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Assessing the impact of the Potassium cycle on stand growth and resource-use in tropical Eucalypt plantations: a process-based modeling approach

Modélisation mécaniste de l'influence du cycle du Potassium sur la croissance et l'utilisation des ressources des plantations d'Eucalyptus en zone tropicale

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sous la direction de **Nicolas DELPIERRE**, maître de conférences
et la co-direction de **Guerric LE MAIRE**, directeur de recherche

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Chapter 1

Introduction

1.1 The global limiters of terrestrial primary productivity
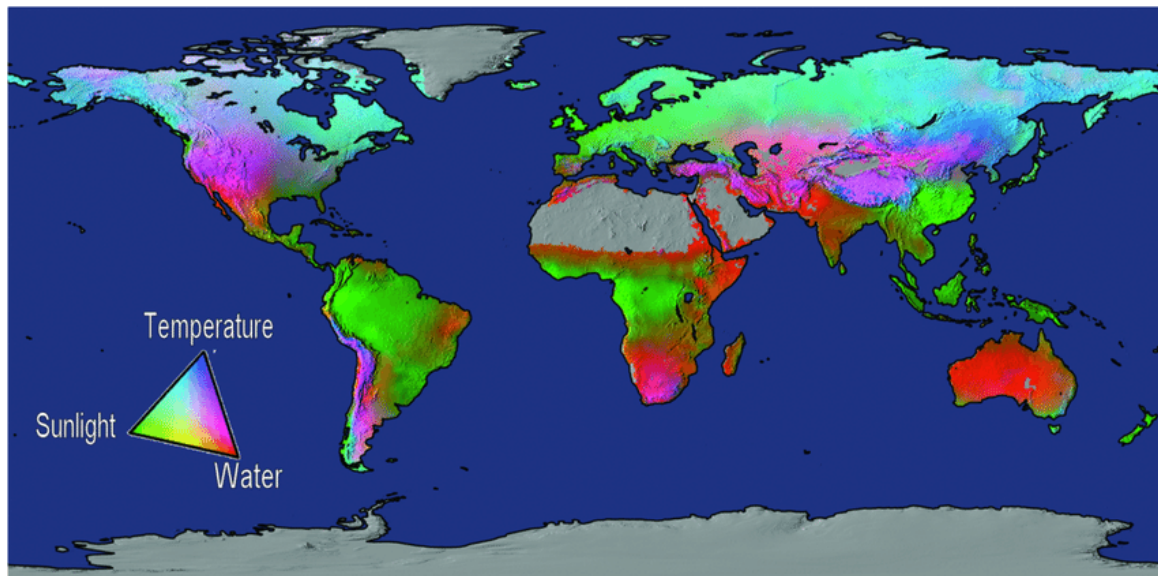
Figure 1.1: A global map of the most limiting factor (light, water or temperature) for the net primary productivity of ecosystems (Figure from Boisvenue and Running, 2006).

1.1.1 Light, water and temperature

It is generally admitted that light, water and temperature are the most limiting environmental factors when it comes to global Net Primary Productivity (NPP). Net primary productivity is the result of gross primary productivity (photosynthesis) minus the autotrophic respiration fluxes. In the rest of the document the above definition will be used. The limitation of NPP by the aforementioned factors is not spread out equally around the globe (Fig.1.1) and these limiting factors have generated specific adaptations of the vegetation (Körner, 2018).

While global change can increase the productivity in some ecosystems that are limited by temperature (Melillo et al., 1993; Myneni et al., 1997), it will likely increase the constraints posed by water in many ecosystems. Tropical regions are more limited by sunlight and water (Zuidema et al., 2022) while temperate regions are more sunlight and temperature limited. Drought stress and atmospheric water stress have already increased and are likely to increase in the future (Yuan et al., 2019; Zhao and Running, 2010). Moreover extreme temperatures could also soon become a problem for vegetation productivity (Wahid et al., 2007) in tropical regions (Horton et al., 2016). This could potentially reshape the maps of limiting factors, as water or temperature could become the principal limiting factor around the tropics.

1.1.2   Carbon

The concentration of carbon (C) in the atmosphere is one of the co-limiting factors for the photosynthesis of plants (Taiz et al., 2015). Carbon is a relatively scarce resource with a mean concentration of 419 ppm (as of February 2022, from the Mauna Loa observatory) in the atmosphere. Plants must also operate an optimisation between carbon gain, water loss and thermoregulation (Michaletz et al., 2015). The increasing CO_2 concentration could change this balance and allow more carbon acquisition for the same amount of water loss by a decrease in stomatal conductance and an increase in assimilation (Ainsworth and Rogers, 2007). This leads to an increase in the Water Use Efficiency (WUE) of plants (that is not necessarily linear to the increase in CO_2 concentration De Kauwe et al., 2013).

Under the widely held assumption that plant growth is limited by carbon assimilation (the C-source, GPP), an increase in CO_2 concentration should lead an increased plant NPP. This view has been challenged over the past few years (Körner, 2015) with suggestion that C-sink processes (processes that directly affect the growth of organs themselves) may be more limiting than C-source processes (processes affecting the GPP).

The impact of increasing C access

The impact of elevated CO_2 levels has been studied in crops for the last few decades (Bazzaz, 1990). The response of whole ecosystems to elevated CO_2 has been a more recent endeavour. Since the 1990's, in an attempt to understand the effects of increased CO_2 concentration levels on ecosystems, free air carbon enrichment (FACE) experiments have been set up. By injecting CO_2, these experiments locally increased CO_2 air concentration in a controlled manner (Ainsworth and Long, 2005) that permitted the measurement of the response of ecosystems to elevated CO_2 levels. The first generation of FACE showed that partitioning of the supplementary carbon, soil organic matter dynamics and C-Nitrogen interactions were key in understanding the response of forest ecosystems to elevated CO_2 levels (Norby and Zak, 2011). It was recently shown that the response of photosynthesis to elevated CO_2 in FACE experiments could be underestimated due to rapid oscillations of CO_2 induced by the setup (Allen et al., 2020). This potentially creates a bias when extrapolating FACE results to the response of vegetation to future CO_2 levels. We will not consider this bias when analysing results from the literature but we thought it should be mentioned. Another identified bias was the concentration of FACE experiments in temperate forest in the first generation of FACE setups (Norby et al., 2017). Fortunately this was corrected in the second generation

with new locations in more diverse forest ecosystems.

Evidence for a global CO_2 fertilisation effect on plant productivity is growing (Schimel et al., 2019; Walker et al., 2020). An increase of GPP of 5.8 $gC.yr^{-1}$ per increase of one ppm of CO_2 in the atmosphere was estimated for evergreen broadleaved forests (Chen et al., 2022), that are of interest in this thesis. This translates into an impressive 4% increase of GPP per decade. Elevated CO_2 was also the main reason behind the global greening trend (Piao et al., 2020). However, the effect on plant biomass was moderate compared to the effect on GPP, and different sites showed dissimilar responses (Walker et al., 2020).

Progressive nitrogen limitation

To explain the decrease in the response of ecosystems to elevated CO_2 levels that was observed in some FACE experiments, the progressive nitrogen (N) limitation hypothesis was proposed (Luo et al., 2004). This hypothesis suggests that N availability declines over time at elevated CO_2 levels due to increased immobilisation in plant biomass and/or sequestration in soil organic matter.

At a global level, it seems that while photosynthesis is still responding to elevated CO_2 levels, the slope between the increase in GPP and the increase in CO_2 has been decreasing (Wang et al., 2020). Simply said, the increase in GPP per every extra ppm of CO_2 is slowly reaching zero. The availability of P was shown to limit increases of NPP in the Amazon by 50% under elevated CO_2 (Fleischer et al., 2019b) and results from a FACE experiment on a P-limited mature eucalypt forest (EUCFACE), showed that while there was a significant increase in photosynthesis there was no response of the aboveground productivity (Ellsworth et al., 2017). This experiment also observed an increased allocation of C to the belowground compartment and as a consequence, an increase in soil respiration (Jiang et al., 2020). Concurrently, an increase in N and P mineralisation was observed, suggesting some sort of soil priming effect (Kuzyakov et al., 2000). The absence of response of stand canopy structure to an elevated level of CO_2 was also observed in a temperate forest (Norby et al., 2022). A commentary on this result (Körner, 2022) suggested that this was to be expected since forests are generally nutrient starved and not C-starved.

Simultaneously, measurements showed a decline of leaf nutrition at the European scale (Jonard et al., 2009, 2014) that seemed related to increasing CO_2 concentrations (Penuelas et al., 2020). Similar trends were observed for N at the global scale (Craine et al., 2018). The causes and consequences of the decline in leaf N concentration are open to debate with

Hiltbrunner et al. (2019) suggesting that this decline was mainly due to an increase in leaf non-structural carbohydrates as a result of higher C assimilation and a decrease in N allocation to leaves by plants (since C demand is already met). But Craine et al. (2019) suggested that this decline was mainly due to the oligotrophication of ecosystems that are not actively fertilised. The cited causes for the oligotrophication were elevated CO_2 levels and increased season growing season.

Finally a decrease in transpiration due to elevated CO_2 should also be considered as a factor for the decrease in the nutrition of plants (McDonald et al., 2002; Mcgrath and Lobell, 2013), since part of the nutritional demand of plants is met by mass flow (the movement of soil water containing solutes towards the roots, BassiriRad, 2005). The importance of mass flow was underlined by studies that showed a coupling between nutritional N status and stomatal conductance (Cramer et al., 2009; Matimati et al., 2014) that suggested that transpiration is not only used for thermoregulation but also a useful tool for nutrient acquisition by plants.

1.1.3   Nutrients

Nutrient limitation of plant productivity also occurs in current CO_2 levels, and the idea that nutrients are limiting the productivity is not new (Liebig, 1841). Limitation by N of terrestrial ecosystem productivity (LeBauer and Treseder, 2008) is widespread at all latitudes and in all terrestrial biomes. Limitation by N is however more widespread at high latitudes and phosphorus (P) at lower latitudes (Fig.1.2a), but this is not an absolute rule (Fig.1.2b). N and P concentrations in leaves have a direct impact on photosynthetic capacity (Evans, 1989; Walker et al., 2014) and the productivity of many ecosystems responds to increased nutrient supply, be they macro- (N, P, potassium (K)) or micro-nutrients (Kaspari, 2021).

1.2   Nutrients as limiters of forest productivity

The limitation of forest productivity by nutrients is widespread in tropical (Wright, 2019), boreal and temperate forests (Magnani et al., 2007). In a lowland tropical forest, wood productivity responded to addition of N, P and K (Wright et al., 2018). Soil fertility was shown to positively impact biomass production efficiency (Vicca et al., 2012) and the effect was consistent across forest types and biomes. Evidence for limitation of photosynthesis by a wide range of nutrients in the Amazon forest (Mendes and Marenco, 2015) was also found.

a

In NRE_{dom}/PRE_{dom}

1.02 ▮ N limitation
0.16
−0.16
−0.91 ▮ P limitation

b

P limitation in natural
terrestrial ecosystems

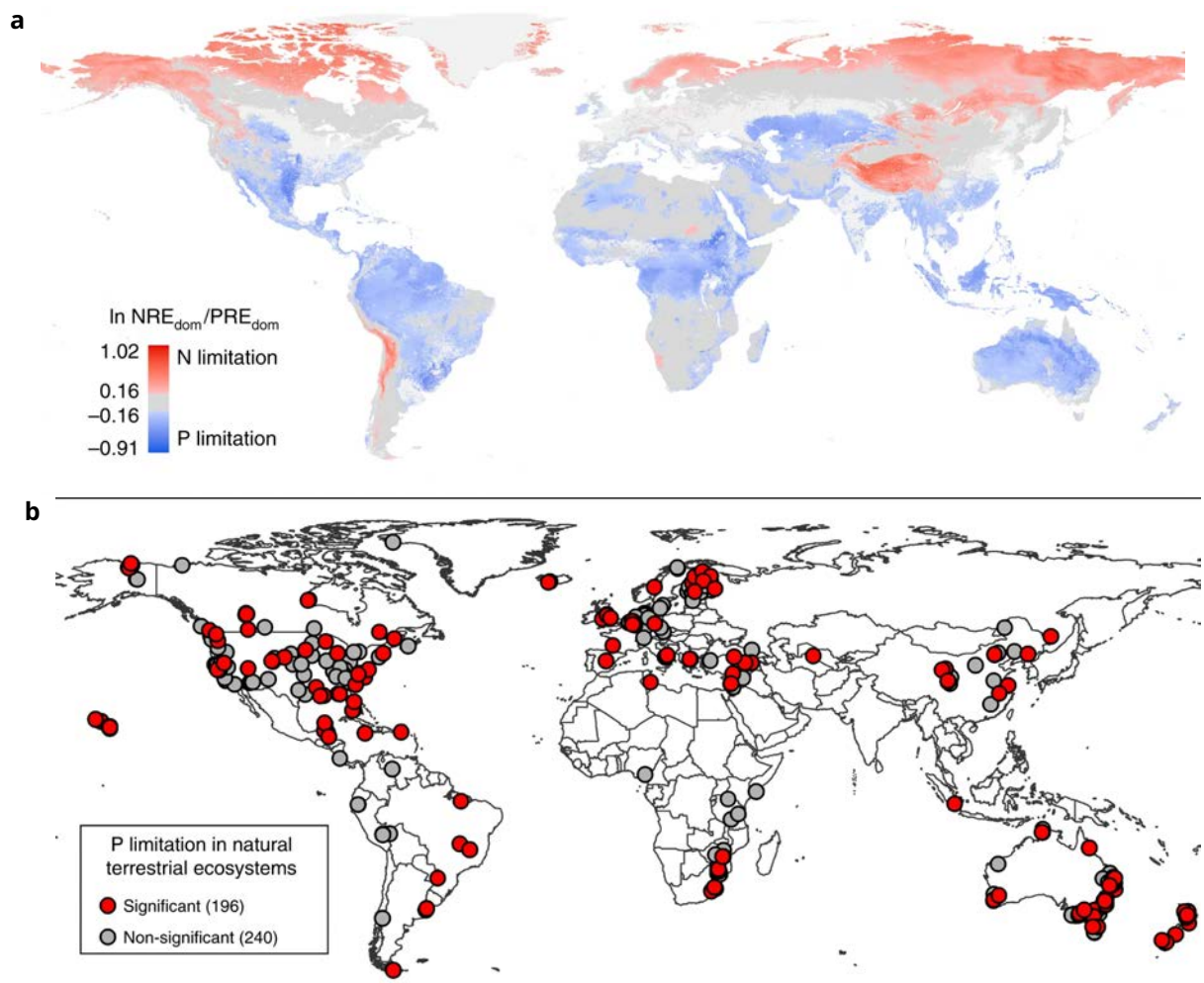● Significant (196)
○ Non-significant (240)

Figure 1.2: a) The limitation of ecosystems by N or P that was determined using foliar resorption efficiencies (Figure from Du et al., 2020); b) the extent of P limitation of plant production by P in natural terrestrial ecosystems determined by addition experiments (Figure from Hou et al., 2020)

Evidence is growing for a non-liebigian world.   As shown above, limitation of forest ecosystems by N or P is a global phenomenon. The liebigian "law of the minimum" states that only one factor (here macro-nutrients) can be limiting at a given time. This assumption is however broken in many cases, leading some to question the relevance of this framework when it comes to understanding nutrient limitation of plant growth (Townsend et al., 2011; Kaspari and Powers, 2016). Many studies show a strong interaction between N and P cycles that goes as far as co-limitation (Harpole et al., 2011). For example, N is necessary for the production of phosphatases that allow the plant to solubilise more P (Deng et al., 2017) that is likely leading to observations of increased P availability after N fertilisation in terrestrial ecosystems (Chen et al., 2020). This multiple nutrient limitation was also observed for litter decomposition (Kaspari et al., 2008) or N-fixation that is co-limited by P and Molybdenum (Wurzburger et al., 2012).

At the community (Danger et al., 2008) and landscape scale (Townsend et al., 2008) co-

limitation is likely to take place due to heterogeneity either in species, soils or micro-environment. This makes it difficult to establish if a particular site is N- or P-limited based on its latitude.

1.3 The cycles of N, P and K

1.3.1 Global stoichiometry of terrestrial ecosystems

Ecological or biological stoichiometry is the study of the ratios of different elements in ecosystems and the effects they have on the functioning of, and the interactions within, this ecosystem (Elser et al., 2000). One milestones in this field of science was the discovery of the so-called Redfield ratio (Redfield, 1934). The stability of the C:N:P ratios in marine plankton (106:16:1) and sea water across oceans came as a surprise and it was proposed that is was the result of a feedback between the biota and their environment (Redfield, 1958). The paradigm was recently extended to soils (Cleveland and Liptzin, 2007) and forests (McGroddy et al., 2004) that both showed constrained C:N:P ratios. In forests, foliar N:P ratios were dependent on the latitude, with tropical biomes having higher C:P and N:P ratios than temperate forests. This could indicate stronger P-limitation of tropical biomes. However this has been called into question with large-scale analyses showing no restriction of either P limitation to the tropics (Elser et al., 2007) or N limitation to the higher latitudes (LeBauer and Treseder, 2008).

An interesting tool to explore the evolutionary advantage of plant stoichiometry can be domestication. Domestication puts a strong selection pressure on organisms and could reveal the importance of stoichiometry for plant yield or allocation. One such study has explored the impact of domestication on plant stoichiometry (by comparing wild ancestors to their domesticated descendants, Delgado-Baquerizo et al., 2016). The authors hypothesized that domestication should have increased leaf N and P concentrations as a mechanism to increase productivity. The observed effects were mainly an increase in leaf P, and the effect size was small. This could have been expected since photosynthetic capacity per unit of leaf surface in its great majority shows little to no improvement in domesticated plants over their wild ancestors (Evans, 1996). The increased P concentration in leaves could be the testimony of increased growth rates since low C:P and N:P ratios are linked to increase allocation to ribosomal RNA molecules that are necessary for fast organ growth (Elser et al., 2000). Unfortunately the response of the whole plants' stoichiometries to different soil nutrient access was not explored (e.g. no information regarding soil stoichiometry was reported, García-

Palacios et al., 2013), as it could have reflected different responses to nutrient deficiency or the effect of allocation on stoichiometry.

1.3.2   The primary sources of N, P and K in terrestrial ecosystems

The N, P and K elements that are used by plants have quite different origins. We will not mention anthropogenic sources of N, P and K here (see below in fertilisation section) and will only provide a synthetic and comparative view of the global nutrient cycles here (for a complete overview see chapter 12 in Schlesinger and Bernhardt, 2013).
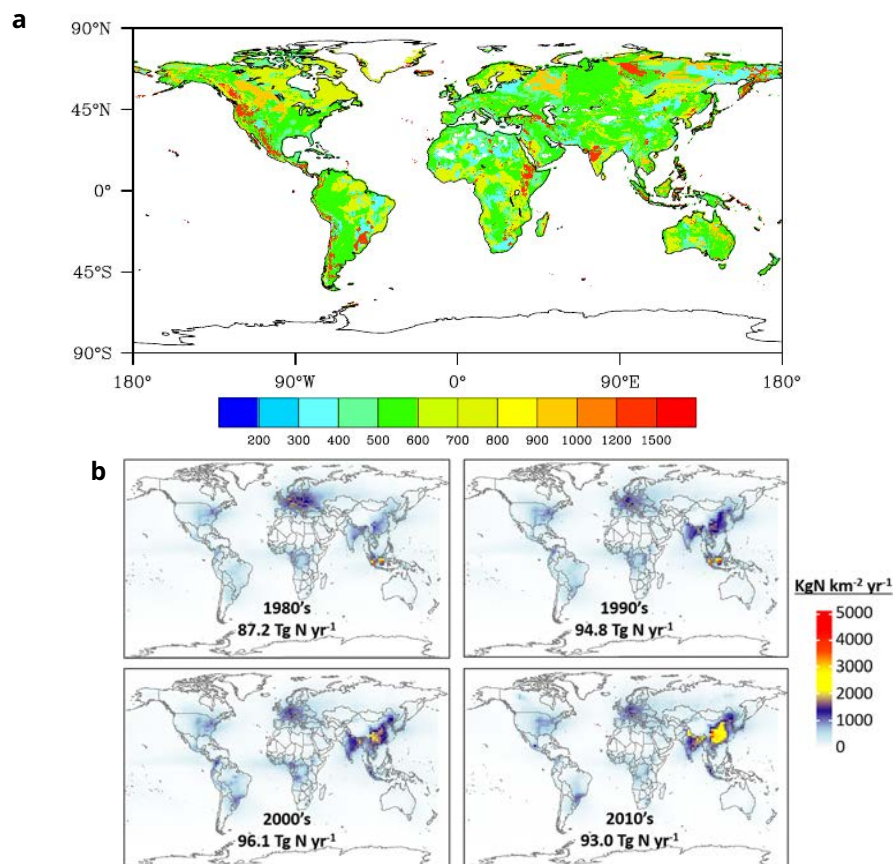
Figure 1.3: a) The map of the P concentration (in ppm) of the soil parent material (figure from Yang et al., 2013) b) The global map of the inorganic N deposition (figure from Ackerman et al., 2019)

Weathering

The weathering of parent material (Fig.1.3a) is the principal source of P (Ruttenberg, 2003; Augusto et al., 2017) and K (Schroeder, 1979; Schlesinger and Bernhardt, 2013) in soils. It can also occur for N (Houlton et al., 2018), but is only a marginal global source of N. There is strong evidence that weathering the parent material containing P and K can be greatly increased by biological activity should it be free living microbes (Pikovskaya, 1978), mycorrhizae (van Schöll

et al., 2008; Landeweert et al., 2001) or roots (Augusto et al., 2019; de Oliveira et al., 2021). These convergent results of "rock-eating" organisms suggest a strong biological component of weathering but to the best of my knowledge, the extent to which this enhanced (compared to physico-chemical weathering) biological weathering is responsible for plant nutrition is still unknown.

Atmosphere and aerosols

While the largest source of P and K are in the parent material of soils, the primary source of N in ecosystems is the atmosphere. The atmosphere is composed of 78% N_2. Nitrogen can be transferred from the atmosphere to the soil by two main mechanisms: biological fixation and lightning strikes. Both these processes require important amounts of energy to brake the triple bond of the N_2 molecule. Lightning strikes transform around 2-8 TgN.yr^{-1} of N_2 to NO_x, with each lightning strike transforming around 3.5 kgN (Schumann and Huntrieser, 2007). Soil fixation requires the use of the nitrogenase enzyme. This enzyme uses Molybdenum (Mo) (Seefeldt et al., 2009), which explains the limitation of N-fixing by Mo deficiency (Barron et al., 2009). The global yearly amount of N fixed in natural ecosystems by free living or symbiotic microbes was estimated to be between 40 and 100 TgN.yr^{-1} (Vitousek et al., 2013).

At a local level, aerosols can also make up an important part of the K and P budget. In the Guianan Amazon forest (Van Langenhove et al., 2020) atmospheric deposition (includes both bulk and dry deposition fluxes) of P was one third of the litter flux, and the K atmospheric deposition flux was superior to the K leaf litter flux. It was hypothesized that a major part of this nutrient deposition originated from Africa and was transported by trade winds.

1.3.3 Losses of N-P-K from the ecosystem

N is a relatively volatile element when compared to P or K. Mineral N in soils can be denitrified by microbes or fire. This returns N back into the atmosphere and is a net loss of N by the ecosystem (Schlesinger and Bernhardt, 2013). These N losses are not without consequence for the climate since the denitrification process in soils generates N_2O (Forster et al., 2007) that is a potent greenhouse gas (Butterbach-Bahl et al., 2013). Phosphorus on the other hand has very few gaseous losses (Roels and Verstraete, 2001). Since P strongly interacts with soil particles (which presents a challenge for uptake by plants), losses from the ecosystem should be low (Yanai, 1992) when the system is not P saturated (e.g. unfertilised). Potassium is also less subject than N to losses from the ecosystem (see below). These losses do not account

for export of nutrients from the ecosystem by harvest. Should it be: grains, trunks or harvest residues, these present an important source of nutrient loss from ecosystems.

1.3.4 Anthropogenic modifications to terrestrial nutrient cycles

Humans have deeply modified the global cycles of several elements. Without even mentioning fertiliser (see below), human activities greatly alter the global nutrient cycles (generally by adding nutrients into the system). It is estimated that the amount of N biologically fixed (by free living and symbiotic microbes) in croplands and grazed savannas is of the same order of magnitude than the amount of N fixed by natural ecosystems (Fowler et al., 2013). There are two major anthropogenic sources for reactive N in the atmosphere (and that ends up being deposited on soils): volatilisation (as NH_3, N_2O and NO_x) after application of fertiliser or manure, and the combustion in industrial processes and transport (as NO_x). These processes create important amounts of reactive N that are then deposited on land (Fig.1.3b). In Europe, which is subject to high N deposition (Schlesinger and Bernhardt, 2013), the N deposition due to human activities was estimated to be responsible for around 10% of the sequestrated C by forests (De Vries et al., 2006). However a subsequent study revealed that at a global scale the impact of N deposition on forest productivity was unclear and that increase were mainly found in boreal forests (Schulte-Uebbing et al., 2022).

Fertiliser

Fertilisers are the biggest contributor to anthropogenic addition of nutrients to ecosystems. Since the discovery that nutrients can limit plant growth (Liebig, 1841), there has been a demand for increasing crop nutrition to increase crop production. It was estimated that around 50% of crop production in the USA is currently attributable to N, P and K fertilisers (Stewart et al., 2005). The invention of the Haber-Bosch process (Haber, 1918) at the beginning of the century, while leading to increased weapons production, has also led to an incredible increase in the production of N fertilisers (Fig.1.4c). This industrial process alone is believed to be responsible for sustaining food production nourishing 44% of the world's population (Erisman et al., 2008). The production of P and K fertiliser has also increased to a lesser extent (Fig.1.4c). As a consequence, stoichiometry of fertiliser production has greatly shifted between the 1950s and now (Fig.1.4d) with N:P and N:K ratios greatly increasing. A plateau was reached recently, maybe representing the optimal N:P:K ratios of crops. The N:K or N:P ratios of fertiliser could be explained in part by the localisation of nutrients in the plant (a
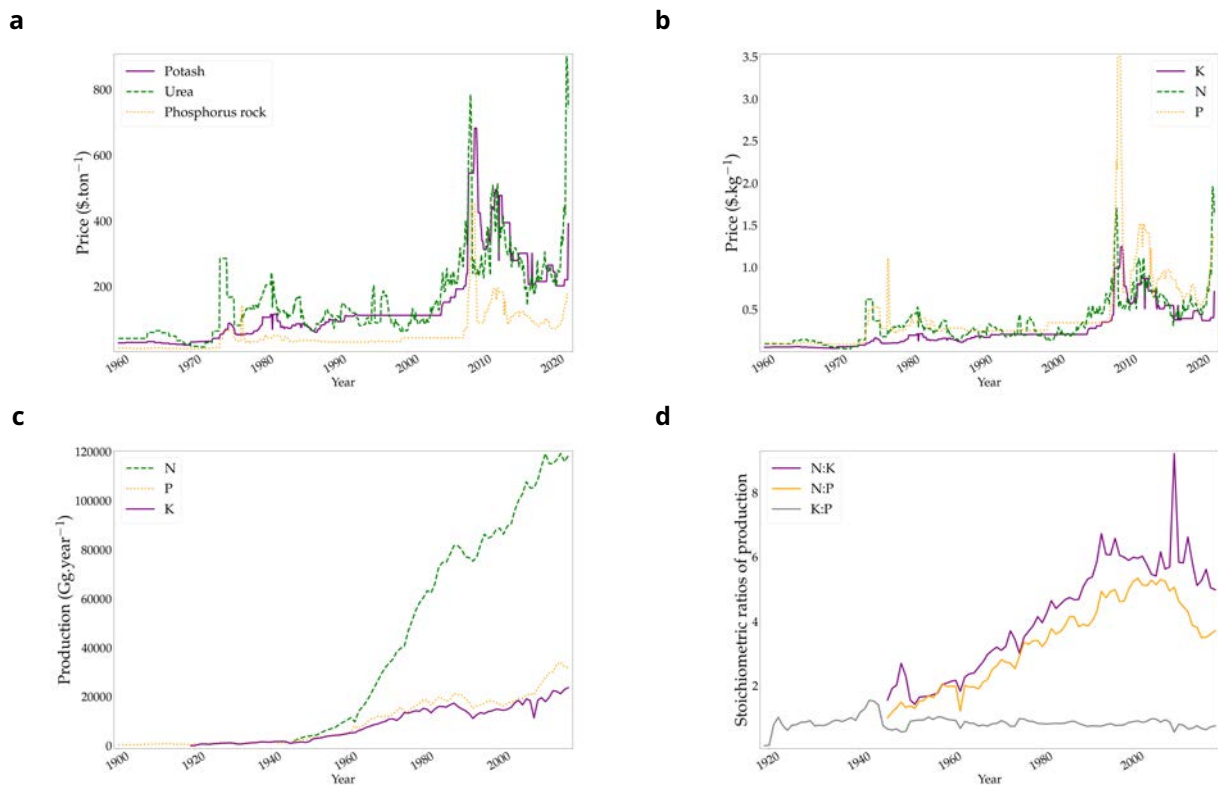
Figure 1.4: The price of fertilizer products (a), the price per kg of N, P and K obtained by converting the price of mining products (using their composition and molar mass of elements) (b), the annual global production of each element (c), and the stoichiometric ratios of the produced elements. The price of fertiliser was found in Bank (2022) and the quantities of fertilisers were found in USGS (2022)

great part of N is concentrated in the exported grains). For example, in winter wheat, N:K ratios in total aboveground biomass at the start of stem elongation and flowering are respectively 2:1 and 1:1 while the N:K ratio of grain biomass is 7:1 (Figs.S1-3 in Weih et al., 2016). This shift was caused by the concentration of K changing between developmental stages and organs while N concentration was relatively stable. The ratio in grain biomass is of the same order of magnitude than the N:K ratio of fertiliser (Fig.1.4d).

In forests, fertiliser is almost never used on non-plantation forest ecosystems (Smethurst et al., 2003). The use of fertiliser in plantation forests is much lower than in agriculture due to a lower global forest cover than crop cover and a lower use of nutrients by the plant per unit GPP. This could be explained by the different stoichiometries between crops and trees. For aboveground biomass, C:N:K:P ratios of herbaceous plants and planted eucalypts (at 6 years of age) were measured at 230:23:5:1 (Reiners, 1986) and 2592:8:4:1 (calculated from Cornut et al., 2021), respectively. This important difference in stoichiometry explains that under the assumption that crops and forests have the same NPP, forest nutrient requirements will be much lower than those of crops. This is counterbalanced by an important part of the annual crops' biomass returning to the soil every year (but also important grain and possibly straw

export) while trees immobilise nutrients in perennial woody organs.

Production limits for fertilisers and alternatives

While N is industrially fixed from the atmospheric N_2 using the Haber-Bosch process, K and P need to be mined. This means that while there is no end in sight to the supply of N since the atmosphere contains 3.9×10^{21}gN and the denitrification process returns fixed N to the atmosphere (Schlesinger and Bernhardt, 2013), P and K fertiliser are a non-renewable resource. Phosphorus demand is expected to outstrip supply by 2035 (Cordell et al., 2011) but some estimates placed that date much later (Fixen and Johnston, 2012). As for potash production, a model has placed its peak around 2060 (Al Rawashdeh, 2020). Fertilisers are also produced in a small number of countries (USGS, 2022) making them subject to strong price fluctuations (Fig.1.4b) as the result of geopolitical instability (Bloomberg, 2022).

Alternatives to mineral fertilisation are starting to be developed with the selection of free ranging nitrogen fixers that could potentially supply the crops' or trees' N demand (Mus et al., 2022), while also potentially minimizing the deplorable losses when using mineral N fertilizer (Schlesinger and Bernhardt, 2013). Free living microbes can be added and increase solubilisation of P in soils (Sharma et al., 2013). Tree plantations can also incorporate legumes that fix atmospheric N (Binkley et al., 1992; Laclau et al., 2008) with the disadvantage of introducing competition between the N-fixer and the tree of interest. Enhanced weathering is another technique that could potentially increase nutrient supply while providing other environmental benefits such as C-fixation (Goll et al., 2021). This technique could be particularly interesting in tropical tree plantations (destined for wood production) where P and K supply can be low and fertiliser requirement is reasonable. For example, andesite has proven to be a good candidate for replacing K fertiliser in tropical eucalypt plantations (Dalmora et al., 2020). All these alternatives are well adapted to planted forests, where demand of nutrients is lower than crops, and demand for sustainability is high (Binkley and Stape, 2004). Alternatives to fertilisers would also have the added benefit of decreasing the impact fertiliser use has on ecosystem functioning worldwide (Rockström et al., 2009) since nutrient use efficiency is potentially higher with these methods.

1.4 Using models to investigate the nutrient limitation of productivity

In highly coupled biogeochemical systems such as Earth's terrestrial ecosystems, models can provide insight into the effects of nutrient supply on plant productivity. Mechanistic models provide a way to test functional hypotheses by building a model based on science-based assumptions, calibrating the model and finally validating the model using measurement or observations. Discrepancies between the model and reality can then be used to identify which of the functional hypotheses were right, wrong or need precising. Models can also be used in a predictive or decision-making capacity to understand the future effects of policies or environmental changes. According to me, these are the reasons (or at least part of them) that have led to the development of many nutrient oriented mechanistic models.

1.4.1 Forest nutrient modelling

C-N models

N was the first element to be introduced in models that mechanistically simulated primary productivity. A complete review of coupled C-N models can be found in Zaehle et al. (2014). This study tested the validity of 11 C-N coupled models on two contrasted FACE sites: a temperate evergreen forest (DUKEFACE) and a temperate deciduous forest (ORNL FACE). These two forests showed contrasted responses to CO_2 fertilisation with DUKEFACE subject to progressive nitrogen limitation and ORNL showing no N limitation of productivity by N due to an increase in N uptake. This analysis showed that models did not manage to reproduce this contrast, underestimated N uptake in the non N-limited site, and concluded that stoichiometric constraints lacked mechanistic backing to explain N-limitation patterns and that deeper process understanding was necessary. Models that simulated N leaf concentration and the feedback on photosynthetic capacity were able to simulate the GPP increase due to elevated CO_2 better than other that used an empirical stoichiometric limitation of photosynthesis. The relative lack of information and representation of belowground processes in the measurements and model respectively was deemed an obstacle for understanding the effect of eCO_2 at the ORNL and DUKEFACE sites.

C-N-P models

Following the relative success of C-N coupled models in replicating some of the patterns of N limitation of productivity, a demand for C-N-P models was introduced (Reed et al., 2015) due to the fact that many forest ecosystems are rather P co-limited or P-limited (Vitousek et al., 2010). Models have mainly focused on the supply of P in the soil while the effect of P on aboveground plant processes has been greatly simplified (Jiang et al., 2019). This is in part explained by the main source of P in ecosystems, weathering (Ruttenberg, 2003; Augusto et al., 2017), and the strong interaction of P with the soil that both explain patterns in P limitation (Soong et al., 2020). In most aboveground parts of the models, the limitation of productivity is mainly the result of a stoichiometric limitation of growth or photosynthesis and not a mechanistic interaction between P availability and organ functioning. By that we mean that P availability does not directly impact a process (e.g. the growth of wood, growth of new root tips, production of root exsudates) but rather empirically affects productivity. This could be in part due to the inheritance from organic matter decomposition models that limit decomposition using stoichiometry (Parton et al., 1988).

Generalised nutrient models

Models of nutrient (N, K, Mg, Ca, S) circulation in forests have first been introduced in the 1990s (Arp and Oja, 1997). We believe they are a response to concomitant reports of acidification of soils and increased N deposition (Arp and Oja, 1997) due to industrial emissions at that time. These models focused primarily on the circulation of cations or anions in the ecosystem and the interaction with standing biomass. ForSVA (Arp and Oja, 1997) and ForNBM (Zhu et al., 2003) simulate a feedback between biomass production and nutrients while the NuCM model focuses mainly on the circulation of cations in the soil (Johnson et al., 1993).

1.4.2   Scale of models

The models that are presented above (CN, CNP and generalised) vary in both temporal and spatial scale. Most of the models that combined the C and N/P cycles were Land Surface models that ran at a relatively fine temporal scale (daily or hourly) since they explicitly simulated carbon assimilation. Their objective being to simulate large swaths of land and the global patterns of primary production, they worked at a large spatial scale (typically 1°) and grouped communities into Plant Functional Types (Diaz and Cabido, 1997), which each had a specific set of parameters (Krinner et al., 2005). Depending on the model different PFTs

could cohabit on the same grid cell.

On the other hand, the cation models worked at a rather coarse temporal scale (monthly or annually) and at a fine spatial scale (stand level). They focused on forests with a reduced number of species and used site specific parameterisations. The low diversity encountered in this model family could be explained by the small extent of their coverage and the fact that these models were used in temperate or boreal forests. They focused on a catchment area and the local nutrient budget.

Box 1: Plant K physiology

Osmotic properties of K. The osmotic properties of K are necessary for a wide range of processes. The increase of K concentration in the leaf drives leaf expansion, while K is also linked to stomatal functioning. Accumulation of K^+ ions in the roots also promotes water uptake. Potassium is essential to response of plants to drought stress by its use in osmotic adjustment and stomatal control. Xylem conductivity is also impacted by K concentrations in the xylem as it apparently plays a role in pit pectin hydration leading to increased pit opening under high xylem sap K concentrations.

Carbon and K interactions. Potassium is linked to a number of functions that can alter the carbon economy of a plant. Photosynthesis can be affected by K deficiency due to it being an essential cation for chloroplast functioning. The changes in leaf morphology caused by K deficiency leads to a decrease of mesophyll conductance that causes a decline in affected leaves. Low K availability is also linked to increased reactive species in leaves that degrade their photosynthetic capacity. Potassium is also an important element for the transport of assimilates from the leaves to the sink organs. It is essential for the loading of sugars into the phloem, the transport by mass flow of phloem sap from C-sources to C-sinks and finally for the unloading of sugars from the phloem to C-sink organs. Recently, K^+ ions have earned a nickname: "mobile battery" due to its role in alleviating local energy demand for the phloem loading process.

This is a very brief summary of Chapter II. References can be found in that chapter.

1.5 Potassium limitation of forests

Potassium is a major limiter of forest growth at the global scale (Tripler et al., 2006). While it had been neglected as a limiting nutrient for forest productivity until quite recently, interest in K has been growing over the past few years (Tripler et al., 2006; Sardans and Peñuelas, 2015; Schlesinger and Bernhardt, 2013; Sardans et al., 2021). Evidence of limitation by K of forest productivity is apparent in both plantations and sub-natural and natural forests. In tropical forests many nutrients addition experiments have shown an ecosystem response to K (Townsend et al., 2011; Wright et al., 2011; Baribault et al., 2012; Wurzburger and Wright, 2015; Wright et al., 2018). However, the positive effect K fertilisation had on tree growth was

not limited to tropical forests or tropical tree plantations (Rocha et al., 2019), and temperate (Tripler et al., 2006) or boreal (Ouimet and Moore, 2015) systems also showed a positive response to K addition.

The reason for the relative neglect of K as an essential nutrient for forest growth when compared to the attention brought to N or P is surprising since it does not seem to be the case in agriculture (Zörb et al., 2014) since K fertiliser use is widespread. The concentration of K in plant biomass is comparable to N and much superior to P (Taiz et al., 2015) so a stoichiometric bias cannot be a reasonable explanation. It is possible that the intense circulation of K in the ecosystem makes it harder to study, or that it is due to its weak interaction with organic matter. Other reasons may include the direct relationship between photosynthetic traits and leaf N or P content (Walker et al., 2014), that is not so evident for K (ref), or the impact N and P can have on decomposition dynamics (Parton et al., 1988). This links N and P directly to the C cycle either through photosynthesis or soil organic matter decomposition. The link between the C-cycle and K is more indirect.

1.5.1 K mainly present in ionic form

Contrary to N are P which are included into organic matter, K is exclusively present as K^+ ions in the plant and the soil. It has major functions in plants that are linked to its high mobility and cationic nature. K circulation in plants is linked to sugar transport (Marschner et al., 1996), energy distribution (Dreyer et al., 2017), stress signaling (Wang et al., 2013), xylem hydraulic conductivity(Nardini et al., 2011), and salt tolerance (Shabala and Cuin, 2008) to cite a few (see Box 1). This makes the roles of K in plants very diverse and still open to debate (Dreyer, 2021).

Sodium as a substitution for K

Surprisingly, sodium (Na) while often described as a competitor of K, has been shown to be a suitable replacement ion in cases of severe K deficiency in tropical eucalypt plantations (Almeida et al., 2010). In the latter reference, the productivity of the stand fertilised with Na was in-between that of a fully fertilised and a K-omission stand. The substitution of K by Na had already been explored and some authors have gone as far as calling Na a functional element (Subbarao et al., 2003). This was somewhat comforted by a recent experiment that showed an increase in growth (de Souza Mateus et al., 2019), photosynthetic rates (by more than one-third) and WUE (Mateus et al., 2021) in eucalypt seedlings following partial K substitution by Na. This amply demonstrates that in some "natrophilic" (Subbarao et al., 2003)

tree species, Na supply can improve functioning.

1.5.2 Exchanges of K between the plant the environment

Uptake of K by trees

The uptake of K from soils takes place through two main mechanisms: mass-flow and diffusion (White and Karley, 2010). It was estimated (in wheat) that mass-flow accounted for around one third of total K uptake (Gregory et al., 1979). Similarly to P only a small part of total soil K is available for absorption by plant roots (Moody and Bell, 2006) but this amount could have been seriously underestimated (Bel et al., 2020). It was long thought that uptake of K^+ ions by roots was the result of a bi-transporter system: low affinity transporters and high affinity transporters (Glass, 2005) that operated at high and low external K concentrations respectively. This was recently called into question by modelling work that demonstrated that both channels (K^+ channel and K^+/H^+ co-transporter) had similar affinities but different energy requirements (Dreyer and Michard, 2020). As a consequence one channel is more adapted to moderate K concentrations (the K^+ channel) and demands less energy per K^+ ion uptaken, while the other operates at the high- and low-end of external K concentrations (the K^+/H^+ co-transporter) and needs more energy to operate.

Losses of K from trees

Since K is mainly present in ionic form, losses of K^+ ions from the plant can happen (in non negligible quantities) in multiple ways: exchanges of K ions between leaves and woody organs and incoming precipitation, losses through leaf, bark and branches fall, and root senescence.

Canopy Leaching. Exchanges of nutrients between the canopy and incoming precipitation are measured by calculating their difference in concentration between canopy throughfall and stemflow, and above-canopy precipitation. Canopy throughfall plus stemflow water will contain the bulk deposition flux plus the result of exchanges with the canopy. An above-canopy rain collector will contain only the bulk deposition and precipitation. This method makes the strong assumption that the above-canopy rain collector will collect the bulk deposition at the same rate than a canopy, while the canopy could act as a filter that intercepts aerosols (McLachlan and Horstmann, 1998). In oligotrophic systems N and P can be in lower concentrations in throughfall (Bellote and Moro, 1995) compared to above-canopy

intercepted rainfall thus showing an uptake of N and P by leaves (Parker, 1983). This has been used as a way of fertilising plants through leaves (Fageria et al., 2009). On the other hand, throughfall is generally enriched in K. When the exchange of nutrients leads to a loss of nutrients from the leaves or woody organs it is called *leaching* (Tukey, 1970). The amount of K leaching has been shown to be proportional to the amount of precipitation (Likens et al., 1994; Crockford et al., 1996).

Litterfall and resorption. Losses of K through leaf fall are moderated because of the re-sorption process, the efficiency of which was shown to depend on the nutritional status of the plant (Vergutz et al., 2012; Achat et al., 2018). The resorption process also takes place in fine roots for N and P (Brant and Chen, 2015; Xu et al., 2021), but we did not find any source documenting K resorption before root fall. The resorption efficiencies for N in fine roots were low (Brant and Chen, 2015) but the same effect of K could provide with a small flux of K returning to the plant.

Contribution of leaching, litterfall and resorption to total K loss. It is hard to make general rules about the contribution of each process to the circulation of K in the ecosystem since estimates of the contribution of resorption efficiency (Vergutz et al., 2012; Achat et al., 2018) and leaching (Laclau et al., 2010; Likens et al., 1994; Duvigneaud and Smet, 1973) vary substantially, while leaf fall and root fall dynamics vary widely among biomes. Resorption of K is also difficult to estimate since leaf leaching can lead to losses in content between mature and senesced leaves. A meta-analysis places the mean at around 50% of foliar K losses taking place through leaching and the other half through leaf fall (Parker, 1983). For N and P, leaf fall makes up a much higher proportion of foliar losses because leaching is low for these nutrients.

Losses of K at the ecosystem level

Here we will focus on forests for the sake of simplicity and concision. The loss of K at the ecosystem can happen by erosion, soil leaching or volatilisation. Volatilisation seldom takes place but can be a contributor to K flux at the continental scale. Volatilisation of K mainly happens during forest fires (Pio et al., 2008). The result of this volatilisation may not be seen in soil K content following fires (Zhang et al., 2015), since part of the K that was immobilised in woody biomass is probably also returned to the soil as a component of ash. Fire can how-ever lead to losses of K from the ecosystem due to increased leaching from ash to streams

(Schindler et al., 1980). Leaching of K from the soil is strongly increased during forest har-vests (e.g. clear-cutting) when a large flux of K (i.e. the K contained in the remnant biomass from the harvest) reaches the soil at once and may be leached (Likens et al., 1994). Erosion is mainly related to agricultural soils (Bertsch and Thomas, 1985) and we will not consider it in detail here.

1.5.3   Is the cycle of K in forest ecosystems worth modelling ?

The extent of K as a limiting element for forest growth and modulator of resource-use effi-ciency is still unknown. As described above, some studies show that K limitation is frequent in forest ecosystems. As a consequence of the large number of roles K occupies in plants, there are multiple ways by which K could be implicated in primary productivity limitation. This makes it hard to disentangle the most important mechanisms when it comes to under-standing the effect of K availability on forest productivity. The limitation of GPP by K (Christina et al., 2015) and the interaction with water has already been explored in a modelling study that has produced evidence as to the consequences of fertilisation on the water status of the stand (Christina et al., 2018): fertilisation increases the water stress during the rotation by increasing transpiration and faster uptake of soil water, which can produce stronger wa-ter stress during dry season, and also lowers the water table. We believe that building upon approach with a mechanistic modelling of the availability of K in the soil, the allocation of K in the plant and its effect on processes would provide more information with regards to K limitation of net primary productivity of forests. Just like models incorporating N are now used to calculate the global land carbon sink (Friedlingstein et al., 2021), and P models are used in prospective studies (Fleischer et al., 2019a), we believe that beyond providing more information on processes, a framework incorporating multiple nutrients (i.e. N, P, K and micro-nutrients) is necessary for accurate simulation of the global carbon cycle since we are in a co-limited world (Kaspari and Powers, 2016). There are currently no C-H_2O-K coupled models and simulating K limitation of forest growth would be the first step in the direction of understanding carbon cycling in a world with a wide range of co-limiting elements (Kaspari, 2021).

