimilation rates and stomatal regulation. There are substantial internal retranslocations of K in senescent eucalypt leaves (Fife et al. 2008) and the rapid release of K during litter decay leads to a very active biological cycle (Laclau et al. 2003, 2004).

Above-ground growth

The response to K fertilization increased over 36 months of the study period. Snowdon (2002) proposed the concepts of type 1 and type 2 responses to silvicultural treatments to model the growth of plantation forests. Type 2 responses occur in treatments which result in a long-term change in site properties, whereas type 1 responses advance the stage

of stand development but do not change the inherent productivity of the site. The improvement of N availability during the early growth of eucalypt trees in this study led to a type 1 response. Canopy closure occurred earlier in the plots with N fertilization and competition between the trees for resources reduced the stand growth earlier than in the −N treatment. By contrast, the response to K fertilization seems to be of type 2 with a long-term enhancement of site fertility. This pattern was expected since the growth of *Eucalyptus* plantations in Brazil is primarily limited by K and P availability (Gonçalves et al. 2004).

Trees shifted their allocation patterns throughout the early development stages, giving priority to leaf production when K was highly deficient (Figure 5F). Plasticity in the partitioning of assimilates between above- and below-ground tree compartments is well documented in *Eucalyptus* plantations in response to water and nutrient availability (Giardina et al. 2004, Stape et al. 2004). However, studies showing that nutrient deficiencies increase the proportion of biomass allocated to foliage production are scarce for fast-growing plantations. The decrease in the proportion of dry matter allocated to produce leaves after alleviation of K deficiency in this study was consistent with the sharp decline in the proportion of litter fall in ANPP as ANPP increases, observed by Binkley et al. (2004) in other Brazilian *Eucalyptus* plantations. The significant increase in the proportion of dry matter allocated to leaves in the third year after planting in the treatment with the lowest growth rate in the N experiment (Figure 5E) suggested that this shift in allocation was related to tree growth rates and was not K specific. A similar behaviour was observed in *L. leucocephala* plantations in the Philippines where stem volume increments were negatively correlated with the leaf turnover rate (Kanazawa and Sato 1986). Leaf lifespan plasticity and shifts in allocation patterns between leaves and stem are well documented in response to the light environment (e.g., King 2003, Vincent 2006).

Conflicting results are found in the literature for the effects of fertilization regimes on GE (Amponsah et al. 2005, Du Toit and Dovey 2005). Mean GE values in this study ranged from 6.1 to 7.9 Mg ha^{-1} $year^{-1}$ LAI^{-1} in the second year after planting and were higher than the values reported by Du Toit and Dovey (2005) in *E. grandis* plantations that peaked at 6 Mg ha^{-1} $year^{-1}$ LAI^{-1} in the third year after planting. Despite strong treatment effects on the leaf area and stand growth, GE remained relatively constant in this study and a decrease in GE was observed in the third year after planting, as reported by Du Toit and Dovey (2005). A positive correlation between GE and resource availability has been reported (Binkley et al. 2004). Growth efficiencies calculated from the data given by Stape et al. (2008) were 9.0 and 12.3 Mg ha^{-1} $year^{-1}$ LAI^{-1} in rainfed and irrigated *Eucalyptus* stands respectively, from 3 to 5.5 years after planting. However, other studies showed that GE was not affected by fertilization in *Pinus radiata* D. Don plantations (Rodriguez et al. 2003) and *Eucalyptus* plantations (Cromer et al. 1993).

Conclusions

Above-ground net primary production was multiplied by a factor of 2 by K fertilization for the first 36 months after planting, whereas N fertilization enhanced tree growth only over the first 24 months after planting. The increase in woody biomass production resulting from K fertilization was mainly accounted for by an enhancement of LAI, since GEs were unchanged, but K fertilization also increased the proportion of dry matter allocated to stem growth. The small differences in foliage production between the –K and +K treatments showed that the shift in LAI due to K fertilization was mainly a result of a longer leaf lifespan. A lessening of the decline in photosynthetic capacity with leaf ageing and an improvement in stomatal control mechanisms, leading to a decrease in the amount of water transpired per area of leaf, were put forward to explain the effects of K fertilization on leaf lifespan and stand foliage biomass.

Various process-based models were developed recently as decision support systems and calibrated for commercial *Eucalyptus* plantations in a large range of environments. As the predictions of stand growth are highly sensitive to changes in LAI (Battaglia et al. 1998, Esprey et al. 2004), which is itself very sensitive to changes in the litter fall rate or its reciprocal leaf lifespan, further studies are required to improve our understanding of the determinants of leaf lifespan.

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