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To cite this version:

Ivan Cornut, Guerric Le Maire, Jean-Paul Laclau, Joannès Guillemot, Louis Mareschal, et al.. Potassium limitation of wood productivity: A review of elementary processes and ways forward to modelling illustrated by Eucalyptus plantations. Forest Ecology and Management, 2021, 494, pp.119275. 10.1016/j.foreco.2021.119275 . hal-03276174

HAL Id: hal-03276174

https://hal.inrae.fr/hal-03276174v1

Submitted on 24 May 2023

Version of Record: https://www.sciencedirect.com/science/article/pii/S0378112721003637
Manuscript_8b952afdb7b7ec81453498c0cb7da115

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

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Summary

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.

Keywords: Potassium, carbon source-sink, tropical plantations, *Eucalyptus*, nutrient limitation, process-based modelling.

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 (Liebig, 1841; Gleeson and Tilman, 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 1 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 2, 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 3, 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 4) of the review, we discuss priorities on how to implement K-related processes in terrestrial ecosystems models.

1. *Eucalyptus* plantations: an ecosystem model to study the cycle of K

1.1. 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 meters 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 (Gonçalves et al., 2008; Laclau et al., 2009; Rocha et al., 2019); see Figure 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).

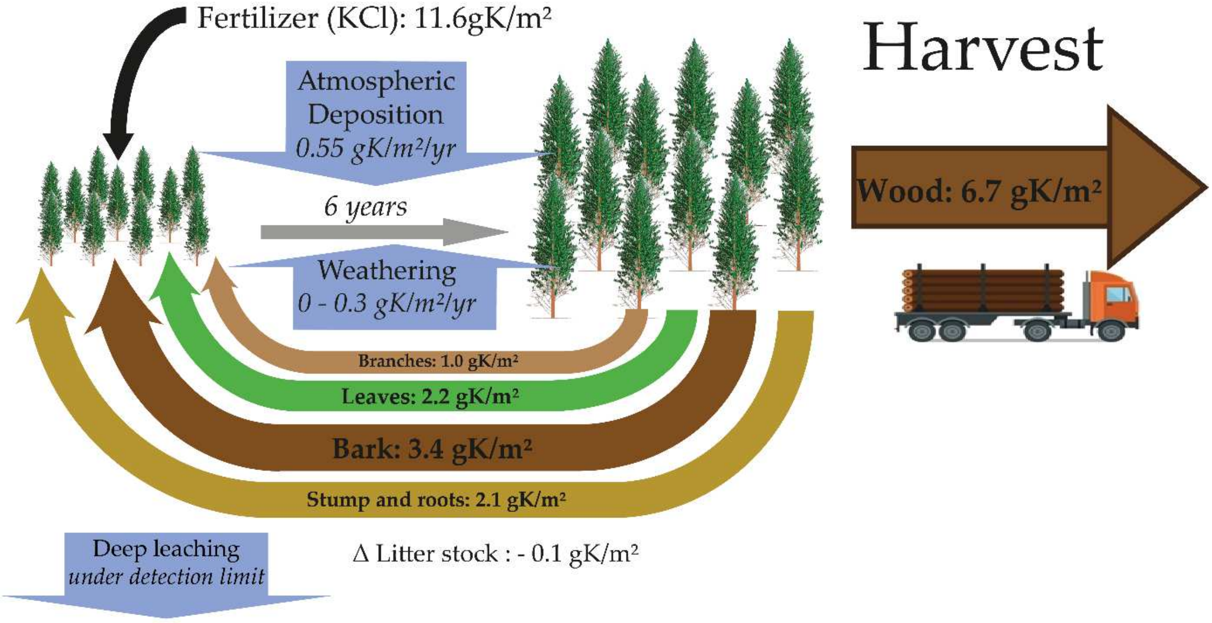

Figure 1. **Main input-output fluxes of K over an entire cycle in experimental eucalypt plantations managed in short rotation with a silviculture representative of commercial plantations in Brazil**. Fertilizer (black arrow) is applied the first 18 months after planting. All the harvest residues are 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.

1.2. 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 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.

1.2.1 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 (Fig. 1 and 2; Laclau et al. 2010). This flux is comparable to the global average of 0.41$gK/m^2/yr$ (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).

1.2.2 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/100g) / 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 Figure S1).