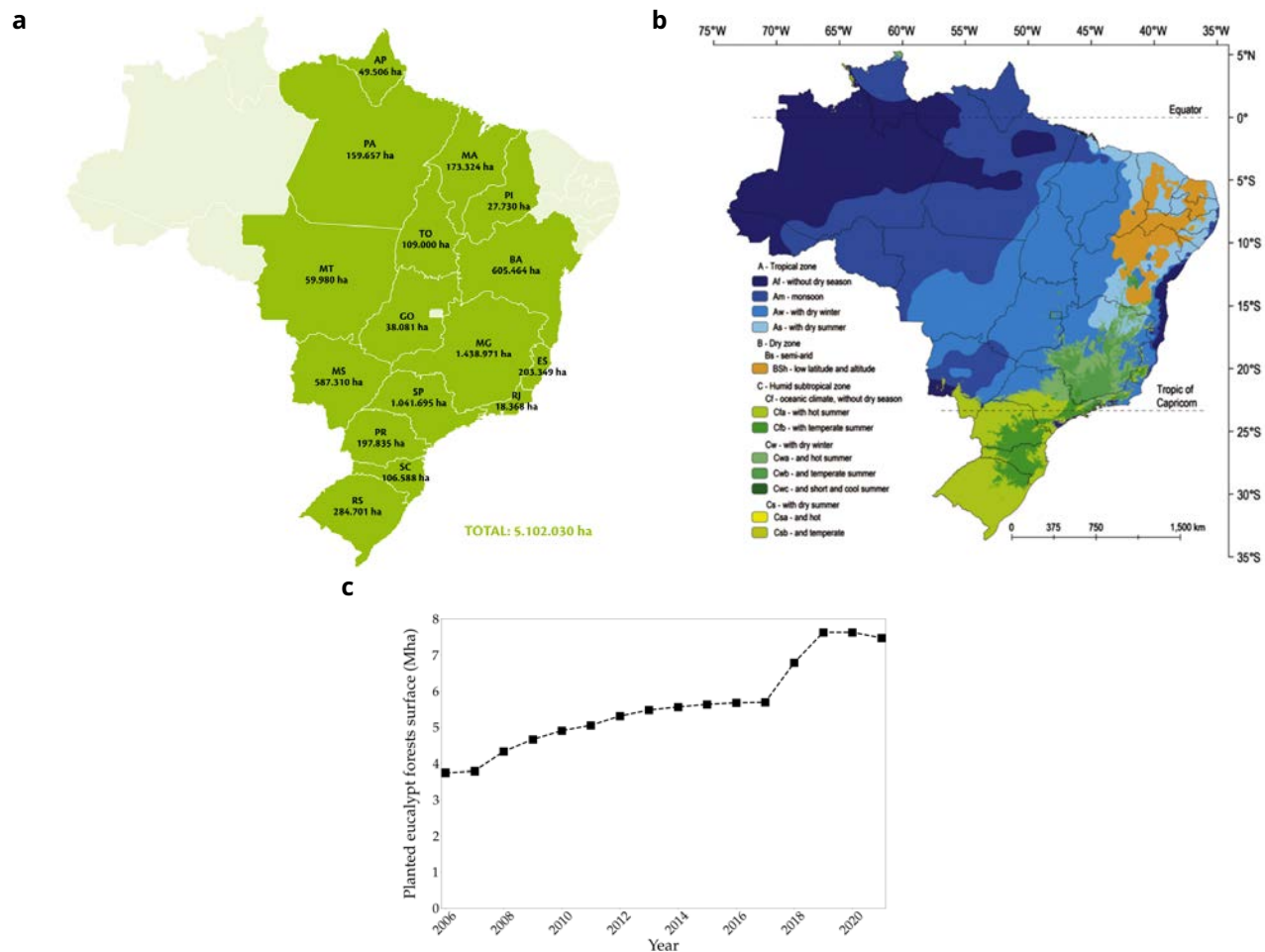## 1.6 Eucalypt plantations as a model ecosystem

a

b

c

Figure 1.5: a) The surfaces of eucalypt plantations per brazilian state in 2012 (figure from ABRAF, 2013) b) The Köppen classification map for Brazil (figure from Alvares et al., 2013) c) Total surface of eucalypt plantations in Brazil (data from IBA, 2019)

Worldwide, eucalypt plantations cover more than 20 Mha (Booth, 2013), of which, in 2020, 7.47 Mha are located in Brazil (IBA, 2020). The plantations cover a wide range of pedo-climatic conditions (Fig.1.5a-b). Between 2014 and 2020, the total surface planted with eucalypts in Brazil has increased by 57% (Fig.1.5c). As of 2020, eucalypt plantations represent 78.2% of all planted forests in Brazil and the mean production per hectare and per year was 36 m^3 with wood productivity up to 100 $m^3.ha^{-1}.yr^{-1}$ in some regions (Colodette et al., 2014). Eucalypt wood is mainly used for pulp, paper, charcoal and wood panel production and as a fast-growing species is a good candidate for use in biomass energy with carbon capture and storage (Azar et al., 2006). A fast-growing eucalypt rotation (from plantation to harvest) lasts between 6 to 8 years. The frequent exports of woody biomass (at harvest) coupled to the weathered nature of soils leads to a nutritional deficit that accumulates over time (even more so if harvest residues are exported) if losses are not compensated by fertilisation (Gonçalves

et al., 2000). At harvest the trunks (and sometimes bark) are exported from the stand. However, trunk wood is not only composed of C but also contains nutrients that were immobilised in wood during the rotation. Despite their low nutrient concentration, trunks are the most important biomass compartment, and as such contain an important nutrient stock (Bauters et al., 2022). As a consequence, at each harvest, an important quantity of nutrients are exported from the stand and thus lost to the stand. This leads to a need for fertilisation of eucalypt stands in terms of both macro- and micro-nutrients (de Barros et al., 2000).

Nonetheless, fertilizer consumption by eucalypt plantations is only a low percentage of consumption by crops in Brazil. If one were to assume that the 7.47 Mha of eucalypt plantations are fertilised (the real figure is evidently smaller since all plantations are probably not fertilised at these levels) with 100 $kg.ha^{-1}$ of N, 80 $kg.ha^{-1}$ of K and 26 $kg.ha^{-1}$ of P (values selected from Melo et al., 2015), and that a rotation lasts 7 years on average, this would mean a maximum consumption of 106 $Gg.year^{-1}$ of N, 85 $Gg.year^{-1}$ of K and, 27 $Gg.year^{-1}$ of P. This corresponds to around 0.08%, 0.31%, 0.08% of global N, K and P production respectively (Fig. 1.4c). At the country scale, this would represent 4.71%, 3.3% and 2.2% of N, K and P fertiliser consumption for crops in Brazil in 2002 (FAO, 2004) respectively. This is the upper bound since not all plantations are fertilised at these levels. It shows that fertiliser consumption from eucalypt plantations is marginal compared to consumption by crops (covering a surface of 38 Mha in Brazil) and per unit surface crops consume ~10 times more fertiliser than eucalypt plantations.

As seen above, frequent nutrient exports, high productivity and weathered soils create the perfect conditions for nutrient limitation in eucalypt plantations. This makes them an ideal system for studying the effect of nutrient limitation on growth. As a consequence, many addition (Stape et al., 2010; Melo et al., 2015; Bassaco et al., 2018) and omission (Laclau et al., 2010; Rocha et al., 2019) experiments have been conducted on these study systems. These experiments though not limited to N, P and K limitation (also micro-nutrients in Rocha et al., 2019) have mainly focused on the effects of these nutrients. All these experiments show a response of eucalypt plantation productivity to K. The response of wood productivity to K was very high in some experiments (Rocha et al., 2019; Laclau et al., 2010) with a reduction in wood NPP reaching more than 50% in stands not fertilized with K. Omission experiments present an opportunity for modelling work since they suppose that in the control (fully fertilised) condition the system is not limited by any nutrient (since fertilisation is very high, Laclau et al., 2010) and the removal of one of the nutrients allows to measure the response of the system to this nutrient without confounding factors.

1.7   Objectives and organisation of the thesis

Nutrients are a limiting factor of the primary productivity in many terrestrial ecosystems. These limitations already strongly constrain productivity in some forests and this proportion might increase as C becomes a more available resource. To reproduce the global patterns of forest productivity, models focusing on the cycles of carbon and water will not be sufficient. Mechanistic models need to include nutrient limitation of growth: models that couple the C, water and N or P fluxes fulfill this function. The use of these models has shown that including these nutrients cycles can greatly change projected future productivity under climate change. Potassium, despite being a limiting element in a number of forests, has not received the same attention, and no models linking the K cycle to the carbon and water cycles presently exist. Tropical eucalypt plantations are an ideal model forest ecosystem to study the nutrient limitation of wood productivity. Due to frequent biomass exports, and poor soils, they are fertilised. This has led to the development of nutrient omission experiments that can measure the limitation of wood productivity by the tested nutrients. Many of such experiments have demonstrated that K is a strongly limiting nutrient in these planted forests.

In that context, my work consisted in identifying and quantifying the processes responsible for the limitation of wood productivity in tropical eucalypt plantations grown on nutrient-poor soils. The achievement of this goal involved a number of steps, identified here as the objectives of this work:

The first objective was to **quantify the effects of K-deficiency on the C-source** (photosynthesis). Limitation of the C-source by K deficiency in eucalypt plantations has been explored through both measurements (Epron et al., 2012) and modelling (Christina et al., 2015) in previous works. Here, the objective was to explore the dynamics of K in the canopy and the processes that limit photosynthesis the most in context of different K availabilities. This objective was also a stepping stone for the next one.

The second objective was to understand if the limitation of the C-source by K availability was enough to explain the observed differences in **wood productivity (the C-sink)** or whether **stoichiometric limitation** was necessary for modeling K limitation of wood productivity in trees. K deficiency has been shown to impact multiple aspects of the cycle of C in the plant, notably photosynthesis, carbon transport from the leaf to the sink organs, and loading of sugars into the sink organs) and as such is a good candidate for studying sink-limitation of wood productivity by nutrients.

The third objective was understanding the effect of **K availability on the resource-use efficiency** of the tropical eucalypt plantations.

These objectives were addressed using a mechanistic model, representing the coupled cycles of carbon, water and potassium in tropical eucalypt stands. This is, to the best of our knowledge, the first model of its kind.

1.8 Approach used in the thesis

In the thesis, we used data from long-standing and large scale experiments to inform a mechanistic model. The large scale experiments were conducted in Brazilian eucalypt stands. The experiments in these stands have taken place over multiple rotations and present a very detailed picture of development, carbon and water fluxes, mineralomass and physiological functioning of eucalypt stands. The collected data was used both to make modelling choices, parameterise simulated processes and validate model results. In the following, we will present the study sites, and then give a succinct presentation of the modelling framework from which we built the coupled C-water-K model.
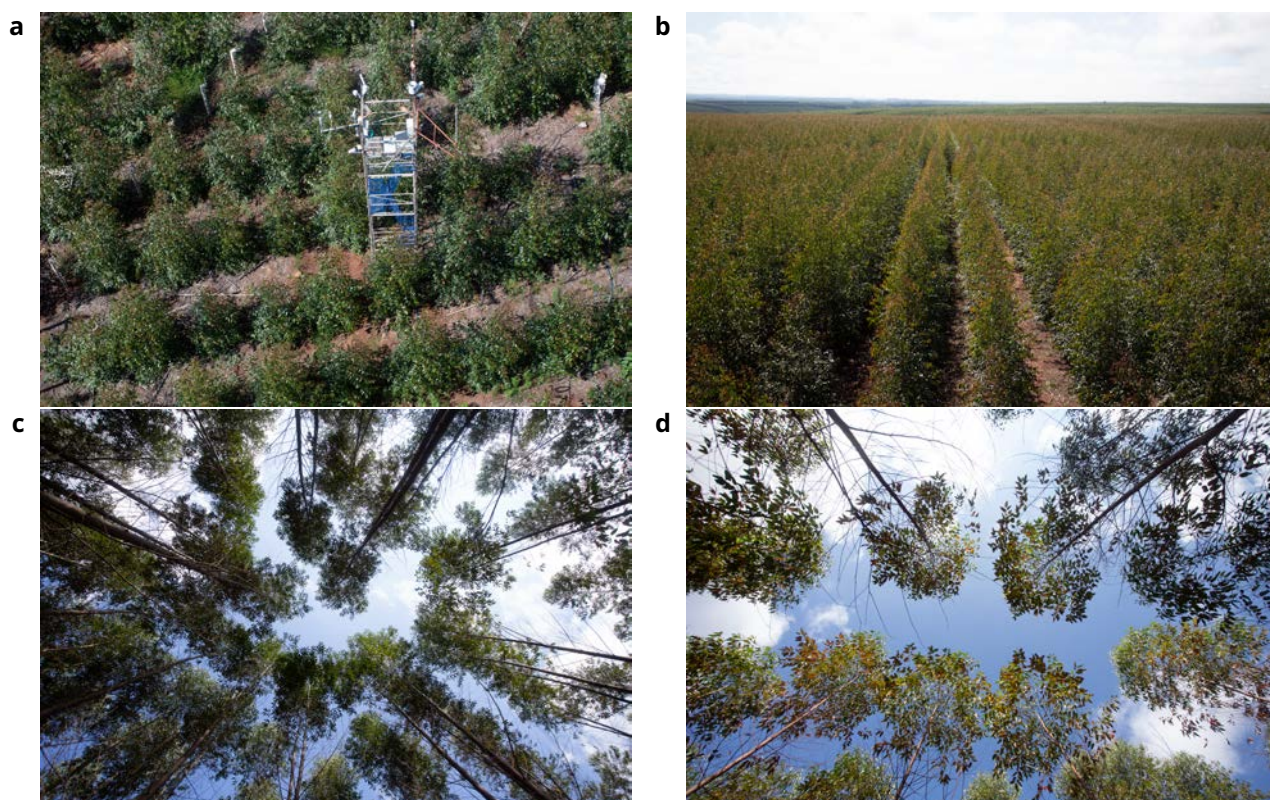
1.8.1 Eucalypt stands

Figure 1.6: a) The flux tower of the Eucflux site two years after the plantation. b) The same stand as viewed from above. c-d) The canopies of the Itatinga eucalypt plantation seen from below (at age 36 months, photo taken with the same focal length) in both the K-fertilised *+K* (c) and K-deficient *oK* (d) stands. The degraded canopy and K-deficiency symptoms are visible in the oK stand.

Most of the work in this thesis was accomplished using data from two eucalypt plantations, hereafter *Itatinga* (a nutrient-omission site) and *Eucflux* (an eddy-covariance site). Both sites are located in the same geographical region (they are separated by a few kilometers)

and were planted at a 1 year interval (2009 and 2010, respectively), making them complementary. The sites were located in south-eastern Brazil (São-Paulo State, transition limit between the Cerrado and Mata Atlantica ecoregions), the precipitation was on average 1430 mm year^{-1}, with a drier season between June and September, and the mean annual temperature was 19.3°C. Soils are deep Ferralsols (>15 m). The plantations considered here were established following multiple eucalypt plantation rotations. The sites were planted with two different fast growing *Eucalyptus grandis* genotypes. The planting density was 1666 trees/ha (equivalent to a 2×3 m spacing) at both sites. We will briefly present the two sites here, but more information can be found in the methods sections of chapters III and IV.
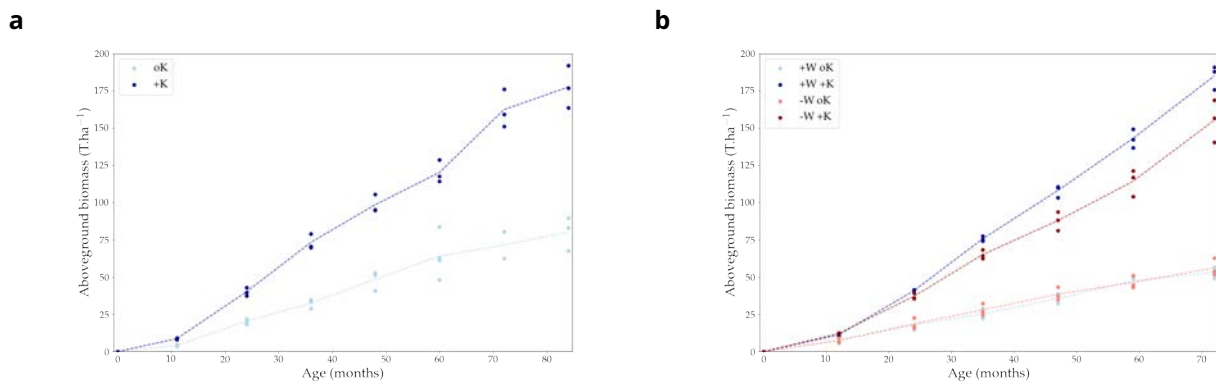
Itatinga: Nutrient omission stands

a
b

Figure 1.7: a) The aboveground biomass of eucalypts in two different fertilisation conditions at Itatinga. This experiment was prior to the one described in detail and was a test of K omission and Na addition with 3 treatments (Sette Junior et al., 2009). b) The aboveground biomass of eucalypt in 4 different fertilisation and water conditions at the Itatinga site. This experiment was subsequent to the one shown in a) and is the one described in the paragraph below.

The "Itatinga" experimental site (23°02′49″S and 48°38′17″W, 860 m asl, University of Sao Paulo-ESALQ) consisted in fertilisation trials. The rotation used in the thesis was planted in June 2010 (there had been previous nutrient omission experiments at this site). It was a split-plot experiment, that tested: rain exclusion, K omission and Na addition. The water exclusion consisted in the reduction by 30% of incoming precipitation. The experimental treatments were the following: +W:+K, +W:oK:+Na, +W:oK, oW:+K, oW:oK:+Na, oW:oK. With oW and oK meaning rainfall exclusion and K omission respectively. In the thesis we used primarily measurements from the +W:+K and +W:oK treatments. The fertilisation in the +K treatment was the following: +K (17.55 gK m^{-2} applied as KCl at planting, with 3.3 gP m^{-2}, 200 g m^{-2} of dolomitic lime and trace elements and 12 gN m^{-2} at 3 months of age). In the oK treatment the KCl fertilisation was not added. This experiment (Fig.1.7b) followed a similar K omission

and Na addition experiment (Fig.1.7a, Sette Junior et al., 2009) that had been conducted at this site.

Eucflux: the flux tower site

Eucflux (Sao-Paulo State, 22°58′04" S and 48°43′40"W, 750 m asl) is a 200-ha eucalypt stand managed by the EucFlux project (http://www.ipef .br/eucflux/en/). The plantation was described in details in Christina et al. (2017); Nouvellon et al. (2010, 2019); Vezy et al. (2018). The clone used here was a fast growing *Eucalyptus grandis* $\times$ *urophylla*. The plantation was established in November 2009 and harvested in June 2017. At the centre of the plot, a flux tower continuously measured meteorological variables as well as the fluxes of CO_2 and water vapour between the plantation and the atmosphere, with the eddy covariance technique. The fertilisation at Eucflux was very high and well above the prescribed amounts for eucalypt plantations (as to be sure no nutrient was limiting): 3.0 g/m² of K_2O, 3.3 g/m² of P_2O_5, 1.8 g/m² of N and 400 g/m² of dolomitic lime and trace elements, then at 3 months with 3.6 g/m² of K_2O, 3.12 g/m² of N, at 10 months with 6.72 g/m² of K_2O, 3.08 g/m² of N and at 20 months of age with 15.12 g/m² K_2O. This amounted to a total of 23.60 gK.m^{-2} from fertilisation and resulted in non-limiting nutrient availability for tree growth.

1.8.2 The CASTANEA model and adaptations

CASTANEA is a mechanistic forest stand model (Dufrêne et al., 2005; Davi et al., 2005). It simulates carbon and water fluxes between a monospecific forest stand and the atmosphere (Fig.1.8). It was initially designed to simulate a temperate beech stand but has since been expanded to simulate both deciduous and evergreen temperate species (Davi et al., 2006; Delpierre et al., 2012; Guillemot et al., 2017). It was chosen as the base model for this work since it had characteristics that were adapted to the simulation of K limitation of wood productivity. Firstly, the model is at the right spatial (stand level) and temporal (both the Eucflux flux tower and the model use a half-hourly timestep) scales for the system we wished to investigate. Secondly, all the tree biomass compartments are included in this model which is useful for both C and K allocation. Thirdly, N (Delpierre et al., unpublished) and P (Cornut et al., unpublished) cycles had been previously included in the CASTANEA model (in a temperate oak stand). All these reasons, made this model a good candidate for our work.
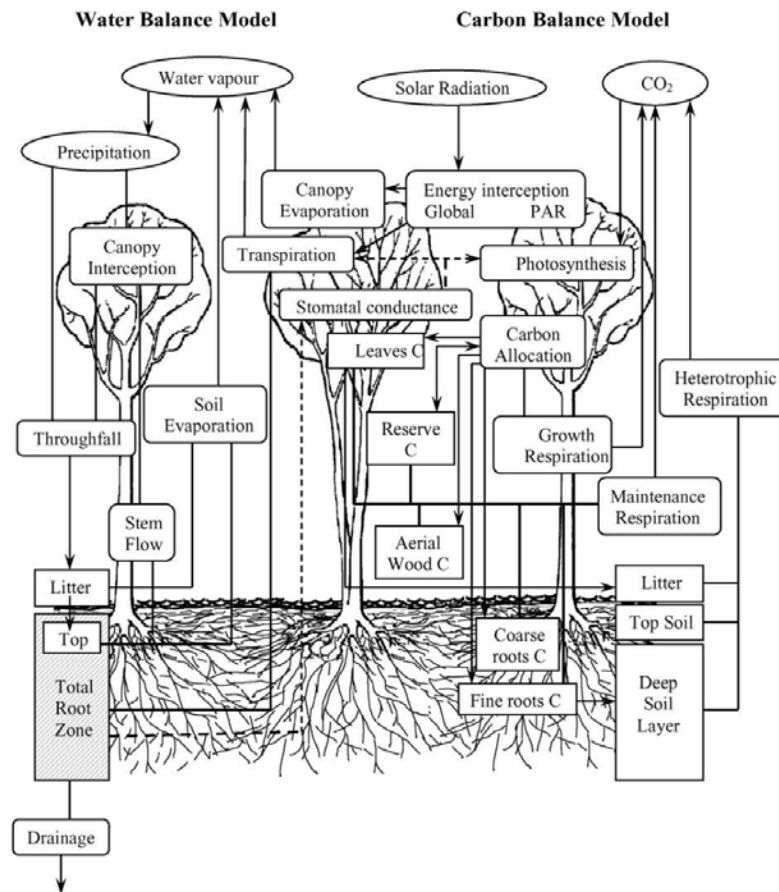
Figure 1.8: The schematic of the first version of the CASTANEA model (figure from Dufrêne et al., 2005).

Canopy

The canopy is one of the main components of the CASTANEA model. It is a 1-dimensional multi-layer continuous canopy model that simulates the propagation of radiation through leaf layers. Photosynthesis and transpiration are calculated independently for each leaf layer by coupling a Farquhar photosynthesis model (Farquhar et al., 1980) and a Ball and Berry stomatal conductance model (Ball et al., 1987). This was well adapted to our monospecific, even-aged, and relatively homogeneous eucalypt plantation canopy.

In the historical CASTANEA model, the diminution of photosynthetic capacity of leaves from the top to the bottom of the canopy is simulated using a LMA gradient. In turn, this decreasing LMA gradient leads to a decreasing N surfacic concentration. Photosynthetic parameters are linearly related to the surfacic N concentration of the leaves.

The photosynthesis and transpiration are simulated at a half-hourly timestep.

Allocation and respiration

The allocation of assimilated carbon is simulated at a daily timestep. A part of the daily GPP is returned to the atmosphere as growth and maintenance respiration. The rest of the C is allocated either to the growing organs or the reserves (the soluble sugars in organs and phloem). There are five biomass compartments in total: leaves, branches, trunk (distinguishing sapwood and heartwood), coarse roots and fine roots.

Growth respiration is calculated assuming a construction cost specific for each organ (depending on the biochemical composition) and maintenance respiration is a function of temperature, the organ's N concentration, and a respiration rate per unit nitrogen. The organ's N concentration is thus used as a proxy for the organ's metabolic activity.

Combining CASTANEA with the MAESPA model

The adaptation of CASTANEA to the Brazilian tropical eucalypt plantations presented a challenge due the continuous phenology (see chapter III) and deep rooting depth (down to 18 m see Christina et al., 2011) that violates the constant rooting-depth assumption of the CASTANEA model.

The MAESPA model had already proven suitable to simulate tropical eucalypt stands (Christina et al., 2015). The MAESPA model (Duursma and Medlyn, 2012) was developed using the above-ground components of the MAESTRA model (Wang and Jarvis, 1990) and the water balance components of the SPA model (Williams et al., 1996). The MAESPA model (Duursma and Medlyn, 2012) is a coupled C and water model and the soil-plant-atmosphere water continuum of water potential is explicitly simulated by MAESPA. It simulates aboveground part of the trees in 3 dimensions and the soil in 1 dimension. Tree canopies are represented by non-dynamic simple 3 dimensional geometric shapes (spheres, ellipsoids, cones). The model simulates the interception of light, the energy balance, and C and water fluxes between the canopy and the atmosphere at a half hourly timestep. The canopy and stand structures can evolve during the simulation, however these dynamics are not simulated by the model and must be forced as inputs to the model. MAESPA was already adapted and has been successfully run on Itatinga and Eucflux plantations (Christina et al., 2017).

The CASTANEA and MAESPA models were thus complementary, and we combined them into one single modelling platform that served as a basis for the development of a mechanistic carbon-water-potassium cycles model named *CASTANEA-MAESPA-K* (described in Chapter III and IV). The photosynthesis and water cycle sub-models were adapted from MAESPA while

the 1-dimensional canopy, C allocation and biomass dynamics sub-models of CASTANEA were conserved. This was done since the photosynthesis and water MAESPA sub-models had been parameterised and validated on the studied eucalypt stands (Christina et al., 2015, 2017, 2018). On the other hand the MAESPA model was incapable of dynamically simulating the biomass compartments of a eucalypt stand or the nutrient cycles. Simulating allocation and biomass was necessary to investigate C-source and sink dynamics. Reducing the 3-dimensional nature of MAESPA to the 1-dimensional nature of CASTANEA also had the added benefit of reducing the calculation time, without losing much precision on radiation interception because the canopy closes rapidly.

1.9   Organisation of the thesis

This thesis is organized in chapters:

1. in Chapter II, we will review the results and literature that describe the K-limitation of tree productivity, focusing on eucalypt plantations,

2. in Chapter III, we will introduce the adaptation of the mechanistic stand model CAS-TANEA to the simulation of the coupled cycles of C, water and K in tropical eucalypt plantations, focusing on photosynthesis and canopy processes,

3. in chapter IV, we will introduce the inclusion in the above-mentioned model of a C and K allocation scheme adapted to fast-growing eucalypt plantations.

The relevance of this work, perspectives and conclusions are presented in Chapters V and VI.

Chapter 2

Potassium limitation of wood productivity: A review of elementary processes and ways forward to modelling illustrated by Eucalyptus plantations

Potassium limitation of wood productivity: A review of elementary processes and ways forward to modelling illustrated by *Eucalyptus* plantations

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ABSTRACT

Potassium (K) is essential for a wide range of physiological functions in plants, and a limiting element for wood productivity in numerous forest ecosystems. However, the contribution of each of the K-sensitive physiological processes to the limitation of wood productivity is poorly known. In trees, K deficiency acts both on the source and the sinks of carbon making it difficult to disentangle its effects on wood productivity. Here, we review the literature dealing with the influence of K-limitation on tree physiological processes. Results from extensively studied tropical *Eucalyptus* plantations are used to illustrate the physiological processes the most impacted by K deficiency. We identify the main processes that limit the availability of K to the trees and influence the circulation of K ions in the ecosystem. Then, we describe the influence of K bioavailability on carbon assimilation, the water economy of trees, and carbon partitioning. We conclude this review by identifying the main priorities towards the process-based modelling of the influence of K on the carbon and water cycles in forest ecosystems. For each process modelling priority, we identify options that could be used in the current conceptual framework of most eco-physiological models.

1. Introduction

Plants are autotrophic organisms that require energy, water, CO_2, macro- and micronutrients inputs as resources to grow, maintain over time and reproduce. The effects of resource limitation (yield limitation sensu (Körner, 2018)) on plant growth has been extensively studied (Gleeson and Timan, 1992)

In the context of current and projected rise in atmospheric CO_2 concentration, much emphasis has been put on the CO_2 fertilisation effect (Haverd et al., 2020; Hyvönen et al., 2007) stemming from the limitation of photosynthesis by leaf internal CO_2 concentration. This C-centric view postulates that while mineral nutrients may influence tree growth, forest ecosystems are principally C-limited. This hypothesis is important for climate change mitigation strategies since it purports that the C-sink activity will increase with increasing atmospheric CO_2 concentration and thus could partially compensate anthropogenic carbon emissions.

To test the validity of this C-centric view, Free Air CO_2 Enrichment experiments have been used over the past three decades. Elevated CO_2 concentrations do lead to a positive effect on tree aerial productivity, but this effect is transient (Norby and Zak, 2011). This shows that other limiting factors than C availability are at play in limiting tree productivity (Leuzinger et al., 2011; Millard et al., 2007). Nitrogen (N), phosphorus (P) (Ellsworth et al., 2017; Fleischer et al., 2019; Terrer et al., 2019) and other nutrients could progressively become limiting factors with more CO_2 available (Dusenge et al., 2019; Luo et al., 2004; Trierweiler et al., 2018; Wieder et al., 2015). Furthermore, leaf nutrient contents in European forests suggest that nutritional stresses are currently increasing (Jonard et al., 2014, 2009; Penuelas et al., 2020). This could negatively impact the assimilation of C by plant leaves, since

the photosynthetic capacity of leaves depends on their nutritional status (Evans, 1989; Walker et al., 2014).

Nitrogen (N) and phosphorus (P) limitation of forest processes have been extensively studied (Crous et al., 2017; Kattge et al., 2009; Reich, 2012; Reich et al., 2009; Walker et al., 2014). With the aim of a better representation of the C cycle, the effect of N (e.g. Corbeels et al., 2005; Dezi et al., 2010; Vuichard et al., 2019) and more recently P (Goll et al., 2017; Thum et al., 2019; Yang et al., 2014) on ecosystem processes has been implemented in many vegetation models. In simulations, representation of N and P limitations can lead to a 25% decrease in the land carbon sink between 1860 and 2100 under a climate change scenario (SRES A1B) (Goll et al., 2012).

A mounting body of evidence has made apparent that liebigian limitation ("one factor limits growth") does not hold in forest ecosystems (Elser et al., 2007; Fanin et al., 2015; Kaspari et al., 2008; Santiago et al., 2012; Townsend et al., 2011; Wurzburger et al., 2012). It has thus become necessary to represent the different elemental cycles in forest ecosystems so that the sensitivity of biomass productivity to these complex interactions can be tested. As such potassium (K) is an essential nutrient for plant growth that can limit productivity in many forest ecosystems currently or in the future (Sardans and Peñuelas, 2015). K's influence on the water budget is expected to be critical in future drier climates.

Contrary to N and P, K is present exclusively in its ionic form (K^+) in the plants and in the soil. K^+ is the most important cation in terms of mass in the plant biomass, and the second nutrient after N. There are two main pools of K in plant cells: the cytosol and the vacuole. While the concentration of K in the vacuole is variable and depends on K availability, cytosolic K concentration remains relatively constant (Walker et al., 1996). In plant cells K+ is essential for enzyme activation, charge balance and osmoregulatory functions (Wakeel et al., 2011).

While evidence of K limitation of forest productivity is scarce in temperate and boreal regions (Bonneau, 1972; Ouimet and Moore, 2015; Wang et al., 2016), K is co-limiting or limiting productivity in many tropical and subtropical forests (Baribault et al., 2012; Bond, 2010; Epron et al., 2012; Laclau et al., 2009; Lloyd et al., 2015; Rocha et al., 2019; Sardans and Peñuelas, 2015; Silveira et al., 1995; Tripler et al., 2006; Wright, 2019; Wright et al., 2011). K availability could influence the productivity of forest ecosystems by influencing either the acquisition (by leaves) and distribution (from leaves to distal organs) of carbon and other resources (a so-called 'source-limitation' of productivity) or the formation of new tissues ('sink-limitation' of productivity), or both. Sink limitation affects the formation of organs and growth of cells and includes processes that can limit growth even when carbon supply is sufficient. For instance, temperature (Hoch et al., 2002) and water stress (Delpierre et al., 2016a; Muller et al., 2011) have been shown to be, for some forest ecosystems, more limiting than carbon for tree growth.

This review aims to identify processes influenced by K limitations that are likely critical for wood growth. We hypothesized that K deficiency could influence wood production through four categories of processes: (1) lower Gross Primary Productivity (GPP) (source limitation), (2) disruption of source-sink dynamics at the leaf level due to disruption of C export to distal organs, (3) modifications of C partitioning, and (4) direct limitation (e.g. stoichiometric constraints) of wood formation (sink limitation). In this review we investigate how wood growth can be influenced by K availability in forest soils. We illustrate this review with tropical *Eucalyptus* plantations managed in short rotations for maximizing wood production. The rationale for the choice of this biological model is that *Eucalyptus* trees have been grown in field experiments manipulating tree nutrition for a long time. The effects of nutrient deficiencies on the main physiological processes have been documented, and *Eucalyptus* plantations are known to be highly responsive to K supply on many tropical soils, e.g. in Brazil and Congo (Laclau et al., 2010, 2009; Rocha et al., 2019).

In Section 2 of this review, we describe the main processes governing the K biogeochemical cycle in forest ecosystems, taking the example of tropical *Eucalyptus* plantations. The main sources of K in the system are identified as well as the bottlenecks that limit its availability to the trees. In Section 3, we review the processes related to the uptake and circulation of K within trees to identify the distribution of this element in the different organs and the main limitations arising from the K biological cycle. In Section 4, we describe the influence of K availability on different processes affecting the acquisition of C and its allocation to wood. While the identification of K-related processes is a prerequisite (and the main objective of this review) it does not allow a ranking of their quantitative influence on wood productivity, which can only be addressed with mechanistic models. Hence in the last section (Section 5) of the review, we discuss priorities on how to implement K-related processes in terrestrial ecosystems models.

2. *Eucalyptus* plantations: An ecosystem model to study the cycle of K

2.1. Introducing Eucalyptus plantations as a biological model

Eucalyptus plantations cover more than 20 million hectares over large climatic and soil gradients in more than 90 countries (Booth, 2013). These plantations have very high growth rates (average of 45 m^3/ha/yr in Brazil), reaching up to 25–30 m tall trees over 6–7 years (Le Maire et al., 2019). Most of the clones in commercial *Eucalyptus* plantations in tropical regions belong to species *Eucalyptus grandis*, *E. urophylla* (ST Blake) or are hybrids including *E. grandis*. The vulnerability of *Eucalyptus* plantations to climate change is of concern (Booth, 2013) and process-based models could be useful tools to help improve management practices in a context of increasing water and nutrient deficiencies.

We chose fast-growing *Eucalyptus* plantations as a biological model in this review because K deficiency is common, with a very strong limitation of wood productivity (up to 50% in absence of K fertilisation) in some tropical areas (Gava and Gonçalves, 2008; Laclau et al., 2009; Rocha et al., 2019; see Fig. 1 for common fertilisation practices). In these plantations, pools of exchangeable base cations in the soil as well as the inputs in the ecosystem are low throughout the rotation in relation to biomass production.. Most of the nutrient requirements to produce biomass are provided through the biological component of the biogeochemical cycle (outside fertilisation). These "Bio" (Legout et al., 2020) sites are particularly sensitive to disruptions in the biological cycle, such as the large exports of stem wood at harvest (Fig. 1; note that the amount of K exported within stem wood is more than compensated by fertilisation to sustain growth rates over successive rotations in commercial *Eucalyptus* plantations).

Experimental designs have been set up in *Eucalyptus* plantations with a positive control fully fertilized (tree growth not limited by the availability of micro- and macro-nutrients) compared to other treatments with the same full fertilization except a single nutrient (omission trials), and a negative control without any fertilization (Laclau et al., 2009). Such experiments made it possible to assess which processes are affected by the deficiency of each nutrient, with or without the confounding interactions with other nutrients (Christina et al., 2015). All data presented in this review for *Eucalyptus* plantations come from omission experiments set up in a nutrient-poor Ferralsol soil at the Itatinga station in Brazil (Laclau et al., 2010).

2.2. Potassium availability in the soil at our study site

In highly weathered tropical soils, K availability is low due to small amounts of K-bearing primary minerals (e.g., illite and vermiculite) likely to release K in the soil solution. The replenishment of the pool of exchangeable K^+ in highly weathered tropical soils comes mainly from atmospheric depositions and from the biological cycle in natural ecosystems, as well as fertilization in agroecosystems. Only a fraction of the
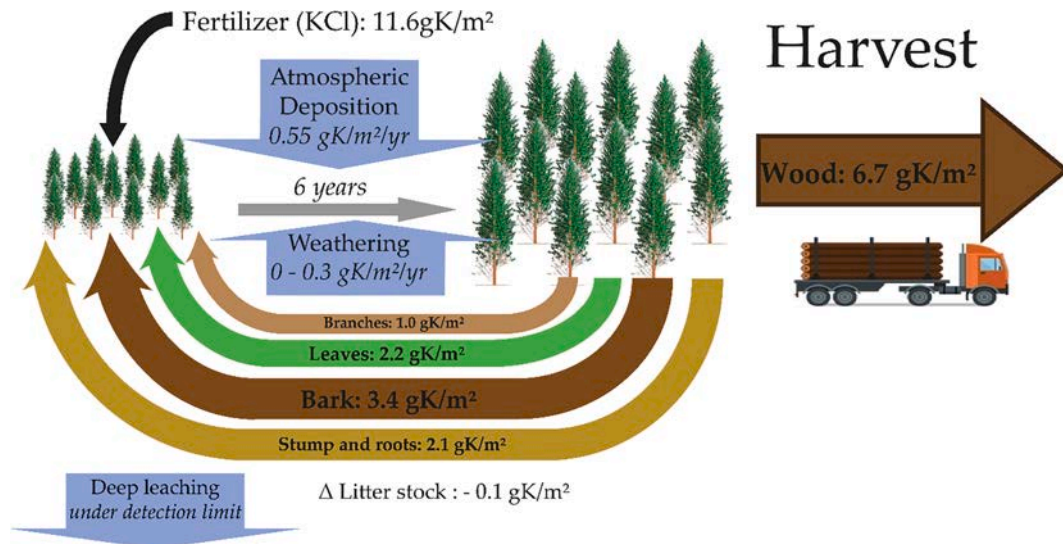
Fig. 1. Main input–output fluxes of K over an entire cycle in experimental eucalypt plantations managed in short rotation with a silviculture representative of commercial plantations in Brazil. Fertilizer (black arrow) is applied the first 18 months after planting. All the harvest residues are left on-site to decompose on the ground (coloured arrows pointing to the left), and only stemwood is exported. Atmospheric deposition and soil weathering are occurring all along the rotation. In some silvicultural practices bark and stumps are also exported. The values of K in the biomass are from Battie-Laclau et al. (2014b). The range of values for weathering come from Maquère (2008) and Pradier et al. (2017). The change in litter stock were calculated by difference between the litter stock measured on a stand at the end of a rotation (Battie-Laclau et al., 2014b) and the litter stock measured at the end of the previous rotation (Almeida et al., 2010). Note that the K balance is not closed: indeed, it was not possible to have precise measurements of change of K content in this very deep soil.

total stock of K in the soil is directly available to the plants and sorption as well as diffusion speed may limit the access of the trees to the pool of K.

2.2.1. K Inputs and outputs in the soil

Atmospheric deposition is an external source of K to *Eucalyptus* plantations. It amounts to about 0.55 gK/m^2/yr in *Eucalyptus* plantations at Itatinga (Figs. 1 and 2; Laclau et al., 2010). This flux is comparable to the global average of 0.41gK/m^2/yr (Sardans and Peñuelas, 2015). This atmospheric deposition flux is higher than mineral weathering, that was considered negligible by Maquère (2008) at the same site based on quantitative mineralogical work. However, a recent study considering the rhizosphere of eucalypt trees suggested that the amount of K released by mineral weathering could be much higher than expected in deep Ferralsols (Pradier et al., 2017). The uncertainty on weathering fluxes is particularly high at our study site because of the difficulty to integrate very low concentrations over considerable rooting depths (*Eucalyptus* roots reach a depth of 16 m five years after planting, Christina et al., 2017). K losses through deep leaching are lower than atmospheric depositions, even after application of K-Cl fertilizer the first year after planting (Laclau et al., 2010). Yet, inputs of K from atmospheric deposition and weathering are not sufficient to sustain productivity in these highly productive *Eucalyptus* plantations where biomass export (mostly tree trunks) is massive (Fig. 1). Highly productive plantations are therefore fertilized, with typical amounts of about 12 gK/m^2 before canopy closure (Fig. 1), which is enough to cover the requirements of the tree throughout the rotation (Almeida et al., 2010). We note that the cycling of K is fast in those plantations, with annual inputs to the soil surface of about 1.0 gK/m^2/yr mostly through leaf litterfall (47%), foliar leaching (42%), and branch litterfall (11%) (Fig. 2).

2.2.2. K Mobility in the soil

K$^+$ is weakly adsorbed on soil particles at our study site. Slopes of the K-buffering curves range from 0.09 to 0.13 (change in exchangeable K (mg/100 g) / change in soil-solution K (mg.L^{-1}); Maquère, 2008) demonstrating the very weak capacity of this soil to buffer a change of the soil solution concentration resulting from an output or an input of K.

These low values are explained by low organic matter contents as well as a mineralogical composition where quartz, kaolinite and oxide are predominant, which leads to limited interaction with dissolved cations (Maquère, 2008). The weak interactions between K$^+$ and the soil solid phase suggest that mass flow (rather than diffusion) could be the main process limiting potassium transfer toward the roots. Moreover, diffusion fluxes measured at our study site show that diffusion per se is sufficient to supply the daily demand of trees in K (Supplementary Fig. S1).

3. The biological cycle of K in the ecosystem

Potassium needs to be supplied in sufficient quantity to maintain a concentration in plant cells that allows for metabolic processes (Marschner, 2011). In the following, we go through the K cycle in trees, considering its absorption in the soil, return to the soil through litter production and foliar leaching, and remobilization from senescing tissues. In K deficient soils, these processes can be bottlenecks limiting the availability of K to tree organs.

3.1. Potassium absorption by plant roots and mycorhizae

The uptake of K from the soil by plants is needed to maintain suitable K$^+$ concentrations in the plant cells. Only a tiny fraction of total soil K is available to plants, comprising the 0.1–0.2% in the soil solution and 1–2% adsorbed on clays (not the case in soils at Itatinga) (Sardans and Peñuelas, 2015). Yet roots seem able to mobilize a fraction of the non-exchangeable K pool in the rhizosphere, altering K-bearing minerals (Pradier et al., 2017). A recent isotopic dilution assay with soil samples covering 3 climatic zones and 5 soil types (including the Itatinga site) suggests that the pools of exchangeable K commonly considered as plant-available (measured by conventional methods) are underestimated by about 50%, and that the additional pool is most likely supported by secondary non-crystalline mineral phases in interaction with soil organic matter (Bel et al., 2020).

Large differences in K absorption efficiency between crops (and among their individual genotypes) are mainly a result of differences in root morphology and density, and to their capacity to mobilize the non-exchangeable K pool (Rengel and Damon, 2008). In soils with low K
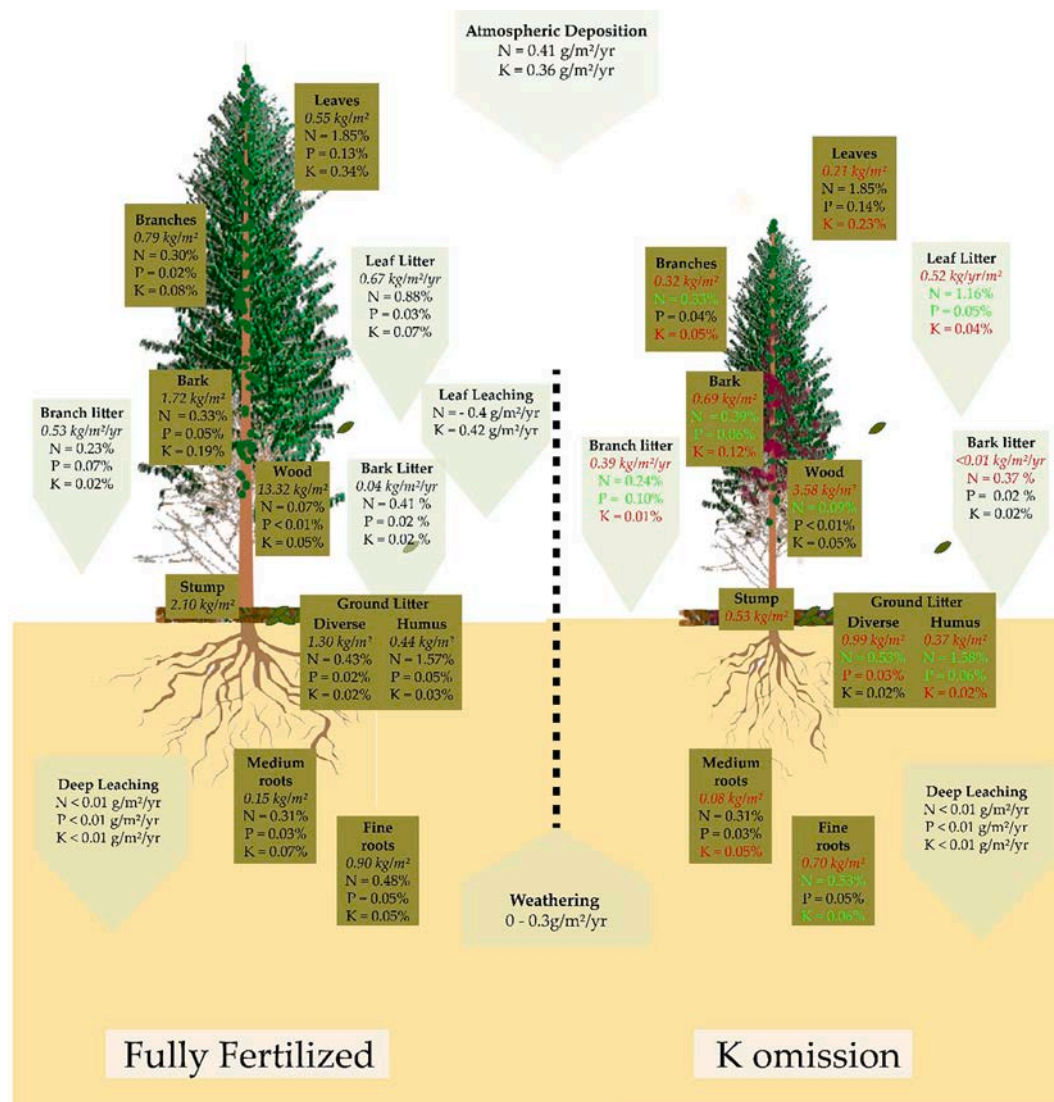
Fig. 2. Main stocks (boxes) and fluxes (arrows) of Carbon, Nitrogen, Phosphorus and Potassium in a Eucalypt plantation of 72 months of age (before harvest). A fully fertilised stand is represented on the left. A K-omission stand is represented on the right. Concentrations or dry masses that are higher in the K omission stand are coloured in green while those that are lower are coloured in red. A description of this experiment can be found in Battie-Laclau et al. (2014b). Atmospheric deposition and leaching fluxes values come from Laclau et al. (2010). Weathering fluxes were obtained by Maquère (2008) and Pradier et al. (2017). Estimation of soil K content is not feasible, due to its very low concentration to integrate on very deep soil (root depth at 16 m at 72 months). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

availability, fine root distribution of trees is skewed towards upper soil layers, compared with richer soils. This is explained by the higher availability of K at the surface in these soils, coming from dry deposition and litter decomposition (Cusack and Turner, 2020). Specific adaptations have been shown in *Eucalyptus* plantations growing on poor sandy soils with a fine root mat above the mineral soil active throughout the year to catch the flux of K (as well as other major nutrients) from the biodegradation of the forest floor, preventing the transfer of dissolved nutrients toward deeper soil horizons (Laclau et al., 2004). However, the root density profile, albeit informative, does not fit the K-absorption potential profile. Fine roots in deep horizons usually show higher K-specific absorption rates as compared to more superficial roots, as demonstrated by experiments with Caesium and Rubidium which are analogues of K+ (Bordron et al., 2019; Göransson et al., 2008; Silva et al., 2011).

Depending on the K^+ concentration in the rhizosphere, K^+ absorption by the roots can be either a « passive » or an « active » process (Glass, 2005; Maathuis and Sanders, 1996). Passive absorption takes place through specific ion channels, also known as low-affinity

transporters (LATS) and requires a high K^+ concentration in the soil solution since it relies on the electrochemical gradient. The active process operates through H^+-cotransporters (symporters) known as "high-affinity" transporters (HATS; Maathuis, 2009), operating at lower K concentrations in the soil solution. However, recent dry laboratory experiments show that this classification may be obsolete for describing the uptake of K by plants (Dreyer and Michard, 2020).

Total K^+ concentration in the root cells vacuoles is variable and could be a signal for HATS (Walker et al., 1996). In *Arabidopsis* roots, HATS are further activated by reactive oxygen species (ROS), that have accumulated at the root tip, quickly after a K deficiency is sensed by the plant (Adams and Shin, 2014). This is the main identified process by which K^+/H^+ symporters are activated, and it is remarkable that ROS signal that activates HATS also favours root tip elongation (Adams and Shin, 2014). There is a tight correlation between the absorptions of $NO3^-$ and K^+, which could participate in maintaining a charge balance in the xylem sap (Raddatz et al., 2020). Sodium (Na+) can act as a substitute to K+ for some osmotic functions, as shown by Na supplementation experiments for *Eucalyptus* in the field (Almeida et al., 2010;

Battie-Laclau et al., 2014b) as well as in nutritive solution (de Souza Mateus et al., 2019), even though high Na concentrations are detrimental. There is also a need for the plant to maintain a balanced K^+/Na^+ ratio (Cuin et al., 2008). In this context, K + HATS can be Na -induced (Glass, 2005), notably at low Na^+ concentrations in the soil solution (Chérel et al., 2014).

It is not straightforward to assess which of the "active" or "passive" absorption processes are mostly operating in highly fertilized tropical *Eucalyptus* plantations. They grow on severely K-deficient soils but are highly supplemented by fertilizer inputs, delivered at the beginning of the rotation (ref; Fig. 1). A shift from LATS- to HATS-dominated K^+ absorption is thus likely along the rotation and down the vertical root profile, correlating with changes in K contents in the soil solution.

