# Potassium limitation of wood productivity: a review of

## elementary processes and ways forward to modelling

# illustrated by *Eucalyptus* plantations

Ivan Cornut<sup>a,b\*</sup>, Guerric Le Maire<sup>b,c</sup>, Jean-Paul Laclau<sup>b,c</sup>, Joannès Guillemot<sup>b,c,d</sup>, Louis Mareschal<sup>b</sup>, Yann Nouvellon<sup>b,c</sup>, Nicolas Delpierre<sup>a,f</sup>

<sup>a</sup> Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique et Evolution, 91405, Orsay,
 France

<sup>b</sup> CIRAD, UMR Eco&Sols, F-34398 Montpellier, France.

- <sup>c</sup> Eco&Sols, Univ Montpellier, CIRAD, INRA, IRD, Montpellier SupAgro, Montpellier, France.
- <sup>d</sup> Department of Forest Sciences, ESALQ, University of São Paulo, Piracicaba, São Paulo, 13418-900 Brazil

<sup>f</sup> Institut Universitaire de France (IUF)

\* Corresponding author: iv.cornut@gmail.com

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#### 1 Abstract

Potassium (K) is essential for a wide range of physiological functions in plants, and a limiting 2 element for wood productivity in numerous forest ecosystems. However, the contribution of 3 each of the K-sensitive physiological processes to the limitation of wood productivity is 4 5 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 6 7 dealing with the influence of K-limitation on tree physiological processes. Results from 8 extensively studied tropical Eucalyptus plantations are used to illustrate the physiological 9 processes the most impacted by K deficiency. We identify the main processes that limit the 10 availability of K to the trees and influence the circulation of K ions in the ecosystem. Then, 11 we describe the influence of K bioavailability on carbon assimilation, the water economy of 12 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 13 14 forest ecosystems. For each process modelling priority, we identify options that could be 15 used in the current conceptual framework of most eco-physiological models.

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

18

## 19 Introduction

Plants are autotrophic organisms that require energy, water, CO<sub>2</sub>, macro- and micronutrients
inputs as resources to grow, maintain over time and reproduce. The effects of resource

22 limitation (yield limitation sensu (Körner, 2018)) on plant growth has been extensively
23 studied (Liebig, 1841; Gleeson and Tilman, 1992).

24 In the context of current and projected rise in atmospheric CO<sub>2</sub> concentration, much 25 emphasis has been put on the CO<sub>2</sub> fertilisation effect (Haverd et al., 2020; Hyvönen et al., 26 2007) stemming from the limitation of photosynthesis by leaf internal CO<sub>2</sub> concentration. 27 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 28 29 mitigation strategies since it purports that the C-sink activity will increase with increasing 30 atmospheric CO<sub>2</sub> concentration and thus could partially compensate anthropogenic carbon 31 emissions.

To test the validity of this C-centric view, Free Air CO<sub>2</sub> Enrichment experiments have been 32 used over the past three decades. Elevated CO<sub>2</sub> concentrations do lead to a positive effect on 33 34 tree aerial productivity, but this effect is transient (Norby and Zak, 2011). This shows that 35 other limiting factors than C availability are at play in limiting tree productivity (Leuzinger 36 et al., 2011; Millard et al., 2007). Nitrogen (N), phosphorus (P) (Ellsworth et al., 2017; 37 Fleischer et al., 2019; Terrer et al., 2019) and other nutrients could progressively become 38 limiting factors with more CO<sub>2</sub> available (Dusenge et al., 2019; Luo et al., 2004; Trierweiler et 39 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., 40 2020). This could negatively impact the assimilation of C by plant leaves, since the 41 42 photosynthetic capacity of leaves depends on their nutritional status (Evans, 1989; Walker et 43 al., 2014).

44 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., 45 46 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 47 et al., 2019; Yang et al., 2014) on ecosystem processes has been implemented in many 48 vegetation models. In simulations, representation of N and P limitations can lead to a 25% 49 decrease in the land carbon sink between 1860 and 2100 under a climate change scenario 50 51 (SRES A1B) (Goll et al., 2012).

52 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 53 al., 2008; Santiago et al., 2012; Townsend et al., 2011; Wurzburger et al., 2012). It has thus 54 55 become necessary to represent the different elemental cycles in forest ecosystems so that the 56 sensitivity of biomass productivity to these complex interactions can be tested. As such 57 potassium (K) is an essential nutrient for plant growth that can limit productivity in many 58 forest ecosystems currently or in the future (Sardans and Peñuelas, 2015). K's influence on 59 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<sup>+</sup>) in the plants and in the
soil. K<sup>+</sup> 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).