2. The Biological cycle of K in the ecosystem

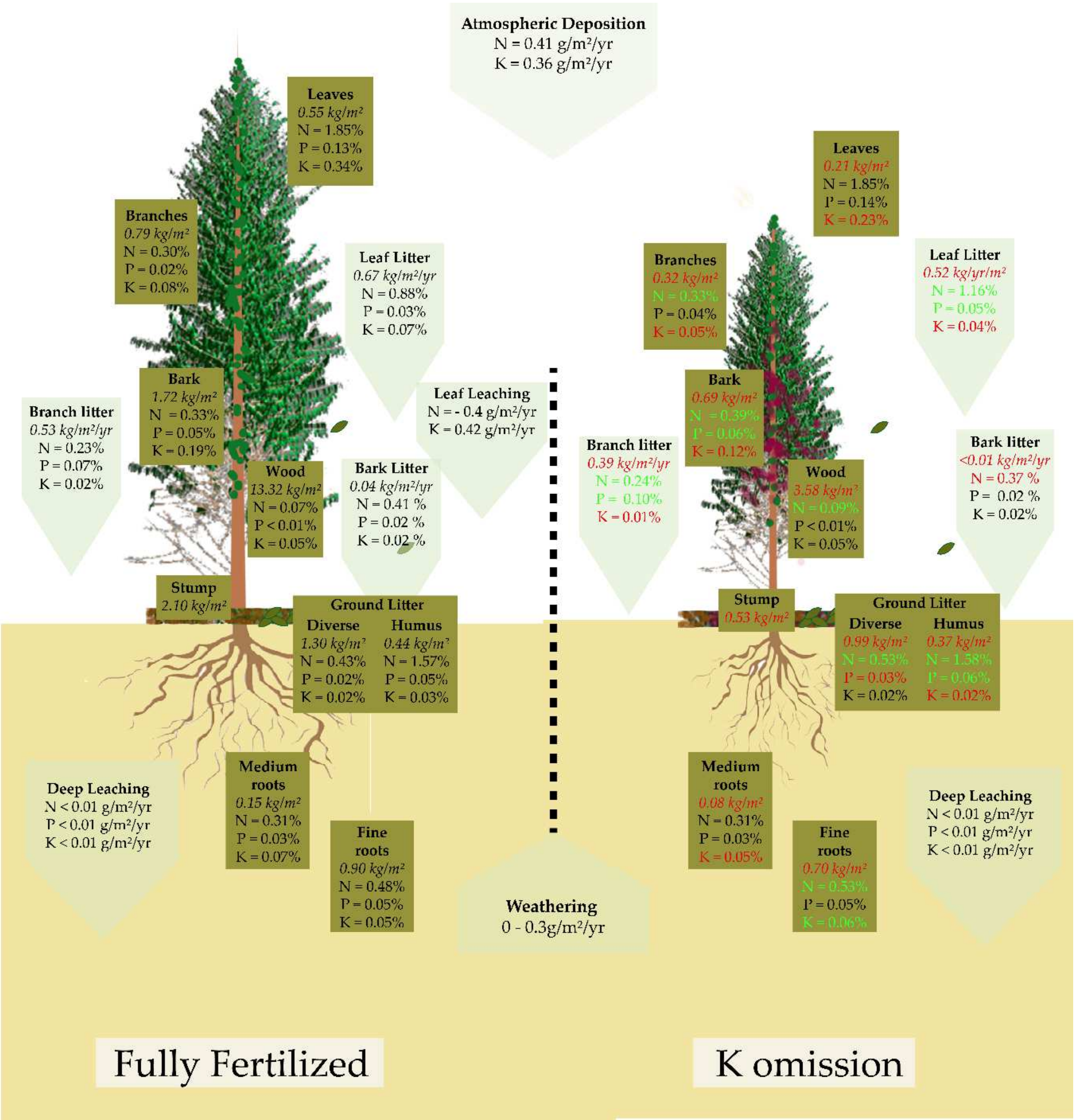

Figure 2. Main stocks (boxes) and fluxes (arrows) of Carbon, Nitrogen, Phosphorus and Potassium in a Eucalypt plantation of 72 months of age (before harvest). A fully fertilised stand is represented on the left. A K-omission stand is represented on the right. Concentrations or dry masses that are higher 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 16m at 72 months).

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.

2.1 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 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.

2.2 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).

2.3 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 $gK/m^2/yr$ 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 2.7g/m²/yr in fertilised *Eucalyptus* plantations (Sette et al., 2013).

2.4 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).