The actual role of the mycorrhizal symbiosis in K absorption is still poorly understood. Ectomycorrhizal fungi have been observed on roots of planted *Eucalyptus* (Lambais et al., 2014; Robin et al., 2019), and a ectomycorrhizal inoculation of *Eucalyptus globulus* growing on ultramafic soils (with toxic levels of heavy metals and low K availability) increased K uptake by plants (Jourand et al., 2014). It is therefore likely that ectomycorrhizae provide part of the K requirements when its availability in the soil is low.

3.2. K Transport in the xylem

Once K has been absorbed by the roots, it can be translocated to newly forming organs. This happens through an upward xylem flux. As for K absorption by roots, a channel for K loading in the xylem is activated by ROS (mainly H_2O_2) that are downregulated in case of high K^+ concentrations (Chérel et al., 2014). K^+ in the xylem ascending flux serves as a counter-ion to the anions and plays a role in electrical neutralization (Maathuis, 2009), as it does in plant cells (Chérel et al., 2014).

3.3. Foliar Leaching, resorption and remobilisation from stemwood

Foliar leaching (also known as "recretion" in some sources) is the passive loss of nutrients by leaves through the exchange of elements between the leaf and the aqueous solution (Tukey, 1970). Along with the washing of dry particles deposited on leaves between rainfall events, foliar leaching brings, via throughfall and stemflow, a non-negligible flux of K to the soil in forests (Dezzeo and Chacón, 2006; Van Langenhove et al., 2020). In subtropical forests one year of foliar leaching can be larger than the foliar nutrient stocks (Lin et al., 2001). In temperate deciduous forests the foliar leaching flux is smaller but still can represent half of the resorption flux (Duchesne et al., 2001). In *Eucalyptus* plantations, however, the foliar leaching flux of K (amounting to 0.42 gK/m²/yr at the Itatinga site, Fig. 2) is much lower than the resorption flux of K. Resorption describes a generally active recycling process that happens during leaf senescence and consists in the remobilisation of nutrients from leaves that can then be re-allocated to growing organs. As for other mobile nutrients, K resorption can be described as a function of K concentration in the foliage with a simplified non-linear equation (Achat et al., 2018). The resorption efficiency computed from K concentration in living and dead *Eucalyptus* leaves at Itatinga was 79%, very close to the generic average value of 80% for trees (Achat et al., 2018). The annual flux of K resorption from leaves was around 1.9 gK/m²/yr in our fertilized *Eucalyptus* plantations (Fig. 2). K resorption from leaves account for 40 to 75% of the annual K requirements in *Eucalyptus* plantations (Laclau et al., 2010), which underlines the importance of this process for K availability at the plant level. Similarly with the foliar resorption flux, a drop in K concentration from the outer rings to the inner rings in stem wood shows that K is strongly remobilized during wood ageing (Ortega Rodriguez et al., 2018; Laclau et al., 2001). The amount of K remobilized in stemwood from 3 to 4 years after planting was estimated at 2.7 g/m²/yr in fertilised *Eucalyptus* plantations (Sette et al., 2013).

3.4. Internal K cycling

Once remobilized from leaves, K is cycled through the phloem. The downward phloem K flux has been estimated to be about 50% of the upward xylem flux (Marschner et al., 1996; Peuke, 2010; Sustr et al., 2019). Since there is low evidence of translocation of nutrients from the phloem to the xylem (Marschner et al., 1996), cycling of potassium through the phloem down to the roots and back into the xylem again can be seen as a way to re-allocate K to where it is most needed (i.e. shoots). Moreover, high potassium concentrations in the phloem make a higher sap flow possible, which in turn enhances photosynthate exports from shoots to roots (Marschner et al., 1996). This effect of sap K concentration on phloem sap flow is most likely due to higher osmotic pressure in sieve tubes (Mengel and Haeder, 1977). Another benefit of high concentrations of K in the xylem (that can only be sustained through high K recycling) is through its use as a counter-ion to anions (Marschner et al., 1996; Peuke, 2010) allowing to maintain the anion-cation balance in the plant. While Dreyer et al. (2017) and Marschner et al. (1996) proposed that phloem K concentration could be used as a signal for K absorption by roots, Peuke (2010) found no evidence of a relationship between phloem K concentrations and uptake of K by the roots and discuss whether the concentration of sugars in the phloem might be a signal of nutrient deficiency. The last reason that could explain the recirculation of K in the phloem is that the K^+ ions act as a 'mobile battery' (Dreyer et al., 2017; Gajdanowicz et al., 2011). This functioning could be useful in the case of low ATP availability for the process of sucrose loading into the phloem (that goes against a concentration gradient). Its working principle is based on the gradient between apoplastic and cytosolic K + concentrations. Specific channels allow K^+ to diffuse to the apoplast and increase an electric gradient which in turn allows sucrose to be transported from the apoplast to the cytosol (Dreyer et al., 2017).

4. Ecophysiology of wood growth limitation by the availability of K

While understanding how the K circulates through the ecosystem is essential to pinpoint the processes limiting the availability of K for trees, it does not reveal why K deficiency has a negative impact specifically on wood production. In the following section, we first present the main effects of K deficiency on the processes that govern the carbon-source activity. We will then present the processes related to the activity of carbon sinks, with an emphasis on wood and root production. All processes described here are summarized in Fig. 3.

4.1. Influence of potassium availability on carbon assimilation

Here we describe the direct effects of K on the carbon assimilation process independently of interactions with the water cycle, through its influence on leaf morphogenesis and the photosynthetic capacity of leaves.

4.1.1. Leaf morphology and development

One of the essential roles that K^+ plays in plants is the maintenance of cell turgor needed for leaf expansion (Marschner, 2011). Fully developed *Eucalyptus* individual leaves have a smaller area under potassium deficiency (Battie-Laclau et al., 2013). The cause of this leaf area difference seems to vary between plants since it is due to smaller final leaf cell size in *Eualyptus* (Battie-Laclau et al., 2013), while it was argued that it was due to a lower number of cells in cotton (Gerardeaux et al., 2010).

However, there is no difference in individual leaf area between K-supplied and Na-supplied trees in these plantations. Pressure-volume curves suggest that the differences in individual leaf area between K-deficient and fertilized trees are mainly due to higher cell turgor shared by potassium and sodium resulting from higher concentrations of
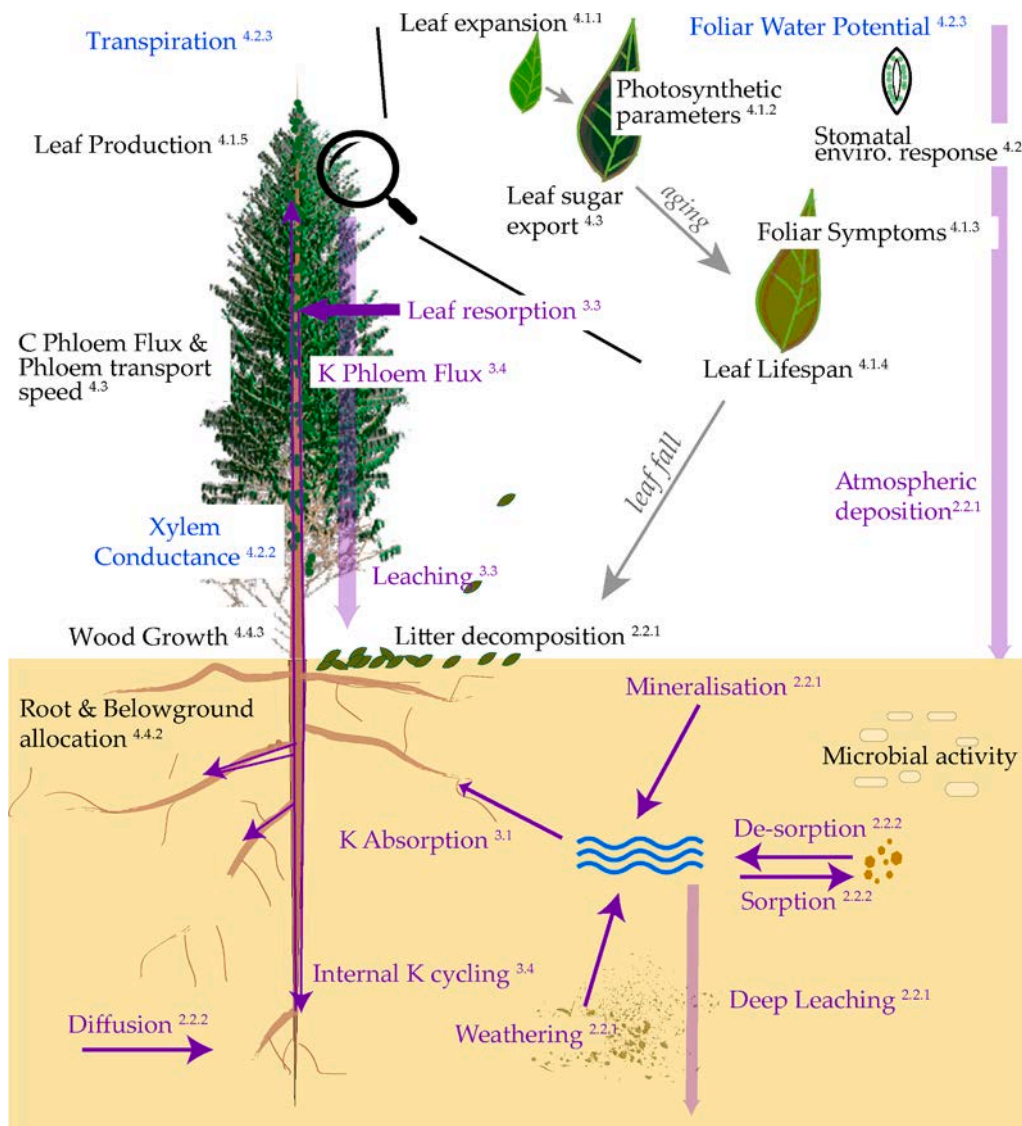
Fig. 3. Processes of interest for the limitation of growth by K. The processes and fluxes directly linked to the K cycle in the system are represented in purple. The processes related to the water cycle are represented in blue. The processes closely linked to the C cycle are represented in black. The numbers appearing in exponents beside process names refer to the section describing this process in the text. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

osmotica increasing both palisade cell diameters and the size of fully expanded leaves. K-deficiency further translates in the loss of leaf mesophyll structure, which leads to a lower leaf intracellular air space in comparison with K-supplied trees (Battie-Laclau et al., 2014a). Both influences of K-deficiency on leaf morphology and leaf anatomy in *Eucalyptus* trees could contribute explaining the decrease of leaf photosynthetic capacity described more precisely below.

4.1.2. Leaf photosynthetic capacity

The relationship between leaf nutrient content and photosynthetic capacity is long-proven and robust (Evans, 1989; Walker et al., 2014). The relationships between leaf nutrient contents and photosynthetic capacities were studied mainly for N and P, which were supposed to be the most limiting nutrients for tree growth in the majority of terrestrial ecosystems (Elser et al., 2007). A much smaller number of studies also dealt with the effects of K deficiency on photosynthetic capacity of leaves. Those studies have shown a good correlation between the leaf photosynthetic capacity and K concentration in almond (Basile et al., 2003), olive (Erel et al., 2015), hickory trees (Shen et al., 2018) and *Eucalyptus* (Christina et al., 2015).

In these studies, K deficiency hampers the leaf photosynthetic capacity mostly through non-stomatal limitations (Hu et al., 2019; Tränkner et al., 2018). Even though soil K availability has a strong effect

on stomatal movement and thus conductance, the lower leaf conductance in K deficient trees seemed to have low or no effects on carbon assimilation. The limitation of assimilation could be explained by multiple other reasons: biochemical effects (through maximum rate of carboxylation, Vcmax, and maximum rate of electron transport, Jmax), mesophyll conductance (g_m) effects (the conductance of CO_2 from substomatal cavities to carboxylation sites) or carbohydrate accumulation (negative feedback on photosynthesis; Ainsworth and Bush, 2011). Studies investigating the influence of K deficiency on biochemical aspects of photosynthesis are contradictory (Gvozdevaite et al., 2018; Jin et al., 2011). On the other hand, the decline of mesophyll conductance in conditions of K deficiency is consistently reported, including in *Eucalyptus* trees (Battie-Laclau et al., 2014a; Lu et al., 2019, 2016; Shen et al., 2018). This decline of g_m has been attributed to a lower area of chloroplasts exposed to intercellular air space and thicker cell walls in K-deficient rice plants (Xie et al., 2020).

The last factor likely to explain the reduction of leaf photosynthetic capacity in K deficient leaves is the accumulation of sucrose in leaves (Cakmak et al., 1994) due to lower phloem sucrose loading (see Section 4.3). Sucrose also serves as a replacement for K^+ 's osmotic properties (Hermans et al., 2006). The accumulation of sucrose in leaves accompanied by a decrease in sucrose stem content has been observed in K-deficient cotton plants (Zhao et al., 2001) and supports the hypothesis of

a lower loading of sucrose into the phloem. In palm trees, both very high K supply (toxic) and low K supply lead to higher leaf dark respiration compared to the control treatment (Cui et al., 2019).. This is a symptom of sucrose accumulation in the leaf because a relationship exists between the leaves' carbohydrate content and dark respiration. Further studies are needed to explain the underlying processes.

4.1.3. Symptoms of K deficiency at the leaf level

K deficiency manifests in leaves through discoloration (e.g. yellowing, or turning purple in *Eucalyptus* trees) and progressive leaf margin necrosis (Ericsson and Kähr, 1993; Battie-Laclau et al., 2013; Silveira et al., 2000). The purple colour is related to the accumulation of anthocyanins, concurrent with a decrease in chlorophyll concentration (Battie-Laclau et al., 2013), which could explain the decrease in photosynthetic capacity associated to symptoms (Battie-Laclau et al., 2014a). The anthocyanins may help with nutrient resorption (Duan et al., 2014; Hoch et al., 2003). They further have a photoprotective function (Close and Beadle, 2003) and could help preventing the photooxidative stress caused by reduced photosynthetic capacity of K-deficient leaves (Marschner and Cakmak, 1989).

4.1.4. Leaf lifespan

Leaf lifespan (LL) can greatly influence the carbon, water, and nutrient cycles through e.g., modifications of leaf area index as well as a faster cycling of nutrients in the system. The changes in LL are central in the response of *Eucalyptus* stands to K availability. While the mean LL of K fertilized *E. grandis* trees was 149 days at the Itatinga site, the LL of K-deficient trees was only 25% to 50% shorter (75 to 111 days) (Battie-Laclau et al., 2013; Laclau et al., 2009). This is consistent with observations of reduced LL under K deficiency in other species such as sugar Maple (Acer saccharum; Wilmot et al. (1996)) and north American spruces (Driessche and Ponsford, 2011). Declining photosynthetic capacities over the ageing of K-deficient leaves, leads to a decline in nutrient use efficiency (the ratio of assimilated carbon to K present in the leaf). This in turn could lead to accelerated senescence that would allow K to be reallocated to newly formed leaves.

4.1.5. Consequences for GPP

Leaf biomass production (leaves produced per unit time) is similar in K-deficient and K-fertilized *Eucalyptus* stands at both the stand scale (Epron et al., 2012) and at the branch scale(Battie-Laclau et al., 2013). However, because of the effects of K availability on leaf development, morphology and lifespan described in Section 4.1, the total leaf surface is lower under K deficiency. Combined with a lower photosynthetic capacity per unit of surface leaf, the GPP is lower in K-deficient stands.

4.2. Potassium-induced changes to the water cycle

4.2.1. Influence at the ecosystem scale

Characterizing the water economy of the plant is essential to understand C-source limitations. Both water and carbon cycles are interdependent (Law et al., 2002) and water availability has a strong impact on GPP through its effects on stomatal opening. K is a central element for the water cycle as it is necessary for stomatal function, but it also plays a role in osmotic adjustment and xylem conductivity as described below.

4.2.2. Effect of K on tree hydraulic conductance

Leaf and xylem hydraulic conductance is essential when considering the water cycle since, in combination with evaporative demand and soil water availability, it influences tree transpiration. Ultimately, this impacts carbon assimilation through the closing or opening of the stomata.

A higher K content in the xylem sap is associated with a higher xylem hydraulic conductivity (Oddo et al. (2020) in grapevine; Gascó et al. (2006) in laurel). The exact mechanism is still unknown, but K^+ concentrations influence the conductivity of the xylem pits, possibly through changes in pectin volume (Nardini et al. (2011)).

However, the positive effect of K fertilization on LAI, caused by both an increase of the leaf individual sizes and leaf lifespan, results in decreased sapwood-to-leaf area ratio (i.e., Huber value) throughout the rotation in K-fertilized *E. grandis* stands (unpublished data). Hence, the whole-tree leaf-specific hydraulic conductance at the end of the rotation (i.e., 6 years after planting) is higher in K-deficient than in K-fertilized stands (unpublished data). K fertilization thus increases the hydraulic constraint on water use in *E. grandis*.

4.2.3. Influence on stomatal conductance and stand transpiration

K deficiency has a negative impact on leaf stomatal conductance. This is explained by the central role K^+ ions play in stomata mobility (Marschner, 2011; Nieves-Cordones et al., 2019). K deficiency impairs the normal functioning of stomatal opening, with, in *Eucalyptus*, a much lower sensitivity of stomatal conductance (g_s) to vapor pressure deficit (VPD) and predawn water potential (ψ_{pdw}) in K deficient trees (Battie-Laclau et al. (2014b)). Reference g_s corrected for daily variations in VPD and seasonal variations in ψ_{pdw} was 2 to 5 times higher in the fertilised (500–1100 $mmolH_2O.m^{-2}.s^{-1}$) than in the non-fertilised trees (200 $mmolH_2O.m^{-2}.s^{-1}$) (Battie-Laclau et al., 2014b).

K-fertilized *E. grandis* stands transpire 1.7 times more than K-deficient stands (Battie-Laclau et al., 2016). A lower LAI explains most of this strong transpiration decrease in K-deficient stands (Battie-Laclau et al., 2014b; Christina et al., 2018). A consequence is that K-deficient stands tap less in the deep soil profile and water table (which follows rooting depth), which is decisive for the stand functioning during droughts (Christina et al., 2018). Hence, the K-deficient stands are less water-stressed than K-fertilized stands. Indeed, both predawn and midday leaf water potentials were higher (i.e. less negative) in K deficient stands, while K-deficiency did not influence the water potential gradient (from root to shoot under transpiration) (Battie-Laclau et al., 2014b). Besides, transpiration per unit leaf area is higher in K-deficient than in K-fertilized stands throughout the rotation of *E. grandis* (Asensio et al., 2020; Battie-Laclau et al., 2016). These evidences of alleviated water stress in K-deficient stands, based on *in-situ* physiological monitoring are further corroborated by omics approaches (Favreau et al., 2019; Ployet et al., 2019).

4.3. Transport limitations

The carbon fixed by the leaves is exported to fuel the growth and metabolic activity of other organs and tissues. Here K also plays a role as it is necessary for the loading of sugars in the phloem. A low availability of K can lead leaves to store C, principally as soluble sugars (Cakmak et al., 1994; Marschner et al., 1996) which in turn downregulates photosynthesis. In *Eucalyptus* stands, while concentration of sugars in the phloem is invariant between K-deficient and K-fertilized trees (Battie-Laclau et al., 2016; Epron et al., 2016), a field study based on ^{13}C labelling showed a strong negative effect of K deficiency on the transport velocity of sugars through the phloem (Epron et al., 2016). This might be a result of changes in phloem anatomy (sieve tubes) that impedes the phloem flow. This low rate of phloem transport could lead in turn to a low rate of sugar export from leaves (Cakmak, 2005), which might lead to degraded photosynthetic capacity of leaves (Battie-Laclau et al., 2014a). This is consistent with the appearance of K deficiency symptoms on leaves (see Section 4.1.3), as anthocyanins could be acting as sinks for excess C in leaves (Pourtau et al., 2006).

4.4. Changes in carbon partitioning

The impacts of soil K availability on wood production depend directly on Gross Primary Productivity (GPP) as described above in detail, but also greatly on the partitioning of C between plant organs. We first present the global effects of K availability on GPP partitioning, then more specifically the effects on roots biomass. We were not able to find any evidence in the literature of a direct influence of soil K availability

on the respiration of organs per unit of organ mass, except for dark leaf respiration (Christina et al., 2015). However, an indirect effect through the reduced living biomass under K deficiency leads to a reduction in stand-scale maintenance respiration. Some authors have also suggested that carbohydrates are retained in shoots and more specifically in leaves (Hermans et al., 2006), which could also impact allocation patterns.

4.4.1. Aboveground partitioning of GPP

Potassium has a strong effect on carbon partitioning among the different organs of trees. As developed in the Section 4.1, the total GPP is lower in K-deficient than in fertilized tropical *Eucalyptus* plantations. On the same species, *in* situ measurements along a full rotation further showed that a lower proportion of GPP was allocated aboveground in K-deficient stands compared to fertilized stands (Epron et al., 2012). Root-shoot ratio was also increased in the mature K deficient stands (Fig. 2, −K: 0.27, +K: 0.19), in contradiction with decreases in R/S ratio under K deficiency observed in other plant species (Gerardeaux et al., 2010).

While the cumulated biomass of leaves produced was similar along a *Eucalyptus* rotation when comparing K-deficient and K-fertilized stands, the ratio of this biomass to cumulated GPP, which is a proxy of the fraction of carbon allocated to leaves, was doubled in K-deficient trees because of the lower GPP (Epron et al., 2012).

4.4.2. Belowground partitioning of GPP

Although fine roots were much less studied than aboveground tree compartments, they are also a major C-sink. There is little information on the response of fine root biomass production to K deficiency. The fraction of GPP allocated belowground is generally reduced in response to fertilization, which leads to a higher aboveground primary production (Ryan et al., 2004). It complies with the theory that carbon allocation tends to optimize resource acquisition to maximize growth (Thornley, 1972).

The response of *Eucalyptus* trees to K fertilization is in accordance with these results: GPP was drastically increased (see Section 4.1) while the total amount of carbon allocated belowground was not significantly affected by K fertilization in a field experiment at Itatinga (Epron et al., 2012). Therefore, the fraction of GPP allocated belowground was decreased by K fertilization.

It seems that the fine root biomass is lower in conditions of K deficiency, contrary to what usually happens in case of N and P deficiencies (Sustr et al., 2019; Fontana et al., 2020). Fine root biomass, specific root tip number and specific root length were shown to increase in the mineral soil in response to K fertilisation in spruce stands (Wang et al., 2016). In *Eucalyptus* plantations, fine root biomass in K-deficient stands was lower than in K-supplied stands, but precise measurements of this compartment remain challenging (Bordron et al., 2019; Christina et al., 2015). The lack of influence of K fertilization on total belowground carbon flux while fine root biomass increased in *E. grandis* plantations (Epron et al., 2012) suggests that K deficiency could decrease fine root lifespan and/or increase C exudation by roots. This pattern should be confirmed by direct measurements.

4.4.3. Stoichiometric limitations of wood growth

Potassium has a direct effect on cambial activity and wood formation (Ache et al., 2010; Langer et al., 2002; Wind et al., 2004) through modulating cell expansion and vessel size (Fromm, 2010). K fertilization influences wood physiological characteristics, with positive effects on fibre length and (weakly) wood density (Sette Jr et al. (2012)). In *Eucalyptus* plantations, wood as a tissue has apparently only little stoichiometric flexibility as shown in Fig. 2 with similar K concentration in the wood between K-fertilized and K-deficient trees (Sette et al., 2013). This contrasts with all the other tree organs (except fine roots; Fig. 2) exhibiting lower K concentrations in K-deficient trees than in fertilized trees. We hypothesize this lack of stoichiometric flexibility as impacting wood growth in two ways in K-deficient soils where K is rare: (1) directly (K-sink limitation of wood growth) because an absence of stoichiometric

flexibility sets a limit to the amount of wood that can be grown by trees, (2) indirectly because the inflexible investment of K in wood restricts its investment in others, stoichiometrically flexible organs and notably leaves (Fig. 2), thereby biomass and thus their photosynthetic activity.

5. Potassium-related processes in forest functioning models

The K-limitation of wood growth can stem from a variety of processes (Fig. 3). Here we identify the priorities when it comes to the integration of K-related processes in eco-physiological models that initially focus on the carbon and water cycles. These a priori modelling choices will need to be refined by implementation, testing and sensitivity analyses in forthcoming studies. We focus here on tropical forests, and in particular our model ecosystem (*Eucalyptus* plantations), while trying to stay as generic as possible. To this aim, the modelling options retained are based on mechanistic formulations. We address: (1) Processes linked to the canopy (influencing GPP), (2) Processes linked to the water cycle, (3) Processes of organ sink activity, (4) Processes of K cycling in the soil and in the plant.

The effects of K availability on leaf biomass and photosynthetic capacity need to be explicitly considered, as experimental observations suggest a strong effect, especially in fast growing species such as *Eucalyptus grandis*. While leaf production in terms of the number of new leaves per unit of time does not change in K-deficient stands, the maximum leaf surface of developed leaves and leaf lifespan were strongly reduced under low K availability (Section 4.1). A leaf-cohort model, such as the one developed for *Eucalyptus* (SLCD; Sainte-Marie et al., 2014) is ideal to this respect. This type of model allows for fine control over leaf development and senescence through functions linking leaf expansion and leaf aging to K availability in the plant, e.g., considered as a function of the xylem K stock (see below).

The impact of K availability on the photosynthetic capacity of leaves can be modelled in two ways: (1) through a direct relationship between the cohort K content and the photosynthetic parameters (e.g. Vcmax, Jmax in the Farquhar et al. (1980) model), (2) through the modelling of the proportion of leaf surface discoloured ("symptoms", Section 4.1.3) in K-deficient leaves and the direct link observed between the symptom surface and the leaf -scale photosynthetic parameters (Battie-Laclau et al., 2014a). Datasets allowing to evaluate the link between leaf K concentration and photosynthetic parameters are scarce for trees, while leaf symptom surface might be easier to measure and implement, and the relationship between leaf symptom surface and leaf photosynthetic capacity is supposedly more generic, advocating for the second option. Whatever modelling options, a modulation of Farquhar photosynthetic parameters should be implemented to represent the direct biochemical limitation of photosynthesis in function of the leaf cohort K content. Furthermore, K-deficiency impacts leaf structure and explicit representation of leaf mesophyll conductance (g_m) would be necessary (Knauer et al., 2019).

The water cycle in forests impacts wood productivity mainly through feedbacks between water availability, stomatal conductance, and water potential inside trees. On top of the indirect effect of K on the water cycle (e.g., through changes in leaf area and thus transpiration, Section 4.1.1), representing the direct impact of K on the forest water cycle is necessary. A model representing plant hydraulics, and the link between the leaf water potential and stomatal conductance (e.g. Tuzet et al., 2003) is a good option for this since it allows to represent the impact of K on both the xylem conductance and stomatal conductance. The leaf K concentration influence on both the residual leaf conductance and the slope between *gs* and carbon assimilation should be integrated in the model. Xylem conductance for water can be modelled as a function of the xylem K concentration.

At this stage, a mechanistic representation of the impact of K availability on the allocation of carbon to the tree organs seems out of reach. For wood, as for roots, the K-limitation of sink activity will require empirical modulation of allocation coefficients (i.e., the share of NPP

directed to each organ, see Delpierre et al. (2016b)). Another constraint could be a direct stoichiometric limitation since wood shows non-flexible K concentrations (Fig. 2, Section 4.4.3).

Circulation of K in the trees is essential since, for instance, it regulates the K concentration of newly formed organs, allows for a feedback on root absorption (Section 3.4) and modulates the xylem hydraulic conductance (Section 4.2.2). An explicit xylem and phloem K circulation model appears thus necessary. These types of models have already been developed for phloem, xylem sap flow and photosynthate export (Hölttä et al., 2006). The modelled xylem K stock would determine the K available for the formation of new leaves. The phloem K stock would allow for the recycling of unused xylem K and the K provided by leaf resorption. Phloem K is then available for allocation to wood and root growth, with eventual stoichiometric limitation. The K phloem content would in turn allow for K tree availability to be a feedback for absorption of K from the soil. Leaf K resorption can be simulated using the linear relationships found between nutrient resorption and leaf K content in temperate species (Achat et al., 2018) and confirmed in *Eucalyptus* (see Section 3.3). Leaf K leaching, an important flux of K in certain systems, can be simulated using relationships that show a linear relationship with throughfall quantity (Crockford et al., 1996; Lin et al., 2001). Remobilisation of K from aging wood can be modelled using the framework developed by Saint-Andre et al. (2002).

Root absorption of K will be a function of the plant demand, resulting from the concentration of K in the phloem and of soil supply that can be modelled using a mass flow and diffusion model (Barber, 1995; Leadley et al., 1997). Depending on the buffer power of the soil, the absorption by roots will be more dependent on mass flow (low buffer power) or diffusion (high buffer power). Soil K availability is determined by four main sources: fertilisation and deposition, primary rock weathering, and the leaching from litter and throughfall. The leaching of K from the litter is very rapid and in our opinion is not a bottleneck for K availability. There is also contradicting evidence as to whether K can be limiting for the decomposition processes of organic matter in the soil: this effect is most likely negligible and should not be considered in a model as a first hypothesis. The flux of K from throughfall can follow the flow of water in the soil. We suggest that measurements and modelling investigations in the future should focus on weathering fluxes. These fluxes are decisive to determine K availability in forest ecosystems. Experimental estimates vary widely (Section 2.2.1) and do not allow to prescribe any specific modelling options. These fluxes will vary greatly depending on the soil type and parent rock. While our review has clearly shown that several processes exist and could be included in carbon and water process-based models, their relative importance compared to other processes will need to be explored in the model through sensitivity analyses. Thankfully, we have seen that the effect K has on processes is rather different from the effects of P and N. We have also found no major interactions between the cycles of other nutrients and K. This indicates that is should be possible to model K effects independently of other nutrients.

6. Conclusion

Potassium is an essential nutrient in forest ecosystems. It can be strongly limiting tree growth in highly weathered soils, as in tropical *Eucalyptus* plantations. In this review, we have highlighted the main processes limiting K availability to the trees and the metabolic processes that are affected by low K availability. K influences with both the water cycle and the carbon cycle as it impacts light interception by the canopy, C fixation and C export from leaves to sinks.

With this review, we identified the major priorities for implementing the K cycle in eco-physiological forest models. Yet, the relative importance of each physiological process influenced by K availability on the response of wood production remains unknown. The mechanistic modelling of key processes is needed to quantify their relative importance. Eco-physiological models already incorporate most of these processes and their functioning can be modulated by K availability. N and P

cycles and their effects on forest functioning have been successfully implemented in eco-physiological models. Since K is generally in ionic form, it has a different behaviour than N and P and some new processes will need to be represented to gain insight into its effects on wood growth. We suggest that the effects of K limitation on leaf ontogeny and photosynthetic capacity are central for determining the acquisition of carbon in K-limited forest ecosystems. Leaf ontogeny has strong effects on the canopy, which is crucial for light interception and the tree water economy. Secondly, we propose a new internal K biological cycle, which in turn will allow for K feedbacks at the tree level. If more information on phloem dynamics become available, this will allow interactions between K availability and C export from leaves, a process that is still hard to quantify. Lastly, we identify the K weathering flux to be central when considering K limitation in forest ecosystems. Simulating these processes is essential to understand K limitation at a global scale, and the evolution of this limitation under future climate change in relation with other nutrient limitations.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119275.

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Chapter 3

Potassium-limitation of forest productivity, part 1: A mechanistic model simulating the effects of potassium availability on canopy carbon and water fluxes in tropical eucalypt stands

Potassium-limitation of forest productivity, part 1: A mechanistic model simulating the effects of potassium availability on canopy carbon and water fluxes in tropical eucalypt stands

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Abstract

The extent of the potassium (K) limitation of forest productivity is still open to debate but it is probably more widespread than previously thought. There is evidence that K-limitation could influence the future response of forests to global change. Tropical Eucalypt plantations in Brazil are a good example of ecosystems that are strongly K-limited. To understand the effects of K-limitation on primary production we have developed the first ecophysiological model simulating the K cycle and representing its effects on the carbon (C) and water cycles. In this first paper of a series of two, we focused on the representation and simulation of the limitation of the gross primary productivity (GPP) by K availability. We used results from large-scale fertilisation experiments as well as C flux measurements in two tropical Eucalypt plantations to parameterize the model. The model was parameterized for fertilised conditions and then run in an unfertilised stand with the same parameterisation excepted the initial fertilisation amount. Simulations showed that K-deficiency could limit GPP by more than 50% during a 6-year rotation, a value in agreement with estimations from literature. Effects of K-deficiency on canopy transpiration and water use efficiency were also reported

and discussed. Through a sensitivity analysis, we used the model to identify the most critical processes to consider when studying K-limitation of GPP. The external inputs of K to the system, such as the deposition and weathering fluxes, and parameters regulating the internal fluxes of K were critical for the response of the system to K deficiency. Litter decomposition processes were of lower importance. The new forest K-cycle model developed in the present study includes multiple K processes interacting with the carbon and water cycle, and strong feedbacks on GPP along forest growth were outlined.

Keywords

GPP, Potassium, Eucalypt plantations, K-limitation, process-based modelling

Contents

1 Introduction

Nutrient limitation of plant growth has been well-established since the 19th century (Liebig, 1841). Several macro- (N, K, P) or micro-nutrients can limit the growth of plants (Townsend et al., 2011). The nitrogen (N), phosphorus (P) and potassium (K) limitation of plant growth is a well established phenomenon, as demonstrated by the widespread use of NPK fertilisers in agriculture. It has however, less extensively been studied in natural ecosystems. This probably stems from the fact that, as opposed to agrosystems which are the subject of recurrent "experiments" of fertilisation, natural ecosystems, and particularly forests, are rarely fertilized. Counter-examples in forestry include amendments assays (Bonneau, 1972; Guitton et al., 1988) and other experiments (Hyvönen et al., 2008). This limitation of primary production by nutrients will get more palpable as the atmospheric concentration of CO_2, one of the substrates limiting photosynthesis, increases (Terrer et al., 2018; Jonard et al., 2014; Penuelas et al., 2020).

For forest ecosystems, the focus has been mainly on N- and P-limitation and co-limitation, since both elements are generally considered to be the most limiting for global forest growth. N-limitation is supposedly more widespread in temperate and boreal forest ecosystems while tropical forest systems are thought to be more P-limited (Du et al., 2020). This paradigm neglects other macro- and micro-nutrients as causes of limitation or co-limitation. In the tropics, evidence from *Eucalyptus* plantations in Brazil suggests that K and micro-nutrients are often the primary limiting elements for productivity (Silveira et al., 2000; Cornut et al., 2021). More generally, the K-limitation of forest growth appears to be a widespread phenomenon, that has been overlooked so far (Tripler et al., 2006; Sardans and Peñuelas, 2015). Beyond its role on forest growth, K is also an element of geopolitical importance (Nardelli and Fedorinova, 2021) since it is an essential component of most agricultural fertilisers and potash sources are spread among few countries (Prakash and Verma, 2016).

Despite its importance for forest ecosystems, few models have so far been developed to investigate the K cycling in forest ecosystems. Some models focused on the impact of anthropogenic perturbations and management on multiple nutrient cycles (Johnson et al., 2000), and among them the cycle of K in temperate forests (e.g. models NuCM, Liu et al. (1992); ForNBM Zhu et al. (2004)). Potassium models for annual crops have also been developed and focused mainly on the K dynamics in soils and uptake by the plants (Seward et al., 1990; Silberbush and Barber, 1984). To the best of our knowledge only one K model, developed for arable crops, has to date formalised the link between K availability and plant pro-

ductivity, through an empirical relationship (Greenwood and Karpinets, 1997). This feedback had previously been deemed necessary to predict K uptake more accurately (Seward et al., 1990). Beside these studies, that explicitly modelled the ecosystem K cycle at a broad scale, some papers have quantified through ecophysiological modelling the sensitivity of ecosystem functioning to the availability of K. For example, the influence of K on the Gross Primary Productivity (GPP) (Christina et al., 2015) and water fluxes (Christina et al., 2018) of tropical *Eucalyptus* plantations has been quantified with the MAESPA model, using a specific parameter set for each of the K-fertilised / non-fertilised treatment. In these works, the K cycle was not explicitly modelled.

Modelling the various aspects of the ecosystem cycle of K is a worthwhile endeavour (see Reed et al. (2015) for P), since K influences the ecosystem water and carbon cycles in many ways (Cornut et al., 2021). Indeed, K availability has a strong influence on the canopy photosynthesis (i.e. the *source* of carbon for the plant) through its role on leaf development and senescence. Under low K availability, leaf expansion is reduced by up to 30% (Battie-Laclau et al., 2013) and leaf lifespan is strongly reduced, with estimated reductions from 25% (Laclau et al., 2009) up to 50% (Battie-Laclau et al., 2013). The resulting loss in leaf area, combined to K-deficiency anthocyanic (purple) symptoms that diminish the leaves' photosynthetic capacity (Battie-Laclau et al., 2014a), lead to a strong reduction of GPP (Epron et al., 2012). While evidence is still scarce, it has been shown that K concentration in the xylem sap has an effect on the xylem conductivity (through a change of xylem pit conductivity, Nardini et al., 2010) and its response to water stress (Ployet et al., 2019). Since the fluxes of water and carbon are tightly coupled through the opening of stomata, this will also have an effect on GPP and on the water-use efficiency of the ecosystem. While it is more challenging to study the activity of the plant's carbon *sinks* (i.e. the transport and use of carbohydrate molecules for the maintenance of tissues, growth, constitution of reserves and defense; (Körner, 2015)), there is evidence that the sinks activity are also influenced by the availability of K. For example, the loading and unloading of sugars from the phloem are affected by K deficiency (Marschner et al., 1996), and more generally, the K nutritional status of the tree has an impact on phloem sap mobility (Epron et al., 2016). Anthocyanic symptoms that develop on leaf margins could be a consequence of the lower ability of K-deficient leaves to export sugars into the phloem sap (Landi et al., 2015). This body of evidence points towards a strong sink-limitation (mostly through the alteration of phloem export capacity) of GPP (Ainsworth and Bush, 2011) under K limitation. More details relating to the influence of K on these sink and source processes can be found in Cornut et al. (2021).

The combined influences of K on C-source and C-sink processes explain the K limitation of productivity. The present study focuses on modelling the influence of K on the C-source (i.e. on GPP), which is a prerequisite before modelling the influence of K on C-sink processes, and a first step to start modelling the K limitation on productivity. Process-based models of the C-source activity (Farquhar et al., 1980) have been developed for more than four decades, which contrasts with models representing the activity of C-sinks (e.g. (Hölttä et al., 2006)) which, while relevant (e.g.Guillemot et al., 2017; Körner, 2015), are relatively new and have not been validated at a large scale. While the N- and P-limitation of GPP have been considered in models at scales from the leaf to the globe (Thum et al., 2019; Goll et al., 2012, 2017; Yang et al., 2014), no process-based model simulating the K cycle and its influence on GPP has been published so far.

The objectives of the present study were thus to:

1. develop a model of the K biogeochemical cycle, coupled to the carbon and water cycles, in forest ecosystems,

2. evaluate the model using carbon and water flux data measured at an eddy-covariance site installed in a fertilised (+K) tropical Eucalypt plantation,

3. quantify the influence of K availability on the carbon (gross primary productivity, GPP) and water (evapotranspiration) ecosystem-atmosphere fluxes and on the water-use efficiency of a tropical Eucalypt stand, through simulations in +K and oK conditions,

4. conduct a sensitivity analysis of the model, with the aim to identify the main processes responsible for the response of GPP to the availability of K at the stand level.

To this end we have developed a new K circulation module in an existing ecophysiological forest model and represented the response of different physiological processes to the availability of K in the plant. The model was parameterized and tested on tropical *Eucalyptus* plantations. Because those ecosystems have a continuous phenology, it required the creation of a leaf cohort model (see e.g. (Sainte-Marie et al., 2014)) that explicitly takes into account the effect of K on different leaf level processes (leaf expansion, lifespan, etc.).

2 Materials and Methods

2.1 Study Sites

2.1.1 Eddy-covariance site (Eucflux)

The Eucflux site is within a 200 ha plantation located in south-eastern Brazil (Sao-Paulo State, 22°58′04″ S and 48°43′40″W, 750 m asl), and managed by the EucFlux project (http://www.ipef .br/eucflux/en/). The precipitation was on average 1430 mm year^{-1}, with a drier season between June and September, and the mean annual temperature was 19.3°C. Soils are deep Ferralsols (>15 m). A clonal plantation of a fast growing *Eucalyptus grandis* × *urophylla* hybrid was established in November 2009 and harvested in June 2017. At the centre of the plot, a flux tower continually measured meteorological variables as well as the fluxes of CO_2 and water vapour between the plantation and the atmosphere, with the eddy covariance technique. The plantation was described in details in Christina et al. (2017); Nouvellon et al. (2010, 2019); Vezy et al. (2018). The plantation was fertilised at planting with 3.0 g/m² of K_2O, 3.3 g/m² of P_2O_5, 1.8 g/m² of N and 400 g/m² of dolomitic lime and trace elements, then at 3 months with 3.6 g/m² of K_2O, 3.12 g/m² of N, at 10 months with 6.72 g/m² of K_2O, 3.08 g/m² of N and at 20 months of age with 15.12 g/m² K_2O. This amounted to a total of 23.60 gK.m^{-2} from fertilisation and resulted in non-limiting nutrient availability for tree growth. This value was higher than the typical 12 gK.m^{-2} added on average in commercial plantations (Cornut et al., 2021).

2.1.2 Fertilisation experiments (Itatinga)

A few kilometres from the eddy-covariance site, under similar climate and soil conditions, a fertilisation trial experiment was installed at the Itatinga experimental station (23°02′49″S and 48°38′17″W, 860 m asl, University of Sao Paulo-ESALQ). A split-plot fertilisation experiment was established there on June 2010, for 6 years. The planted clone was a fast growing *Eucalyptus grandis*. The experimental design was described in detail in Battie-Laclau et al. (2014b). Six treatments (three fertilisation regimes and two water regimes) were applied in three blocks. In the present study, we focus on the +K and oK treatments with normal rainfall regime, which consisted in a non-limiting fertilisation +K (17.55 gK.m^{-2} applied as KCl at planting, with 3.3 gP m-2, 200 g m-2 of dolomitic lime and trace elements and 12 gN m-2 at 3 months of age) and an omission treatment oK where all fertilisation was applied as in +K treatment, except K.

The concentrations of different elements (N, P, K) in the organs (leaves, trunks, branches,

and roots) were measured at an annual time step in 8 individuals of each fertilisation treatment and upscaled to the whole stand using allometric relationships (not shown). Biomass and mineralomass were calculated (using upscaling) from inventories, biomass and nutrient concentration measurements done at 1, 2, 3, 4, 5 and 6 years in each fertilisation treatment. Atmospheric deposition (0.55 gK.m^{-2}.yr^{-1}) and canopy leaching fluxes (0.42 gK.m^{-2}.yr^{-1}) were obtained in a nearby experiment from Laclau et al. (2010).

2.2 Complementary foliar measurements

Surface, mass and K-deficiency symptom development of individual leaves were measured for the studied sites to parameterize the new leaf cohort sub-model and the K-deficiency-symptom area sub-model described below. To this aim, we used the scan pictures (tabletop scanner device model HP Scanjet G4050, 300 dpi) of leaves collected during the biomass samplings at both sites (every six-months at Eucflux and annually at Itatinga), on at least 6 trees per date and treatment and at three crown levels. Individual leaf surfaces as well as the proportion of anthocyanic symptoms on individual leaves were automatically computed from the images. The leaf-scale metrics were up-scaled to stand averages using linear regressions with individual tree D²H (i.e. the product of squared diameter with tree height), for each canopy thirds. Regression were done using the *scikit-learn* python library (Pedregosa et al., 2011). The resulting parameters and functions were then applied to the D²H of trees using inventories of diameter and height of plots. This allowed the upscaling of leaf individual area and symptomatic leaf area in order to compute their plot averages.

2.3 CASTANEA-MAESPA general model presentation

The soil-vegetation-atmosphere carbon and water balance were simulated with the CASTANEA-MAESPA model for the Eucflux and Itatinga Eucalypt plantations. CASTANEA-MAESPA was the merging of the CASTANEA model (Dufrêne et al., 2005) with the MAESPA model (Duursma and Medlyn, 2012), the latter being modified as in Christina et al. (2017). CASTANEA is an ecophysiological model simulating the fluxes of carbon and water between a forest stand (average tree) and the atmosphere at an half-hourly time step. In its basic version, it includes no representation of the hydraulic soil-plant-atmosphere continuum, which is however critical in the context of a coupled carbon-water-potassium model. The MAESPA model (Duursma and Medlyn, 2012) was developed using the above-ground components of the MAESTRA model (Wang and Jarvis, 1990) and the water balance components of the SPA model (Williams et al., 1996). MAESPA is a three dimensional model of light interception, energy balance and carbon and water fluxes. These fluxes are computed from prescribed description of individual trees along time, and at the scale of small volumes of leaves within each tree crown. The soil-plant-atmosphere water continuum is explicitly simulated by MAESPA.

It was not possible to adapt the CASTANEA model, initially developed on temperate Beech (*Fagus sylvatica*) forests (Dufrêne et al., 2005), to the particular study case of tropical *Eucalyptus* plantations, as we did previously for several temperate and Mediterranean species (e.g. Delpierre et al., 2012; Davi et al., 2006; Le Maire et al., 2005). Indeed, tropical *Eucalyptus* plantations grow roots deep in the soil at a very fast pace (Christina et al., 2011), which violates the CASTANEA assumption of a constant rooting depth over the simulation period, and the use of a simple soil water bucket model. The MAESPA model does not have this constraint and can easily be adapted to simulate an increasing amount of extractible water (Christina et al., 2017). Moreover, MAESPA had already been parameterized and applied at the Eucflux and Itatinga sites (Christina et al., 2015, 2017). However, although it simulates fluxes of carbon and water, MAESPA, is not a full carbon balance model, in the sense that it does not simulate the carbon allocation within the plant, litterfall, soil organic matter decomposition, etc. As such, contrary to CASTANEA, MAESPA did not provide alone the structure required to simulate the K balance. The merging of both models in CASTANEA-MAESPA model was therefore chosen as an efficient modelling way, previous to the implementation of the K processes as described below.

The modules of CASTANEA simulating light interception, water interception, carbon allocation and the growth of organs and organ respiration were coupled with the modules

of MAESPA simulating soil water dynamics, leaf photosynthesis, transpiration, and plant hydraulics. Note that in the coupled model, the leaf photosynthesis module of MAESPA was applied to canopy layers of CASTANEA. As such, the coupled model takes the 1-D vertical structure of CASTANEA. This simplified assumption of canopy horizontal homogeneity is valid in these homogeneous plantation at least after canopy closure.

2.4 Model of *Eucalyptus* canopy dynamics

2.4.1 Overview of the leaf cohort model

Highly productive tropical eucalypt plantations in Brazil grow from seedlings to 25 meter high trees in the span of 6-7 years. The plantations present a continuous foliar phenology with leaf production and leaf fall throughout the year. These problematic has previously led to the development of a canopy dynamics model (Sainte-Marie et al., 2014). While this model was sufficient to explain leaf production and leaf fall dynamics, we found it necessary to develop a new cohort-based canopy dynamics model (Summarised in Fig.1). The creation of this model stemmed from the need for the simulation of both K cycling in the canopy and the effects of K on foliar ontogeny. We chose to implement leaf cohorts as the elementary objects for the simulation of the canopy dynamics. The use of a leaf cohort model stemmed from the continuous phenology of *Eucalyptus* trees as well as the importance of K on leaf ontogeny (Laclau et al., 2009; Battie-Laclau et al., 2013). A daily time step was necessary for the simulation of expansion and fall of the leaves of each cohort. All leaves within a cohort were considered to have the same physiological characteristics, same growth and same lifespan. One cohort was characterised by a number of leaves per square meters of ground, individual leaf surface and mass. This new leaf cohort model is described in the next sections, in the case of no limitation by K.

2.4.2 Leaf cohort production

A new cohort was initialised daily. The number of leaves N produced in the cohort was a function of the height increase of the trees. Indeed, in these fast-growing system, most of the new leaves are produced in the top-most part of the crown. The increase in tree height can be computed in the CASTANEA-MAESPA model as the result of increase in trunk biomass, and with allometric parameters relating stand biomass and stand height (see article 3).

The relationship between daily height increase and leaf production was corrected by a

flattening factor. This means that even if the daily height increase was close to zero or even null, leaf production would still happen at a slower but positive rate. The model generated a number of new leaves per m² at a daily time-step following this function:

$$N = \frac{\Delta H + f_p}{1 + f_p} \times \kappa \tag{1}$$

Where N was the daily number of leaves produced in number of leaves per m² and ΔH (m) was the increase in tree height. f_p was the flattening factor, meaning that if $f_p = 0$ then leaf production was linearly related to height increase and as f_p increased, P_{leaf} tended towards a constant function. κ is a conversion factor from height increment to number of new leaves in number of leaves per m of vertical growth per m² of ground. The parameters used here were fitted using experimental data from the fully fertilised stand.