67 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 68 69 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 70 71 Peñuelas, 2015; Silveira et al., 1995; Tripler et al., 2006; Wright, 2019; Wright et al., 2011). K 72 availability could influence the productivity of forest ecosystems by influencing either the 73 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 74 75 ('sink-limitation' of productivity), or both. Sink limitation affects the formation of organs and 76 growth of cells and includes processes that can limit growth even when carbon supply is 77 sufficient. For instance, temperature (Hoch et al., 2002) and water stress (Delpierre et al., 78 2016a; Muller et al., 2011) have been shown to be, for some forest ecosystems, more limiting 79 than carbon for tree growth.

80 This review aims to identify processes influenced by K limitations that are likely critical for 81 wood growth. We hypothesized that K deficiency could influence wood production through 82 four categories of processes: (1) lower Gross Primary Productivity (GPP) (source limitation), 83 (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 84 85 constraints) of wood formation (sink limitation). In this review we investigate how wood 86 growth can be influenced by K availability in forest soils. We illustrate this review with 87 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 88 in field experiments manipulating tree nutrition for a long time. The effects of nutrient 89

90 deficiencies on the main physiological processes have been documented, and *Eucalyptus*91 plantations are known to be highly responsive to K supply on many tropical soils, e.g. in
92 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 93 94 cycle in forest ecosystems, taking the example of tropical *Eucalyptus* plantations. The main 95 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 96 97 within trees to identify the distribution of this element in the different organs and the main 98 limitations arising from the K biological cycle. In section 3, we describe the influence of K 99 availability on different processes affecting the acquisition of C and its allocation to wood. 100 While the identification of K-related processes is a prerequisite (and the main objective of 101 this review) it does not allow a ranking of their quantitative influence on wood productivity, 102 which can only be addressed with mechanistic models. Hence in the last section (section 4) of 103 the review, we discuss priorities on how to implement K-related processes in terrestrial 104 ecosystems models.

105

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

107

## **108 1.1.** Introducing *Eucalyptus* plantations as a biological model

109 Eucalyptus plantations cover more than 20 million hectares over large climatic and soil 110 gradients in more than 90 countries (Booth, 2013). These plantations have very high growth 111 rates (average of 45 m<sup>3</sup>/ha/yr in Brazil), reaching up to 25-30 meters tall trees over 6-7 years 112 (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.

117 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 118 absence of K fertilisation) in some tropical areas (Gonçalves et al., 2008; Laclau et al., 2009; 119 120 Rocha et al., 2019); see Figure 1 for common fertilisation practices). In these plantations, pools 121 of exchangeable base cations in the soil as well as the inputs in the ecosystem are low 122 throughout the rotation in relation to biomass production.. Most of the nutrient requirements 123 to produce biomass are provided through the biological component of the biogeochemical 124 cycle (outside fertilisation). These "Bio" (Legout et al., 2020) sites are particularly sensitive to 125 disruptions in the biological cycle, such as the large exports of stem wood at harvest (Fig. 1; 126 note that the amount of K exported within stem wood is more than compensated by 127 fertilisation to sustain growth rates over successive rotations in commercial Eucalyptus 128 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

136 experiments set up in a nutrient-poor Ferralsol soil at the Itatinga station in Brazil (Laclau et

## 137 al., 2010).



139	Figure 1. Main input-output fluxes of K over an entire cycle in experimental eucalypt
140	plantations managed in short rotation with a silviculture representative of commercial
141	plantations in Brazil. Fertilizer (black arrow) is applied the first 18 months after planting. All
142	the harvest residues are left on-site to decompose on the ground (coloured arrows pointing
143	to the left), and only stemwood is exported. Atmospheric deposition and soil weathering are
144	occurring all along the rotation. In some silvicultural practices bark and stumps are also
145	exported. The values of K in the biomass are from Battie-Laclau et al. (2014b). The range of
146	values for weathering come from Maquère (2008) and Pradier et al. (2017). The change in
147	litter stock were calculated by difference between the litter stock measured on a stand at the
148	end of a rotation (Battie-Laclau et al., 2014b) and the litter stock measured at the end of the
149	previous rotation (Almeida et al., 2010). Note that the K balance is not closed: indeed, it was
150	not possible to have precise measurements of change of K content in this very deep soil.