3 Ecophysiology of wood growth limitation by the availability of K

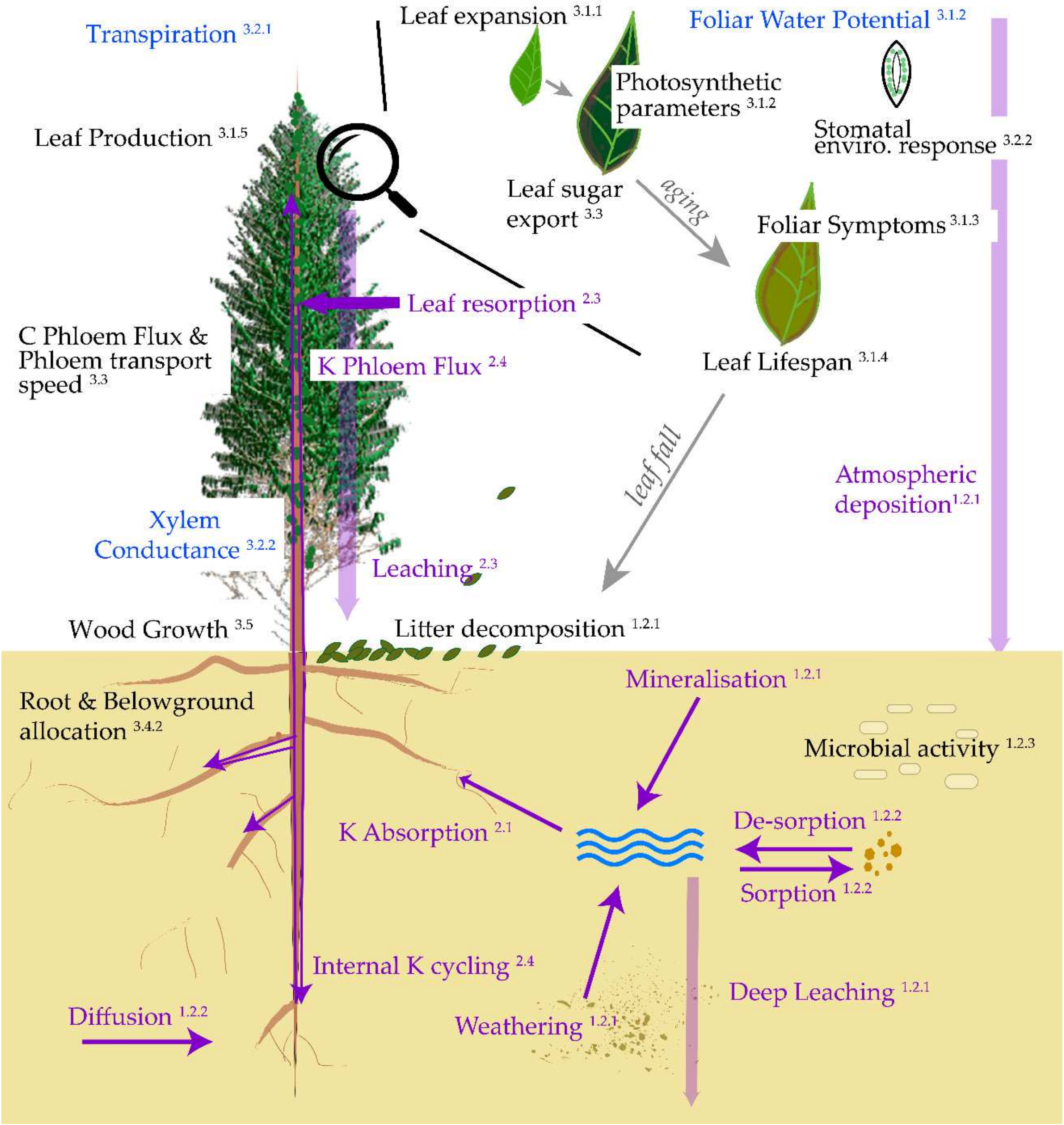

Figure 3. Processes of interest for the limitation of growth by K. The processes and fluxes directly linked to the K cycle in the system are represented in purple. The processes related to the water cycle are represented in blue. The processes closely linked to the C cycle are represented in black. The numbers appearing in exponents beside process names refer to the section describing this process in the text.

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 Figure 3.

3.1 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.

3.1.1 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 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.

3.1.2 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 CO2 from sub-stomatal 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 4.2). 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.

3.1.3 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).

3.1.4 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.

3.1.5 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 3.1, 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.

3.2 Potassium-induced changes to the water cycle

3.2.1 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.

3.2.1 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.*

3.2.2 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).

3.3 **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 3.1.3.2), as anthocyanins could be acting as sinks for excess C in leaves (Pourtau et al., 2006).

3.4 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.

3.4.1 Aboveground partitioning of GPP

Potassium has a strong effect on carbon partitioning among the different organs of trees. As developed in the section 3.1, the total GPP is lower in K-deficient than in fertilized tropical *Eucalyptus* plantations. On the same species, i*n* 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).

3.4.2 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 3.1) 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, Soukup, et Tylova 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.

3.5. **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.

4 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 3.1). 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 3.1.3) 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 3.1.1), 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 3.5).

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 2.4) and modulates the xylem hydraulic conductance (section 3.2.2). 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 2.3). 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 1.2.1) 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.

5 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.

6 Acknowledgments

Ivan Cornut was funded by the ANR under the "Investissements d'avenir" programme with the reference ANR-16-CONV-0003 (CLAND) and by the Centre de coopération Internationale en Recherche Agronomique pour le Développement (CIRAD).

The data acquired on *Eucalyptus* stands at Itatinga station, Brazil, and partly re-analysed here, were funded by Universidade de São Paulo, CIRAD, Agence Nationale de la Recherche (MACACC project ANR-13-AGRO-0005, Viabilité et Adaptation des Ecosystèmes Productifs, Territoires et Ressources face aux Changements Globaux AGROBIOSPHERE 2013 program), Agropolis Foundation (program "Investissements d'avenir" ANR-10-LabX-0001-01) and from the support of the Brazilian state (Programa de Cooperacão internacional capes/Fundacão AGROPOLIS 017/2013'). The experimental site belongs to the SOERE F-ORE-T, which is supported annually by Ecofor, Allenvi and the French National Research Infrastructure ANAEE-F (http://www.anaee-france.fr/fr/).

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