2.4.3 Leaf cohort lifespan

As long as K was not limiting, the lifespan of a cohort was considered to be constant since the leaf lifespan deduced from leaf biomass and leaf fall measurements in fully fertilised stand did not show major trends along the rotation and amplitude of seasonal changes in lifespan was limited (Fig.S3e). Since no mechanistic explanation was available, we abstained from implementing it in the model. For sake of simplicity, we did not consider in the present simulations the fall of leaves subsequent to extreme events (drought, frost, heatwave). Indeed, in the studied sites no large leaf fall due to extreme events were observed. Here the leaf lifespan (LLS) in non-limiting K conditions was fixed to the average measured value of 480 days.

2.4.4 Leaf expansion in surface in the cohort

For a given cohort, individual leaf surface *S* expands from a virtually null surface at initialisation of the cohort, up to a surface of S_{max} (mm^2). The leaf surface followed a sigmoid function (Fig.2a, Battie-Laclau et al., 2013). Leaf surface was a function of time and not thermal time (as for instance in the original CASTANEA model) since no calibration data were available and it was not deemed necessary for this model. Therefore, the daily leaf surface expansion was forced to follow the sigmoid derivative function:

$$\frac{\Delta S}{\Delta t} = \frac{k_S \times S_{max} \times e^{-k_S(t-t50_S)}}{(e^{-k_S(t-t50_S)} + 1)^2} \tag{2}$$

Where $\frac{\Delta S}{\Delta t}$ (mm^2.day^{-1}) was the daily growth in surface of an individual leaf a given cohort, t (days) was the number of days since leaf cohort creation, S_{max} (mm^2) was the (non-limited)

maximum leaf surface, k_S (mm².days^{-1}) was a slope parameter, $t50_S$ (days) was the inflexion point of the original sigmoid of leaf surface increase, therefore was the date of maximum leaf surface increase, and also the date when half S_{max} was reached. The parameters S_{max}, k and $t50_S$ were fitted from measured leaves in expansion (Battie-Laclau et al., 2013) in non-limited fertilisation conditions. Parameters k_S and $t50_S$ were assumed not to vary along the stand rotation. S_{max} was also assumed to be constant since the leaf scans did not show any explainable trends of mean leaf surface during the rotation (Fig.S4).

The total leaf surface of a given cohort was given by the product of S, the surface of an individual leaf and N, the number of leaves in the cohort. The total leaf surface of the stand at a given date was calculated by adding up all the cohort surfaces.

2.4.5 Leaf expansion in mass in the cohort

Individual leaf mass increase within a cohort was similar in shape to the leaf surface increase, but with a temporal shift since leaf mass per area continues to increase when the maximum leaf surface is attained:

$$\frac{\Delta BF}{\Delta t} = \frac{k_{BF} \times BF_{max} \times e^{-k_{BF}(t-t50_{BF})}}{(e^{-k_{BF}(t-t50_{BF})} + 1)^2} \tag{3}$$

Where $\frac{\Delta BF}{\Delta t}$ (g.day^{-1}) was the daily growth in mass of an individual leaf in a given cohort, t (days) was the number of days since leaf cohort creation, BF_{max} (g) was the maximum individual leaf mass, k_{BF} (g.day^{-1}) was a slope parameter, and $t50_{BF}$ (days) was the inflexion point of the original sigmoid of leaf mass increase, therefore it was the date of maximum leaf surface increase, and also the date when half BF_{max} was reached. The parameters k_{BF} and $t50_{BF}$ were calibrated using individual leaf biomass data and results from Laclau et al. (2009).

Specific leaf area (SLA) of individual leaves showed a decreasing relationship with tree height (Fig.S5a), while S_{max} was more constant as described before (Fig.S4). We thus assumed that BF_{max} increased with tree height:

$$BF_{max} = min\Big(BF_{max}^{rotation}, s_{BF} \times H^P\Big) \times TC \tag{4}$$

Where BF_{max} (gC) is the maximal mass of an individual leaf of a cohort at the end of leaf expansion in mass, $BF_{max}^{rotation}$ (gDM) is the maximum mass of an individual leaf throughout the rotation, s_{BF} and P are the parameters of the power function between leaf mass and tree height H (m), and TC (gC.gDM^{-1}) is the leaf carbon content.

2.4.6 Leaf water content

In non-limited nutrient conditions, leaf cell expansion in surface was associated with a leaf water inflow in order to maintain an optimum leaf turgor. This water inflow was computed as:

$$W_{xylem \to leaf} = \Gamma \times \frac{\Delta S}{\Delta t} \tag{5}$$

where $W_{xylem \to leaf}$ (mL.day^{-1}) was the water inflow into the expanding leaf (this was "structural" water associated to the creation of new tissues, not to be confounded with the water used for leaf transpiration), S the leaf surface of the cohort (mm^2), computed in eq. 2, and Γ (mL.mm^{-2}) was the surfacic water content, i.e. the amount of leaf water per leaf surface at full turgor. Γ was assumed to be a constant.

Experimental data have shown that at the end of leaf surface expansion, when the leaf has reached its maximum surface, there was some water outflow, defined further as water expulsion (Laclau et al., 2009). This water expulsion, probably corresponding to a loss of cell wall extensibility (Pantin et al., 2012) during the maturation of leaf tissue, was limited in quantity and in duration. Hence the overall leaf water content dynamic starts increasing until a maximum at the end of the leaf surface expansion, followed by a small decrease until a constant plateau. This plateau corresponds to the water content necessary to maintain a constant leaf turgor in optimal conditions. The water expulsion flux was computed as:

$$W_{leaf \to phloem} = -min\Big(\alpha \times (1 - \frac{W_{leaf}}{W_{leaf}^{turgor}}), 0\Big) \tag{6}$$

Where $W_{leaf \to phloem}$ (mL.day^{-1}) was the flux of water leaving the leaf at the end of leaf expansion, α (mL.day^{-1}) the rate of water expulsion, W_{leaf} (mL) was the amount of water in an individual leaf in previous day, and W_{leaf}^{turgor} (mL) the amount of water found in the leaf at the final plateau. W_{leaf}^{turgor} was computed as $\Gamma \times S_{max}$.

Finally, the variation of leaf water content for an individual leaf in a cohort (W_{leaf}, in mL) was computed by adding the daily net flow $\frac{\Delta W_{leaf}}{\Delta t}$ given by:

$$\frac{\Delta W_{leaf}}{\Delta t} = W_{xylem \to leaf} - W_{leaf \to phloem} \tag{7}$$

2.5 Ecosystem model of the K cycle

We now introduce the *CASTANEA-MAESPA-K* model which simulates cycle of K in the plantation, and its interactions with the ecosystem carbon and water cycles (Fig.1). K remains in its

ionic (K^+) form throughout the cycle (Marschner, 2011). A model of K circulation within the plant as well as between the plant and the soil was necessary since K^+ was a cation of high mobility (Marschner, 2011). As for the leaf cohort model, a daily time step was used for the K cycle model. The K cycle was modelled using seven explicit K pools (Fig.1): soil K (subdivided in the fractions of soil K available and not available for root uptake, respectively), soil K fertiliser, litter K, xylem sap K, phloem sap K, leaf K and other plant organs K. These K pools were connected with fluxes (soil uptake, resorption, leaching, etc.), and K inputs (fertilisation, atmospheric deposition and rock weathering) entered this open system (Fig.1).

K entered the soil through fertiliser inputs, atmospheric deposition and rock weathering. After uptake by roots, K circulated through the plant in the xylem and into the phloem which provided the K necessary to the leaves and organs as well as the K needed for phloem functioning. Part of the K in the phloem was recirculated back into the xylem and thus created a feedback for absorption. Indeed, soil K uptake by roots depends on the gradient between soil and xylem K. Leaves contribute to the cycle through resorption, canopy leaching and litterfall. The K in the litter was leached following a rate that depended on throughfall amount. It then entered the soil, to be once again available for uptake. The only outgoing flux from the system is the soil deep K leaching, and the trunk K exported from the stand at harvest. K was accumulated in organs (trunk, branches, roots) but this allocation sub-model will be presented in the companion paper (Part 2). This K cycle allowed us to create a feedback between K availability and GPP through the actions it has on leaf expansion, leaf lifespan and photosynthetic parameters (see below).

2.5.1 Soil K

Soil K initialisation   Soil K content (K_{soil}, in gK.m^{-2}) was initialised in the model at the tree planting date (eucflux: 07/10/2009, itatinga: 01/06/2010) with a measured value $K0_{soil}$, calculated using K concentration in soil, and soil bulk density at different depths (Maquère, 2008). Then, this value was updated daily with incoming and outgoing fluxes.

Litter leaching   The K that is added daily to the K litter pool (K_{litter}) is the K that falls to the ground through leaf fall, bark fall, branch fall and fine root turnover (see article 3). Instead of a fixed decomposition rate of K in litter, the model considered K release from litter to be mainly coming from leaching with water since K is an ionic element, that is not strongly adsorbed on organic surfaces. Litter K release measurements done at the experimental site

Figure 1: Schematic representation of the soil and plant pars of the K cycle, and their links with the leaf cohort model and other sub-models. Purple boxes are K state variables, and purple arrows are K fluxes. K fluxes simulated with a simple Ohm's law form are represented with resistance symbols. Black arrows represent a functional link a variable has on another variable or process. The numbers in exponent correspond to the number of the equation in the text.

(Maquère, 2008) showed near identical K release rates for branches, bark and leaves further confirming this hypothesis. Moreover, K is released faster than either C, N or P contained in the litter, suggesting a leaching process independent of litter decomposition. The following equation was used for K leaching from the litter to the soil:

$$K_{litter \rightarrow soil} = \sigma \times P_{ground} \times K_{litter} \qquad (8)$$

Where, $K_{litter \rightarrow soil}$ (gK.m^{-2}.day^{-1}) was the litter K leaching flux, P_{ground} (mm.day^{-1}) was the daily amount of precipitation that falls to the ground, σ (mm^{-1}) was the conversion factor between the K litter leaching rate and ground precipitation, and K_{litter} (gK.m^{-2}) was the amount of K in the litter. σ was estimated on annual data by dividing the measured K leaching rate (Maquère, 2008) by the annual precipitation that falls on the ground (throughfall).

Fertilisation   K fertilisation was brought at the beginning of the rotation at several dates, in a solid form (crystals of KCl), and located close to the Eucalyptus seedling. The flux of K from this solid fertiliser compartment ($K_{fertiliser}$ in gK.m^{-2}) to the soil K compartment was simulated using the following equation:

$$K_{fertiliser \to soil} = s_{fertiliser} \times K_{fertiliser} \tag{9}$$

Where $K_{fertiliser \to soil}$ (gK.m^{-2}.day^{-1}) was the the flux of K from the fertiliser compartment to the accessible soil K pool, and $s_{fertiliser}$ the decomposition rate of K fertiliser in day^{-1}. It was assumed that fertiliser dissolved quickly at Eucflux and Itatinga (less than two months).

Atmospheric deposition   Amospheric K deposition is modelled as a constant flux. We used the values measured at Itatinga (Laclau et al., 2010). They amounted to a mean input of $K_{atmosphere \to soil}$ of 0.55 gK.m^{-2}/year distributed uniformly throughout the year. This amount enters directly into the total K_{soil} pool.

Mineral weathering and soil deep leaching   Deep soil K leaching was included in the model, but was parameterized to be a null flux as measured in the plantations under study (Maquère, 2008). The K entrance to the soil pool from mineral weathering was simulated as a constant flux. K flux from weathering is directly added to the accessible soil since this process mainly takes place in the rhizosphere (Pradier et al., 2017). However, as for deep leaching, there is no clear evidence of this flux in the soils under study, where values between 0 and 0.3 gK.m^{-2}/year are given (Cornut et al., 2021) : we therefore also set this flux to zero.

Leaching from canopy leaves   Leaching K flux from living leaves and entering soil K ($K_{leaves \to soil}$) was computed within the Leaf K submodel, described below (eq. 27).

Soil K accessible for root uptake.   Only a portion of K_{soil} was accessible to the roots at the beginning of the rotation because of the time spent for root horizontal and vertical expansion. Because K was mainly located in the top soil layers (Maquère, 2008), and because root growth in depth was very fast (Christina et al., 2011), only the horizontal root exploration was considered in the model. An empirical relationship between tree height and surface root radius around individual trees was described in Gonçalves (2000):

$$Root_{Radius} = 0.80 \times H - 0.075 \tag{10}$$

Where $Root_{Radius}$ (m) was the average radius of the horizontal root front around a tree and H (m) the tree height (article 3). Since the planting density was 1666 trees/ha, a full exploration of the soil was obtained when tree had explored a circle of 6 m²-area:

$$K_{soil}^{accessible} = \frac{(Root_{Radius})^2 \times \pi}{6} \times K_{soil} \tag{11}$$

Where $K_{soil}^{accessible}$ (gK.m^{-2}) is the soil K accessible for te plant uptake, K_{soil} (gK.m^{-2}) is the total soil K. The fraction is the ratio of root accessible soil to total soil, bounded between 0 and 1.

Because of the root exploration dynamics, the initial K in the system $K0_{soil}$ was progressively available to roots, at a proportion following the increase in the root explored area. Following the same logic, the K coming from the litter decomposition and atmospheric deposition entered the total soil K pool K_{soil}, but only a part of this K_{soil} was available for plant uptake (called $K_{soil}^{accessible}$). However, the three other incoming fluxes of K to the soil were considered to be directly accessible for root uptake, i.e. they enter directly in the $K_{soil}^{accessible}$ pool: 1) the fertiliser flux since fertilisers are applied at the base of the seedlings; 2) the K flow coming from soil weathering because most of the weathering takes place in the rhizosphere (Pradier et al., 2017; de Oliveira et al., 2021); and 3) the canopy leaching flux because it enters the soil mostly below the crown foliage.

2.5.2 Uptake of soil K and cycling in xylem and phloem

Optimal K concentration in the phloem To calculate the K soil uptake by the trees and the fluxes of K in the plant it was necessary to calculate the optimal quantity of K in the phloem sap. Furthermore, K in phloem sap is essential to a wide range of processes (e.g. loading/unloading of sugars)(Cornut et al., 2021) . For these processes, the plant maintains a fairly constant K phloem sap concentration $[K]_{phloem}$. To compute this K quantity in the phloem, values of optimal K concentration in the phloem sap ($[K]_{phloem}^{opti}$), minimum K concentration in the phloem sap ($[K]_{phloem}^{min}$) and phloem sap volume (V_{phloem}) were needed.

$[K]_{phloem}^{opti}$ was considered to be the maximum concentration of K in the phloem sap measured in the fully fertilised stand (Battie-Laclau et al., 2014b). $[K]_{phloem}^{min}$ was assumed to be the minimum concentration of K in the phloem sap measured in the K omission stand of the same experiment (Battie-Laclau et al., 2014b).

Estimating V_{phloem} was done through relationships between phloem sap volume and xylem sap volume since no direct measurements or estimates were available. Xylem sap volume

was considered to be a function of basal area, sapwood area at DBH (Guillemot et al., 2021), height of the tree, and branch and root biomass. The trunk cross section was divided in sapwood area and heartwood area. The trunk (respectively heartwood) volume was modelled as a cone with a base disk of surface equal to the basal area (respectively equal to the heartwood area). Trunk sapwood area was estimated as the difference between trunk volume and heartwood volume. Branch and root sapwood volume were deduced from their biomass, considering that branches and root biomass are entirely composed of sapwood. Their volume are computed using the density of *Eucalyptus* sapwood. The lumen volume of the xylem (i.e. the xylem sap volume) was considered to be 13.6% of total xylem volume as reported in general for Angiosperms (Zanne et al., 2010) since no *Eucalyptus*-specific data were available. Following Hölttä et al. (2013), and considering the relatively similar lumen proportion between both xylem and phloem (Nobel, 2005), phloem sap volume was considered to be 2% of the total xylem sap volume.

Uptake of soil K   Uptake of K from the soil by the trees was a function of demand by growing organs, remobilisation of K from senescent organs, and soil supply. The amount of K available for uptake was computed in eq. 11. K demand by the trees needs to be calculated. To that end:

First, the objective amount of K in the phloem was calculated as:

$$K_{phloem}^{obj} = [K]_{phloem}^{opti} \times V_{phloem} + K_{NPP} + K_{leaf}^{demand} \tag{12}$$

Where K_{phloem}^{obj} is the objective amount of K in the phloem sap in gK.m-2, $[K]_{phloem}^{opti}$ is the optimal K concentration in the phloem sap in gK.L^{-1}, V$_{phloem}$ is the volume of phloem sap in L, K$_{NPP}$ is the optimal quantity of K needed for organ growth and K_{leaf}^{demand} is the optimal quantity of K needed for leaf development.

Finally the demand for K uptake from then soil is the following:

$$K_{soil \to xylem}^{demand} = K_{phloem}^{obj} + K_{xylem}^{obj} - \left(K_{phloem} + K_{remob} + K_{xylem} \right) \tag{13}$$

With $K_{soil \to xylem}^{demand}$ (gK.m^{-2}) the quantity of K uptake necessary for optimal tree functioning, K_{phloem}^{obj} from eq.12, K_{xylem}^{obj} (gK.m^{-2}) the objective amount of K in the xylem sap, $Kphloem$ (gK.m^{-2}) the amount of K in the phloem sap, K_{remob} (gK.m^{-2}) the amount of K remobilised from the woody organs (see part 2) and K_{xylem} (gK.m^{-2}) the amount of K in the xylem.

Uptake of K from the soil to the xylem sap is the minimum between the soil "offer", i.e. what can be uptake from the soil knowing the soil K content and the soil to root K resistance,

and the xylem K "demand":

$$K_{soil \to xylem} = min\left(\frac{K_{soil}^{accessible}}{R_{soil \to xylem}}, K_{soil \to xylem}^{demand}\right) \tag{14}$$

With $K_{soil \to xylem}$ (gK.m^{-2}.day^{-1}) the uptake flux, K_{soil} (gK.m^{-2})the amount of K in the accessible soil, $R_{soil \to xylem}$ (days) the resistance to absorption by plant roots, and $K_{soil \to xylem}^{demand}$ (gK.m^{-2}.day^{-1}) the uptake demand from eq. 13.

K fluxes between phloem and xylem.   In the model, internal K cycling (Marschner et al., 1996) was a necessary process that provides feedback for the uptake of K from the soil, maintaining K homeostasis in the phloem sap and linking organ remobilisation and allocation of K for growth. In the K circulation model (Fig.1), two K fluxes are represented, one from the phloem sap to the xylem sap (representing a flux mainly happening in roots *in planta*, though the model was not topological) and one from xylem sap to phloem sap (mainly happening in the shoots). These representations allowed the phloem sap to maintain a K content of phloem close to optimal values (eq. 12).

Firstly, the flux of K from the xylem sap to the phloem sap was calculated. It was a function of phloem "demand" and xylem sap K of the previous time step. We assumed that all the K available in the xylem sap could potentially be transferred to the phloem sap the next day:

$$K_{xylem \to phloem} = min\left(max(K_{phloem}^{obj} - K_{phloem}, 0), K_{xylem}\right) \tag{15}$$

Where $K_{xylem \to phloem}$ (gK.m^{-2}.day^{-1}) was the flux of K from the xylem to the phloem, K_{xylem} (gK.m^{-2}) the amount of K in the xylem sap, K_{xylem} (gK.m^{-2}) the amount of K in the phloem sap, and K_{phloem}^{obj} from eq. 12.

The transport of K from the phloem to the xylem took place if K concentration in the phloem sap was higher than its optimal value (e.g. following leaf resorption):

$$K_{phloem \to xylem} = max\left(K_{phloem} - K_{phloem}^{obj}, 0\right) \tag{16}$$

Where $K_{phloem \to xylem}$ (gK.m^{-2}.day^{-1}) was the flux of K from the phloem to the xylem, and K_{phloem}^{obj} was from eq. 12.

2.5.3   K cycling in the leaves

Leaf K balance   The leaf K balance equation of the individual leaf of each leaf cohort was given by the following sum of fluxes:

$$\frac{\Delta K_{leaf}}{\Delta t} = K_{phloem \to leaf} - K_{leaf \to soil} - K_{leaf \to phloem} - K_{leaf \to litter} \tag{17}$$

Where $\frac{\Delta K_{leaf}}{\Delta t}$ (gK.day^{-1}) was the daily variation of the quantity of K in an individual leaf of a given cohort, $K_{phloem \rightarrow leaf}$ was the amount of K entering the leaf during leaf expansion (see eq. 22), $K_{leaf \rightarrow soil}$ was the canopy leaching flux (see eq. 27), $K_{leaf \rightarrow phloem}$ was the sum of K following water expulsion at the end of leaf expansion (eq. 24), the maximum between K resorption driven by the phloem demand (eq. 25) and the K resorption at leaf senescence (eq. 26), and $K_{leaf \rightarrow litter}$ was the K flux occurring the last day of the cohort, when the leaf was simulated to fall.

K flux from phloem to leaf: modulation by K offer and demand Leaf K inflow ($K_{phloem \rightarrow leaf}$) was computed as a function of the K offer by the phloem and K demand for leaf growth at the canopy scale and organ growth at the tree scale.

The calculation of the water inflow in the leaf during leaf expansion was calculated first in the case of no K limitation ($W_{xylem \rightarrow leaf}$ in eq. 5). This allowed the calculation of a theoretical optimal K flux entering the expanding leaf, $K_{phloem \rightarrow leaf}^{nonlimited}$, computed considering an optimal concentration of K in the water entering the leaf, $[K]_{leaf}^{max}$ (gK.mL^{-1}). This value was approximated as the maximum concentration found in the leaf water on different measurement campaigns (Battie-Laclau et al., 2013; Laclau et al., 2009). The resulting K flux was the non-limited rate of K entrance in the expanding leaf:

$$K_{phloem \rightarrow leaf}^{nonlimited} = [K]_{leaf}^{max} \times W_{xylem \rightarrow leaf} \qquad (18)$$

Where $K_{phloem \rightarrow leaf}^{nonlimited}$ (gK.day^{-1}) was the maximum entrance of K$^+$ ions in the expanding leaf.

However, restriction of this flux occurs due to the phloem limitation of K supply at canopy scale that may not attain the K demand for optimal growth. A reduction of the K inflow in the leaf was therefore applied if the leaf demand at canopy scale K_{leaf}^{demand} was high compared to the K_{phloem} available (the "offer").

K_{leaf}^{demand} ($gK.m^{-2}$) was the K demand of all expanding leaves of the stand, and was computed as the sum of $K_{phloem \rightarrow leaf}^{nonlimited} \times N$ for all leaf cohorts (with N the number of leaves of each cohort, see eq. 1):

$$K_{leaf}^{demand} = \sum_{i=1}^{t} \left(K_{phloem \rightarrow leaf\ i}^{nonlimited} \times N_i \right) \qquad (19)$$

To calculate the phloem sap "offer" the following relationship was used:

$$K_{phloem \rightarrow organs} = min\left(K_{phloem} - [K]_{phloem}^{min} \times V_{phloem},\ K_{NPP} + K_{leaf}^{demand} \right) \qquad (20)$$

Where $K_{phloem \rightarrow organs}$ (gK.m^{-2}) is the amount of K available for leaf expansion and organ growth in the phloem sap, K_{phloem} (gK.m^{-2}) is the total amount of K in the phloem sap,

$[K]^{min}_{phloem}$ (gK.L^{-1}) is the minimal concentration of K in the phloem sap, V_{phloem} (L)is the phloem sap volume and K_{NPP} (gK.m^{-2}) is the optimal amount of K for organ growth (article 3), and K^{Demand}_{leaf} (gK.m^{-2}) the demand for optimal leaf expansion.

Then a the limitation of K for leaf expansion was calculated as a ratio of available ("offer") K to K demand:

$$L_K = \frac{K^{available}_{phloem}}{K_{NPP} + K^{Demand}_{leaf}} \tag{21}$$

Where L_K was the ratio of available K in the phloem sap to demand of K from organ growth and leaf expansion, $K_{phloem \rightarrow organs}$ (gK.m^{-2}) was available phloem K (eq. 20), K_{NPP} and K^{Demand}_{leaf} were organ and growth demands (both gK.m^{-2}, see above).

The quantity of K entering the expanding leaf was thus defined as the following:

$$K_{phloem \rightarrow leaf} = K^{nonlimited}_{phloem \rightarrow leaf} \times L_K \tag{22}$$

Where $K_{phloem \rightarrow leaf}$ (gK.day^{-1}) was the amount of K$^+$ ions that enter the expanding leaf in limited K conditions, $K^{nonlimited}_{phloem \rightarrow leaf}$ was computed in eq. 18 and L_K was computed in eq. 21

K flux from leaf to phloem: expulsion and resorption. The K outgoing flux from leaf to phloem (Fig.2b) can be decomposed into:

$$K_{leaves \rightarrow phloem} = K_{expulsion} + max(K^{phloem}_{resorption}, \ K^{senescence}_{resorption}) \tag{23}$$

Where $K_{expulsion}$ (gK.m^{-2}.day^{-1}) was the K flux leaving the leaf during leaf maturation (eq. 24), $K^{phloem}_{resorption}$ (gK.m^{-2}.day^{-1}) was the resorption flux driven by phloem sap demand (eq. 25), and $K^{senescence}_{resorption}$ (gK.m^{-2}.day^{-1}) was the resorption flux driven by leaf senescence (eq. 26).

$$K_{expulsion} = W_{leaf \rightarrow phloem} \times \frac{K_{leaf}}{W_{leaf}} \tag{24}$$

where $W_{leaf \rightarrow phloem}$ was calculated in eq. 6, W_{leaf} was the previous day leaf water content, calculated in eq. 7, and K_{leaf} was the previous day leaf K content of the cohort.

The K resorption flux $K_{resorption}$, from the leaf to the phloem could be activated by low phloem K content. This was a mechanism to maintain homeostasis in the phloem since K was essential for many phloem functions (Cornut et al., 2021). Evidence was also provided by leaves losing K during their lifespan, especially in K-deficient trees (Battie-Laclau et al., 2013). Another piece of evidence was the high concentrations of K in the petiole compared to other leaf parts (Fig.S8d). This was not the case for N (Fig.S8c) and suggests an intense circulation

of K to and from the leaf. The resorption of the leaf towards the phloem was:

$$K_{resorption}^{phloem} = \frac{K_{leaf}}{R_{leaf \to phloem}} \times (1 - L_K) \tag{25}$$

Where $K_{resorption}^{phloem}$ (gK.day^{-1}) was the cohort phloem driven resorption, K_{leaf} (gK) was the K content of leaves in the cohort, $R_{leaf \to phloem}$ (days) was the resistance to resorption, and L_K was the K limitation computed in eq. 21.

The leaf K resorption flux during leaf senescence $K_{resorption}^{senescence}$ was fast (Battie-Laclau et al., 2013). The amount of resorbed K follows a sigmoid function:

$$K_{resorption}^{senescence} = \frac{e^{-k_r(t-LLS)}}{(e^{-k_r(t-LLS)} + 1)^2} \tag{26}$$

Where $K_{resorption}^{senescence}$ (gK.day^{-1}) was the resorption flux occurring at leaf senescence, just before leaf fall. LLS (days) was the leaf lifespan, which was also the inflexion point of the sigmoid, and k_r was the parameter corresponding to the speed of the resorption flux at the inflexion point. We approximated the time it took for active K resorption to be one week as K$^+$ ions are highly mobile and evidence from chlorophyll degradation at senescence suggest extremely fast dynamics (Mattila et al., 2018).

K flux from leaf to soil: canopy leaching. We assumed that the daily canopy leaching flux strength was proportional to the throughfall that occurs during precipitation as observed previously in a *Eucalyptus* forest (Crockford et al., 1996):

$$K_{leaves \to soil} = \lambda \times W_{tip} \times K_{leaf} \tag{27}$$

Where λ ($mm_{throughfall}^{-1}$) was the fraction of leaf K that was leached per mm of daily throughfall, W_{tip} (mm) was the throughfall and K_{leaf} (gK) was the amount of K in the leaf. λ was calibrated considering the leaf area index and leaf K content of a well fertilised canopy as well as canopy K leaching measurements (Laclau et al., 2010).

K flux from leaves to litter: leaf fall. Finally, the K flux accompanying the leaf fall, $K_{leaf \to litter}$, happened following one of the two conditions: when leaf cohort lifespan LLS was reached, or when the K concentration in leaf water ($\frac{K_{leaf}}{W_{leaf}}$) was below a threshold value $[K]_{min}$ of 9.25e^{-5} gK.mL^{-1}. At one of these dates the leaf cohort was shed and $K_{leaf \to litter} = K_{leaf}$. This $[K]_{min}$ threshold value was either reached after resorption during senescence or through other processes (phloem demand, eq. 25; leaching, eq. 27) thus diminishing the leaf lifespan in K deficient trees. Indeed, leaf fall was related to strong K deficiency in several studies (Laclau et al., 2009; Battie-Laclau et al., 2013).

2.6 Impact of K limitation on the cohort growth model

2.6.1 Number of leaves produced at cohort initialisation

Since leaf production was a function of tree height which itself is a function of tree trunk biomass, K availability could have an indirect impact on leaf production through its impact on tree trunk production (see the companion article Part 2). No specific impact of K deficiency was included in the model since experiments have shown that leaf generation speed at the branch level is not impacted by K availability and leaf biomass production is not extremely different in K omission and fully K fertilised stands (Cornut et al., 2021).

2.6.2 Impact of K limitation on individual leaf surface

When there was no K limitation, in optimal conditions, leaf expansion in surface was computed as in eq. 2, and the water inflow was simply simulated to follow this leaf expansion as in eq. 5. However, under K limitation, individual leaf surface was strongly affected by K availability (Battie-Laclau et al., 2013). Mechanistically, the increase of leaf surface was driven by a water flux entering the leaf, because the turgor pressure participates to the cell expansion, following the logic of the Lockhart model (Lockhart, 1965). The Lockhart model was simplified in the present study due to the important number of parameters of the original model that had not been measured in our context and the difficulty regarding their calibration. This model allowed to relate the K availability in the phloem sap and the expansion of leaves at the individual leaf level on a daily time step. Using the dynamic water content of leaves during expansion, K demand for the cohort at each time step was calculated. The availability of K in the phloem sap then determined a K-limited water flux and thus the leaf expansion rate (Fig.2d).

First, K availability limit the water entrance flux ($W_{xylem \to leaf}$, eq. 5) in the leaf during leaf expansion since there was a lower limit of osmotic potential required for the entrance of water in the leaf cells.

$$W_{xylem \to leaf}^{Klimited} = W_{xylem \to leaf} \times max(\frac{K_{phloem \to leaf}}{K_{phloem \to leaf}^{nonlimited}}, r)$$ (28)

Where $W_{xylem \to leaf}^{Klimited}$ (mL.day^{-1}) was the flux of water entering the leaf during leaf expansion reduced with K limitation, $K_{phloem \to leaf}$ from eq. 22 and $K_{phloem \to leaf}^{nonlimited}$ from eq. 18, and r a parameter $r \in [0, 1]$ of the same order of magnitude than the ratio of K limited individual leaf surface compared to non-limited leaf surface.

Secondly, leaf water content W_{leaf} was re-computed using eq. 7 with $W_{xylem \rightarrow leaf}^{Klimited}$ instead of $W_{xylem \rightarrow leaf}$.

Finally, the non limited leaf surface expansion increment $\frac{\Delta S}{\Delta t}$ computed in eq. 2 was updated with a new K limited leaf surface expansion increment $\frac{\Delta S_{Klimited}}{\Delta t}$, considered to be directly proportional the water flux entering the leaf:

$$\frac{\Delta S_{Klimited}}{\Delta t} = W_{xylem \rightarrow leaf}^{Klimited} \times \frac{1}{\Gamma} \tag{29}$$

Where $\frac{\Delta S_{Klimited}}{\Delta t}$ (mm².day^{-1}) was the surface increase of the expanding leaf computed after accounting for K limitation, $W_{xylem \rightarrow leaf}^{Klimited}$ was obtained from eq. 28, and Γ $(mL.mm^{-2})$ was the leaf surfacic water content.
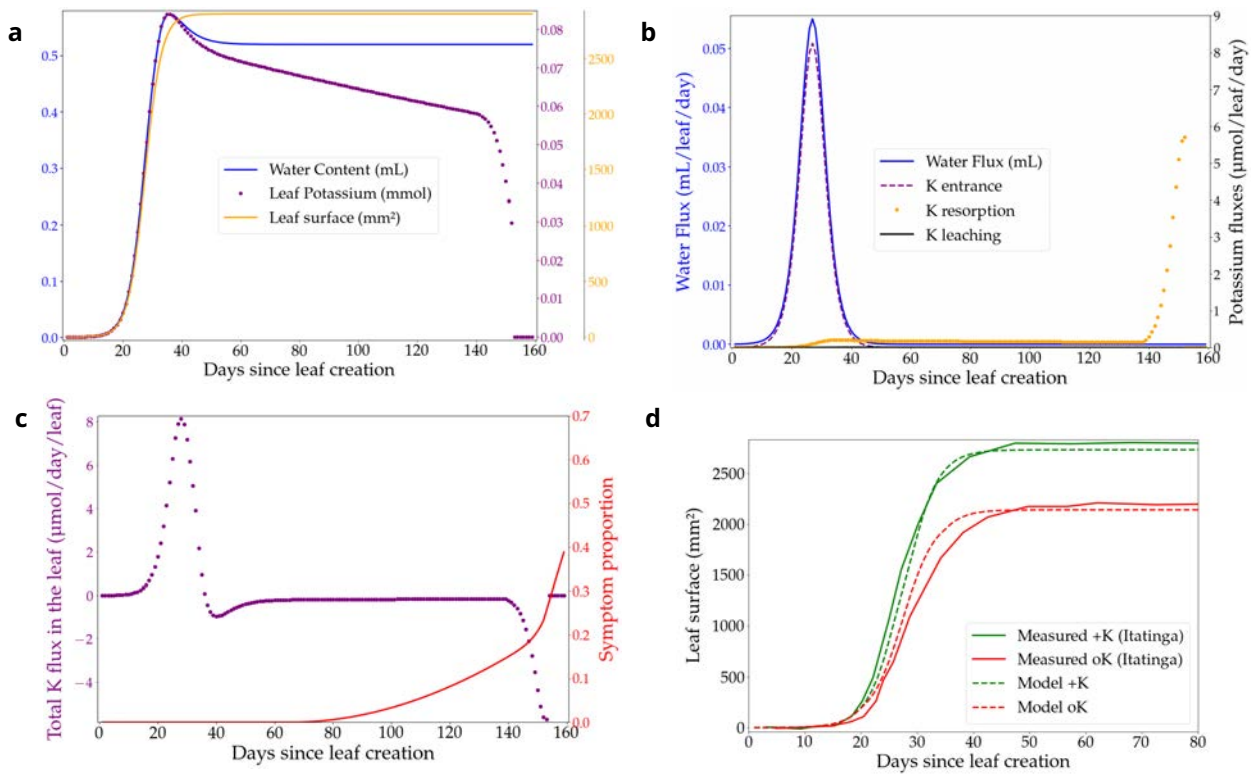

Figure 2: Outputs of the theoretical leaf cohort expansion model over the course of the lifespan of a single leaf in the cohort: state variables that are produced by the model (a); fluxes of water and K at the individual leaf scale (b); total flux of K at the leaf scale showing the transition from K sink (positive flux to the leaf) to K source (negative flux from the leaf) (c); comparison of the model to the individual leaf surface data from Battie-Laclau et al. (2013) in two contrasted K availabilities (d).

2.7 Leaf K-deficiency symptoms and implication for leaf photosynthesis

2.7.1 Leaf K-deficiency symptoms

When leaves experience strong K deficit, they display anthocyanic symptoms (i.e. they turn purple from the leaf margins, Gonçalves, 2000). This has a strong impact on the photosynthetic capacity of affected areas (Battie-Laclau et al., 2014a). We assumed that leaf K-deficiency symptom surface results from the history of K deficiency the leaf has experienced since the beginning of its growth. This was modelled as function of the accumulation of K-deficit in the leaves over time, called "deficit days" (DD). The daily increase in DD was computed as:

$$\frac{\Delta DD}{\Delta t} = max\Big(([K_{leaf}]_{max} \times W_{leaf}) - K_{leaf},\ 0\Big) \tag{30}$$

where $\frac{\Delta DD}{\Delta t}$ (g) was the daily increase of the deficit days, $[K_{leaf}]_{max}$ (gK.mL^{-1}) was the optimal (maximal) foliar concentration of K, W_{leaf} (mL) was the amount of water in the individual leaf (after K limitation, eq. 7), and K_{leaf} (gK) was the leaf K content.

The proportion of symptoms in a leaf (Fig.2c) was then computed as:

$$SP = min\Big(DD \times \Theta,\ SP_{max}\Big) \tag{31}$$

where SP the leaf surfacic symptom proportion, DD the accumulated deficit days computed in eq. 30, Θ a conversion factor from deficit days to symptom proportion and SP_{max} the maximum proportion of symptom area on a single leaf, with $0 < SP < SP_{max}$.

2.7.2 Impact of symptoms on leaf photosynthesis

Leaves, even with symptoms, continue to intercept radiations. In the model, it means that the light interception submodel was not affected by symptoms surface, i.e. the total leaf area of each cohort was taken into account. Note that the total leaf area under K deficiency was reduced through various processes such as lower number of produced leaves because of lower growth in height (eq. 1), reduction of individual leaf sizes (eq. 29), and through the shorter lifespan of leaves because of K-deficiency associated leaf fall (section 2.5.3).

However, leaf symptoms have a strong effect on leaf-scale photosynthesis. Indeed, experimental results (Battie-Laclau et al., 2014a) have demonstrated that the leaf scale photosynthesis was strongly reduced when there was K-deficiency symptoms. This decrease was

almost linear, suggesting that we could model leaf photosynthesis as fully active in the non-symptomatic areas of the leaves, and null in the symptomatic area, i.e. the photosynthesis was reduced by the proportion of symptoms in the leaf.

For sake of simplicity, this was implemented in the model by reducing the two leaf scale photosynthetic parameters Vc_{max} and J_{max} according the leaf area proportion affected by symptoms:

$$Vc_{max}^{lim} = Vc_{max} \times (1 - SP) \tag{32}$$

$$J_{max}^{lim} = J_{max} \times (1 - SP) \tag{33}$$

Where Vc_{max} and J_{max} are respectively the maximum carboxylation rate and the maximum rate of electron transport, SP was described in eq. 31.

2.8 Model parameterisation and initialisation

Most of the parameters of the model were obtained from (Christina et al., 2017), except the parameters of the new cohort model and of the new K cycle model, for which the parameterisation was described along the equation descriptions of sections 2.4 to 2.7, and reported in Tables S1,2. The beginning of the simulation was considered to be the plantation of the trees. They were considered to be 10-cm high. The canopy was initialised with a very small, but not null, amount of leaves: 10 leaves of 30 mm² each per m² (eqv. to 0.0003 m²leaf/m²soil). The soil was divided into 50 layers of 33-cm (for the three top ones) or 50-cm depth each, and soil properties for each layer were obtained from (Christina et al., 2017). Initial values of water content of the soil on the planting day were set as measured at the Eucflux site (Christina et al., 2017). The model was initialised with both K present in the soil and in the litter compartment. The amounts of K present in the litter were determined using measurements of the mass and elemental dosages of the litter present on the ground at the beginning of the rotation in the fertilisation experiment. This amounted to 1.92 gK.m^{-2} (Laclau et al., 2010). The amount of K present in the soil compartment at the start was deduced from soil K concentration and bulk soil density measurements at different depths (Maquère, 2008). It amounted to 0.507 gK.m^{-2} (it was converted from gK.m$_{soil}^{-3}$). The simulations were run on Eucflux site.

2.9 Sensitivity analysis

A sensitivity analysis was conducted with a One-At-a-Time (OAT) approach, in both K-fertilised (+K) and K-omission (oK) conditions to test the sensitivity of GPP to the different processes.

The sensitivity of GPP to all the parameters of the new sub-models was tested. The method used was the following: in each fertilisation condition (+K and oK) the parameter was increased and decreased by 10%, except the fertilisation parameters which was fixed to their +K and oK treatment values. The model was then run for each combination of fertilisation and parameter values. The total average GPP of the simulated rotation was compared to the simulated average GPP of the rotation with the same fertilisation regime and the normal value of the parameter. The percentage of difference gives the response of the simulated GPP to the variation of the chosen parameters.

3   Results
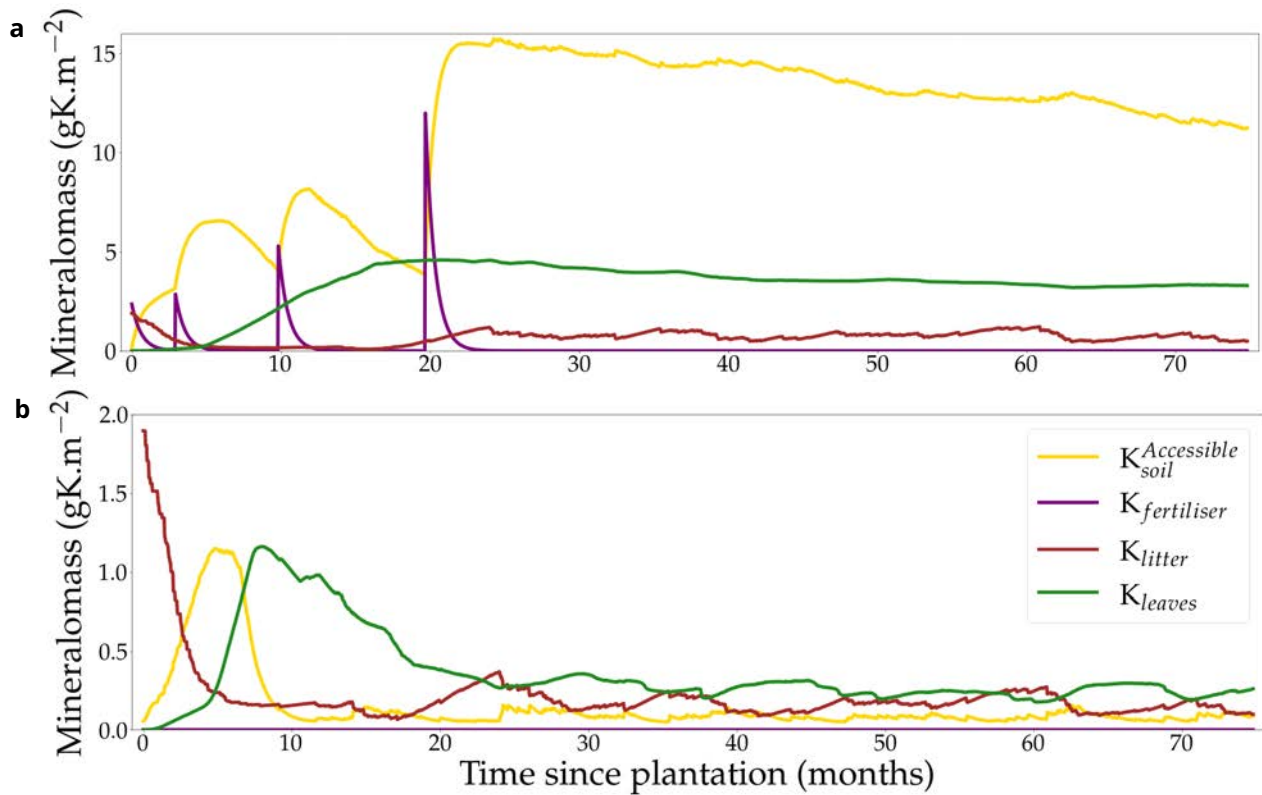
3.1   Ecosystem K cycle

Figure 3: Simulated stocks of K in the soil, litter, fertiliser and canopy compartments, in a non K-limited (+K) stand (a) and in the same K-limited (0K) stand (b). Note differences of the y-axis scales for better visualisation.

The quantity of K accessible in the soil for the plant was on average 62 times as high in the +K (Fig.3a) compared to the 0K (Fig.3b) fertilisation treatments. While the K stored in the canopy was only a small fraction (23%) of the total K in the system in the +K stand, leaves represented more than half of the total K stock in the 0K stand (52%). In both stands, the quantity of K stored in the litter was small, representing 3.8% of total K in +K treatment and 27% in 0K (Fig.3, Tab. 1a). In the +K stand the amount of K in the leaves increased until 2 years after which it remained stable during the rotation (Fig.3a). In the 0K stand however, the increase only lasted for one year and was quickly followed by a strong decrease (Fig.3b). The strong decrease in K_{leaves} is concurrent to an important decrease of $K_{soil}^{accessible}$ as the initial litter stock is depleted while the plant demand is still high. In the +K stand, the fertiliser quickly compensates for the decrease in initial litter K, increasing the $K_{soil}^{accessible}$ to high values.

In the +K treatment, over the course of the rotation, the fluxes of fertiliser, atmospheric

Stocks (gK.m^{-2})	+K	oK
$K_{soil}^{Accessible}$	11.18	0.16
K_{litter}	0.59	0.20
K_{canopy}	3.68	0.39

a

Fluxes (gK.m^{-2}.yr^{-1})	+K	oK
$K_{fertiliser \rightarrow soil}$	3.60	0
$K_{atmosphere \rightarrow soil}$	0.55	0.55
$K_{litter \rightarrow soil}$	1.71	0.66
$K_{leaves \rightarrow soil}$	0.27	0.01
$K_{soil \rightarrow xylem}$	4.67	1.29
$K_{leaves \rightarrow phloem}$	2.04	0.77

b

Table 1: Mean value of simulated K stocks (a) and mean value of simulated yearly fluxes of K (b) in two contrasted fertilisation regimes: +K and oK.

deposition, litter leaching (eq. 8) and canopy leaching were respectively 59%, 9%, 28%, 4% of the total amount of K that entered the soil (Tab. 1b). In the oK stand, they were respectively 0%, 43%, 56%, 1% (Tab. 1b). So while the litter stock was small (Tab. 1a), the cumulated flux of K from the litter to the soil was important for K cycling in both fertilisation regimes. In both stands, the resorption flux from leaves ($K_{leaf \rightarrow phloem}$) was more important than the sum of canopy leaching ($K_{leaves \rightarrow soil}$) and litter leaching flux ($K_{litter \rightarrow soil}$, Tab. 1b), highlighting the role of the tree internal K cycling.

In the +K treatment, leaf resorption ($K_{leaves \rightarrow phloem}$) was equal to 43% of the average uptake flux ($K_{soil \rightarrow xylem}$, Tab. 1b). In the oK, this proportion was higher (60%) thus showing the importance of the internal K recycling for the maintenance of a correct K supply.

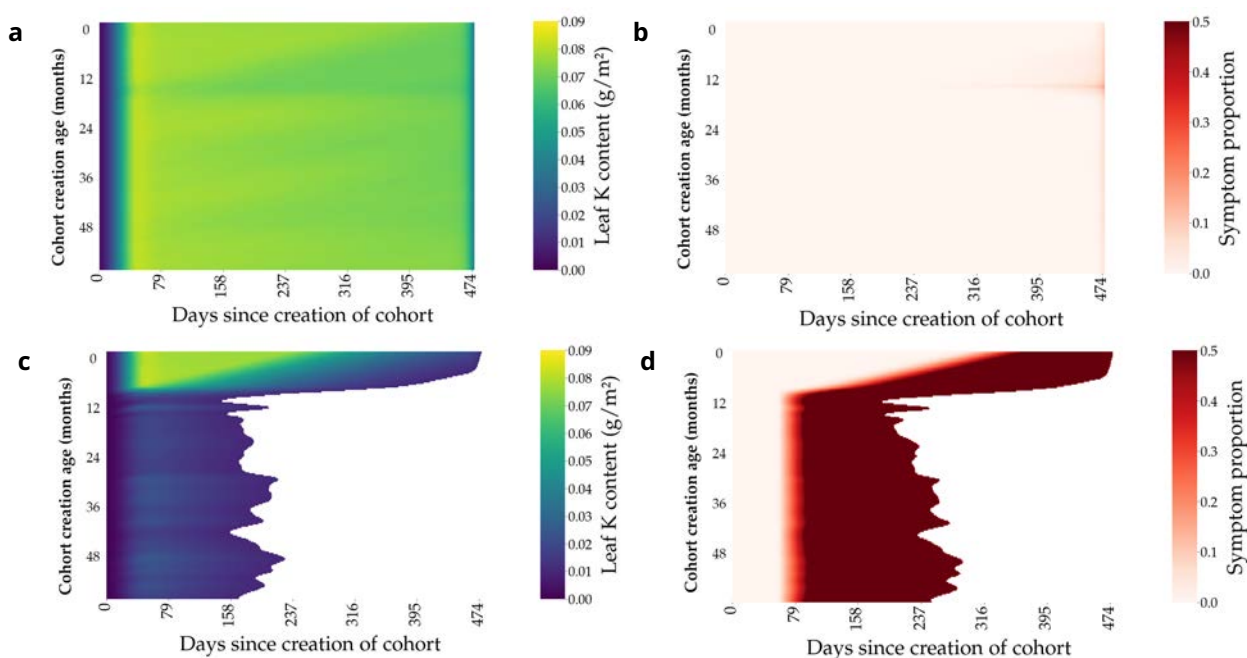## 3.2 Leaf cohort model and canopy dynamics

Figure 4: Outputs of the leaf cohort model in two contrasted K fertilisation regimes. The K content present in each individual leaf of the cohort is represented through the lifespan of a cohort (x-axis) for the different cohort created along the first 60 months of the rotation (a, c). The symptom area proportion for each leaf of the cohort is also represented (b, d). Top subplots (a, b) were simulated in +K conditions, while bottom subplots were 0K simulations (c, d).