151

**152 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<sup>+</sup> 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.

160

## 1.2.1 K inputs and outputs in the soil

161 Atmospheric deposition is an external source of K to *Eucalyptus* plantations. It amounts to about 0.55 gK/m<sup>2</sup>/yr in *Eucalyptus* plantations at Itatinga (Fig. 1 and 2; Laclau et al. 2010). This 162 163 flux is comparable to the global average of 0.41gK/m<sup>2</sup>/yr (Sardans and Peñuelas, 2015). This 164 atmospheric deposition flux is higher than mineral weathering, that was considered negligible by Maquère (2008) at the same site based on quantitative mineralogical work. 165 However, a recent study considering the rhizosphere of eucalypt trees suggested that the 166 167 amount of K released by mineral weathering could be much higher than expected in deep 168 Ferralsols (Pradier et al., 2017). The uncertainty on weathering fluxes is particularly high at 169 our study site because of the difficulty to integrate very low concentrations over considerable 170 rooting depths (Eucalyptus roots reach a depth of 16 m five years after planting, Christina et 171 al. 2017). K losses through deep leaching are lower than atmospheric depositions, even after 172 application of K-Cl fertilizer the first year after planting (Laclau et al., 2010). Yet, inputs of K 173 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<sup>2</sup> 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<sup>2</sup>/yr mostly
through leaf litterfall (47%), foliar leaching (42%), and branch litterfall (11%) (Fig. 2).

180

## 1.2.2 K mobility in the soil

181 K<sup>+</sup> 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 182 183 (mg.L<sup>-1</sup>); Maquère 2008) demonstrating the very weak capacity of this soil to buffer a change 184 of the soil solution concentration resulting from an output or an input of K. These low values 185 are explained by low organic matter contents as well as a mineralogical composition where 186 quartz, kaolinite and oxide are predominant, which leads to limited interaction with 187 dissolved cations (Maquère, 2008). The weak interactions between K<sup>+</sup> and the soil solid phase 188 suggest that mass flow (rather than diffusion) could be the main process limiting potassium 189 transfer toward the roots. Moreover, diffusion fluxes measured at our study site show that 190 diffusion per se is sufficient to supply the daily demand of trees in K (Supplementary Figure 191 S1).

192

## 2

## 2. The Biological cycle of K in the ecosystem



## **Fully Fertilized**

## K omission

193 194 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 195 is represented on the left. A K-omission stand is represented on the right. Concentrations or dry 196 197 masses that are higher in the K omission stand are coloured in green while those that are lower 198 are coloured in red. A description of this experiment can be found in Battie-Laclau et al. (2014b). 199 Atmospheric deposition and leaching fluxes values come from Laclau et al. (2010). Weathering 200 fluxes were obtained by Maquère (2008) and Pradier et al. (2017). Estimation of soil K content is 201 not feasible, due to its very low concentration to integrate on very deep soil (root depth at 16m at 72 months). 202

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.

## 209 2.1 Potassium absorption by plant roots and mycorhizae

210 The uptake of K from the soil by plants is needed to maintain suitable K<sup>+</sup> concentrations in 211 the plant cells. Only a tiny fraction of total soil K is available to plants, comprising the 0.1-212 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-213 214 exchangeable K pool in the rhizosphere, altering K-bearing minerals (Pradier et al., 2017). A 215 recent isotopic dilution assay with soil samples covering 3 climatic zones and 5 soil types 216 (including the Itatinga site) suggests that the pools of exchangeable K commonly considered 217 as plant-available (measured by conventional methods) are underestimated by about 50%, 218 and that the additional pool is most likely supported by secondary non-crystalline mineral 219 phases in interaction with soil organic matter (Bel et al., 2020).

220 Large differences in K absorption efficiency between crops (and among their individual

221 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
- 223 low K availability, fine root distribution of trees is skewed towards upper soil layers,
- 224 compared with richer soils. This is explained by the higher availability of K at the surface in