The leaf expansion model was successful in simulating the influence of K on both the dynamics and maximum value of the individual leaf area (Fig.2d). Positive fluxes of K into the leaf took place during the expansion process (Fig.2b,c). Foliar leaching, K expulsion after leaf expansion and resorption were responsible for fluxes of K going out of the leaf across its lifespan (Fig.2b). This model allowed us to represent leaf K content in the leaves at the organ scale and also revealed the variation of K availability at the leaf level during the rotation. In +K condition, K availability was high during the whole rotation with symptom surface proportion of the canopy always below 2.5% (Fig.5b) during the leaf lifespan, that reached its maximum, fixed value (LLS). On the other hand, in 0K simulations, leaf lifespan was greatly reduced (less than half of the leaf lifespan of fertilised stands, Fig.4c) and symptom proportion reached more than 40% during a major part of the rotation (Fig.4d,5b). The patterns of the leaf K content in the different cohorts during the 0K rotation had two phases (Fig.4c): a first phase of the rotation where K availability was high and a second phase with very low K concentrations in leaves. This mirrors the K availability in the soil and litter sub-system (Fig.3b). The first phase corresponds to a high initial litter decomposition flux (litter originat-

ing from the preceding rotation which was fertilised with K), in the second phase the only fluxes of K to the soil were the litter leaching flux (recycling) and atmospheric deposition (external input). These cumulated fluxes were not sufficient to satisfy the plant K demand.
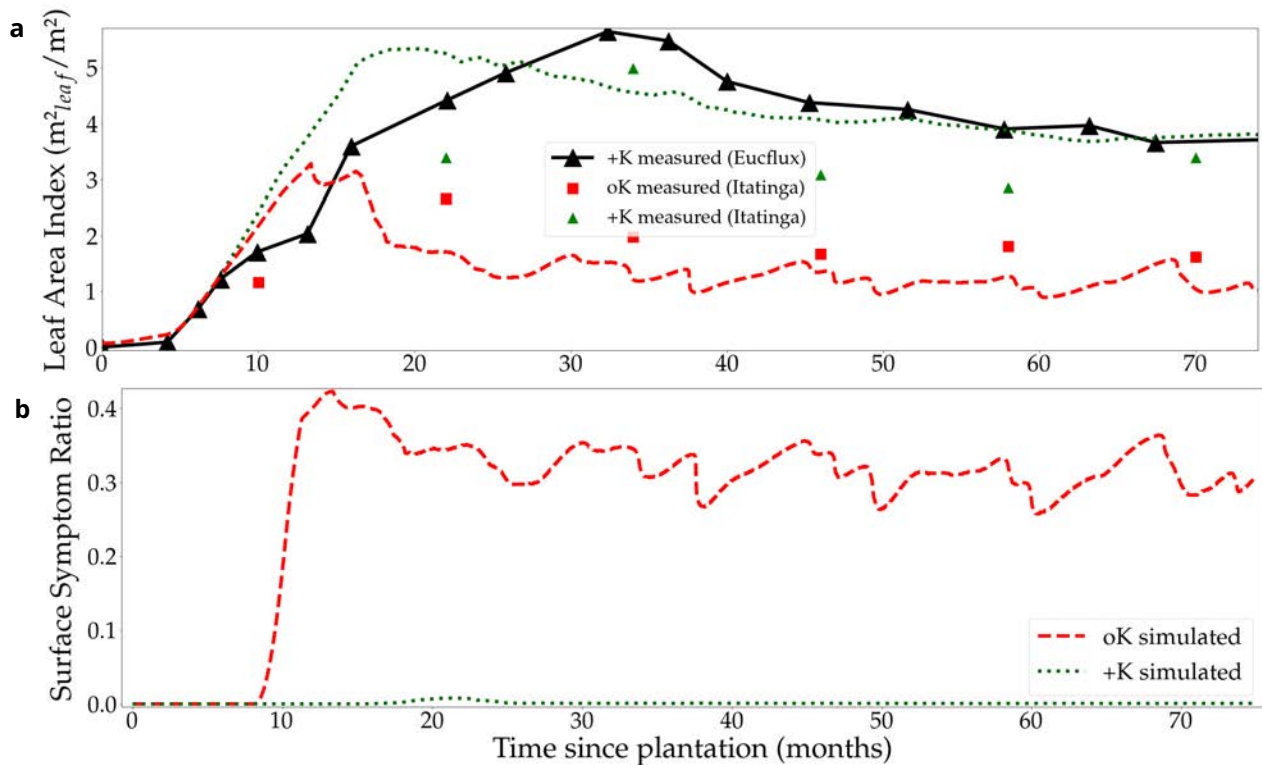

Figure 5: Simulated Leaf Area Index in both the fertilised +K and non fertilised oK treatments, and the Leaf Area Index measured at the Itatinga experiment and at the eddy-covariance site Eucflux (a). Canopy average proportion of leaf surface with symptoms in both fertilisation treatments (b).

The difference of leaf area between the +K and oK simulated stands was higher than observed in the +K and oK treatments of the Itatinga fertilisation experiments. The mean leaf area of the oK stands were 58% of the leaf area of the +K stand in the experiment versus 43% in the model (Fig.5a). This could be explained by different response to K deficiency between the genetic material (different Eucalypt clones) being used at Eucflux and at Itatinga. Another possibility was an underestimation of K availability in the oK stand in our simulations. For example, a small change in the mineral weathering flux from 0 to a realistic value of 0.3 $gK.m^{-2}.yr^{1}$ (Cornut et al., 2021) led to the simulated leaf area in the oK stand being 53% of the +K stand (not shown).

In the oK condition, symptoms appeared very early during the leaves' lifespan (Fig.4d). The proportion of symptomatic leaf area was slightly higher in the simulations of the Eucflux site than measurements at the Itatinga site (Fig.S6). This could be due to an overestimation of the leaves' limitation by K or a difference in response of the genetic material to K availability.
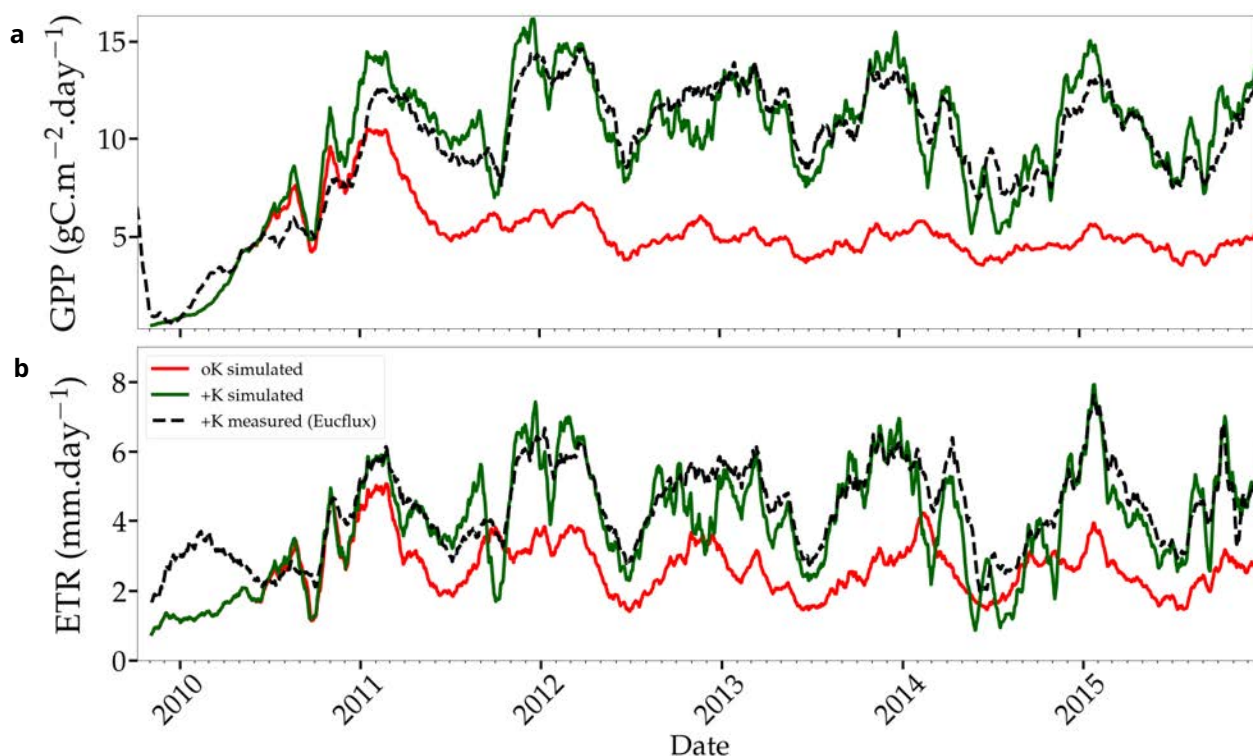
3.3   Carbon and water fluxes

Figure 6: Simulated and measured daily gross primary productivity (a) and evapotranspiration (b) fluxes simulated in two stands with contrasted fertilisation regimes. The measurements are from the Eucflux site (a +K stand, fully fertilised). A rolling average of 30 days was applied to the observed and simulated time series for sake of clarity.

Simulated GPP was greatly reduced under 0K conditions (Fig.6a) and the cumulated GPP in the 0K stand was only 50% of the +K stand on average (Table 2). Seasonal fluctuations of GPP between dry and wet seasons were clearly visible in both simulations, however the seasonal variability was higher in the +K stand (Fig.6a) due to lower access to soil water in the +K stand. This was a consequence of higher cumulated ETR in the +K stand compared to the 0K stand (Fig.6b). The difference of GPP between fertilisation regimes was not constant during the rotation. During the first phase (i.e. the first year), the difference was small due to similar low leaf areas in both fertilisation conditions resulting in low K demand, fulfilled by sufficient K availability for both treatments (Fig.4a,c). The difference was also quite small during the major 2014 drought (Fig.6a) where water-limitation dominated in the +K stand. The simulated GPP were similar to both measurements (Epron et al., 2012) and simulations conducted at Itatinga with the MAESPA model (Christina et al., 2015) (Table 2).

Our simulations showed reduced evapotranspiration under K deficiency (Fig.6b). This is expected since K deficiency had a strong impact on leaf area (Fig.5a). We compared our

	Estimated GPP (Itatinga) from Epron et al. (2012) (gC.m^{-2}.yr^{-1})	Modelled GPP (Itatinga) from Christina et al. (2015) (gC.m^{-2}.yr^{-1})	Modelled GPP (Eucflux) in this study (gC.m^{-2}.yr^{-1})
Age (years)	+K − oK	+K − oK	+K − oK
0 → 1	... − ...	1300 − 800 (61%)	1129 − 1083 (95%)
1 → 2	... − ...	3500 − 2500 (71%)	3926 − 2519 (64%)
2 → 3	... − ...	4600 − 2900 (63%)	4541 − 1782 (39%)
3 → 4	... − ...	... − ...	3971 − 1636 (41%)
4 → 5	4440 − 2540 (57%)	... − ...	3653 − 1670 (45%)

Table 2: Annual GPP at the study sites, under contrasted K availabilities. Values from Epron et al. (2012) were inferred from fluxes and biomass increment measurements. These results were obtained from a previous fertilisation experiment at the Itatinga site. Values from Christina et al. (2015) were simulated by the MAESPA model. Percentages between parentheses indicate the ratio of GPP between the oK and +K treatments for each experiment. The data presented are different from those on Fig.6b that display evapotranspiration.

transpiration simulation results with those obtained using the MAESPA model at the Itatinga stand. The MAESPA simulated transpirations had been validated using sap-flow measurements. While in the first part of the rotation the difference between treatments simulated by our model was lower than simulated by MAESPA, in the following years our simulations were close to MAESPA results (Table 3). Total 5-year cumulated transpiration in the oK plot was 54% of that of the +K plot in our simulation of the Eucflux site. This was a slightly higher proportion than for GPP, i.e. GPP was more impacted than transpiration by K deficit. As a consequence, the simulated WUE for GPP was higher in +K condition in our simulations (Tab.3).

	Modelled Transpiration (Itatinga) in Christina et al. (2018) (mm.yr^{-1})	Modelled Transpiration (Eucflux) in this study (mm.yr^{-1})	WUE$_{GPP}$ this study (mmolC.molH$_2$O^{-1})
Age (years)	+K − oK	+K − oK	+K − oK
0.5 → 1.5	947 − 654 (69%)	969 − 858 (88%)	14.3 - 13.2
1.5 → 2.5	1365 − 881 (64%)	1605 − 791 (49%)	12.8 - 11.24
2.5 → 3.5	1438 − 753 (52%)	1344 − 649 (48%)	13.9 − 12.0
3.5 → 4.5	1323 − 774 (58%)	1458 − 678 (46%)	13.0 − 11.5

Table 3: Annual transpiration fluxes in contrasted K availabilities both in our study and in a previous modelling work that used the MAESPA model (Christina et al., 2018). Percentages between parentheses indicate the ratio of transpiration between the oK and +K treatments for each experiment.

3.4 Sensitivity analysis

Sensitivity analysis was done separately on a K fertilised and a non-fertilised stand (i.e. with parameters the fertilisation amount of +K and oK treatments of Itatinga experiments). The simulated GPP cumulated over the whole simulation period was highy sensitive to few sub-models parameters, but this sensitivity was strongly dependent on the fertilisation treatment (Fig.7a). Among the tested parameters, in the +K condition, GPP was sensitive to parameters related to the leaf phenology, especially the ones driving maximum leaf surface and maximum leaf lifespan. Increase (resp. decrease) in maximum leaf surface (S_{max}, number of leaves produced by height increment (κ) and maximum lifespan (LLS) parameters resulted in GPP increases (resp. decrease) in the +K simulations. These parameters had an impact on the leaf area of trees, thus directly affecting photosynthetic area. This shows that under non-limiting, +K conditions, the model's gross primary productivity was mainly limited by leaves developmental aspects among the parameters tested here, i.e. the ones directly involved in processes related to K cycle.

Under oK conditions, GPP was sensitive to a greater number of parameters but a pattern still emerged. In this case, variations in the parameters controlling the values of K inputs to the ecosystem ($K_{atmosphere \rightarrow soil}$, K^{ini}_{litter}, K^{ini}_{soil}) produced a strong response in simulated GPP, highlighting the strong limitation of GPP by K availability. The amplitude of their response was in line with their respective contribution to the total K entrance in the system at the rotation scale (Tab. 1b). For instance, a small increase in atmospheric deposition is accumulated through the entire rotation and has a larger impact that small changes in the initial value of
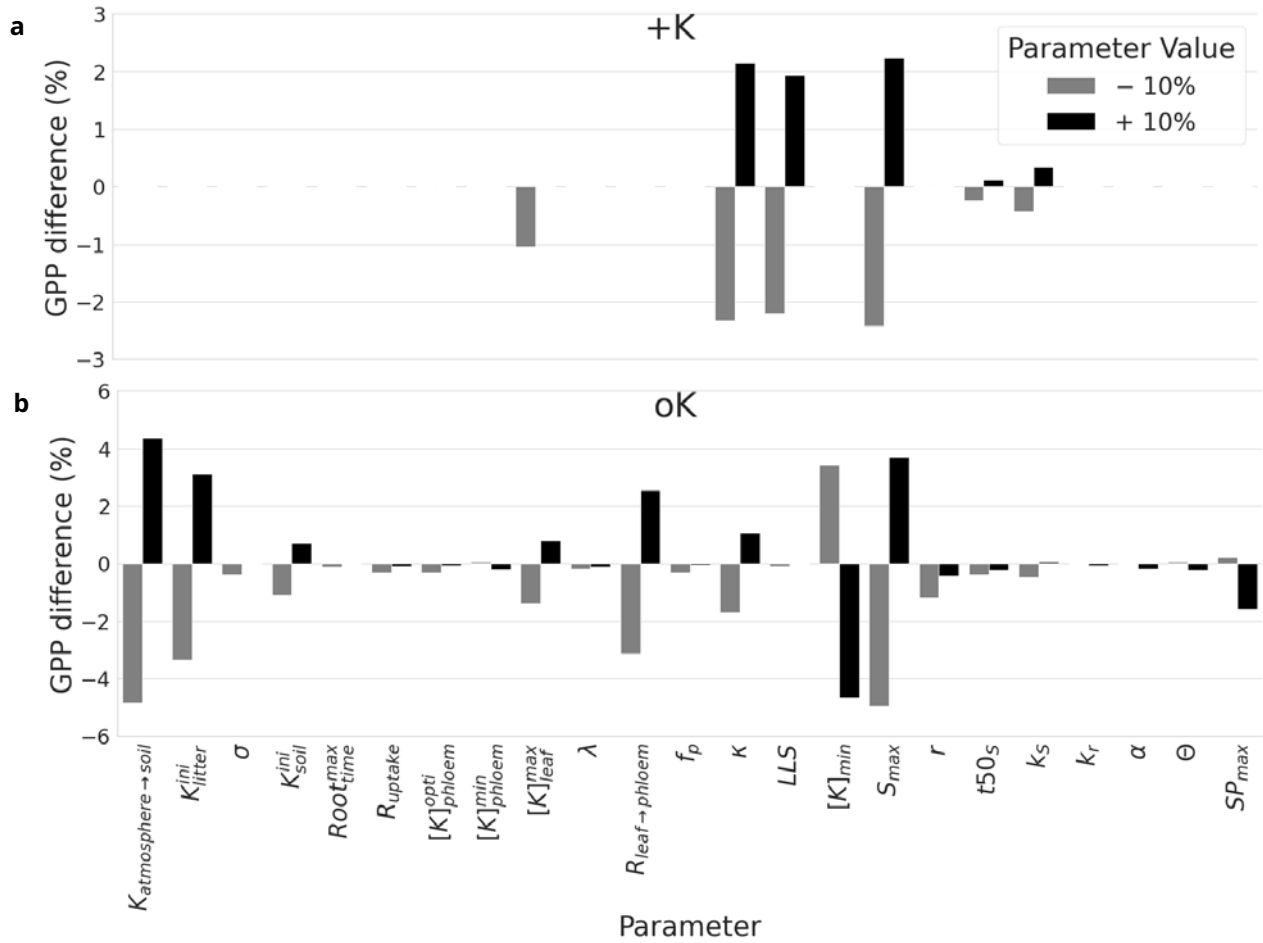
Figure 7: Sensitivity of GPP cumulated over a rotation to a ±10% change in parameters related to soil availability, diffusion resistances and response of leaves development to K. For each parameter, the sensitivity analysis was done in the two contrasted K conditions. Note differences on the y-axes scales, for sake of clarity.

K content in the litter or in the soil. In the oK condition, contrary to +K, the model was not sensitive to the parameter controlling maximum leaf lifespan (LLS, Fig.7. Indeed, the maximum leaf lifespan was almost never reached because of earlier leaf fall due to K limitation (Fig.4c). Other parameters ($t50_s$, k_s) controlling maximum leaf growth had also a much lower impact for similar reasons. Sensitivity of simulated GPP to the leaf maximum individual surface (S_{max}) in the oK stand was high, as in the +K case. Indeed, this parameter is used both in the +K and oK case because the surface increment, depending on this target value, is modulated when a leaf cohort experience a K deficit (eq. 2 and 29). This led to a variation in leaf area of each cohort which affected directly the GPP. The second most important leaf parameter in the oK stand was the resistance to K flux from the leaf to the phloem ($R_{leaf \rightarrow phloem}$, Fig.7b). This parameter was important since it controlled the competition for the K resource between new leaves (demanding K) and old leaves (providing K through resorption). In our

simulations, an increase (+10% in Fig.7b) in resistance to K flux between the leaves and the phloem had a positive impact on GPP, at least in the range of values considered. Indeed, increasing the resistance ($R_{leaf \rightarrow phloem}$) led to a higher conservation of K in the leaves, which kept the leaf K concentration longer above the leaf shedding K threshold, which increased the leaf realised lifespan, which in turn increased canopy surface. Since LAI in the oK stand was low (Fig.6a), a small increase in LAI can have an important impact.$[K]_{min}$ is the K concentration value below which leaves start their senescence. An increase of this value caused earlier leaf fall because this value was reached sooner, and GPP therefore decreased. Finally, the parameter related to symptoms area SP_{max} was also sensible in the model, i.e. the GPP is reduced when the symptoms of surface increase.

4 Discussion

In this work, we developed a process-based model simulating the influence of K on the gross primary productivity and transpiration fluxes of tropical Eucalypt plantations. Such models have rarely been published in the literature, and we identified it "a worthwhile endeavour" (Reed et al., 2015) owing to the importance of K limitation of productivity in forests around the world (Sardans and Peñuelas, 2015). We considered tropical Eucalypt plantations as our primary study system, since nutrient limitation has been extensively studied there, they are typically highly fertilised, and K-omission experiments show a very strong response of wood productivity to K deficiency (Laclau et al., 2010). Our K model incorporates parts of the K cycle that were essential in determining K availability at the plant level. We focused on the modelling of the carbon-source activity on canopy processes and fluxes, starting with the demography of leaves and the impact of K availability on their functioning. In particular, we first considered the impacts of K on leaf development, photosynthetic capacity and senescence. We included processes that we identified as central (Cornut et al., 2021) regarding the K-limitation of GPP in these plantations. While adding processes to a mechanistic model is pertinent from a realism perspective, one must consider if the implementation of new processes increases or decreases the predictive power of the model in a given context (Famiglietti et al., 2021). Here, the model additions were clearly necessary since the CASTANEA model, into which we developed the K modules, was initially incapable of reproducing the effect of K limitation on GPP and no mechanistic model of the effect of K on plant productivity at the stand level existed. This development also broadly followed several of the guidelines posited by Famiglietti et al. (2021) in their paper addressing the question of models' structural complexity: 1) the use of datasets (here multiple experiments over multiple rotations) to constrain model parameters, 2) the new developments led to increased forecast ability (since no forecast of K deficiency was previously possible), and 3) we sought to calibrate unmeasured parameters. We adopted a reductionist approach, typical of the development of mechanistic model, by formulating and parameterising the model on dedicated experiments conducted at the organ scale. Only a few parameters were calibrated on carbon and water fluxes measured at the ecosystem scale. It is noticeable that the model was parameterized in a fully fertilised stand, and then allowed to run in a virtual K omission stand with, as the only difference, a reduced amount of K fertiliser brought at beginning of the stand rotation. The results showed a strong impact on fluxes.

In fertilised condition, our model was able to simulate GPP and water fluxes similar to the

observed flux at the Eucflux experimental site, both in terms of seasonality and magnitude (fig.6). Compared to our model, the MAESPA model presents a very fine-scales modelling of water and carbon fluxes (Christina et al., 2018, 2015) in both fertilisation regimes, but uses a different parameterisation of the model in +K and oK, i.e. without simulating the K cycling and its impact on the parameters (which is a feature of CASTANEA-MAESPA-K). It is possible that the CASTANEA-MAESPA-K model presented here lost some accuracy in the prediction of carbon and water fluxes compared to MAESPA alone, due to the inclusion of new processes linked to K cycle instead of a direct parameter forcing with measurements. It also did not use the 3D representation of trees of MAESPA which had probably improved the simulation of fluxes during the first year of the rotation, before canopy closure (Christina et al., 2018). At the rotation scale, however, the differences between the measured accumulated GPP and the simulated accumulated GPP flux are small (Fig.S1).

The difference in cumulated GPP between the +K and oK stands simulated by the model was large on average, but varied during the rotation. In the first year the difference in GPP between oK and +K (table 2) was underestimated in our model compared to Christina et al. (2015). The leaf cohort model also showed that leaves were not K-limited at the beginning of the oK stand (Fig.2c). Both leaf K content and symptomatic leaf area showed similar dynamics between the simulated oK and +K stands up until around 1 year of age (Fig.6b). These results suggest that up until this time, K was not more limiting in oK than in +K. The simulated plant available K in the soil was similar in both treatments at the beginning of the rotations, which suggests that either K availability was in fact high at the beginning of the oK simulation (through litter remaining at harvest and K available in the soil from the previous rotation) and/or that our model overestimated K soil access the first year.

The simulated water-use efficiencies (WUE, Tab.3) were at the high end of the spectrum for C3 woody plants (Lambers and Oliveira, 2019) but resulted from simulated transpiration and GPP fluxes that compared well with observations (Tab.3 and 2). Our simulations showed a decrease of both GPP and transpiration in the oK stand that was consistent with evidence from the MAESPA model (Christina et al., 2015, 2018) and from experiments (Epron et al., 2012). WUE was higher in the simulated +K, as opposed to oK condition (Tab.3). Unexpectedly, this result from our model simulations was in accordance with experimental data on wood WUE but differed from experimental data on leaf intrinsic WUE, for which the opposite was reported (i.e. lower WUE in +K as opposed to oK) (Battie-Laclau et al., 2016). The observed difference was was small and in their study, Battie-Laclau et al. (2016) explained the difference between wood WUE and intrinsic leaf WUE by differences in the post-GPP processes

of carbon allocation in +K vs. oK. This could suggest that our approach of restricting the effects of symptoms to the photosynthetic capacity was insufficient and that a direct effect on stomatal response or mesophyll conductance would be necessary for our model to agree with experimental data. Part of the effects of K on leaf functioning could also be ignored by our approach of direct proportionality between the surface of symptoms and the reduction of leaf photosynthetic capacity. Studying the response of leaf functioning to a gradient of individual leaf K content (Basile et al., 2003; Shen et al., 2018) may be useful to diminish the uncertainty regarding this response (see section 6.6).

The submodel we implemented for the simulation of plant K uptake was a simple demand model, dampened by a resistance meant to represent diffusion and the different impediments to the uptake of K ions from the soil. It was similar to models used successfully in ForNBM (Zhu et al., 2003) and ForSVA (Arp and Oja, 1997), that are based on the law of diminishing returns (van den Driessche, 1974). Except for the soil access equation (eq. 10), our model did not consider K uptake kinetics to depend on root density. This was in part due to the highly dynamic growth of Eucalyptus, that goes from saplings to 20-meter trees in less than six years (the same being true for roots down to 16-m depth (Christina et al., 2011)). However, the sensitivity analysis showed that GPP was not greatly affected by the resistance to uptake in both fertilisation conditions. This is in accordance with results from the Itatinga site, where K^+ ions appeared weakly sorbed to this sandy soil, hence the process of diffusion was probably not limiting (Cornut et al., 2021). This could be further amplified by the fact that uptake of K by roots can take place directly in the litter (Laclau et al., 2004) thus bypassing the soil entirely. Taking K-soil interactions into account might however be necessary if one were studying leaching of K ions in the soil.

The importance of the accurate measurement of K sources in the system was underlined by the results of the sensitivity analysis. The simulated GPP of the oK stand was sensitive to variables relating to K influx. The GPP showed a strong response to small changes in the yearly influx from atmospheric deposition. This mirrors modelling results that show a strong response of NEP to increasing N deposition (Zaehle and Friend, 2010; Dezi et al., 2010). The response of GPP to initial K litter stock underlined the importance of harvest residues in the maintenance of plot fertility. It was apparent that the model shifted from developmental (leaf production, base leaf lifespan, leaf surface) and pedoclimatic limitations of GPP in the +K treatment to biogeochemical limitations in oK. For example, the level of mineral weathering had an important impact on the GPP flux of the oK stand (not shown here, see Part 2), but uncertainty regarding this flux is high (Cornut et al., 2021; Pradier et al., 2017; de Oliveira et al.,

2021). We believe these results confirm the importance of studying biological weathering of minerals in situations of strong K limitation in forests.

The analysis of the model also showed the importance of internal K cycling, especially the resorption flux between the leaves and the phloem. The intense cycling of K in plants has been amply demonstrated (Marschner and Cakmak, 1989). Measurements are still lacking to evaluate whether our phloem demand simplification to explain the variation in leaf K content is true in different conditions. On the other hand, at least in the studied system, the GPP of the oK stand showed little to no response to the circulation of K in the soil and its uptake by the plant.

5   Conclusions and perspectives

This study is the first attempt to simulate the potassium cycle in a forest ecosystem, and its intimate link to the carbon and water balance at different time and space scale. It was developed based on data and processes observed in Eucalypt fast-growing plantations under contrasting fertilisation regimes. The model was tested against stand-scale measurements and showed reliable results for both K-fertilised and K-omission simulations. First analysis show that K amounts present at the beginning of the rotation (in litter, soil or fertilisation) and atmospheric deposition are essential to explain the overall amounts of K in foliage. Then the internal K cycling dominates the K availability to leaves, which in turn influence strongly leaf development, leaf area index and GPP.

The coupled Carbon-water-Potassium forest process-based model developed in this study represents an important step in the endeavour to understand the nutrient limitation of forest productivity. This study, focusing on the canopy and C source processes will be followed by a second part (Cornut et al., in prep.) which will investigate the C-sink limitation of growth under low K availability. It also provides a framework for the development of modules that will incorporate other ionic nutrients such as Mg or Ca. The leaf cohort model developed is also good starting point for accurately simulating nutrient fluxes in tropical forests that follow a continuous phenology. This work was enabled by long-term omission experiments and detailed data collection at these sites (Cornut et al., 2021). This further underlines the necessity of these large scale manipulation experiments for nutrient modelling work. These modelling frameworks can then be adapted to other similar systems.

Acknowledgements

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6 Supplementary material

6.1 Parameters

Parameter	Symbol	Value	Units	Source
Atmospheric deposition	$K_{atmosphere \rightarrow soil}$	0.5	$gK.m^{-2}.yr^{-1}$	Measured in Laclau et al. (2010)
Initial K contained in litter	K_{litter}^{ini}	1.92	$gK.m^{-2}$	Measured in Laclau et al. (2010)
Initial K contained in soil	K_{soil}^{ini}	0.507	$gK.m^{-2}$	Calculated from Maquère (2008)
Litter K leaching response to rainfall	σ	0.002005	mm^{-1}	Calculated from average rainfall and K litter dynamics measured by Maquère (2008)
Resistance to uptake from the soil	$R_{soil \rightarrow xylem}$	30	days	Assumed
Optimal K concentration of phloem sap	$[K]_{phloem}^{opti}$	0.33	$g.L^{-1}$	Maximum measured value in phloem sap (Battie-Laclau et al., 2014b)
Minimum K concentration of phloem sap	$[K]_{phloem}^{min}$	0.07	$g.L^{-1}$	Minimum measured value in phloem sap (Battie-Laclau et al., 2014b)

Table S1: Parameters related to the circulation of K in the system

Parameter	Symbol	Value	Units	Source
Objective K concentration in leaf water	$[K]_{leaf}^{max}$	5.85	$g.L^{-1}$	(Battie-Laclau et al., 2013)
Leaf K leaching coefficient	λ	0.000090	mm^{-1}	Calculated from average rainfall, leaf K concentration in the +K stand and Laclau et al. (2010)
Resistance to leaf to phloem K flux	$R_{leaf \rightarrow phloem}$	130	days	Assumed from leaf lifespan in oK stand (Battie-Laclau et al., 2013)
Flattening factor	f_p	4	unitless	Calibrated using leaf production on the fully fertilised Eucflux stand
Number of leaves produced by height increment	κ	380	$nb_{leaves}.m^{-2}.m_{tree}^{-1}$	Calibrated using leaf production on the fully fertilised Eucflux stand
Leaf Lifespan	LLS	380	days	Calibrated using leaf production, biomass and fall measurements on the fully fertilised Eucflux stand
Minimum K concentration in leaf water	$[K]_{min}$	0.78	$g.L^{-1}$	Minimum measured K concentration in leaf water (Battie-Laclau et al., 2013)
Objective leaf surface	S_{max}	3500	mm^2	measured in scans (Fig.S4)
Maximum leaf surface reduction due to K	r	0.8	mm^2	Measured in scans from Itatinga and Battie-Laclau et al. (2013)
Half time of leaf expansion	$t50_s$	30	days	Calibrated on leaf expansion data (Battie-Laclau et al., 2013)
Rate of leaf expansion	k_s	538	$mm^2.days^{-1}$	Calibrated on leaf expansion data (Battie-Laclau et al., 2013)
Resorption rate	k_r	0.2	$.days^{-1}$	Assumed from Battie-Laclau et al. (2013)
Water expulsion rate	α	0.1	$mL.day^{-1}$	Calibrated using measurements in Laclau et al. (2009)
Conversion factor from deficit days to symptoms	Θ	0.44	unitless	Calibrated using measurements in Battie-Laclau et al. (2013)
Maximum leaf symptom proportion	SP_{max}	0.44	$m_{symptoms}^2.m_{leaf}^2$	Calibrated using max symptom surface proportion in Battie-Laclau et al. (2013)

Table S2: Parameters related to the leaf cohort sub-model

Parameter	Symbol	Value	Units	Source
Curvature parameter	θ	0.5	unitless	Found in Grassi et al. (2002)
Quantum efficiency	α	0.24	mol.mol^{-1}	Found in Grassi et al. (2002)
Empirical coefficient in two-slope Tuzet model	G_{11}	8	unitless	Calibrated on Eucflux flux data
Empirical coefficient in two-slope Tuzet model	G_{11}	25	unitless	Calibrated on Eucflux flux data

Table S3: Photosynthetic parameters that were modified from Christina et al. (2017). The values of the other parameters related to the MAESPA model can be found in Table S1 of Christina et al. (2017).
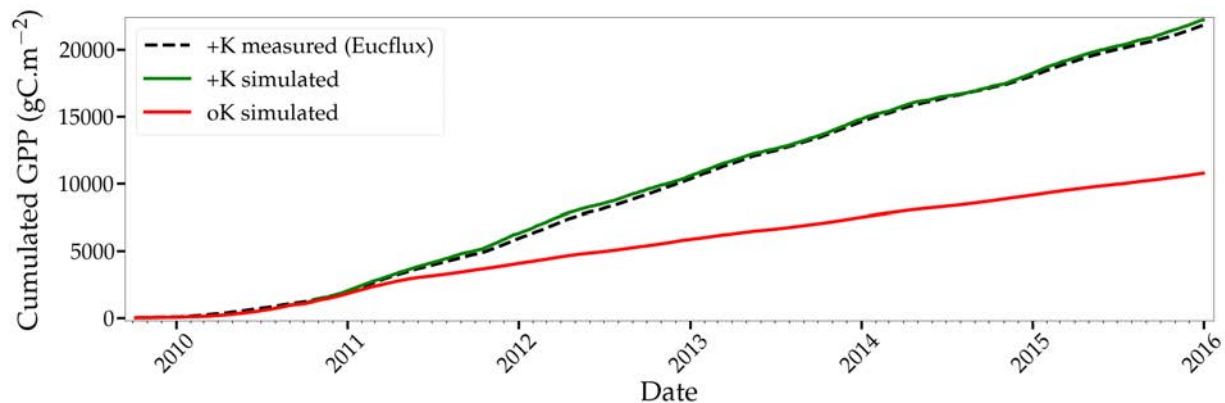
6.2 Cumulated GPP

Figure S1: Measured and simulated GPP over the course of a rotation.

6.3 Leaf lifespan

The lifespan of leaves was measured in a Eucalypt stand planted in 2018 in place of the Eucflux experiment described above. Leaf lifespan was measured on 4 trees that were chosen due to their proximity with the flux tower, thus allowing for easy access to branches. Leaf lifespan and production were followed by tagging axes. Every 50 cm along the trunk (primary axis) a secondary axis was tagged and all subsequent nth order axes on the secondary axis were tagged (Fig.S2). If an axis exceeded 10 leaves tags were placed every 10 leaves from the base. Every two weeks, the number of leaves for each tag was counted and tags were added as needed. This methodology hinged upon the hypothesis that on a series of 10 leaves of the same axis, there could not be leaf production and leaf fall at the same time. It was possible to make this assumption since new leaf production was very fast.

The experiment lasted 15 months to be able to guarantee a good measurement of seasonal leaf production and leaf lifespan dynamics. Overall, 5597 leaves were followed from production to senescence. The biological material (i.e. clone) that was used for these measurements is different from that of the Eucflux experiment described in the main text. This
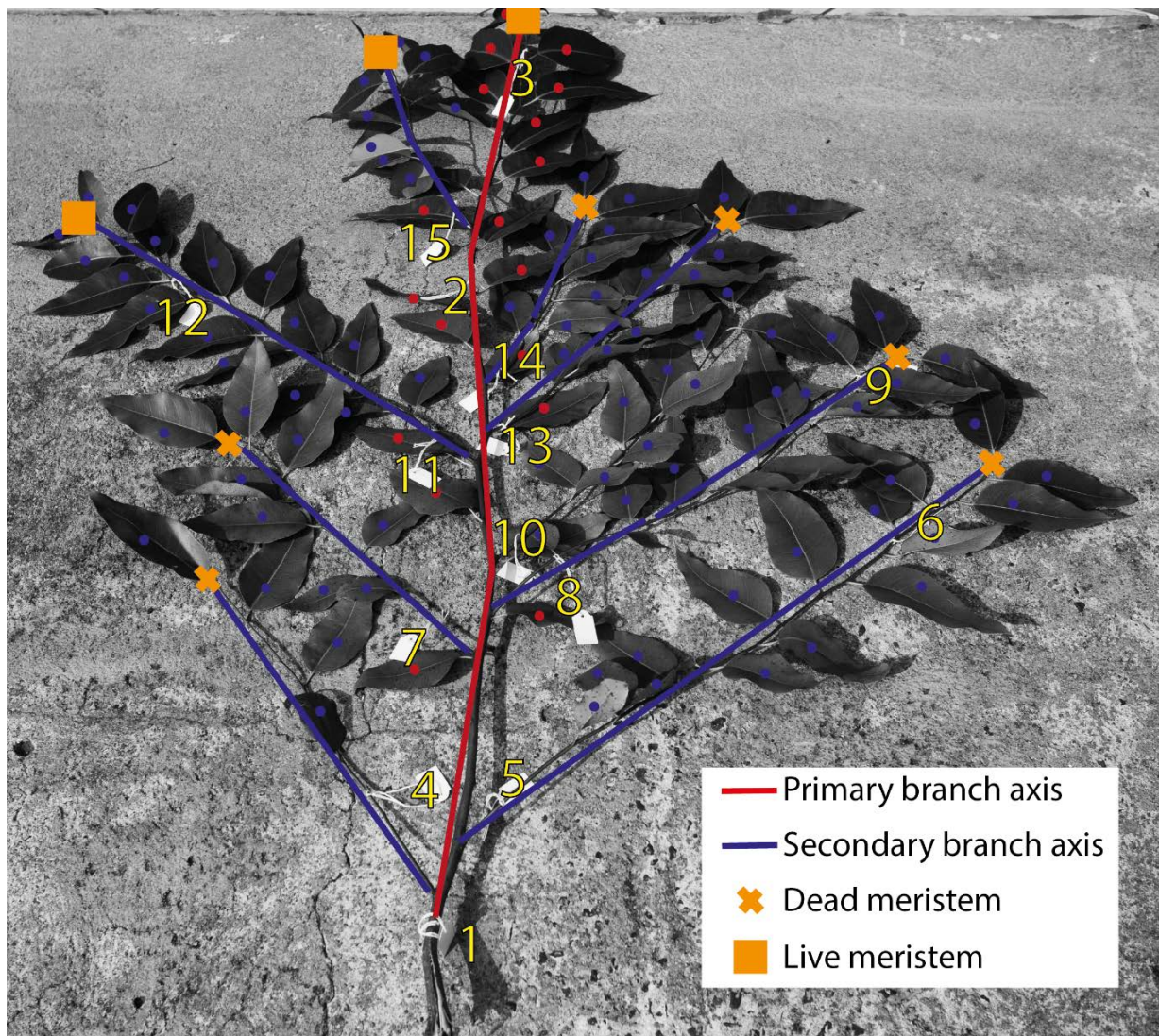
Figure S2: An example of the leaf tagging protocol on a cut branch. The numbers correspond to the number of the individual tags.

explains why leaf lifespan values are different.

While leaf lifespans followed a seasonal pattern (Fig.S3a-e) there was no link between the horizontal position of leaves on the axis and their lifespan (Fig.S3f). This suggests that leaf lifespan was not related to shading-induced C sink-source dynamics at the leaf level.
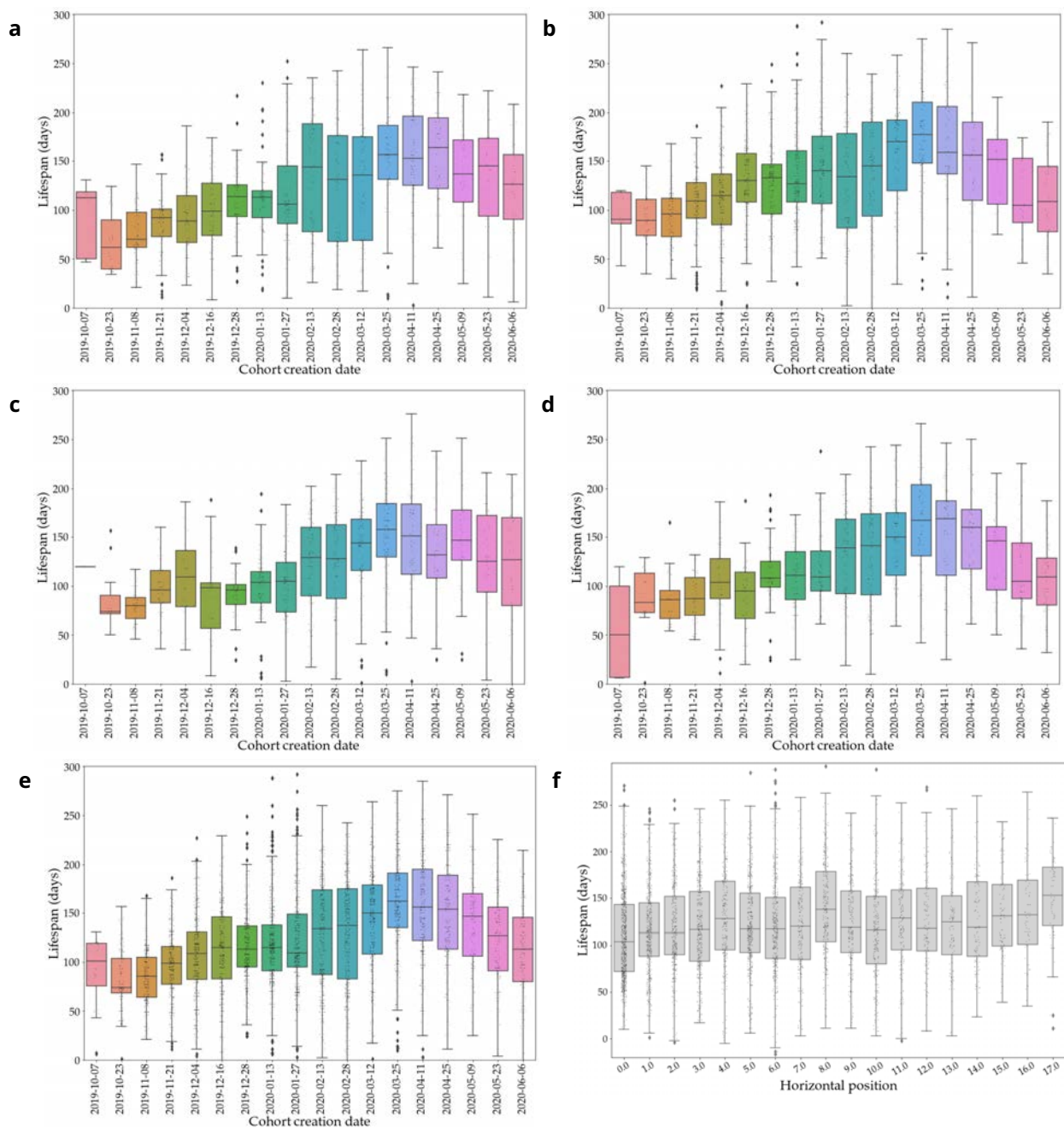
Figure S3: a,b,c,d boxplot of the lifespans of individual leaves of different cohorts from trees 1, 2, 3, and 4 respectively. e) The lifespans of the leaves from all trees when the datasets are joined together. f) Leaf lifespan in function of the leaves' position on the horizontal axis (number of the tertiary axis where the leaf is found: 1 is close to the trunk and 16 is far).

6.4 Leaf surface and mass

While there was variation of mean surface of individual leaves during the Eucflux rotation, no temporal trend was found after 15 months (Fig.S4). The difference between two locations of Eucflux stand, one close to the flux-tower (soil more sandy) and the other further to the flux-tower, on a more clayey soil, was also small. The lower mean leaf surface at 12 months of age in the Clay site could be a consequence of high leaf production and low total leaf surface (meaning that expanding leaves represent a higher proportion of leaves).
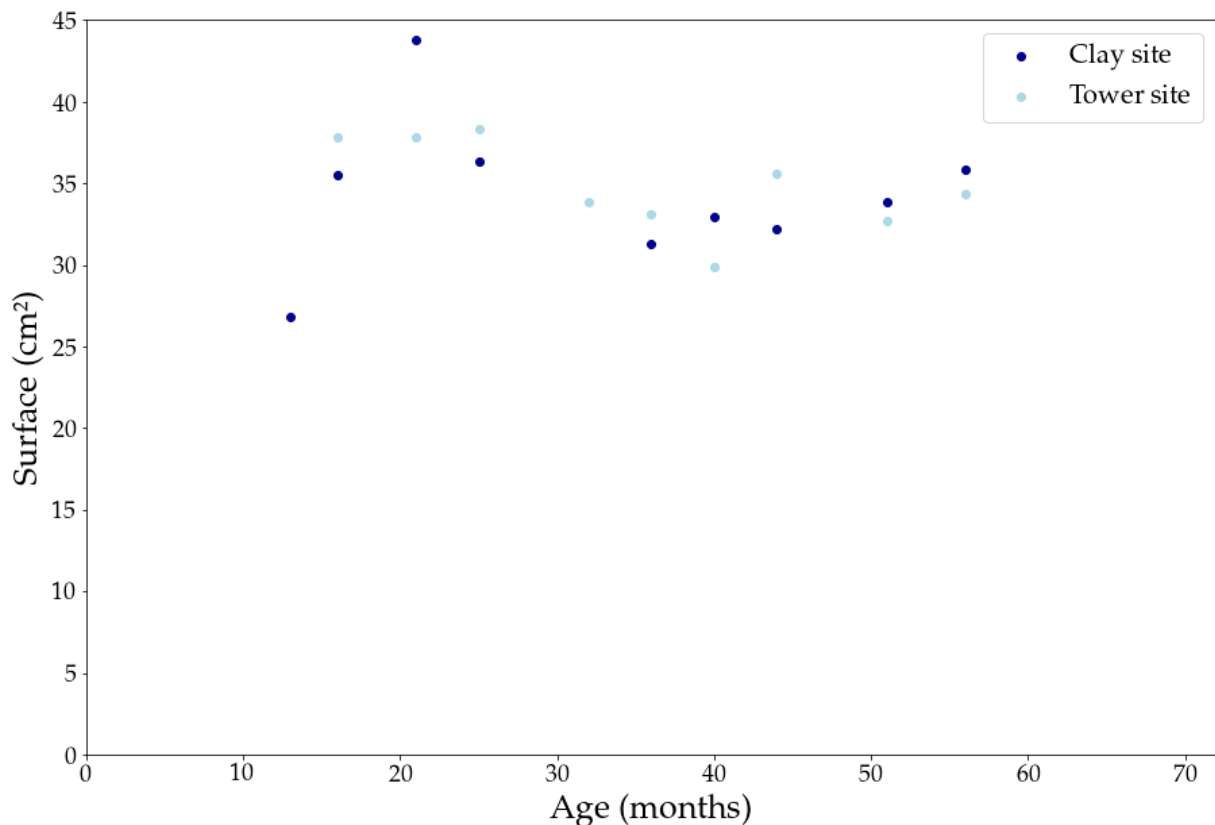

Figure S4: Upscaled mean leaf surfaces at two locations of Eucflux stand: The tower site (mainly sandy soil) in close proximity to the flux tower measurement and the Clay site (more clayey soil) further away from the tower but still on the Eucflux stand

As a rule SLA decreased with tree height. This decrease of SLA with tree age (strongly related to height in these fast growing eucalypt plantations) has been observed at other sites (Fig.2 in le Maire et al., 2011). A two-slope relationship was apparent (Fig.S5a) but could not be mechanistically explained. It could be related to the shift in leaf morphology that happens at the beginning of the rotation (Fig.S5b).
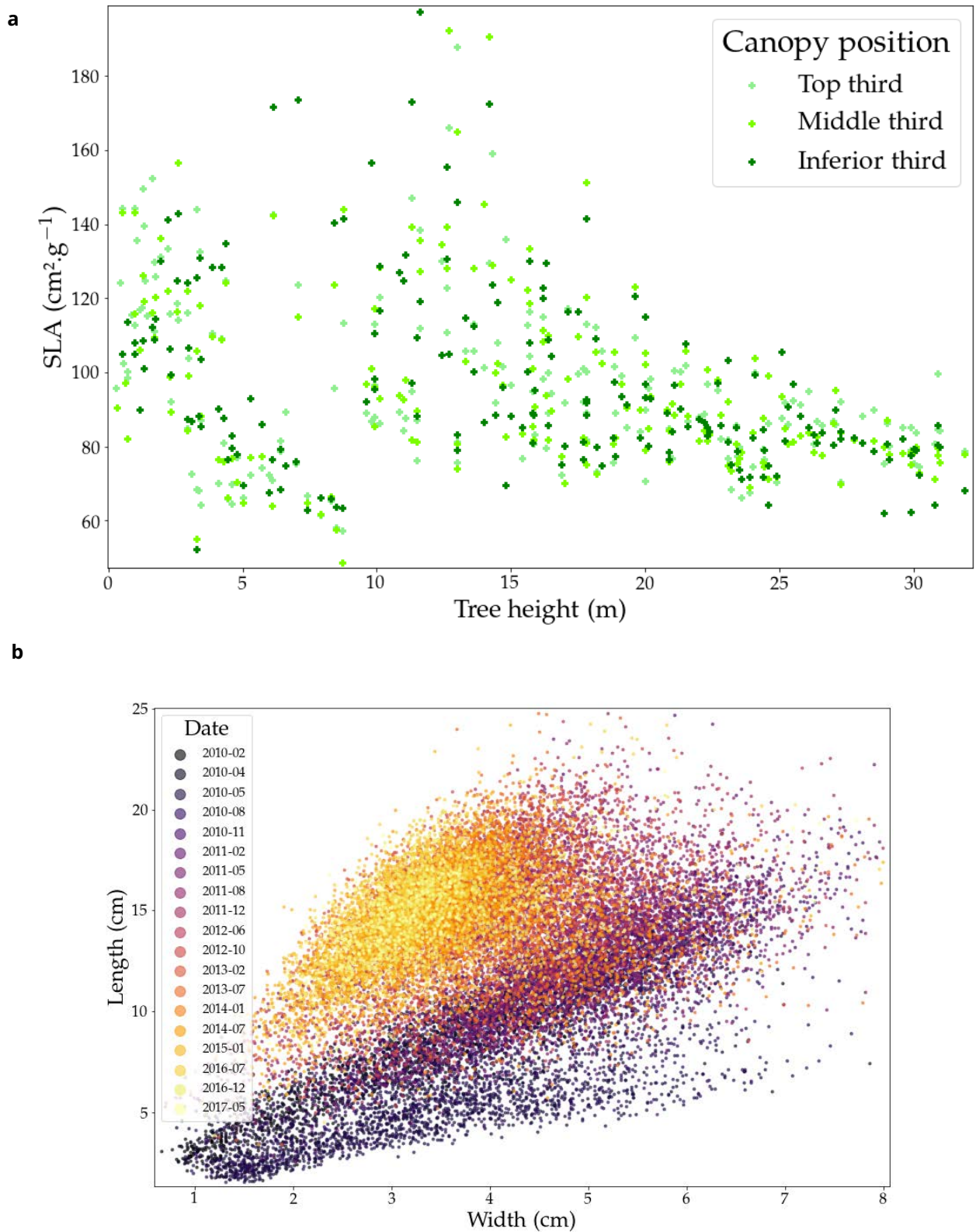
Figure S5: (a) Specific leaf areas of leaves at the Eucflux site in function of tree height. The canopy was cut into 3 thirds that show no difference in the response of SLA to tree height. (b) The leaf width in function of leaf length shows that there is a strong shift in leaf morphology over the course of the rotation. The colors represent the date at which the leaves were sampled. Each dot is an individual leaf that was scanned.

6.5 Leaf symptoms

Leaf symptoms were measured on the Itatinga experiment using leaf scans by using a classification algorithm based on the purple colour of the anthocyans.
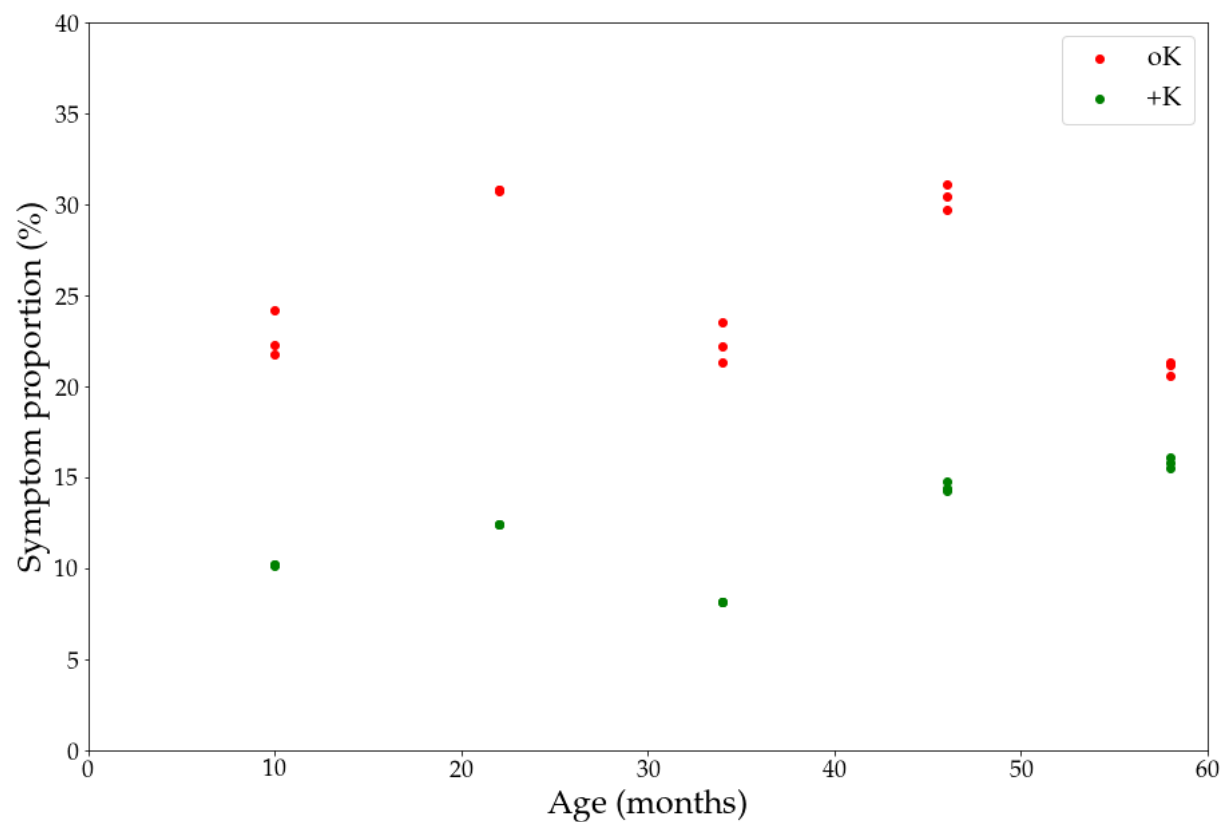

Figure S6: Upscaled mean leaf symptom proportion at the Itatinga experiment

6.6 Leaf Photosynthesis and nutrient content

In an attempt to understand the link between the K content of leaves and their photosynthetic capacity in planted eucalypts, a measurement campaign was set up. The site was an eucalypt plantation with a fully fertilised and K omission stands.

Eight trees in total were selected: 5 in the 0K stand and 3 in the fully fertilised stand. These trees were cut in the field. On every tree, 4 branches were selected. One at the top of the canopy, one at the middle exterior of the canopy, one at the middle interior of the canopy and one at the bottom of the canopy. These branches were cut under water to prevent cavitation (Verryckt et al., 2020) and were brought back to the lab. There, on each branch 3 fully expanded leaves were selected. One close to the tip, one at the middle and one close to the base of the branch.

For each of the leaves a rapid A-Ci response curve (RACiR) was performed. The RACiR allows the phenotyping of more leaves than the traditional A-Ci curves (Stinziano et al., 2017). For each measurement series, an empty chamber calibration was performed (Fig.S7a-c, to measure the response of the CO_2 measurement to the CO_2 concentration ramp). This accounts for the offset and delay between the two IRGA cells that measure CO_2 concentrations (Stinziano et al., 2017). Then the reference CO_2 in the camber was continuously decreased from 620 to 50 ppm and increased in a second ramp from 1100 to 530 ppm. This protocol had previously been developed and tested on different eucalypt plantations and compared to classical A-Ci curves (personal communication, SUZANO). Photosynthetic traits *Vcmax* and *Jmax* were fitted on RACiR data collected for each leaf using the plantecophys R package (Duursma, 2015).

Each leaf was then scanned, weighed (both wet and dry weight) and the concentration in N, P and K were measured. Using the dry weight and leaf surface determined by the scans, we calculated the leaf mass per area (LMA, g m^{-2}). This was needed to calculate the surfacic concentration of N, P and K (g of element m$^{-2}_{leaf}$). We then related the surfacic nutrient content of leaves with their photosynthetic traits (Fig.S8a-b). We observed no significant relationship between the leave's K surfacic concentration and photosynthetic traits in our dataset (Fig.S8b). This could be the consequence of the restricted, and overall high range of K surfacic concentrations measured here. Indeed, values of surfacic K concentrations in this 0K experiment (1.0-2.0 gK m$^{-2}_{leaf}$, Fig.S8b) were higher than the observed values of the +K stand at Itatinga (i.e. the range at the Itatinga experimental site was 0.28 (0K) to 0.85 (+K) gK m$^{-2}_{leaf}$, data not shown).
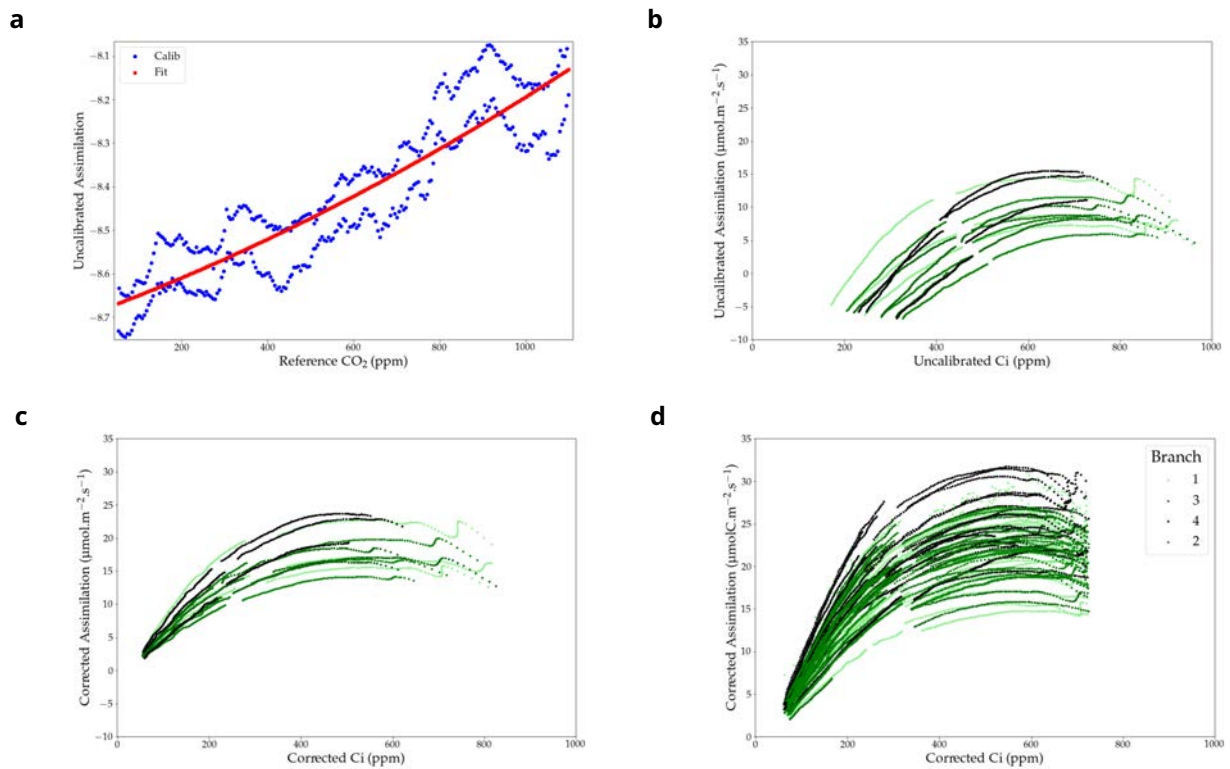
Figure S7: (a) The empty chamber calibration that is used in the RACiR method. (b) The uncorrected RACiR curves. (c) The same curves after correction by the calibration performed in a. (d) The RACiR curves of all the leaves that were used in this experiment. The number of measured leaves (62) was lower than the theoretical number of leaves that we planned to measure (96) due to technical difficulties.
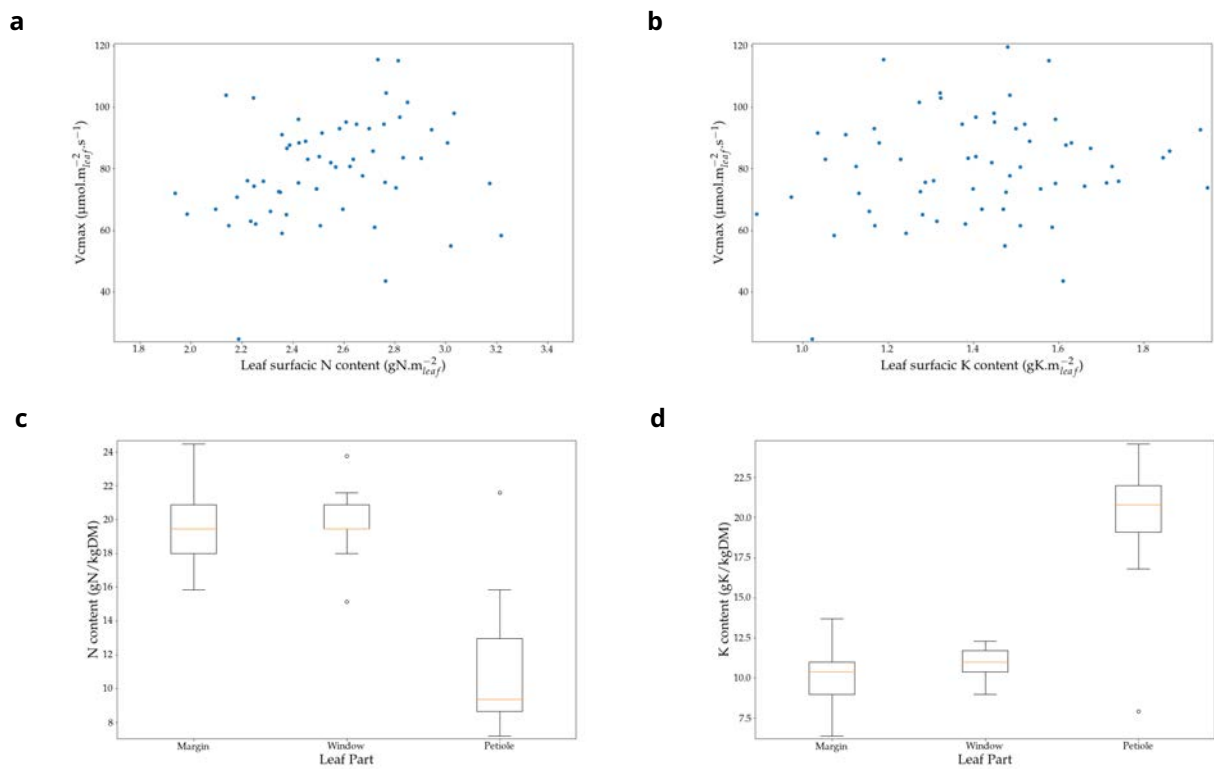
Figure S8: (a) The response of the maximum carboxylation rate *Vcmax* to the leaf N surfacic concentration (b) The response of the leaves' *Vcmax* to the K surfacic concentration. (c) The N mass concentration of each leaf part that was cut (d) The K mass concentration of each leaf part that was cut. Differences in the organ pattern of concentrations can be seen between N and K.

Chapter 4

Potassium-limitation of forest productivity, part 2: Lack of potassium limits the wood productivity of tropical Eucalypt plantations by reducing photosynthesis, not by imposing stoichiometric limitation on tissue formation.

Potassium-limitation of forest productivity, part 2: Lack of potassium limits the wood productivity of tropical Eucalypt plantations by reducing photosynthesis, not by imposing stoichiometric limitation on tissue formation.

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Abstract

After applying the CASTANEA-MAESPA-K model to the study of the limitation of GPP by K in tropical eucalypt plantations in the first part of this two series-paper. In this second part, we built upon the model and used it as a tool to understand if the simulated decline in C-source under K deficiency was sufficient to explain the K-limitation of wood productivity. We developed allocation schemes for both C and K and included them in the mechanistic model. No direct limitations of the C-sink activity, nor direct modifications of the C-allocation by K availability were included in the model. Simulation results show that the model was successful in replicating the observed patterns of wood productivity / growth / NPP limitation by K deficiency. Simulations also show that the response of NPP is not linear with increasing K fertilisation. Carbon use efficiency and water use efficiency decrease with decreasing levels of K availability. Simulating a direct stoichiometric limitation of wood productivity / growth / NPP was not necessary to reproduce the observed decline of productivity under K shortage, suggesting that K stoichiometric plasticity could be different than that of N and P. Confirming

previous results from the literature, the model simulated an intense recirculation of K in the trees, suggesting that process was essential for tree functioning. Optimal K fertilisation levels calculated by the model were similar to nutritional recommendations currently applied in tropical Eucalypt plantations, paving the way for validating the model at a larger scale and using at a decision-making tool.

Keywords

Potassium - Biogeochemistry - nutrient limitation - NPP - eucalypt -

Contents

1 Introduction

Large scale fertilisation experiments of tropical eucalypt stands have been conducted over multiple rotations (Laclau et al., 2010; Battie-Laclau et al., 2016; Gazola et al., 2019; Gonçalves, 2000). These experiments have shown that nutrients can strongly affect tree growth in these systems. These nutrient limitations can be explained in part by low nutrient supplies from the soil, and in part by the frequent export of trunk wood (every 6-7 years) from the stands. The frequent export of trunk wood in these fast-growing plantations leads to the export of massive amounts of nutrients that are immobilised in wood (Cornut et al., 2021). In commercial plantations this issue is solved through the use of fertilisers (NPK and micro-nutrients).

Potassium (K) has been identified as the most limiting element in many of those nutrient limitation of wood productivity (Gonçalves, 2000; Rocha et al., 2019). Potassium impacts wood growth through different physiological mechanisms that have been reviewed in detail (Sardans and Peñuelas, 2015; Cornut et al., 2021). In brief, K deficiency is thought to impact the assimilation of carbon by the plant (C-source processes, Gross Primary Production) as well as allocation and use of carbon by the plant for growth (C-sink processes, Net Primary Production).

The study of the limitation of GPP (C-source) by K deficiency was explored at the stand level in Part 1 of this series of two papers, using a coupled C-H_2O-K mechanistic model (CASTANEA-MAESPA-K). The simulations showed a strong response of GPP to K deficiency. The GPP in the simulated K omission stand was less than half of that in the simulated fertilised stand (Tab.2, Part 1). These results were consistent with previous measurements (Epron et al., 2012) and modelling work (Christina et al., 2018). The strong response of GPP to K availability was due to a reduction in canopy surface and the photosynthetic capacity per unit surface of leaf. The reduction in canopy surface was due in part to a slight reduction in leaf production, in part to a decrease in individual leaf surface and in part to a strong decrease in leaf lifespan (Fig.4, Part 1). The reduction in photosynthetic capacity of the canopy was the consequence of leaf symptoms appearing in the K-deficient (0K) stand. The impact of symptom surface on leaf photosynthetic capacity was sufficient to explain most of the reduction in leaf-scale assimilation in the unfertilized case. A decrease of WUE$_{GPP}$ in the simulated 0K stand was also observed / simulated?. A sensitivity analysis of the model parameters showed that competition between the organs (trunk, branches, bark and roots) and leaves for K access had an important impact on GPP in the 0K stand (the leaf to phloem resorption resistance, $R_{leaf \rightarrow phloem}$, Fig.7 Part 1). This underlined the need for a precise understanding of K circula-

tion and stoichiometry in the plant.

The impact of K deficiency on net primary productivity (NPP) is a widely observed phenomenon in non-planted forests (Tripler et al., 2006; Baribault et al., 2012) and in planted forest omission experiments (Laclau et al., 2010; Battie-Laclau et al., 2016; Gazola et al., 2019). One main question would be how well does the negative influence of K deficiency on GPP explain the decrease in trunk NPP. Various processes have been described that could explain a sink-limitation of tree growth under K deficiency. Indeed, potassium deficiency impacts phloem mobility (Epron et al., 2016; Marschner et al., 1996), loading and unloading of sugars into and from the phloem (Doman and Geiger, 1979; Cakmak et al., 1994; Dreyer et al., 2017) and could directly impact organ growth by stoichiometric limitation (through its role as an enzyme co-factor for example) independently of or in interaction with GPP. The present paper focuses on the simulation of the relationship between K availability and the NPP of the different tree organs and is an attempt to understand if an explicit C sink-limitation is necessary to replicate the observed patterns of K-limited wood productivity.

The objectives of the present study are to understand:

1. the impact of K deficiency on the NPP of a tropical eucalypt plantation,

2. if the influence of K availability on GPP is enough to explain the differences in wood productivity between fertilised and K-limited stands,

3. the link between C partitioning and K availability in the plant-soil ecosystem,

4. which parts of the K cycle are the most critical when it comes to K limitation of wood productivity,

5. if K:C stoichiometry can explain the observed patterns of organ NPP.

To accomplish these objectives we have built on the results relating to the K-GPP relationship obtained in Part 1. Whereas Part 1 focused on the carbon fluxes between the atmosphere and the plant, this study focuses on the internal fluxes of C and K in the plant. To this end, CASTANEA-MAESPA-K was adapted and specific efforts were made to adapt the C allocation scheme to the planted eucalypt stands as well as including an allocation scheme for K. Modelling results were compared to a K fertilisation-omission experiment in order to validate the modelling choices. To test the hypothesis of sink limitation of wood NPP, the parsimony principle was applied and the model did not include any explicit sink-limitation process in the model. If the model was able to replicate observed productivity patterns, that

meant that C-source limitation was sufficient to explain wood productivity limitation by K deficiency.

2 Methods

2.1 Site presentation

A fertilisation trial experiment was installed at the Itatinga experimental station (23°02'49"S and 48°38'17"W, 860 m asl, University of Sao Paulo-ESALQ). The precipitation was on average 1430 mm year^{-1}, with a drier season between June and September, and the mean annual temperature was 19.3°C. A split-plot fertilisation experiment was established there on June 2010, for 6 years. The planted clone was a fast growing *Eucalyptus grandis*. The experimental design was described in detail in Battie-Laclau et al. (2014). Six treatments (three fertilisation regimes and two water regimes) were applied in three blocks. In the present study, we focus on the +K and oK treatments with normal rainfall regime, which consisted in a non-limiting fertilisation +K (17.55 gK m^{-2} applied as KCl at planting, with 3.3 gP m^{-2}, 200 g m^{-2} of dolomitic lime and trace elements and 12 gN m^{-2} at 3 months of age) and an omission treatment oK where all fertilisation was applied as in +K treatment, except K.

The concentrations of different elements (N, P, K) in the organs (leaves, trunks, branches, and roots) were measured at an annual time step in 8 individuals of each fertilisation treatment and upscaled to the whole stand using allometric relationships. Biomass and mineralomass were calculated (using upscaling) from inventories, biomass and nutrient concentration measurements done at 1, 2, 3, 4, 5 and 6 years in each fertilisation treatment. Atmospheric deposition (0.55 gK m^{-2} yr^{-1}) was obtained in a nearby experiment from Laclau et al. (2010).

2.2 CASTANEA-MAESPA-K model

CASTANEA-MAESPA-K is a coupled C-H$_2$O-K mechanistic model that simulates forest growth at the stand level. The original CASTANEA model (Dufrêne et al., 2005), generally used to simulate temperate forest stands was adapted to tropical eucalypt plantations. It was merged with the MAESPA model (Duursma and Medlyn, 2012; Christina et al., 2017) since it does not simulate the water-plant-atmosphere hydraulic continuum natively and the assumption of a fixed root depth made by CASTANEA did not hold true in the studied system (Christina et al., 2011). More information on the construction of the CASTANEA-MAESPA-K model can be

found in Part 1 of this two series article.

While Part 1 focused on the response of GPP to K availability, the second part focuses on NPP. This led to a focus on the C and K allocation models (Fig.1). All the sub-models (leaf cohorts, external K cycling, uptake) from Part 1 were re-used albeit sometimes with different parameter values (Tab.S1-2) since the simulated experimental sites were different. New modules simulating the carbon allocation, the availability of K for organ growth and the remobilisation of K from organs were developed for this work and are presented below.
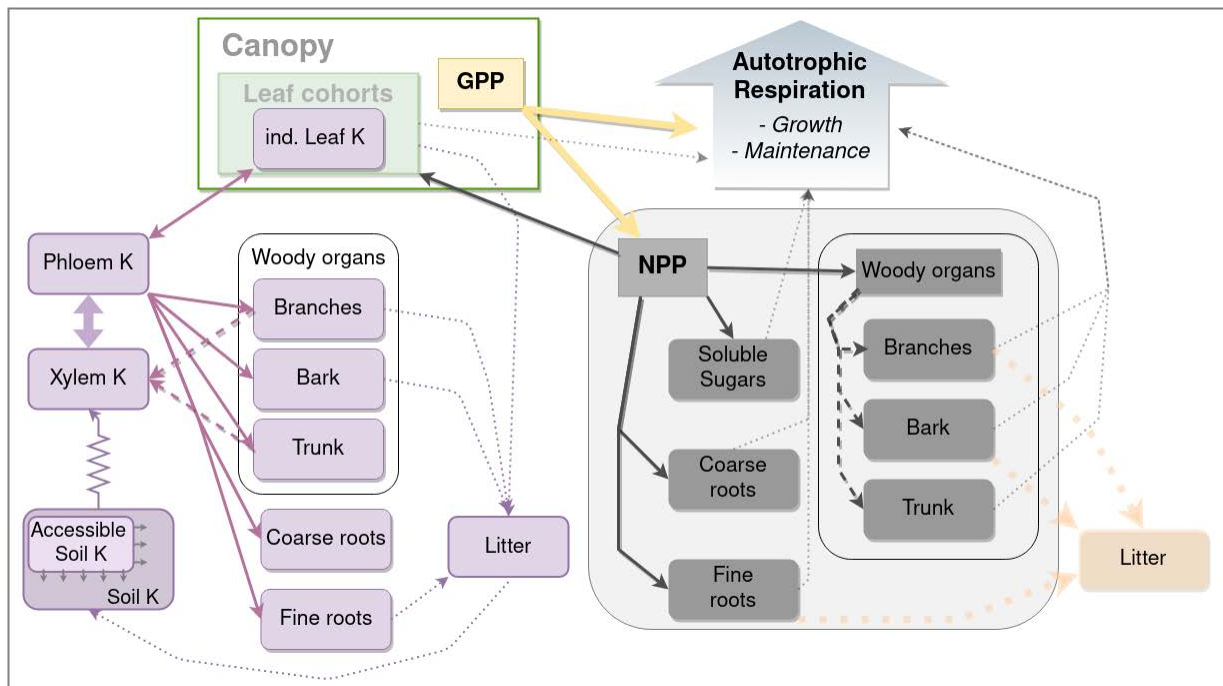
Figure 1: Schematic representation of soil and plant K balance, and its link with the allocation model. Purple boxes are K state variables, while purple arrows are K fluxes. Dashed purple arrows are remobilisation fluxes. The K uptake flux simulated with a simple Ohm's law form is represented with resistance symbols. Grey boxes represent C biomasses. Dark grey arrows represent allocation of NPP to the different organs. Small dotted grey arrows represent the influence of the organ biomass on respiration.

2.3   Carbon allocation

In the CASTANEA model, carbon of assimilates was allocated to organ growth and soluble sugars (SSs), after a part of it was released to the atmosphere through maintenance respiration and growth respiration processes. SSs are not localized in the model which, for the carbon part, has no topology. So SSs are hypothesized to be part of the phloem and other tissues, indistinctly. This is different from the K content of the plant, that we localized either

in organs or the semi-explicit phloem and xylem saps.

The growth of all organs was a fraction of the daily NPP (Fig.1). The allocation coefficients of each organ except leaves (i.e. fine roots, coarse roots, woody organs) were calculated at a daily time-step and were the result of NPP and allometric relationships among organs. The generation of leaves and their growth was a process that was not directly dependent on NPP (see Part 1), and had priority for the allocation of carbon. Leaf growth could however be limited if demand for growth was higher than available C in the SSs compartment.

2.3.1 Leaves

In the model, leaves had carbon priority over other organs. This means that carbon was firstly allocated to leaves and what was left could be allocated to the other organs. Leaf production in the model was driven by the increase in tree height (see Part 1 and eq.8 below). The parameters used here were fitted using experimental data from the +K stand.

2.3.2 Soluble Sugars

The optimal biomass of SSs (BSS_{max}) was a function of woody organ biomass (eq. S1). The parameters of the function relating optimal SS biomass to woody organ biomass assumed in a range of realistic values since no data was available on SS content. The allocation coefficient to SSs with an objective corresponding to this optimal biomass was calculated as:

$$G_{SS} = max\Big(0, GSS_{max} \times min\Big(1, (1 - \frac{B_{SS}}{BSS_{max}}) \times \frac{1}{p_{SS}}\Big)\Big) \tag{1}$$

Where G_{SS} was the (daily) allocation coefficient of soluble sugars, B_{SS} (gC m^{-2}) the biomass of soluble sugars, BSS_{max} (gC m^{-2}) the optimal biomass of soluble sugars and p_{SS} the sensitivity of the response of the allocation coefficient to soluble sugar deficiency.

2.3.3 Roots

In accordance with experiment evidence in the fertilisation experiments, the allocation coefficient of coarse roots was set to a constant:

$$G_{CR} = 0.01 \tag{2}$$

The allocation coefficient of carbon to fine roots was similar to Marsden et al. (2013). It used an objective function, where the fine root objective was a function of leaf area index:

$$G_{FR} = min\Big(1 - G_{CR} - G_{SS}, max\Big(0, 0.5 \times min\Big(1, (1 - \frac{B_{FR}}{\lambda \times L}) \times \frac{1}{p_{FR}}\Big)\Big)\Big) \tag{3}$$

Where G_{FR} was the allocation coefficient to fine roots, G_{CR} and G_{SS} the allocation coefficients of coarse roots (eq. 2) and SSs (eq. 1) respectively, B_{FR} (gC.m^{-2}) the fine root biomass, λ (gC.$m^{-2}.m_{leaf}^{-2}$) the conversion coefficient between leaf area and objective root biomass, L ($m_{leaf}^2.m_{soil}^{-2}$) the leaf area index of the stand and p_{FR} a sensitivity parameter.

2.3.4   Woody organs

The remaining C available after allocation of NPP to leaves, roots and SSs was allocated to the woody organs (trunk, branches and bark):

$$G_W = max(0, 1 - G_{FR} - G_{CR} - G_{SS}) \tag{4}$$

Where G_W was the allocation coefficient to woody organs, and G_{FR}, G_{CR} and G_{SS} the allocation to fine roots (eq. 3), coarse roots (eq. 2) and soluble sugars (eq. 1) respectively.

The C allocated to woody organs was then distributed to the different woody organs (trunk, branches and bark) using allometric relationships.

Branches   Parameters of the function linking the allocation of woody NPP to branches in function of total woody biomass were fitted on experimental data. The following equation was used in the model:

$$G_{Br} = 0.437 \times e^{-0.00240 \times (B_{trunk} + B_{Br} + B_{bark}) + 0.102} \tag{5}$$

Where G_{Br} was the ratio of woody NPP allocated to branch production, B_{trunk}, B_{Br}, B_{bark} the biomasses (gC.m^{-2}) of the trunk, branches and bark respectively.

Bark   Following experimental data, the allocation of woody NPP to bark was considered to be constant:

$$G_{Bark} = 0.10 \tag{6}$$

Trunk   All the C remaining after allocation of woody NPP to the bark and the branches was used for trunk wood production.

$$G_{trunk} = 1 - G_{Bark} - G_{Br} \tag{7}$$

Where G_{Bark} was from eq.6 and G_{Br} from eq.5.

Height The increase in height was a function of trunk biomass. The relationship was fitted in the +K stand using biomass and inventory data from Itatinga (Fig.S1):

$$H = 22.67 \times (1. - e^{-0.00029 \times B_{trunk}})^{0.4989} + 1 \qquad (8)$$

Where H (m) was the height of the stand and B_{trunk} (gC.m^{-2}) the biomass of the trunk.

2.4 Autotrophic Respiration fluxes

2.4.1 Growth respiration

Each organ in the model had an associated construction cost. The growth respiration corresponded to the carbon allocated to the organ minus the construction cost (see Dufrêne et al., 2005).

2.4.2 Maintenance respiration

The hourly maintenance respiration for all organs (except leaves which had a respiration rate based on their vertical position in the canopy, Christina et al., 2015) was a function of their respective respiration rate per nitrogen unit, nitrogen content and surface temperature (Dufrêne et al., 2005).

Respiration rates per unit nitrogen Firstly the respiration rates per unit nitrogen were calculated. For the trunk, we used data from Ryan et al. (2009) to calculate the maintenance respiration rate per unit nitrogen, as a function of trunk biomass:

$$MRN_{Trunk} = 0.0073 - 1.16 \times 10^{-6} \times B_{Trunk} \times 10^{-6} \times 3600 \times \frac{1}{12} \times \frac{1}{N_{TV}} \qquad (9)$$

Where MRN_{Trunk} (mol CO$_2$.gN^{-1}.hr^{-1}) was the respiration rate of the trunk per nitrogen unit, B_{trunk} the trunk biomass in gC.m^{-2}, 3600 the number of seconds per hour, 12, the molar mass of carbon and N_{TV} the concentration of N per unit mass of trunk (gN gDM^{-1}). The respiration rate per nitrogen unit of roots (MRN_R) and branches (MRN_{Br}) was assumed to be equal to twice MRN_{Trunk}.

N content of organs The N content of roots was fixed at 0.0050 gN.gC^{-1} since no variation was visible in the experimental data. The N content of branches and trunks was a decreasing

exponential function of their respective biomasses that was calibrated using experimental data (Fig.S2):

$$N_{branches} = min(0.5, 0.256 \times e^{-0.00966 * B_{branches}} + 0.2604) \times 0.005$$

$$N_{trunk} = min(0.5, 0.256 \times e^{-0.00854 * B_{trunk}} + 0.0759) \times 0.005$$

(10)

Where $N_{branches}$ and N_{trunk} were the respective N concentrations (gN.gC^{-1}) of the branches and the trunk, and $B_{branches}$, B_{trunk} the respective biomasses (gC.m^{-2}) of the branches and the trunk. The N content of leaves and bark were not simulated since N content did not influence the respiration of leaves in our model and bark had no maintenance respiration.

Maintenance respiration   Following Dufrêne et al. (2005), the maintenance respiration of an organ (except leaves, see below) was:

$$RM_{organ} = B_{organ} \times MRN_{organ} \times N_{organ} \times Q_{10}^{T_{org} - T_{MR}/10}$$

(11)

Where RM_{organ} (CO$_2$.hr^{-1}) was the respiration rate of the organ, MRN_{organ} the respiration rate per unit nitrogen (CO$_2$.gN^{-1}.hr^{-1}, eq. 9) and Q_{10} the exponential relationship between the respiration rates and temperature.

The maintenance respiration of leaves was their dark respiration (inhibited during the day), Rd, and the values from Christina et al. (2017) were used.

2.5   Organ turnover

With the exception of coarse roots and the trunk the other organs were subject to turnover. Branches, bark, fine roots and leaves each had lifespans.

In these simulations, the theoretical (independently of K limitation effects) lifespan of leaves (LLS) was considered to be constant throughout the rotation. This option was chosen since we were unable to mechanistically model the observed variations in leaf lifespan. The realised lifespan of leaves was influenced by their K status (see Part 1). We assumed that the lifespans of bark ($BarkLS$, Fig.S3b), branches ($BrLS$, Fig.S3a) and fine roots ($FRLS$, Lambais et al. (2017)) depended neither on tree age nor on the nutritional status of the organs.

With the exception of dead branches, the other dead organ biomass was allocated to different litter pools. Dead branches were allocated to the dead branch pool which has its own turnover rate. These dead branches fell at a fixed rate and were then added to the litter.

Resorption of K took place during the senescence of leaves (see Part 1) and branches (Fig.S4a). K remobilised from these two organs was added to the phloem sap K pool. While the resorption rate for leaves was dependent on the nutritional status of the tree and their theoretical lifespan, for branches it was fixed.

2.6 K allocation, remobilisation and turnover

The allocation of K to organs was a function of the optimal K concentration of newly formed organ tissue, organ NPP and K availability in the tree. Firstly, organ NPP was calculated by allocating part of GPP to the organs after subtracting the respiration. Then, the total K quantity required was calculated by multiplying the growth of each organ by its optimal K concentration (the concentration of newly formed organs in the fully fertilised stand). If the quantity of available K in the phloem sap was inferior to the demand, K allocation to the organs was limited without affecting C allocation to the organ's growth. This was equivalent to flexivle stoichiometry in other models.

$$K_{NPP} = NPP_{org} \times \left([K]_{wood}^{opti} \times G_{trunk} + [K]_{Br}^{opti} \times G_{Br} + [K]_{Bark}^{opti} \times G_{Bark} + [K]_{CR}^{opti} \times G_{CR} + [K]_{FR}^{opti} \times G_{FR} \right) \quad (12)$$

Where K_{NPP} (gK.m^{-2}) was the quantity of K necessary for optimal stoichiometry of newly formed organ biomass, NPP_{org} (gC.m^{-2}.day^{-1}) the daily net primary production minus the allocation to the leaves, K_{org}^{opti} (gK.gC^{-1}) the optimal concentration of the considered organ (eq.15-18) and G_{org} the allocation coefficient of that organ (eq. 2 to 4).

The quantity of available K was a function of K content in the phloem sap and the minimal quantity of K in the phloem sap (Part 1):

$$K_{available} = K_{phloem} - K_{phloem}^{min} \quad (13)$$

Where $K_{available}$ (gK.m^{-2}) was the amount of K available for organ growth, K_{phloem} (gK.m^{-2}) the amount of K in the phloem sap, K_{phloem}^{min} ($gK.m^{-2}$) the minimal amount of K in the phloem sap (see Part 1).

The limitation of K allocation to newly formed organ mineralomass was simply the ratio between available K and K demand:

$$Lim_{org}^{K} = \frac{min\left(K_{available}, K_{NPP}\right)}{K_{NPP}} \quad (14)$$

Where $K_{available}$ was from eq. 13 and K_{NPP} ($gK.m^{-2}$) the amount of K needed for optimal stoichiometry of newly formed organs (eq.12).

The cycle of K in the leaves is described in Part 1 since it is an integral part of the canopy cohort model.

2.6.1 Wood

Due to the continuous phenology of tropical eucalypt trees, K dynamics in wood were simulated through daily cohorts of wood. This was also the preferred modelling choice since it provided a mechanistic explanation for wood remobilisation (that we considered to be leaching of K from sapwood). The trunk NPP was allocated daily to a cohort. In parallel, the optimal K concentration of newly formed wood ($[K]_{Trunk}$) was constant and equal to the maximum trunk concentration measured at the fertilisation experiment (Fig.S5), i.e. the K content of cohort i at its creation was the following:

$$K^i_{phloem \to Trunk} = [K]^{opti}_{Trunk} \times Lim^K_{org} \times NPP_{trunk} \tag{15}$$

Where $K^i_{phloem \to Trunk}$ ($gK.m^{-2}.day^{-1}$) was the flux of K to the cohort i at the time of its creation, $[K]^{opti}_{Trunk}$ ($gK.gC^{-1}$) the optimal concentration of newly formed wood, Lim^K_{org} the limitation by K availability (eq. 14) and NPP_{trunk} ($gC.m^{-2}.day^{-1}$) the daily trunk increment.

Since K concentration of the total trunk tissue decreases with trunk biomass, it was necessary to implement wood K remobilisation in the model. A model where the remobilisation rate was dependent on wood production was the best suited for this task since it showed the best fit with experimental data when compared to a model where remobilisation was independent of wood production. The following equation was used:

$$K^i_{trunk \to xylem} = K^i_{Trunk} \times T_{KTrunk} \times NPP_{trunk} \tag{16}$$

Where $K^i_{trunk \to xylem}$ ($gK.m^{-2}$) was the remobilisation of K from the cohort i, K^i_{Trunk} ($g.m^{-2}$) the K mineralomass of the trunk cohort i, T_{KTrunk} ($.gC^{-1}$) the remobilisation rate per unit of trunk production, and NPP_{trunk} ($gC.m^{-2}.day^{-1}$) the daily trunk increment. Remobilised K was allocated to K_{xylem}. If the K concentration of the cohort ($[K]^i_{Trunk}$) was lower than a threshold value $[K]^{min}_{Trunk}$ ($gK.gC^{-1}$), there was no remobilisation ($K^i_{trunk \to xylem} = 0$). The threshold, $[K]^{min}_{Trunk}$, was determined from the minimum asymptot of the relationship between trunk biomass and trunk K concentration at the fertilization experiment (Fig.S5). This measured value was assumed to be the minimum concentration of a cohort since it was assumed that at a high enough wood biomass, the contribution of newly formed wood to the total K mineralomass was negligible (Augusto et al., 2000). This meant that the measured concentration of

wood as a whole was similar to the minimum concentration of K in the trunk at high enough trunk biomass.

2.6.2   Branches

The optimal K concentration of newly formed branches was a function of the branch biomass.

$$[K]_{Br}^{opti} = 0.00707 \times e^{-0.00854 \times B_{Br}} + 0.000759 \tag{17}$$

Where $[K]_{Br}^{opti}$ was the K concentration of the newly formed branches in gK.gC^{-1} and B_{Br} was the branch biomass in gC.m^{-2}. This decreasing function was fitted on experimental mineralomass and biomass data collected in the fertilised plots.

Before falling as litter to the ground, branches that die stay attached to the tree. Whenever dead branches are mentioned, we mean dead branches still attached to the trunk. During branch death, part of branch K was remobilized into K_{xylem}. The remobilisation efficiency ($R_{KBranch}$, eq.16) was considered constant and was calculated using the difference between dead branch and live branch K concentration in experimental data. The value that was used here was calculated as the remobilisation rate in the first year (Fig.S4). This was done as we assumed that the dead branches that were dosed at that moment had potentially spent less time as dead branches (than dead branches later on in the rotation) and we would minimise the leaching effect. Since we could not know what proportion of the K loss between the living branches and dead branches was due to leaching or remobilisation we assumed that this was the best methd to avoid error.

2.6.3   Bark

The optimal K concentration of newly formed bark was a function of the bark biomass.

$$[K]_{Bark}^{opti} = 0.00204 \times e^{-0.0057 \times B_{Bark}} + 0.00147 \tag{18}$$

Where $[K]_{Bark}^{opti}$ was the K concentration of the newly formed bark in gK.gC^{-1} and B_{Bark} was the bark biomass in gC.m^{-2}. The parameters for this function were fitted on experimental data collected in the fertilised plots. No remobilization was considered for bark since it is not a living tissue.

2.6.4   Roots

The optimal K concentration (in gK.gC^{-1}) of coarse ($[K]_{CR}^{opti}$) and fine roots ($[K]_{FR}^{opti}$) was a fixed value independent of tree age or biomass. Due to the absence of data regarding this process,

the model did not simulate remobilisation from roots. The K mineralomass of dead fine roots was added to the K litter pool, which in turn leached into the soil available K and could be uptaken by other living roots.

2.6.5   Total remobilisation

Total remobilisation was the flux of K from the woody organs to the xylem. It was calculated as the following:

$$K_{remob} = K_{trunk \rightarrow xylem} + R_{Kbranches} \times K_{branches}^{mortality} \tag{19}$$

Where K_{remob} (gK.m^{-2}.day^{-1}) was the total remobilisation flux, $K_{trunk \rightarrow xylem}$ (gK.m^{-2}.day^{-1}) the remobilisation rate of wood, $R_{Kbranches}$ the remobilisation rate of dying branches and $K_{branches}^{mortality}$ (gK.m^{-2}.day^{-1}) the flux of K from living branches to dead branches.

2.7   Simulations

The simulation initialisations were conducted to resemble as closely as possible the omission experiment. The +K simulated stands were simulations where the K fertiliser pool was initialised at the same fertilisation values as the fertilised control in the experiment (i.e. 17.5 gK m-2) corresponding to a one-time application of fertiliser. The 0K simulations shared the same initialisation except that the fertiliser pool was initialised with 0 gK.

To investigate the effects of a fertilisation gradient, 10 linearly spaced values of K pool initialisation were chosen between the fertilisation values of the 0K and +K stand.

To test whether the fertilisation regime could have an impact on tree productivity, two fertilisation regimes were simulated. One where the K dose was brought all at once (as in the experiment) and one where the same K fertiliser dose was broken up into 4 sub-doses that were temporally spaced (equivalent to the Eucflux experiment see Part 1).

2.8   Analysis

To test the accuracy of model prediction, the Root Mean Square Errors of simulations' output variables were calculated using measurements at the experimental site. The mean of the 3 experimental blocs (there were 3 blocs per experimental condition) was used. To normalise this metric and have a relative Root Mean Square Error, the RMSE was divided by the measured rotation mean of the considered output variable.

To describe the response of resource use efficiency (RUE) to different levels of K availability, we used the following metrics.

2.9 Carbon use efficiency

The carbon-use efficiency was calculated as the simulated NPP flux divided by the simulated GPP flux. It is in fact a measure of the proportion of assimilated carbon that was not lost to respiration.

2.9.1 Water use efficiency

The water use efficiencies of NPP (WUE$_{NPP}$) and trunk NPP (WUE$_{trunk}$) were calculated by dividing the total NPP or trunk NPP by the amount of transpired water during the period over which NPP and trunk NPP were calculated.

2.9.2 Potassium use efficiency

Potassium use efficiencies of GPP (KUE$_{GPP}$), total NPP (KUE$_{NPP}$) and trunk NPP (KUE$_{trunk}$) were calculated by dividing the respective C-based metric by the maximum amount of K that was immobilised in the plant during the rotation. For example in the case of (KUE$_{NPP}$):

$$KUE_{NPP} = \frac{\sum_{i=0}^{k} NPP_i}{K_{plant}^{max}} \tag{20}$$

With KUE_{NPP} (gC.gK^{-1}) the K-use efficiency of total NPP, k the number of days in the rotation (days), NPP (gC.m^{-2}.day^{-1}) the daily NPP of the rotation, and K_{plant}^{max} (gK.m^{-2}) the maximum of K that was immobilized in the plant during the rotation (the maximum of total simulated plant K during the rotation). For calculating KUE$_{GPP}$ and KUE$_{trunk}$ the numerator of the above fraction can be replaced by GPP or NPP$_{trunk}$ respectively. There are many alternative ways to calculate nutrient use efficiencies in forests (Turner and Lambert, 2014). Here, we decided to use total nutrient immobilisation instead of uptake since circulation of K in the system was high and we think that the maximum amount of K immobilized in standing biomass is a more relevant representation of total system K demand. Indeed, the maximum K immobilized in standing biomass is a proxy of the amount of K necessary in the system and along the rotation for the plant considering its biomass. In systems where there is less restitution to the soil, it would be equivalent to the soil nutrient uptake.