225	these soils, coming from dry deposition and litter decomposition (Cusack and Turner, 2020).
226	Specific adaptations have been shown in <i>Eucalyptus</i> plantations growing on poor sandy soils
227	with a fine root mat above the mineral soil active throughout the year to catch the flux of K
228	(as well as other major nutrients) from the biodegradation of the forest floor, preventing the
229	transfer of dissolved nutrients toward deeper soil horizons (Laclau et al., 2004). However, the
230	root density profile, albeit informative, does not fit the K-absorption potential profile. Fine
231	roots in deep horizons usually show higher K-specific absorption rates as compared to more
232	superficial roots, as demonstrated by experiments with Caesium and Rubidium which are
233	analogues of K+ (Bordron et al., 2019; Göransson et al., 2008; Silva et al., 2011).
234	Depending on the $K^+$ concentration in the rhizosphere, $K^+$ absorption by the roots can be
235	either a « passive » or an « active » process (Glass, 2005; Maathuis and Sanders, 1996).
236	Passive absorption takes place through specific ion channels, also known as low-affinity
237	transporters (LATS) and requires a high K <sup>+</sup> concentration in the soil solution since it relies on
238	the electrochemical gradient. The active process operates through H <sup>+</sup> -cotransporters
239	(symporters) known as "high-affinity" transporters (HATS; Maathuis, 2009), operating at
240	lower K concentrations in the soil solution. However, recent dry laboratory experiments
241	show that this classification may be obsolete for describing the uptake of K by plants (Dreyer
242	and Michard, 2020).
243	Total K <sup>+</sup> concentration in the root cells vacuoles is variable and could be a signal for HATS

244 (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

246 the plant (Adams and Shin, 2014). This is the main identified process by which  $K^+/H^+$ 

247 symporters are activated, and it is remarkable that ROS signal that activates HATS also

248 favours root tip elongation (Adams and Shin, 2014). There is a tight correlation between the 249 absorptions of NO3<sup>-</sup> and K<sup>+</sup>, which could participate in maintaining a charge balance in the 250 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 251 et al., 2010; Battie-Laclau et al., 2014b) as well as in nutritive solution (de Souza Mateus et al., 252 253 2019), even though high Na concentrations are detrimental. There is also a need for the plant 254 to maintain a balanced K<sup>+</sup>/Na<sup>+</sup> ratio (Cuin et al., 2008). In this context, K+ HATS can be Na-255 induced (Glass, 2005), notably at low Na<sup>+</sup> concentrations in the soil solution (Chérel et al., 256 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<sup>+</sup> absorption is thus
likely along the rotation and down the vertical root profile, correlating with changes in K
contents in the soil solution.

263 The actual role of the mycorrhizal symbiosis in K absorption is still poorly understood.

264 Ectomycorrhizal fungi have been observed on roots of planted *Eucalyptus* (Lambais et al.,

265 2014; Robin et al., 2019), and a ectomycorrhizal inoculation of *Eucalyptus globulus* growing

266 on ultramafic soils (with toxic levels of heavy metals and low K availability) increased K

267 uptake by plants (Jourand et al., 2014). It is therefore likely that ectomycorrhizae provide

268 part of the K requirements when its availability in the soil is low.

269

#### 270 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<sub>2</sub>O<sub>2</sub>) that are downregulated in case of
high K<sup>+</sup> concentrations (Chérel et al., 2014). K<sup>+</sup> 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).

277

#### 278

#### 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 279 280 leaves through the exchange of elements between the leaf and the aqueous solution (Tukey, 281 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 282 283 forests (Dezzeo and Chacón, 2006; Van Langenhove et al., 2020). In subtropical forests one 284 year of foliar leaching can be larger than the foliar nutrient stocks (Lin et al., 2001). In 285 temperate deciduous forests the foliar leaching flux is smaller but still can represent half of 286 the resorption flux (Duchesne et al., 2001). In Eucalyptus plantations, however, the foliar 287 leaching flux of K (amounting to 0.42 gK/m<sup>2</sup>/yr at the Itatinga site, Fig.2) is much lower than 288 the resorption flux of K. Resorption describes a generally active recycling process that 289 happens during leaf senescence and consists in the remobilisation of nutrients from leaves 290 that can then be re-allocated to growing organs. As for other mobile nutrients, K resorption 291 can be described as a function of K concentration in the foliage with a simplified non-linear

292 equation (Achat et al., 2018). The resorption efficiency computed from K concentration in 293 living and dead *Eucalyptus* leaves at Itatinga was 79%, very close to the generic average value 294 of 80% for trees (Achat et al., 2018). The annual flux of K resorption from leaves was around 1.9 gK/m<sup>2</sup>/yr in our fertilized *Eucalyptus* plantations (Fig. 2). K resorption from leaves 295 296 account for 40 to 75% of the annual K requirements in Eucalyptus plantations (Laclau et al., 297 2010), which underlines the importance of this process for K availability at the plant level. 298 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 299 300 Rodriguez et al., 2018; Laclau et al., 2001). The amount of K remobilized in stemwood from 3 301 to 4 years after planting was estimated at 2.7g/m<sup>2</sup>/yr in fertilised *Eucalyptus* plantations (Sette 302 et al., 2013).