2.9.3 Fertiliser use efficiency

Fertiliser use efficiencies of stands at different fertilisation levels were computed as the difference of cumulated NPP between the simulated unfertilized stand (0K) and stands simulated with different fertilisation levels, and dividing it by the amount of K fertiliser added. This allowed us to compute the growth gain in carbon per unit of K fertiliser used:

$$FUE_{NPP}^f = \frac{\sum_{i=0}^{k}(NPP_i^f - NPP_i^{oK})}{K_{fertiliser}^{added}} \tag{21}$$

With FUE_{NPP}^f (gC.gK^{-1}) the fertiliser use efficiency of NPP for a given level of fertilisation, k the number of days in the rotation (days), NPP^f (gC.m^{-2}.day^{-1}) the daily NPP of the currently considered stand, NPP^{oK} (gC.m^{-2}.day^{-1}) the NPP of the K omission stand and $K_{fertiliser}^{added}$ (gK.m^{-2}) the amount of fertiliser that was added in the considered stand. To obtain FUE_{GPP} or FUE_{Trunk}, this relationship can be applied to either GPP or NPP_{trunk}.

3   Results

3.1   Prediction of changes in NPP caused by GPP

The model was capable of replicating most of the NPP and biomass differences between the +K and 0K stands (Fig. 2). In the +K stand, the five-year cumulated GPP, NPP and trunk NPP (NPP$_{trunk}$) were respectively 19830 gC.m^{-2} (i.e. 3966 gC.m^{-2}.yr^{-1} on average), 9950 gC.m^{-2} (1990 gC.m^{-2}.yr^{-1}), 5795 gC.m^{-2} (1159 gC.m^{-2}.yr^{-1}). In the 0K stand, they were respectively 8907 gC.m^{-2} (1781 gC.m^{-2}.yr^{-1}), 3578 gC.m^{-2} (715 gC.m^{-2}.yr^{-1}) and 1781 gC.m^{-2} (414 gC.m^{-2}.yr^{-1}). The GPP, NPP and NPP$_{trunk}$ were respectively 55%, 64% and 70% lower in the 0K compared to the +K stand. The reduction in GPP was in line with what was simulated at the Eucflux site (Table 2 of Part 1) and GPP estimations using the TBCA method (Fig.S6), Giardina and Ryan, 2002). The reduction of trunk NPP$_{trunk}$ was comparable to data (Fig. 2b). The same could be said for the bark (Fig. 2d) and the branches (Fig. 2f). This led to simulated biomasses in line with measurements in the +K and 0K stands for branches (Fig. 2e, bark (Fig. 2c) and trunk (Fig. 2a). In the +K stand the RMSEs (and normalised RMSEs in parentheses) for trunk, branches, bark, leaves and total aboveground biomass were respectively: 385 (12%), 50 (17%), 34 (9%), 48 (19%), and 363 gC.m^{-2} (9%). In the 0K stand they were respectively: 155 (16%), 48 (37%), 25 (17%), 31 (26%), and 193 gC.m^{-2} (15%). The errors between measurements and simulation of total aboveground biomass at 59 months were an underestimation

of 24 gC.m^{-2} (-1%) in the +K stand and an overestimation of 161 gC.m^{-2} (6%) in the oK stand. This overestimation of aboveground biomass was concurrent to an underestimation of root biomass (Fig. 2i).

3.2 Changes in allocation (of GPP) between oK and +K stands

The model allowed the study of allocation in the trees under different K fertilisation regimes. The simulated allocation patterns did not differ greatly between the fertilised and omission stands (Fig 3a). However, simulated carbon use efficiency (defined as the ratio of NPP to GPP) was reduced by 23% in the omission stand (0.52 vs 0.40). The ratio of wood productivity to GPP (CUE$_{trunk}$) was reduced by the same proportion (21%) showing that the reduction of NPP$_{trunk}$ followed the same dynamic than total NPP. Moreover the difference in CUE between the two fertilisation treatments increased over the time of the rotation (3% the first year, 32% the fifth). The trend was similar for CUE$_{trunk}$. The difference in CUE between the two treatments was mainly due to an increase of maintenance respiration in the oK stand where it represented 48% of the GPP compared to 34% in the +K stand. This was further amplified by leaf NPP representing 13% of GPP in oK compared to 7% in +K.

The model was also capable of simulating the response of the different carbon fluxes, along the stand rotation, to a gradient of initial K fertilisation (Fig. 3b). It showed that the responses of GPP, NPP and wood productivity to fertilisation all saturated at around 11 gK.m^{-2} for a five-year rotation. The simulated carbon fluxes did not show any sensitivity to the fertilisation application regime (one or four time application, Fig.S7a). The simulations conducted with the one-time application and the four-time application of the same amount of fertiliser show little to no differences in GPP, NPP and NPP$_{trunk}$ (Fig. S7a). The wood productivity was the same in all fertilisation treatments in the first year of the rotation (Fig. 3). This result was similar to experimental data that shows that the difference in organ NPP only appears in the next years of the rotation (Fig. 2). While the response of CUE$_{NPP}$ resembled a linear function before it saturated at a fertilisation of 11 gK.m^{-2}, the response of CUE$_{trunk}$ followed a non linear response (Fig.S7b) by increasing from 0 to 2 gK.m^{-2} of fertilisation, saturating between 2 and 4 gK and increasing linearly between 4 and 11 gK.

3.3 The sensitivity of K cycling in the trees

The model showed that the main sink of K in both the +K and oK stands were the woody organs (trunk, bark and branches). Despite the remobilisation of K in the trunk, the quantity
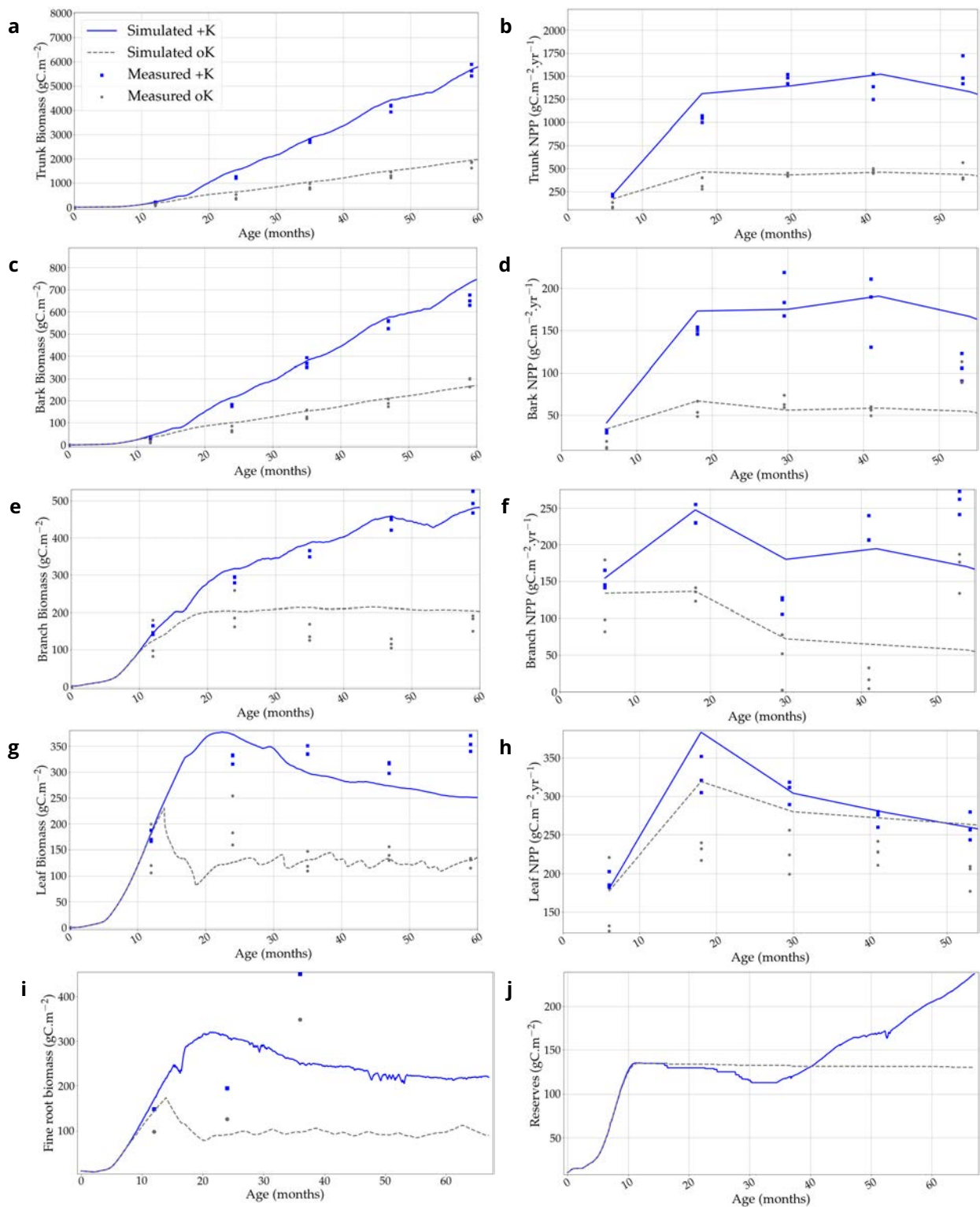
Figure 2: Simulated biomass of the different organs in two contrasted K availability scenarios (no K fertilisation, *oK*, and full K fertilisation, *+K*): a) trunk, c) Bark, e) Branches, g) Leaves, i) Fine roots and j) Reserves. On the right column, the respective measured and simulated annual NPP of each organ: b) trunk, d) Bark, f) Branches, h) Leaves.
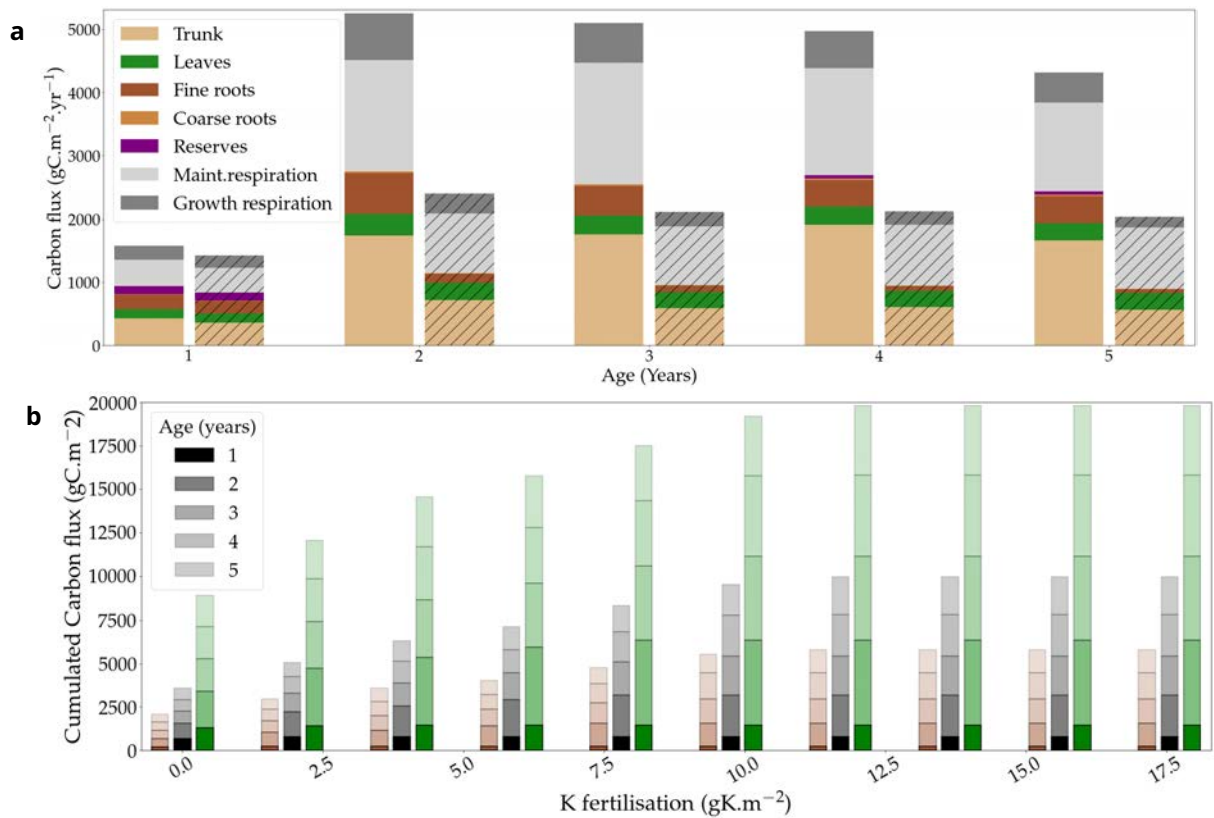
Figure 3: a) The simulated allocation of assimilated carbon to the different organs and respiration fluxes in 2 contrasted fertilisation conditions (oK is hatched). b) The response of simulated carbon fluxes, cumulated over five years, to different fertilisation levels. Total GPP is in green, total NPP in black and trunk NPP in brown.

of K immobilised in the trunk increased linearly with time in both treatments (Fig. 4) thus constituting an important K sink.

The theoretical minimum concentration of K in the xylem sap (assuming no recirculating K) of our trees was calculated by dividing the daily simulated flux of K that circulated in the xylem sap (uptake, wood and branch remobilisation) by the simulated transpiration flux of each day. The mean simulated minimum xylem sap K concentration over the course of a rotation was 0.30 mM (0.012 gK.L^{-1}) in the fully fertilised stand and 0.11 mM (0.004 gK.L^{-1}) in the K omission stand. When including the K content of the phloem sap and leaf resorption (which means the total circulating K in the tree) in this calculation, the values were respectively 1.66 mM (0.065 gK.L^{-1}) and 0.46 mM (0.018 gK.L^{-1}).

The simulation of internal and external K fluxes in the system (Tab. 1) showed that in the fully fertilised and K omission stands, wood remobilisation represented the most important flux of K. Implementing in the model this process of K remobilisation from wood increased the model accuracy substantially (not shown here) by buffering the amount of K available for

organ growth. When added to branch and leaf resorption, the total amount of K remobilised represented 1.8 times the K uptake in the fertilised stand versus 1.4 times in the omission stand. In the simulated oK stand, K uptake was very similar to the sum of the litterfall, leaching and atmospheric deposition fluxes, in all but the first year of the rotation (Tab. 1). The deposition flux represented more than 50% of the uptake flux in these K deficient conditions. Moreover, in the K omission stand, an increase of the simulated weathering flux from 0 to 0.3 $gK.m^{-2}.yr^{-1}$ (in the range of possible values, see Cornut et al., 2021) led to an increase of 23, 28 and 30% of the rotation-cumulated GPP, NPP and NPP_{trunk} respectively. This showed that small differences in K input can lead to big differences in outcome for wood productivity.

The difference in the K flux of canopy leaching between the two simulated stands (much lower in the omission stand, Tab. 1) was in line with results obtained on eucalypt plantations at K-rich and K-deficient sites (Laclau et al., 2010). This was the result of lower leaf K concentration and supports the validity of the leaching model used here (see Part 1).

	Wood remob.	Branch remob.	Leaf resorption	Uptake	Litterfall	Leaching
Age	+K − oK	+K − oK	+K − oK	+K − oK	+K − oK	+K − oK
$0 \rightarrow 1$	0.35 − 0.19	0.12 − 0.10	0.36 − 0.75	5.61 − 2.90	0.07 − 0.05	0.03 − 0.02
$1 \rightarrow 2$	7.71 − 1.13	0.41 − 0.26	1.96 − 0.92	7.39 − 0.96	1.49 − 0.45	0.25 − 0.01
$2 \rightarrow 3$	9.21 − 1.13	0.44 − 0.24	2.68 − 0.70	4.39 − 1.00	2.30 − 0.42	0.26 − 0.01
$3 \rightarrow 4$	10.01 − 1.19	0.43 − 0.21	2.23 − 0.69	4.39 − 0.92	1.90 − 0.40	0.15 − 0.01
$4 \rightarrow 5$	8.73 − 1.12	0.41 − 0.19	2.07 − 0.66	3.86 − 0.99	1.80 − 0.39	0.15 − 0.01

Table 1: Simulated yearly fluxes of K (in $gK.m^{-2}.yr^{-1}$) in a fully fertilised and K limited condition. This table contains both internal fluxes (wood, branch and leaf remobilisation) and exchange fluxes (uptake, litterfall and canopy leaching). Not shown here is the constant atmospheric deposition flux (0.5 $gK.m^{-2}.yr^{-1}$).

3.4   Resource-use efficiencies

Simulated transpiration decreased by 51% between the +K and oK stand. The reduction (13%) of simulated GPP water use efficiency (WUE_{GPP}) between the +K (0.0035 $gC_{GPP}.gH_2O^{-1}$) and oK (0.0031 $gC_{GPP}.gH_2O^{-1}$) stands was comparable to results obtained on the Eucflux site in Part 1. On the other hand, simulated WUE_{NPP} showed a much stronger response to K defi-
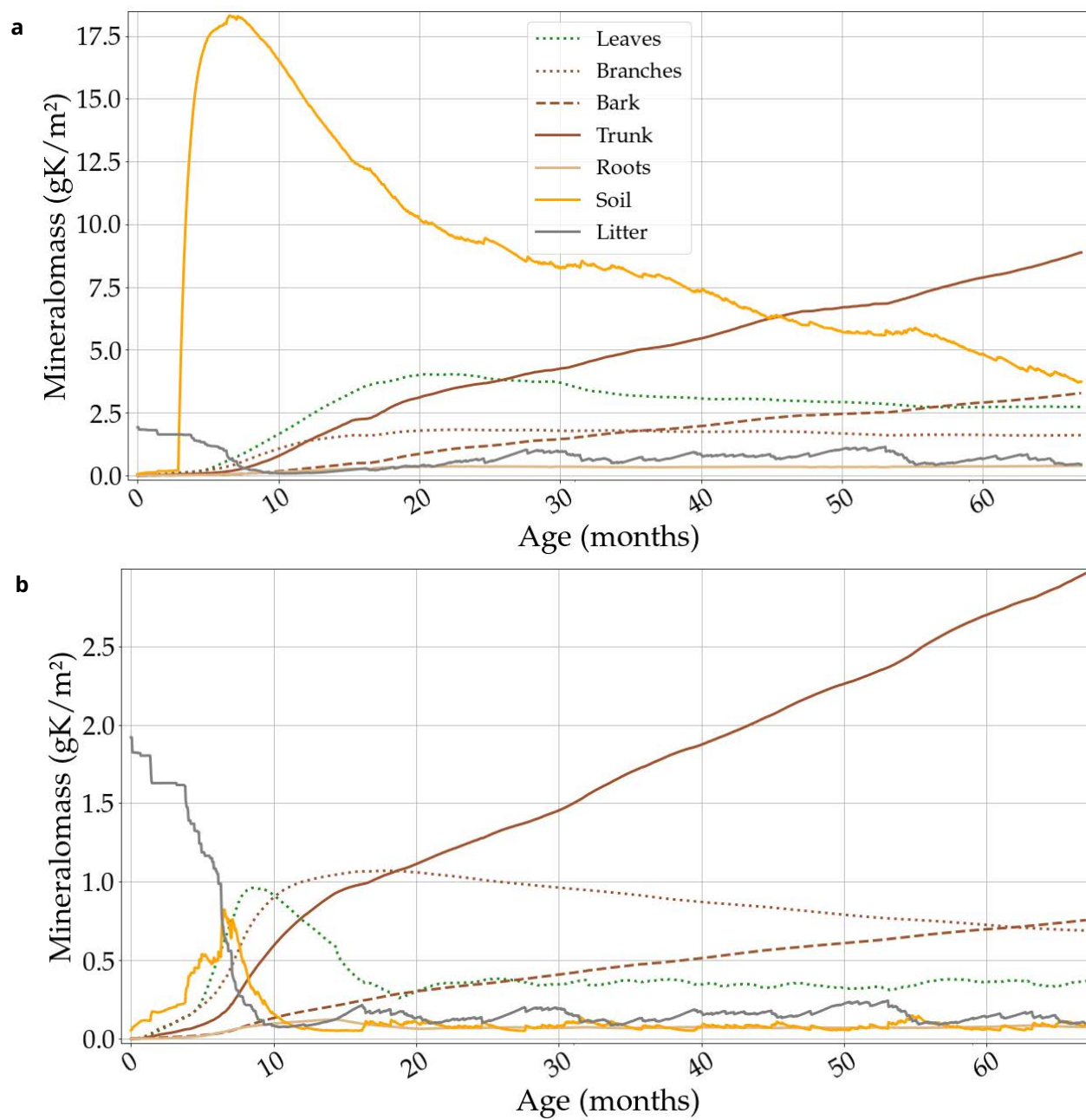
Figure 4: Simulated mineralomass of all the compartments containing K. Two contrasted K availability scenarios are displayed: a) high fertilisation (+K in the main text), b) no K fertilisation (oK in the main text). Note differences in the y-axis scale.

ciency. The reduction was on the order of 33% with WUE_{NPP} at 0.0018 and 0.0012 $gC.gH_2O^{-1}$ in the +K stand and oK stand respectively. The simulated water use efficiency of trunk wood was reduced by the same amount between the +K and oK stand. The WUE_{trunk} values in the +K and oK stands were respectively 0.0011 and 0.0007 $gC.gH_2O^{-1}$ (a reduction of 32%).

In the following paragraph, potassium use efficiency (KUE) is understood as the ratio of a cumulated carbon flux at the end of the rotation and maximum value of K immobilized in the tree (eq.20 during the rotation (not necessarily the end of the rotation). The simulated KUE_{GPP} were 1281 and 1994 $gC.gK_{plant}^{-1}$ in the +K and oK stands, respectively, an increase of +55%. In contrast, the simulated KUE_{NPP} and KUE_{trunk} only increased by 19% (owing to decreased CUE in the oK stand) between the +K and oK stands. The simulated KUE_{trunk} were 387 and 462 $gC.gK_{Plant}^{-1}$ in the +K and oK stands, respectively.

FUE generally decreased with increasing fertilisation (Fig.S8). However, a two-slope relationship was apparent: at low levels of fertilisation, increases in fertilisation led to strong increases in NPP. However, as fertilisation increased more, there is a declining returns in productivity per unit of K. At intermediate levels of fertilisation (between 6 to 10 $gK.m^2$) the FUE was almost constant or slightly increased. At higher levels of initial fertilisation the FUE linearly decreased (consequence of a stable NPP with linearly increasing fertilisation, Fig. 3b).

3.5 Stoichiometry of organs

Potassium concentrations in the trunk total wood and in branches were correctly simulated (Fig. 5) using a simple limitation of the K flux entering organs in function of organs K optimal concentrations (Eq.12-18). The mean K concentrations of total tree biomass were 0.0048 $gK.gDM^{-1}$ in the +K stand and 0.0030 $gK.gDM^{-1}$ in the oK stand. This corresponded to a decrease of 36% of the K concentration between the +K and oK stands. This revealed that total plant stoichiometric flexibility was high in the model in accordance with measurements.

The new model of wood growth and K remobilisation was validated by the simulated concentrations that were in line with experimental measurements both in the fully fertilised an K omission treatment (Fig. 5a) without the need for additional forcing. However, the simulated concentration of K in branches (Fig. 5b) was overestimated in the oK stand. An important amount of K was also stored in bark and branches in the simulated K omission stand (Fig. 4b) and it was the most important K stock at the beginning of the oK rotation.
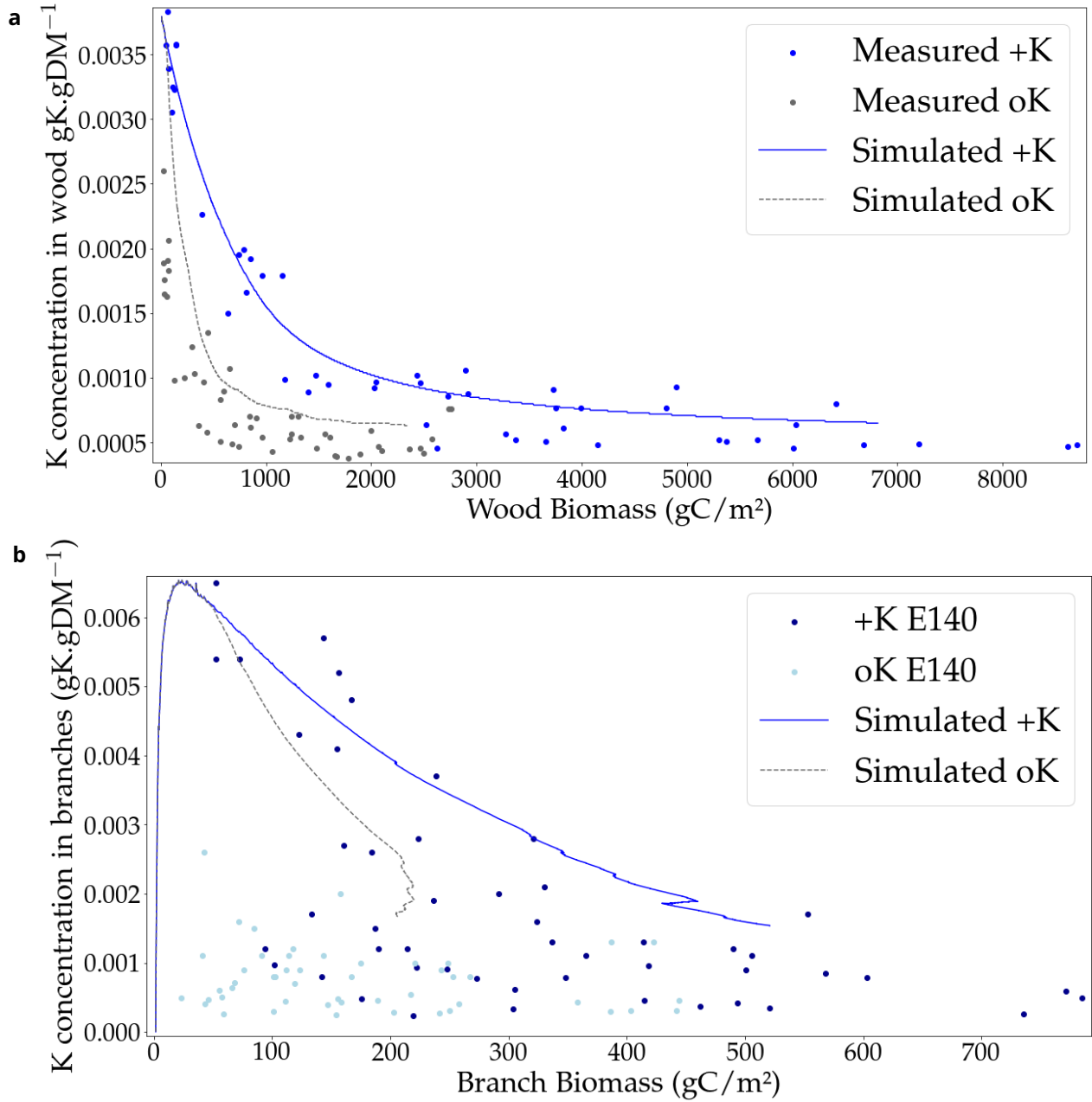
Figure 5: Simulated concentrations of wood (a) and branches (b) in two contrasted K availability scenarios compared to measurements conducted at the fertilisation experiment.

4 Discussion

4.1 GPP-limitation of NPP and partitioning of photosynthates

The CASTANEA-MAESPA-K model was largely successful in reproducing the limitation of wood productivity induced by K deficiency (Fig.2). This makes it the first mechanistic model to simulate the interaction between the K cycle and forest NPP. The model was most successful in its representation of woody biomass productivity. Combined with the fact that partitioning in the model was not directly impacted by K availability (there was no mechanism through which K directly impacted carbon allocation to wood), this tends to show that the limitation of wood productivity in the absence of K fertilisation was mainly due to GPP-limitation. However NPP limitation under K deficiency was higher than that of GPP. This was due to a decrease in CUE at low levels of fertilisation. This is similar to global results that show a decrease in forests' BP-GPP ratio (a proxy for CUE) with decreasing fertility (Vicca et al., 2012). Here, the partitioning of GPP to the different organs was not strongly affected by K availability (except for leaves going from 7% in +K to 13% of NPP in oK). The reduced CUE was mainly the result of an increased autotrophic respiration in proportion to the biomass of organs mirroring the increase in the ratio of ecosystem respiration to GPP in nutrient-poor forests (Fernández-Martínez et al., 2014). In this last study their was no significant relationship between GPP and Net Ecosystem productivity at low fertility forest sites, this was not the case for GPP and NPP in this study.

Only simulated fine root biomasses were under-estimated in both the +K and oK stands (Fig.2j). This leads us to believe that simulating a root objective biomass that is function of leaf area (Marsden et al., 2013) might not be appropriate in this instance (since the shape of root biomass is qualitatively different). One other cause could be a misestimation of root lifespan since measurements of fine root turnover have yielded a wide range of values (Jourdan et al., 2008; Lambais et al., 2017). The estimation of fine root turnover had also been an impediment to simulating N mineralisation rates in Australian eucalypt stands with the G'DAY model (Corbeels et al., 2005). The values of GPP that were simulated here (a mean of 3986 $gC.m^{-2}.yr^{-1}$ in +K and 1709 $gC.m^{-2}.yr^{-1}$ in oK), while even underestimated compared to TBCA measurements (a mean of 4606 $gC.m^{-2}.yr^{-1}$ in +K and 2157 $gC.m^{-2}.yr^{-1}$ in oK), were on the high range of values expected for terrestrial ecosystems (Baldocchi and Penuelas, 2019; Luyssaert et al., 2007), especially considering this 6 year mean included the year after planting. They were however similar to values deduced using TBCA measurements in highly

productive eucalypt plantations (Ryan et al., 2004, 2010) and clonal experiments at the Eucflux site (personal communication from Yann Nouvellon, see Part 1 for the site description).

The K fertilisation level value at which K-limitation was totally alleviated in simulations (Fig.3b) was similar to the 12 gK.m^{-2} of fertilisation that are typically added to commercial eucalypt plantations in Brazil (Cornut et al., 2021).

4.2   Resource-use efficiency is affected by K availability

The RUEs of NPP and NPP$_{trunk}$ were strongly affected by K availability (modelled here as a change in fertilisation levels). Variations of WUE$_{trunk}$ are in line with experimental results that showed a decrease in WUE$_{trunk}$ in the K omission stand at the Itatinga site (Battie-Laclau et al., 2016). While simulations showed a decrease in WUE of 33% of WUE$_{trunk}$ between the +K and oK stand, measurements showed a decrease of 37% (Battie-Laclau et al., 2016). This confirms the relevance of the model based approach in studying the effect of K availability on WUE. However, the model diverged from measurements in the same stand at 50 months of age that showed that WUE of the K omission stand was reduced by 75% as compared to the WUE of the +K stand (Asensio et al., 2020), where CASTANEA-MAESPA-K only showed a reduction by 39% of WUE between these two stands at this age. Since the trunk NPP simulated by the model agreed with measurements (Fig.2b) and the model simulated a reduction in transpiration consistent with different approaches (see Part 1), we believe that trunk WUE in the oK stand might have been underestimated by the measurements presented in Asensio et al. (2020).

Both the variation of KUE and FUE along increasing K fertilisation gradient showed some interesting results. While the increase in KUE under K deficiency was very strong for GPP, the same could not be said for NPP or trunk NPP (Fig.S8). This was a consequence of reduced CUE. FUE results demonstrate that the response of wood productivity is not a linear function of fertilisation and that at low levels of fertilisation, small increases in K fertilisation levels produce a strong increase in NPP. Maximum NPP is obtained with the highest fertilizer amount, however the trend is asymptotical, with more than 95% of trunk NPP (Fig.3b) already reached at around 10 gK.m^{-2}, a value classically used in plantations in these areas. Partitioning of the K fertilisation in only one or in several amounts did not changed the wood production, considering that no deep leaching occurs in these systems.

4.3 Circulation of K in the plant and stoichiometry

Our work pinpointed the necessity of a K circulation model in the plant. The remobilisation flux of K from branches, the trunk and leaves was superior to uptake at all fertilisation levels. In C-N (Zaehle et al., 2010; Thum et al., 2019) or C-N-P (Goll et al., 2017) coupled models, stoichiometry of organs can be a direct limiter of organ growth. This is similar to historical models of organic matter decomposition in soils (Parton et al., 1988). In the present model, which provides no such mechanism (there is no lower bound for organ K concentration), the reduction in NPP was enough to compensate the reduction in K availability such that the simulated stoichiometries of organs do not vary more than they do in the measurements (Fig.S5). Potassium may also be a nutrient with more stoichiometric flexibility than N or P. This is consistent with observations of wood K content, which depends mainly on abiotic conditions while P wood content depends mainly on the species (Bauters et al., 2022). Our model shows that leaves have a higher stoichiometric flexibility than wood (not shown here), in agreement with observations in a Mediterranean forest environment (Sardans et al., 2012). However, the model failed at reproducing the patterns of stoichiometric plasticity (variability in K concentration of organs) that were observed between the woody organs, in particular in branches (measurements show high stoichiometric flexibility in branches). This suggests that not all organs have the same necessity to maintain K homeostasis. The failure of the model to reproduce stoichiometric flexibilities in wood and bark (not shown here) could potentially have had an impact on the amount of K available for leaf expansion thus creating a more severe limitation than reality. This is further compounded by the importance of K stored in bark and branches in the simulated K omission stand , especially at a moment where the model showed a strong K limitation of leaves (between the 10th and 20th month since plantation).

The simulated amount of K immobilised in wood at the end of the rotation in the +K stand was an order of magnitude lower than what is observed in tropical forests (Bauters et al., 2022). This is due to a low total biomass in a short planted rotation compared to a natural forest since the simulated K concentrations of wood were well in range of measured values in old-growth tropical forests. The yearly increase was also well into the range of observed values (see Fig.1 in Bauters et al., 2022) both for the oK and +K stands. This suggests that tropical eucalypt plantations are a relevant model system for certain parts of the K cycle. The quantity of K that was allocated daily to wood and remobilised gradually (see eq.7), acted as a buffer that prevented an overestimation of K limitation once K in the soil reached very low

values. This shows that wood can act as a storage organ for K and can alleviate low uptake of K (under drought for example, Sardans and Peñuelas, 2007; Touche et al., 2022).

While the K trunk remobilisation fluxes were an order of magnitude higher in our model than what was previously calculated using other methods (a mean of 7.6 $gK.m^{-2}.yr^{-1}$ vs 0.64 $gK.m^{-2}.yr^{-1}$ in (Laclau et al., 2010)), the amount of K that transited in the xylem sap every day was low compared to the amount of transpiration. This led to very low xylem sap K concentrations if the quantity of K in the K contained in the phloem sap was not considered. Since values of xylem sap K concentrations that have been measured on different plants are one order of magnitude higher (Nardini et al., 2010; Siebrecht et al., 2003), it either suggests that xylem sap K concentrations are very variable between plants or that an intense recirculation of K between xylem and phloem is taking place. The first hypothesis is supported by evidence from temperate conifers that show a variation of an order of magnitude (the lower bound is similar to values calculated from our simulations) of xylem sap K^+ concentration during the growing season (Losso et al., 2018). The last hypothesis seems more plausible since K is necessary to maintain xylem hydraulic conductivity (Oddo et al., 2011; Nardini et al., 2011) and that adding the K contained in the phloem made the calculated K xylem sap concentrations more in line with measurements from the literature. It also supports evidence that K^+ ions are an essential part of many processes at the plant level (Dreyer and Michard, 2020): energy source (Dreyer et al., 2017), counter-ion for NO_3^-, signaling (Anschütz et al., 2014), protection against abiotic stress (Cakmak, 2005), among others; this intense recirculation from xylem to phloem and back serving as a way to maintain homeostasis. The order of magnitude of this recirculation would have to be determined experimentally. Previous measurements have shown that up to 25% of K^+ ions are recirculated in tomato plants (Armstrong and Kirkby, 1979) and up to 50% in *Ricinus communis* seedlings (Marschnert et al., 1997). Results from the model suggest that the figure could be higher in eucalypt trees (maybe owing to remobilisation from wood absent from tomato plants).

5   Conclusion

The results shown here demonstrate the relevance of using a mechanistic model to explore the links between K availability and forest NPP. The model was able to reproduce results from fertilisation experiments with a good degree of accuracy while being able to also simulate a gradient of K availability. The model allowed us to formulate the following conclusions:

1. The decrease in GPP caused by K deficiency explained most of the difference in wood productivity between K-rich and K deficient stands. There was no need for a direct modification of the partitioning process or stoichiometric limitations to explain the observed patterns of productivity;

2. Potassium-use efficiency increases with diminishing K availability suggesting that the plant is able to compensate for lower K content in tissues, through reduced carbon-use efficiency;

3. The major importance of external inputs (weathering and deposition mainly) already observed in GPP simulations (see Part 1) is also critical for the ecosystem's productivity;

4. The importance of internal K fluxes in the trees that provide buffering against temporally localised K limitations and confirms that K performs important functions in plants.

Acknowledgements

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6 Supplementary Material

6.1 Parameters

Parameter	Symbol	Value	Units	Source
Number of leaves produced by height increment	κ	345	$nb_{leaves}.m^{-2}.m_{tree}^{-1}$	Calibrated using leaf production on the +K Itatinga stand
Leaf Lifespan	LLS	400	days	Calibrated using leaf production, biomass and fall measurements on the +K Itatinga stand
Objective leaf surface	S_{max}	2750	mm^2	Measured in scans from the +K stand

Table S1: Parameters related to the leaf cohort sub-model that were modified from Part 1

Parameter	Symbol	Value	Units	Source
Sensitivity parameter for soluble sugar allocation	p_{ss}	0.1	unitless	Assumed
Sensitivity parameter for fine roots allocation	p_{FR}	0.1	unitless	Assumed
Conversion from LAI to objective root biomass	λ	80	$gC.m_{leaves}^{-2}$	Calibrated on the +K stand
Optimal wood K concentration at creation	$[K]_{Trunk}^{opti}$	0.0038	$gK.gDM^{-1}$	Maximum K wood concentration measured on the +K stand
Minimal wood K concentration in a cohort	$[K]_{Trunk}^{min}$	0.0005	$gK.gDM^{-1}$	Minimum K wood concentration measured on the +K stand
NPP driven rate of remobilisation of K in wood	T_{KTrunk}	0.00216	unitless	Calibrated on K wood concentrations measured on the +K stand
remobilisation efficiency of K in dying branches	$R_{KBranches}$	0.8	unitless	Measured difference in K content between live branches and dead branches in the +K stand
Annual turnover rate for branches	$M_{Branches}$	0.31	$.yr^{-1}$	Calculated from biomass and necromass measurements in the +K stand
Annual turnover rate for fine roots	M_{FR}	0.71	$.yr^{-1}$	(Lambais et al., 2017)
Annual turnover rate for bark	M_{Bark}	0.001	$.yr^{-1}$	Calculated from biomass and necromass measurements in the +K stand

Table S2: New parameters related to C and K allocation

6.2 Figures
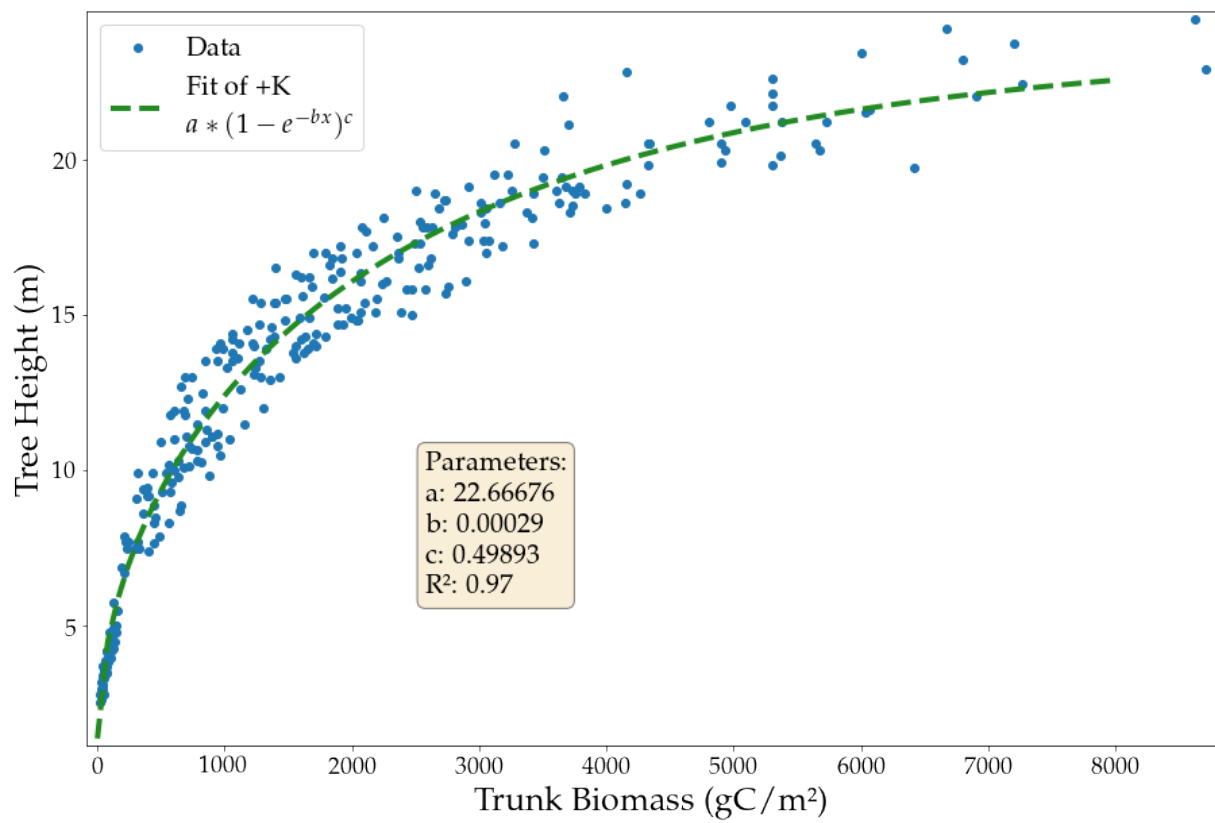
Figure S1: Tree height as a function of trunk biomass. The function was well adjusted.
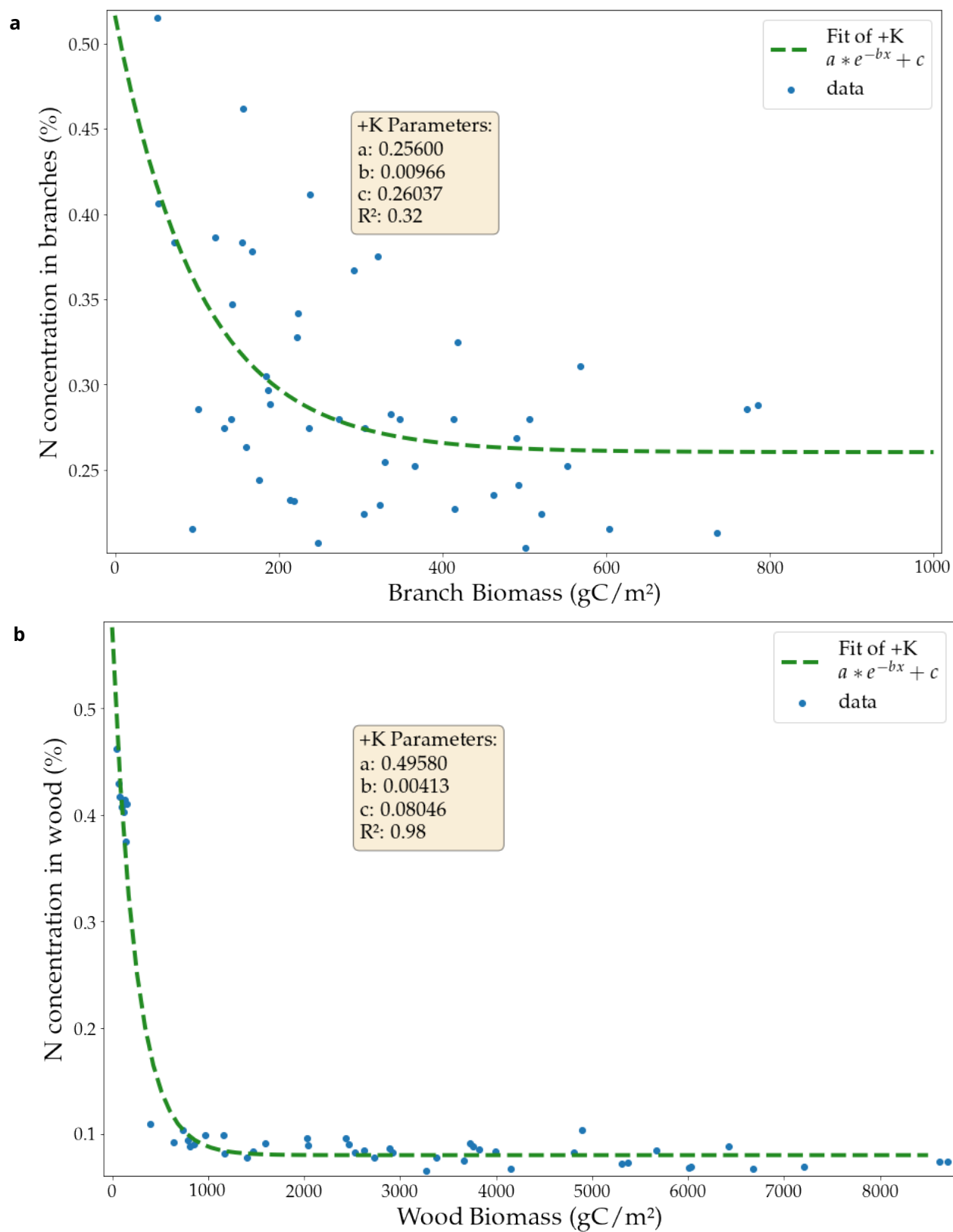
Figure S2: a) Branch N content in function of the biomass of living branches b) The trunk's N content in function of the trunk biomass.
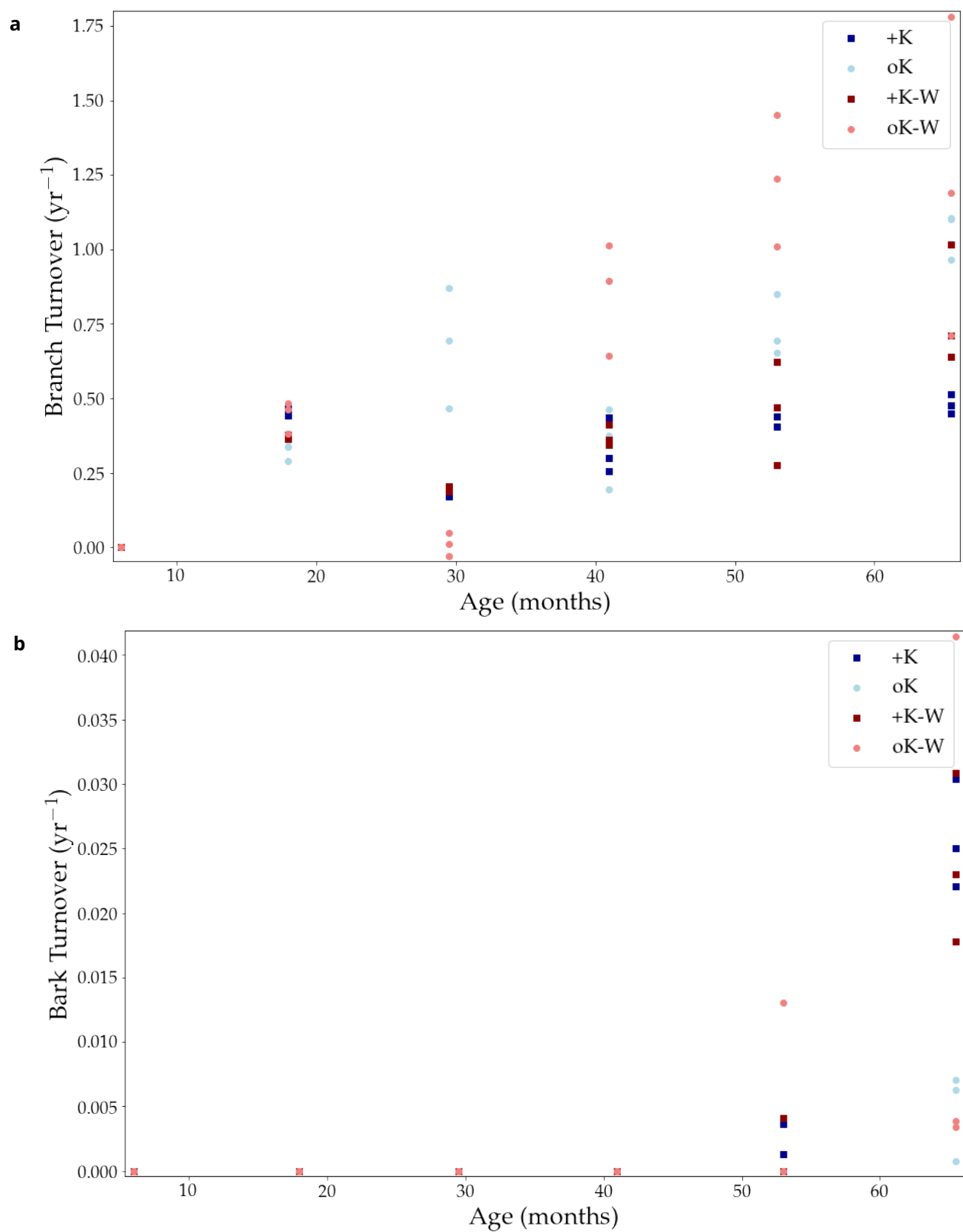
Figure S3: a) Turnover of bark in different fertilisation and rainfall exclusion plots (-W is 30% of rainfall removed). Each data is a separate data point. b) The turnover of branches in the same conditions.
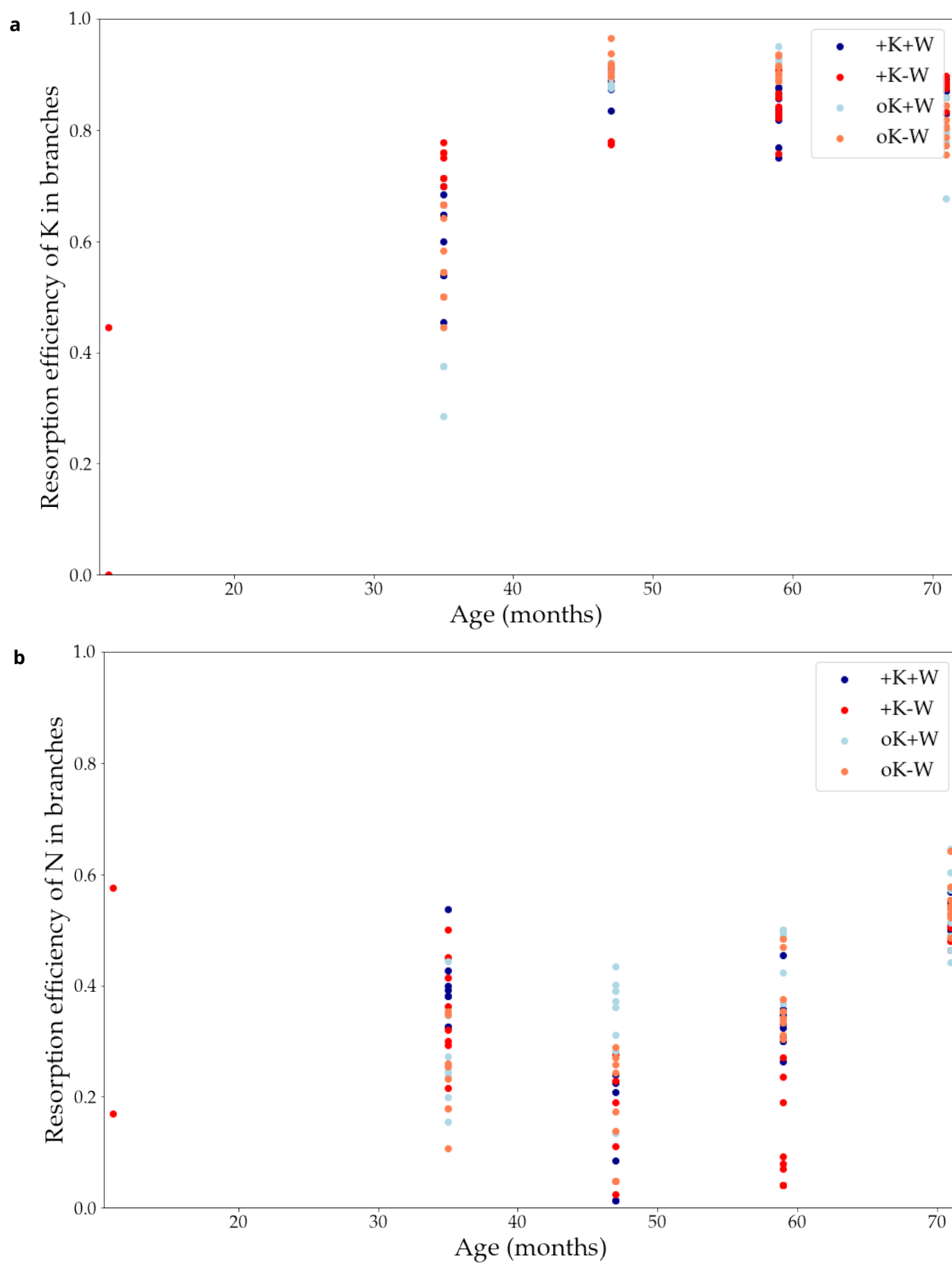
Figure S4: Branch resorption efficiencies for K (a) and N (b) that were calculated using annual measurements of K concentrations of live and dead branches on the same tree. Each data point is a tree in each treatment.
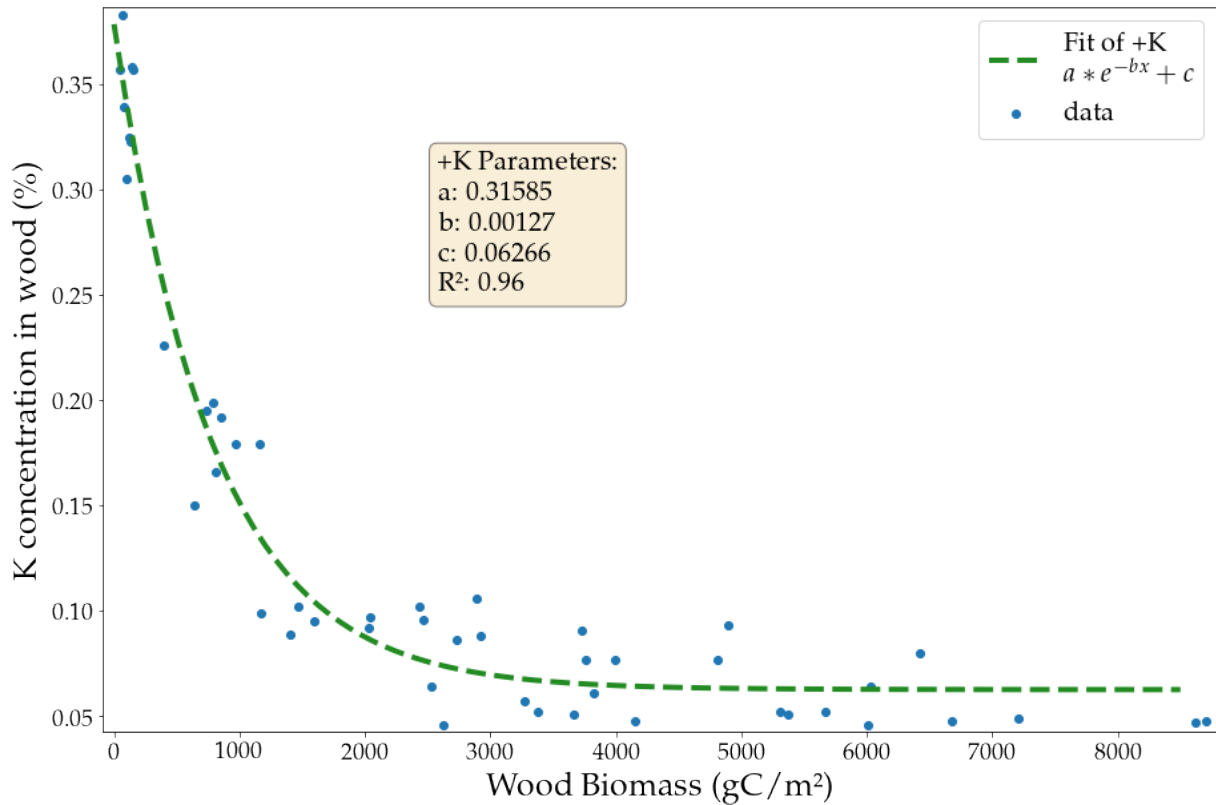
Figure S5: Wood K content as a function of trunk biomass. A decreasing function was adjusted to the data. This function was not used in the model but the parameters were used to parametrise the K wood cohort model. The non-limited wood concentration at the creation of the cohort was equal to $a+c$ of the function shown in the inset and the minimal wood K content was similar to c (but corrected to account for the newly created cohorts in trunk wood).

a
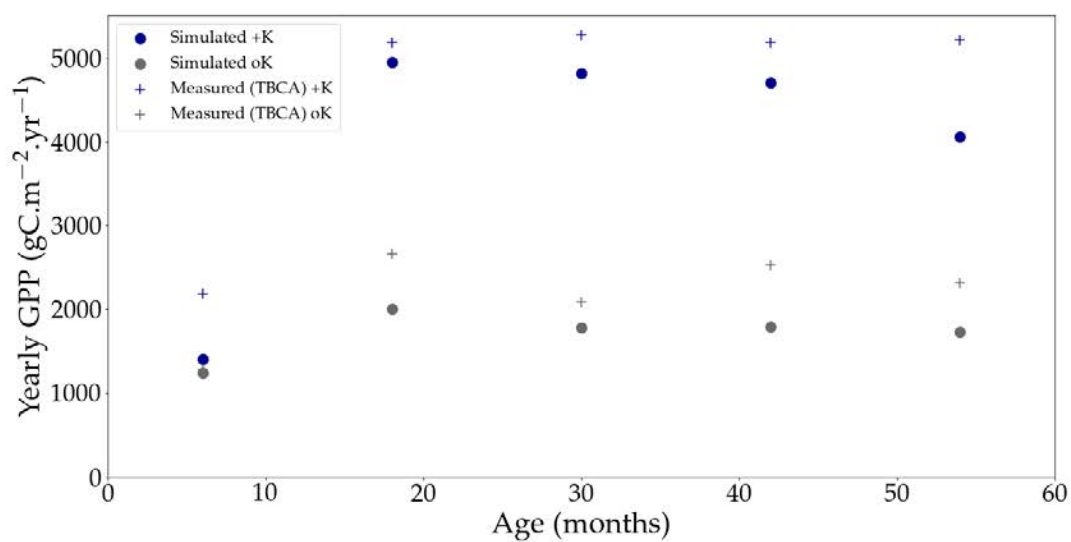
b
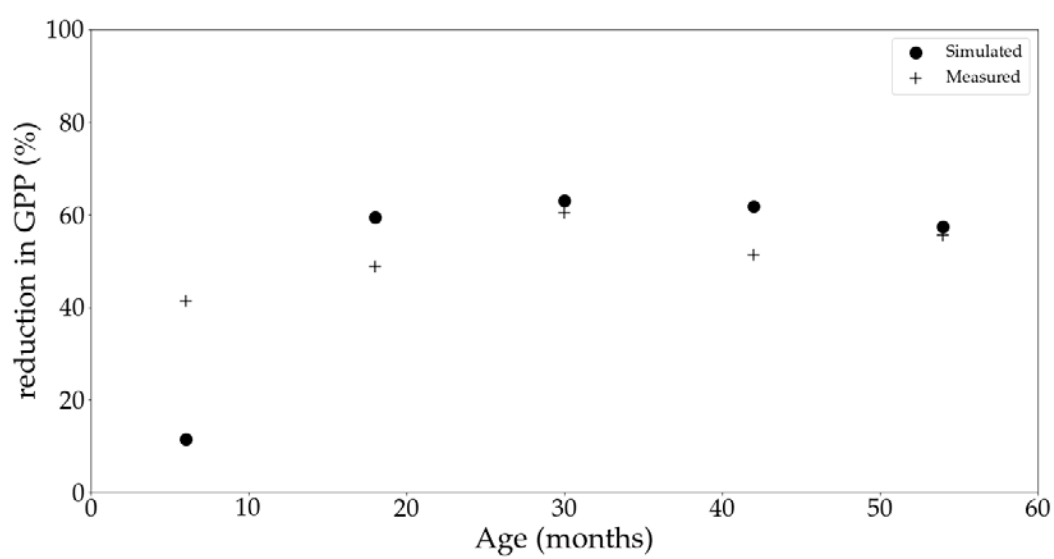
Figure S6: a) The annual GPPs simulated by the model and calculated using the TBCA method. b) The relative reduction of GPP in the oK stand compared to the +K stand in both simulation and measurments.
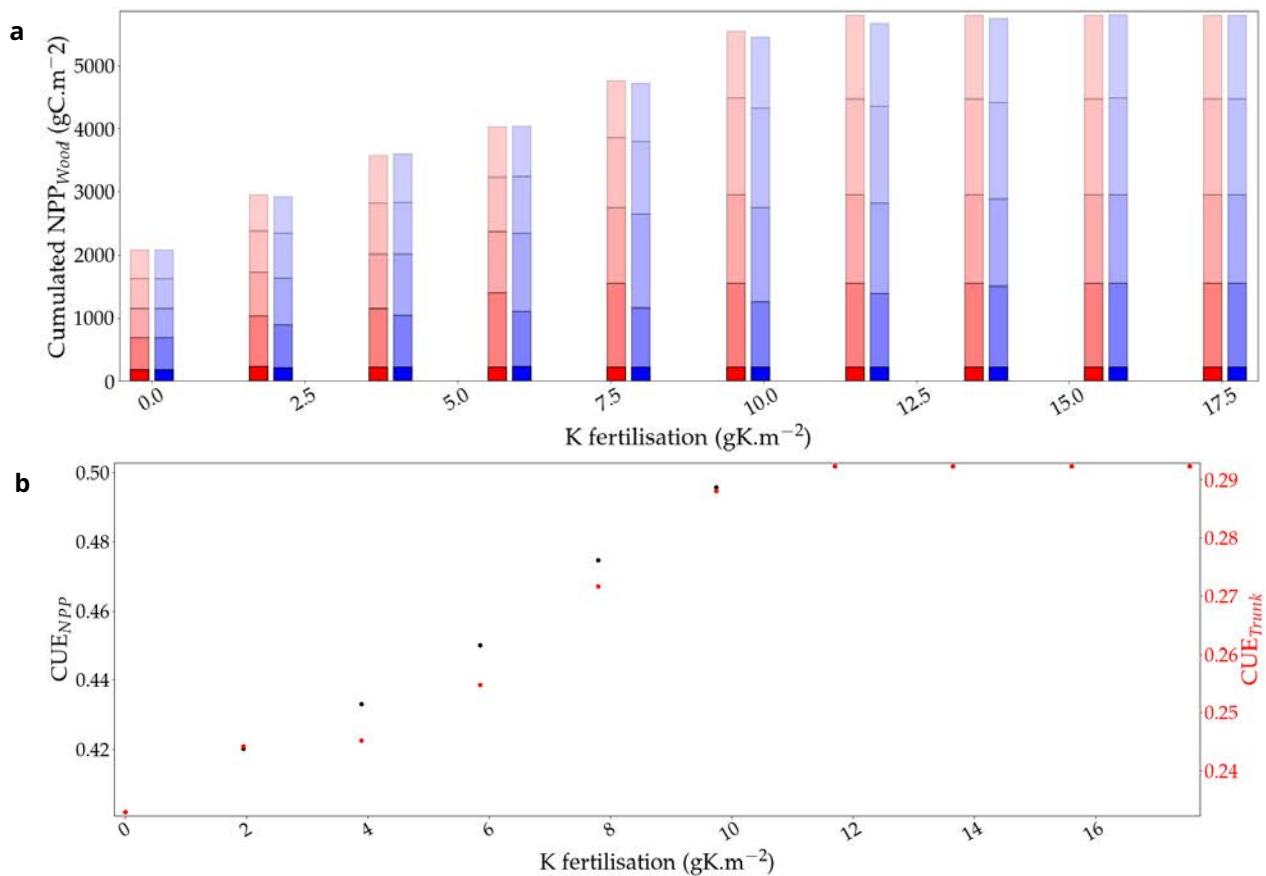
Figure S7: a) The response of cumulated NPP$_{trunk}$ to two different fertilisation regimes (one-time in red and four-time in blue) along a fertilisation gradient. b) The response of simulated whole-rotation NPP and trunk CUE to a gradient of K fertilisation.
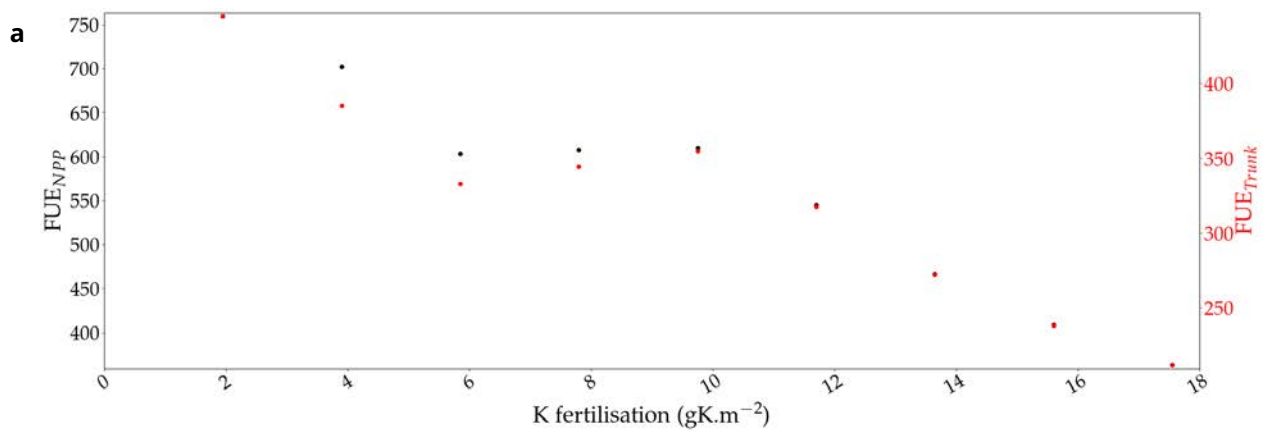
Figure S8: The fertiliser use efficiencies of NPP and wood in function of the fertilisation level of the simulated stand.

Chapter 5

General discussion

At the beginning of the thesis we started by identifying which elements were limiting to growth in tropical eucalypt plantations. As it would soon become clear, all plant essential macro or micro nutrients (Kaspari et al., 2008) are potentially limiting wood production in Brazilian tropical eucalypt plantations (Gonçalves, 2000). It is obvious that the highly productive nature of these managed ecosystems (Binkley and Stape, 2004) plays a role. The high biomass export levels combined to the wide span of territory covered by eucalypt plantations make these plantations the perfect testbed for nutrient limitation of primary productivity. While N and P get all the credit when it comes to the nutrient limitation of NPP at a global scale, observations in plantations demonstrate that other nutrients deserve to be considered as well.

As an example in the identification of "forgotten" nutrients as limiters of primary productivity, this work was an investigation on the widespread K-limitation of wood productivity in tropical eucalypt plantations. In the following, we summarize and discuss what we have learned from the development and use of a mechanistic carbon-water-K model as a tool for the identification of the key processes that control wood productivity in K-deficient tropical eucalypt plantations.

5.1 Concluding remarks on the potassium limitation of wood productivity

5.1.1 C-source or C-sink limited ?

Simulation results (Chapter IV) have clearly indicated that in the current version of the model, a limitation of the C-sink activity by K availability was not necessary to reproduce the observed patterns of wood productivity in the K-omission (0K) and fully fertilised (+K) experimental stands. The reduction in C-source activity (Chapter III) and the reduction in carbon use efficiency were enough to explain the strong reduction in wood productivity (Fig.1.7b). Nevertheless the conclusion that eucalypt are C-source limited when it comes to K deficiency is an outcome of our modeling hypotheses. We concluded that K-limitation of the C source was enough to explain the decreased wood productivity in the model simulations. We drew this conclusion on the basis of our modelling results that (i) were supported by the demonstrated model ability to simulate growth in both the +K and 0K stands and (ii) involved the most parsimonious modelling hypotheses. However, we cannot exclude that, beside our modelling

results, the modulation of the C-sink activity by K availability was also contributing to the limitation of productivity *in natura*. Potassium deficiency symptoms do not appear instantaneously, instead they correspond to a cumulative K deficiency of the leaves. This means that they could be the sign of an impediment of the export of sugar from the leaves (see Chapter II). This impediment could be caused by a slow loading into the phloem or a slow phloem transport, that we attributed to the "C-sink limitation" family of processes (Chapter II). A reduction in phloem velocity under K deficiency was shown in the K omission experiment at the Itatinga site (Epron et al., 2016). However it was perfectly proportional to assimilation by leaves making it impossible to know if this reduction in phloem velocity was the consequence or the cause of reduced C-source activity, and the authors suggested that K was not responsible for the majority of the phloem turgor in eucalypts, meaning that changes in K phloem sap concentration would not have a big effect on phloem movement (under the mass-flow Münch hypothesis, Knoblauch and Peters, 2017). This does not support the hypothesis of a C-sink limitation caused by K deficiency via a reduction of phloem mobility.

The issue of categorizing basic physiological processes as modulating growth "from the source" or "at the level of the sink" was not specific to our work since C-source activity, sugar transport and C-sink activity are tightly coupled (Ainsworth and Bush, 2011; Lacointe, 2000). Illustrating this tight coupling, detailed mechanistic models of coupled assimilation and phloem functioning show that a down-regulation of stomatal opening by phloem sugar concentration is necessary for the stability of simulations (Nikinmaa et al., 2013). This mechanism could provide a modeling framework for the coupling between hydraulics, C and K that goes beyond the effect of K deficiency symptoms on photosynthetic traits. In such a framework, K availability at the leaf level could influence the rate of photosynthate export to the phloem thus creating a feedback on photosynthesis.

5.1.2 Is the hypothesis of stoichiometric homeostasis relevant for the K-limitation of productivity?

A direct limitation of growth by stoichiometry (that would have been simulated as a restriction of allocation to wood in cases of lack of K despite C abundance, e.g. under the hypothesis of a fixed C/K ratio) was not necessary and the model confirmed that the observed stoichiometric plasticity could be quantitatively (e.g. trunk wood) and qualitatively (e.g. branches) reproduced by a simplistic demand and supply model with no direct effect on C allocation (Chapter IV, Figure 5). In the plant, K can be stored in two different compartments in plants:

the cytoplasm and vacuoles. The cytoplasm is described as homeostatic for K and the vacuole has a variable K concentration (Walker et al., 1996). This tow-compartment storage could have produced the apparent stoichiometric flexibility of organs.

When it comes to the observed differences of stoichiometric plasticity between organs (i.e. trunk wood vs. branches) the debate is still open. In this case the model was incapable of replicating the observations (Chapter IV). The living branches showed an important K concentration variation in measurements that was not observable in trunk wood. The model correctly estimated the variation in concentration for wood but underestimated that of branches. We note that branches are subject to leaching (Tukey, 1970), a process which was not represented in our model. This could be the cause of the disparity between observations and simulations, an hypothesis that does not involve stoichiometric plasticity at branch creation.

5.1.3 Allocation of K in the trees

We chose a semi-explicit representation of the K cycle in the trees since K is a very mobile element in plants (Marschner, 2011). This was supported by the importance of implementing K allocation and remobilisation (Chapter IV) in the model tree for the stability of simulations (not shown, personal observation). By stability we mean that without these processes the response of the model to varying soil K fertilisation levels was erratic and the K-limitation of GPP or NPP appeared suddenly in the simulations. The implementation of wood remobilisation was the biggest step towards model stability in K-deficient simulations, and this process represented a very important part of total resorption/remobilisation fluxes (Table 1, Chapter IV). This confirmed the role of wood as a compartment to act as a nutritional buffer (Chapter IV and see Bauters et al., 2022). Here, our results echo reports from the NuCM multiple-nutrient model, that identified the lack of internal re-translocation and accumulation in biomass as a cause of the poor accuracy of K cycle simulations (Johnson et al., 2000).

In our simulations, leaf K was considered a stock that was filled from the phloem. Active resorption of K from the leaves, driven by the phloem, was possible before the expected resorption occurring during leaf senescence in cases when phloem K concentrations passed below a threshold. In the K-deficient simulations, the GPP flux was sensitive to the leaf-to-phloem resistance parameter controlling this resorption flux, unrelated to senescence (Chapter III). This process of active K resorption driven by phloem demand was implemented to represent the decline in leaf K concentration that was observed during the lifespan of

leaves in the K deficient stand (Battie-Laclau et al., 2014). We argue that just as roots could provide the link between K in the phloem sap, K uptake and K in the xylem sap (Marschnert et al., 1997), leaves may also provide a link between K in the xylem sap, carbohydrate export and K in the phloem sap. The leaves' K content could be the result of an equilibrium between the ascending of K in the xylem sap and the exporting of K in the phloem sap. This hypothesis is supported by the important K accumulation in mistletoes (up to 13 times the K concentration of the host plant and it might contain 50% of the total K quantity contained in the tree-mistletoe couple , Lamont, 1983) that are connected to their hosts' xylem but not phloem. Moreover, albino leaves of a citrus trees (*Citrus sinensis*) and oleander (*Nerium oleander*) also showed an accumulation of K (2 to 3 times the K concentration of green leaves; it was less the case of other nutrients) and it was hypothesized (Lo Gullo et al., 2012) that this was due to the lack of phloem export in albino leaves (since there were not photosynthates produced in these leaves).

To conclude, there seems to be a tight coupling between the C and K cycles that takes place at the leaf level and should be investigated further (e.g. by using isotopic markings) and could be a potential way forward for mechanistically simulating a dynamic K circulation in leaves that would link the assimilation and export of C from the leaf, to the import-export dynamics of K in the leaf.

5.1.4 The belowground blind spot

While it can be said that the simulations of aboveground biomasses were successful in different K availability scenarios, the same cannot be said for simulation of the belowground biomass. The accuracy of fine root biomass simulations was a weakness (Chapter IV) of the model that we developed if we are to trust root biomass measurements at Itatinga. This was due to the poor performance of the empirical sub-model that links the objective root biomass to leaf area (Marsden et al., 2013) at the Itatinga site (eq. 3 in Chapter IV). The lack of a mechanistic representation of roots in forest process-based models (a misnomer in this case) is common, in part since it does not seem to strongly influence simulation outcomes (Warren et al., 2015) but could impact model performance in elevated CO_2 scenarios where the canopy is potentially unaffected (Norby et al., 2022) but allocation to the belowground compartment increases (Jiang et al., 2020). Belowground allocation was also a major source of uncertainty when comparing the performance of 11 C-N coupled Terrestrial Biosphere Models (TBM) (Zaehle et al., 2014).

The lack of a mechanistic root sink activity sub-model driving the allocation to fine roots (i.e. in our model allocation to roots was a fraction of daily NPP) was mirrored by the absence of mechanistic representation of the dynamics of K in the soil. Diffusion and sorption dynamics were not considered to be the limiting element for K availability to the plant, so a sorption-desorption (Tinker and Nye, 2000) and diffusion (Barber, 1995) sub-model was not identified as a priority. Moreover, we did not implement in the model a representation of the biologically-enhanced weathering of K in the rhizosphere. The lack of information regarding mineral weathering was already identified as a bottleneck 20 years ago (Johnson et al., 2000). The availability of nutrients is known to increase in proximity to roots but to the best of our knowledge no TBM integrates this process in their uptake sub-model (Hinsinger et al., 2011; Goll et al., 2017).

5.1.5 The scale of the model

Our model was relatively fine scaled both temporally and spatially. This was necessary since it was the scale of the measurements that were available for building model hypotheses and informing parameter values. The choice of the stand as an ideal spatial was guided by viewing as a "functional unit" since the productivities of stands were related to their homogeneity (Stape et al., 2010) and it is probable that the clones selected by growers are selected by their productivity as a stand and not as isolated individuals. We believe the stand scale is also the relevant level of information and links fine-scale physiological processes to the biosphere. Our goal was not describing global patterns of NPP so approximations such as PFTs were not necessary. On the other hand, nutrient cycles can only be calculated at the scale of multiple trees. Despite being composed of only one clone, a certain level of variability is present in these plantations so using a stand level reduces the uncertainty. Moreover, nutrient availability is subject to fine scale variability (for K in a field see Fig.1 in Jin and Jiang, 2002) that is not necessary for comprehension of K-limitation in forests.

5.2 Eucalyptus plantation: a forest managed as a crop ?

While eucalypt plantations are forests by most definitions (Chazdon et al., 2016), in some aspects they are very similar to crops (Binkley and Stape, 2004). As most crops, they are: grown in clonal monocultures, planted as rows with high density, on short rotations, herbicides are used at plantation, fertiliser is applied, they rapidly develop during the rotation and harvest

is conducted very similarly to that of a field of corn (in appearance). Likewise, they are also the subject of controversy when it comes to biodiversity, land use, water use and carbon sequestration (Fleischman et al., 2020). Does this mean that eucalypt plantations are unlike secondary growth or primary growth forests and that one should not use them as a model ecosystem to study ecological phenomena relevant to a wide range of forests?

Here we argue that beyond the importance of eucalypt plantations for a wide array of services (IBA, 2020) and the global surface they cover, these fast growing tree plantation can also be useful models for the fundamental understanding of nutrient dynamics in forests. They display a multi-layer canopy, a continuous phenology similar to other evergreen broadleafs, produce wood, a deep rooting system (Christina et al., 2011), and the cycling of nutrients involves the same basic processes in eucalypt plantations as in natural forests: uptake, allocation, resorption, remobilisation, canopy leaching and litter fall. These plantations are also interesting from a modelling perspective since the eucalypts that are used in these plantations have undergone a strong artificial selection for wood production. This means that we can more easily make the assumption that these trees are optimised for C sequestration in the trunk (which is one of the reasons why all the carbon that was left after allocation to the essential organs was then allocated to the trunk without limits, see Chapter IV). Moreover, *Eucalyptus grandis* is considered as a long-lived pioneer species (Tng et al., 2012) which has led some authors to comparing fast-growing eucalypt plantations to early stages of forest regeneration (Christina et al., 2017). Furthermore, eucalypt plantations have successfully been used to regenerate Atlantic-type forests (Brancalion et al., 2019, 2020). This body of evidence indicates that while eucalypt plantations might not be a good model ecosystem for old-growth, diversified forests, they are potentially an interesting model for nutrient dynamics in forest regeneration.

Chapter 6

General conclusion and perspectives

6.1   General conclusion

Let us return to the main goal of the thesis: Identifying the processes responsible for the limitation of wood productivity in tropical eucalypt plantations grown on nutrient-poor soils. This initial goal was refined to identifying the processes related to the K-limitation of wood productivity since it was the most limiting nutrient at the Itatinga experimental site, and is still a neglected nutrient. To achieve this goal we used a process-based modelling approach that led to the development of the first coupled C-H_2O-K process-based model. The model was then used to investigate the effect of the availability of K in the plant-soil system on the C source-sink dynamics and resource-use efficiency of the stand. We will briefly summarize the main highlights of the thesis here:

- **Limitation of GPP (the C-source) by K deficiency is quantitatively important** and is driven by **leaf ontogeny** and plant **K circulation** dynamics.

- **Limitation of the C-source by K is sufficient** to successfully replicate **differences in NPP** between K-deficient and K-rich eucalypt stands in our simulations.

- A **direct stoichiometric limitation of growth** in CASTANEA-MAESPA-K is **not necessary** to simulate both the reduction of growth and lower organ K concentration in K-deficient, as compared to K-fertilized, stands.

- Implementing representations of the **circulation**, **immobilisation** and **re-translocation** of K in trees in CASTANEA-MAESPA-K was **essential** for **model stability** and accurate representation of the **K-limitation** of wood productivity.

- **Potassium deficiency** caused a **decrease** in the **water-use efficiency** and **carbon-use efficiency** of NPP in our simulations.

- Our modelling showed that **Potassium-use efficiency** of NPP was higher at **lower levels of K availability**.

To conclude, the first C-H_2O-K process model (CASTANEA-MAESPA-K) was successful in replicating the patterns of K limitation observed at experimental stands. However, a specific effort still needs to be made on belowground C allocation, root architecture, uptake and soil K dynamics for the model to reach a higher level of genericity. We are hopeful that the model we developed can be the first step in a long series of new generation process-based forest models that include N, P as well as other less investigated, though essential, nutrients. We believe

this to be essential from a quantitative perspective (Modelling for numbers, Rastetter, 2017) and from a fundamental comprehension perspective (Modelling for understanding) when studying nutrient limitation of forest ecosystems.

Large scale ecosystem manipulations   The work that was presented throughout this thesis was only made possible by the exhaustive dataset that was painstakingly acquired over more than two decades at the Itatinga experimental site. We wish to emphasize here the absolute necessity of these large scale nutrient omission or addition experiments to inform process based models. We are grateful that many years ago, some people found it a worthwhile endeavour to setup forest nutrition experiments at Itatinga followed by long-term and exhaustive monitoring. This has made building CASTANEA-MAESPA-K easier. The choice of nutrient omission (where the control is fully fertilised), has proven fruitful for modelling work since notwithstanding very strong nutrient interactions, it guarantees that only one nutrient is limiting at a time.

6.2   Perspectives

In what follows, we describe what we envision as possible pathways for further research, in the continuation of our work.

6.2.1   The use of sodium as an investigative tool

Sodium could potentially be a useful tool for modellers since it replicates only part of K functions in the plant. It is believed that the Na^+ cation is a substitute for the osmotic functions of the K^+ cation (Wakeel et al., 2011). Luckily, eucalypt plantations have proven to be natrophilic (Almeida et al., 2010) so they can be used as a test-bed for testing the differential effects of K or Na addition. As an example, the leaves in the Na addition experiment at Itatinga had a lifespan in-between that of the K omission and K fertilised stands. This could indicate that part of the decrease in leaf lifespan was the result of problems in leaf water retention (solved by Na addition) and the other part was the result of carbon export issues.

6.2.2   Genericity of the model

Eucalypt plantations cover a large area in Brazil. Consequently, eucalypt plantations face very diverse environmental (pedoclimatic) conditions. This means that achieving model genericity

is essential if we are to use the model as a tool at a larger scale, since the site effect, the clonal effect and the interaction of the two (Gonçalves et al., 2013) on wood productivity are important, even when discounting nutrient limitation (Binkley et al., 2017). We believe that the main obstacle to genericity is the diversity of clones that are used in tropical eucalypt plantations. The plantations use fast-growing eucalypt clones that are the outcome of an intense artificial selection. This, combined to improved management (Gonçalves et al., 2004) is the reason for the significant increase in mean wood productivity of eucalypt stands in the last 50 years. The effect of genetics on productivity is high (more than 50% variability in wood productivity, Binkley et al., 2017) and was appearing in our dataset by a strong differences in the mean GPP between the Itatinga and Eucflux stands (amounting ~ 1000 $gC.m^{-2}.y^{-1}$ despite very similar pedoclimatic conditions). Whether this difference is the result of the measurement methods (one was deduced from eddy-covariance while the other used the TBCA method) or underlying tree physiology remains unclear. Making the model able to simulate a wide diversity of stands will demand an important database building and model parametrisation effort. Potential issues regarding the genericity of the model concern two major components: the canopy and the soil. Both will be succinctly discussed here.

The model was capable of replicating part of the canopy dynamics at our stands (Chapter III). However, the seasonal variation of leaf area was not reproduced by the model and, more generally, we chose not to represent in the model variations in leaf lifespan caused by other drivers (e.g. the leaf C balance or water stress) than K. This was a choice since we had no functioning hypotheses (verified by measurements) about the environmental or C balance determinants of leaf lifespan. Recent observations have shown a severe effect of a major drought on leaf fall at the Eucflux site (personal communication, Joannès Guillemot). Following the intense drought, leaf area was severely reduced (this has also been observed on a natural eucalypt forest, Pook et al., 1997). It is likely that implementing processes linking leaf ontogeny and the environment (e.g. water stress) will be necessary for the model genericity. For example, leaf water potential has been used as an integrating variable for hydraulics (De Swaef et al., 2022). This variable is already simulated by CASTANEA-MAESPA-K and could be used to inform processes related to leaf ontogeny (e.g. leaf expansion, senescence induced by embolism).

Genericity in the representation of soil processes could potentially be harder to reach due to the relative lower number of studies documenting root dynamics and absorptive capacity, and nutrient cycles in the soil, as compared to aboveground compartments (Fatichi et al., 2019). Integrating a model of nutrient movement in the soil should be the first step. Global

maps of soil properties (Batjes et al., 2020) and local measurements could be used to validate the model on different soil types. This approach could also benefit from a meta-modeling approach of both root growth dynamics (for a meta-model of a architectural root model see Pagès et al., 2020) and solute movement in the soil. This meta-modeling approach is relevant with the goals here since it can replicate the behaviour of complex models but reduce the run time by using simplified equations. This method is potentially useful for calibration when numerous simulations must be run multiple times.

6.2.3   Can the model be used in a predictive capacity

The next step for model validation, would be the comparison of simulation outputs of the 0K and +K combined with the precipitation omission at Itatinga (see Figure 1.7 in Chapter I). This would be a relevant test of local genericity of the model since the model was calibrated on the *+K:+W* treatment but neither on the *+K:oW* nor the *oK:oW* treatments. It would then be possible to investigate whether the response of the simulation is the same as reality: a decrease in NPP in the *+K:oW* compared to the *+K:+W*, and no difference in NPP between *oK:oW* and *oK:+W* treatment.

One last line of investigation would be determining the optimal quantity of K fertilisation that optimises the long term productivity of the stand and takes into account the effects of drought. In this study we identify that the fertilisation optimum (where the maximum NPP is reached) is similar to recommendations ($\sim$10 gK.m^{-2}). At the sites studied here there is a recharging of the water table between two rotations. The trees are cut, and the water table recharges until the transpiration of the next stand exceeds the recharging. The water table is essential to the resilience of the eucalypt plantations to drought (Christina et al., 2017) since the roots are able to directly access the water stored in the water table (Christina et al., 2011). Due to repeated droughts over the past few years (2014 - 2021), the water table was unable to sufficiently recharge between the Eucflux rotation presented in this document (period 2009-2017) and the current one (that started in year 2018). This led to a severe drought, strongly impacting eucalypt productivity and physiology (severe loss of leaf area) in 2021 (J. Guillemot, personal comm.). The fertilisation level has an effect on transpiration levels (Chapter III and Christina et al., 2018). Thus, adapting the fertilisation plan could be an option for increasing the sustainability of the eucalypt plantation over multiple rotations. To simulate this we could take advantage of the continuous response of the model. This way, we would use the model as a decision-aiding tool, to identify the optimal level of fertilisation needed for

maintaining wood productivity while increasing the resilience of eucalypt plantations over multiple rotations in a context of increasing drought frequency and severity (Geirinhas et al., 2021).

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Chapter 7

Synthèse en français

De nombreux facteurs édaphiques et climatiques peuvent limiter la croissance végétale. Ces limitations ont un impact direct sur la capacité des écosystèmes terrestres à stocker du carbone. Le concentration atmosphérique de CO_2 est un des éléments qui peut limiter la productivité des écosystèmes terrestres. L'augmentation de la cocentration atmsophérique de CO_2 aurait du et devrait conduire à une augmentation de la productivité (et potentiellement du carbon stocké) des forêts. Cependant plusieurs expériences n'ont mis en évidence aucun effet ou un effet transitoire de cette augmentation de CO_2 sur la productivité des forêts. Ces résultats renforcent l'idée d'une limitation de la productivité des forêts par d'autres éléments: les macro-nutriments N, P et K ainsi que divers micro-nutriments.

Les nutriments ont été identifiés comme une cause majeure de la limitation mondiale de la productivité forestière à la fois dans des expériences de fertilisation à large échelle ainsi qu'à l'aide de modèles intégrant l'effet de la disponibilité des nutriements sur divers processus du fonctionnement des forêts. Les plantations tropicales d'eucalyptus sont un bon exemple d'un écosystème fortement limité par les nutriments. Les plantations couvrent une grande surface au Brésil ($\sim$7.5Mha) Des expériences d'omission de nutriments (N, P, K) à large échelle ont donc été menées sur de multiples rotations et une base de données cohérente de la réponse de ce système à la disponibilité des nutriments a été construite. Dans plusieurs de ces expériences le Potassium (K) a été identifié comme l'élément le plus limitant de la production de bois. Cela rejoint les résultats d'autres expériences menées sur différents écosystèmes forestiers qui montrent une réponse positive de la productivité nette à la fertilisation en K. Le K est présent dans l'écosystème uniquement dans sa forme cationique. Il joue un rôle fondamental dans le fonctionnement des plantes. Il est essentiel pour les processus d'expansion cellulaire, de régulation osmotique, et de transport du carbone des

sources vers les puits. Le K joue également un rôle central dans le fonctionnement stomatique et la photosynthèse. Au délà de l'effet de la déficience en K sur la production de bois, les plantations d'eucalyptus déficientes en K montrent une surface foliaire réduite ainsi que des symptômes foliaires importants.

Les modèles forestiers mécanistes ont démontré leur intérêt pour explorer la réponse des écosystèmes forestiers aux limitations par l'azote (N) et plus récemment le phosphore (P). Ils permettent à la fois de comprendre les méchanismes en jeu dans la limitation de la productivité par les nutrtiments mais également de quantifier cette limitation à des échelles globales. Dans ce travail de thèse, nous avons utilisé une approche de modélisation basée sur les processus en créant le premier modèle couplé C-H_2O-K pour quantifier et identifier les processus responsables de la limitation de la production de bois par le K. Ce modèle est issu de la fusion de 2 modèles méchanistes: un modèle forestier travaillant à l'échelle de la parcelle, CASTANEA (utilisé principalement pour l'allocation de carbone et l'interception de la lumière) et MAESPA (pour la photosynthèse et le cycle de l'eau) qui a été utilisé précédemment sur les plantations d'eucalyptus. Ce modèle hybride a été complété par différent sous-modules ayant trait à la phénologie des eucalyptus et au cycle du K dans la plante, développés pendant la thèse. Cet outil a été utilisé afin de répondre à trois questions principales: 1) Quel est l'impact de la disponibilité du K au niveau de la plante sur la photosynthèse (source de C)? 2) La limitation de la source de C est-elle suffisante pour expliquer la limitation de la production de bois par la déficience K dans les plantations tropicales d'eucalyptus ? 3) Quel est l'impact de la disponibilité du K sur l'efficience d'utilisation des ressources des plantations tropicales d'eucalyptus ? Ces questions se placent dans un contexte plus large de compréhension de la limitation de la productivité végétale par les puits ou la source de carbone. Cette approche est particulièrement pertinente dans le cas de la limitation par le K car c'est un élément qui a été identifié à la fois comme limitant des processus ayant trait aux puits ainsi qu'à la source de carbone.

Afin de réaliser le travail de modélisation en connsaissance de cause, les processus impactés par la disponibilité du K au niveau de l'arbre ont été identifiés dans une revue de la littérature avec un accent mis sur l'impact de la disponibilité du K sur les processus dans une plantation d'eucalyptus au Brésil. Le jeu de données récolté dans les expériences de manipulation des nutriments a été utile pour introduire des processus propres au K ainsi que la paramétrisation du modèle. Ce travail a permis d'établir un bilan de masse du K dans l'écosystème, identifier les processus prioritaires pour la modélisation et replacer la limitation de la production de bois dans les plantations d'eucalyptus dans un contexte scientifique

plus large. Cette synthèse a permis de concentrer les efforts sur la création d'un modèle de cohortes foliaires intégrant les effets de la disponibilité du K sur l'expansion foliaire, la durée de vie des feuilles et leur capacité photosynthétique. Un sous-module de circulation et d'allocation du K dans le système sol-plante a également été développé. Le modèle complet a ensuite été utilisé afin de simuler des parcelles avec différents niveaux de fertilisation K et de comparer ces simulations aux données expérimentales.

Le travail de modélisation a confirmé que l'assimilation du C a été grandement réduite par la déficience K. Cette diminution était semblable aux données expérimentales ainsi qu'à de précédents travaux de modélisation. Les simulations monrtrent aussi une plus faible saisonnalité de la photosynthèse en situation de déficience de K grâce à une consommation en eau plus faible. Cette baisse de la photosynthèse était le résultat d'une diminution de la surface foliaire et la capacité photosynthétique par unité de surface de feuille. L'effet de la disponibilité du K sur l'assimilation de carbone par les arbres est sensible aux paramètres ayant trait au dévelopement des feuilles ainsi qu'à la résorption du K dans les feuilles. Les simulations ont montré que la réduction de l'activité des sources de carbone était suffisante pour expliquer la réduction de la production de bois. Ce résultat est le produit des sous modules d'allocation du C et K dans la plante sans modification des paramètres du modèle entre les parcelles simulés à différents niveaux de fertilisation. Les simulations à différents niveaux de fertilisation ont permis de montrer que la réponse de la production de bois à la fertilisation était non-linéaire avec une réponse de la productivité à la quantité de K ajouté plus forte à de faibles niveaux de fertilisation K. Ce travail a aussi montré l'importance de la circulation et de la remobilisation interne du K (majoritairement au niveau du tronc) qui est nécessaire au maintien d'une offre stable de K au niveau des feuilles et des organes en croissance. Il démontre aussi l'absence d'une limitation stoichiométrique de la croissance des organes par le K. Le dévelopement de ce modèle est une première étape vers l'inclusion de nutriments essentiels supplémentaires dans les modèles mécanistes de forêts.

Titre: Modélisation mécaniste de l'influence du cycle du Potassium sur la croissance et l'utilisation des ressources des plantations d'Eucalyptus en zone tropicale

Mots clés: Potassium - modèle mécaniste - production primaire - écophysiologie

Résumé: Les nutriments sont une cause majeure de la limitation mondiale de la productivité forestière. Les plantations tropicales d'eucalyptus sont un bon exemple d'un écosystème fortement limité par les nutriments. Les plantations couvrent une grande surface au Brésil (~7.5Mha) Des expériences d'omission de nutriments (N, P, K) à large échelle ont donc été menées sur de multiples rotations et une base de données cohérente de la réponse de ce système à la disponibilité des nutriments a été construite. Dans plusieurs de ces expériences le Potassium (K) a été identifié comme l'élément le plus limitant de la production de bois. Les modèles forestiers mécanistes ont démontré leur intérêt pour explorer la réponse des écosystèmes forestiers aux limitations par l'azote (N) et plus récemment le phosphore (P). Ici nous avons utilise une approche de modélisation basée sur les processus en créant le premier modèle couplé C-H$_2$O-K pour quantifier et identifier les processus responsables de la limitation de la production de bois par le K. Cet outil a été utilisé afin de répondre à deux questions principales: 1) Quel est l'impact de la disponibilité du K au niveau de la plante sur la photosynthèse (source de C)? 2) La limitation de la source de C est-elle suffisante pour expliquer la limitation de la production de bois par la déficience K dans les plantations tropicales d'eucalyptus ? Les processus impactés par la disponibilité du K au niveau de la plante ont été identifiés dans une revue de la littérature. Le jeu de données récolté dans les expériences de manipulation des nutriments a été utile pour introduire des processus propres au K ainsi que la paramétrisation du modèle. L'assimilation du C a été grandement réduite par la déficience K. C'était le résultat d'une diminution de la surface foliaire et la capacité photosynthétique par unité de surface de feuille. L'importance de la circulation interne du K a aussi été soulignée. Les simulations ont aussi montré que la réduction de source de C était suffisante pour expliquer la réduction observée de la production de bois dans la parcelle d'omission K et qu'une limitation stœchiométrique n'était pas nécessaire. Le dévlopement de ce modèle est une première étape vers l'inclusion de nutriments essentiels supplémentaires dans les modèles mécanistes de forêts.

Title: Assessing the impact of the Potassium cycle on stand growth and resource-use in tropical Eucalypt plantations: a process-based modeling approach

Keywords: Potassium - Process based model - GPP - NPP

Abstract: Nutrients are central in the limitation of forest productivity. Due to frequent biomass exports and poor soils, tropical eucalypt plantations are an example of strongly nutrient-limited ecosystems. The plantations cover a wide surface ($\sim$7.5 Mha) in Brazil. Large-scale nutrient (N, P, K) omission experiments have been conducted over multiple rotations, and an important coherent data set of the response of this system to nutrient availability is available. In many of these experiments, Potassium (K) was identified as the major limiter of wood productivity. Mechanistic forest models have proven to be relevant tools to explore the response of forest ecosystems to nutrient limitations by Nitrogen (N) and recently, Phosphorus (P). In this thesis we created the first coupled C-H_2O-K process-based model in an attempt to quantify and identify processes responsible for the limitation of wood productivity by K. We used the model as a tool to explore two main questions regarding the K-limitation of wood productivity in tropical eucalypt plantations: 1) What is the impact of K plant availability on photosynthesis (C-source)? 2) Is the limitation of the C source enough to explain the limitation of wood productivity by K deficiency in tropical eucalypt plantations ? To this end, the processes impacted by plant K availability were identified in a literature review (Chapter II). In the modelling work, a specific focus was thus put on leaves (Chapter III), the recycling of K in the plant and allocation of K to the different organs (chapter IV). The assimilation of C was greatly reduced under K deficiency. This was mainly the result of a decrease in leaf area combined to a decline in photosynthetic capacity per leaf area. The importance of processes governing K internal plant recycling was also underlined (chapter IV). Simulations also showed that this reduction in C assimilation was enough to explain the observed reduction of wood productivity in the K omission stand and that no stoichiometric limitation was necessary (chapter IV). This model is the first step for including more essential nutrients in forest process based models.