303

#### 304 2.4 Internal K Cycling

Once remobilized from leaves, K is cycled through the phloem. The downward phloem K 305 flux has been estimated to be about 50% of the upward xylem flux (Marschner et al., 1996; 306 307 Peuke, 2010; Sustr et al., 2019). Since there is low evidence of translocation of nutrients from 308 the phloem to the xylem (Marschner et al., 1996), cycling of potassium through the phloem 309 down to the roots and back into the xylem again can be seen as a way to re-allocate K to 310 where it is most needed (i.e. shoots). Moreover, high potassium concentrations in the phloem 311 make a higher sap flow possible, which in turn enhances photosynthate exports from shoots 312 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). 313 314 Another benefit of high concentrations of K in the xylem (that can only be sustained through

315 high K recycling) is through its use as a counter-ion to anions (Marschner et al., 1996; Peuke, 316 2010) allowing to maintain the anion-cation balance in the plant. While Dreyer et al. (2017) 317 and Marschner et al. (1996) proposed that phloem K concentration could be used as a signal 318 for K absorption by roots, Peuke (2010) found no evidence of a relationship between phloem 319 K concentrations and uptake of K by the roots and discuss whether the concentration of 320 sugars in the phloem might be a signal of nutrient deficiency. The last reason that could 321 explain the recirculation of K in the phloem is that the K<sup>+</sup> ions act as a 'mobile battery' (Dreyer et al., 2017; Gajdanowicz et al., 2011). This functioning could be useful in the case of 322 low ATP availability for the process of sucrose loading into the phloem (that goes against a 323 324 concentration gradient). Its working principle is based on the gradient between apoplastic and cytosolic K+ concentrations. Specific channels allow K<sup>+</sup> to diffuse to the apoplast and 325 326 increase an electric gradient which in turn allows sucrose to be transported from the apoplast 327 to the cytosol (Dreyer et al., 2017).

328

## 329 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.

## 343 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.

## 347 3.1.1 Leaf morphology and development

One of the essential roles that K<sup>+</sup> 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

359	in the loss of leaf mesophyll structure, which leads to a lower leaf intracellular air space in
360	comparison with K-supplied trees (Battie-Laclau et al., 2014a). Both influences of K-
361	deficiency on leaf morphology and leaf anatomy in <i>Eucalyptus</i> trees could contribute
362	explaining the decrease of leaf photosynthetic capacity described more precisely below.
363	
364	3.1.2 Leaf photosynthetic capacity
365	The relationship between leaf nutrient content and photosynthetic capacity is long-proven
366	and robust (Evans, 1989; Walker et al., 2014). The relationships between leaf nutrient
367	contents and photosynthetic capacities were studied mainly for N and P, which were
368	supposed to be the most limiting nutrients for tree growth in the majority of terrestrial
369	ecosystems (Elser et al., 2007). A much smaller number of studies also dealt with the effects
370	of K deficiency on photosynthetic capacity of leaves. Those studies have shown a good
371	correlation between the leaf photosynthetic capacity and K concentration in almond (Basile
372	et al., 2003), olive (Erel et al., 2015), hickory trees (Shen et al., 2018) and Eucalyptus (Christina
373	et al., 2015).
374	In these studies, K deficiency hampers the leaf photosynthetic capacity mostly through non-
375	stomatal limitations (Hu et al., 2019; Tränkner et al., 2018). Even though soil K availability
376	has a strong effect on stomatal movement and thus conductance, the lower leaf conductance
377	in K deficient trees seemed to have low or no effects on carbon assimilation. The limitation of
378	assimilation could be explained by multiple other reasons: biochemical effects (through
379	maximum rate of carboxylation, Vcmax, and maximum rate of electron transport, Jmax),

380 mesophyll conductance (g<sub>m</sub>) effects (the conductance of CO2 from sub-stomatal cavities to

381 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 gm 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 389 leaves is the accumulation of sucrose in leaves (Cakmak et al., 1994) due to lower phloem 390 391 sucrose loading (see section 4.2). Sucrose also serves as a replacement for K<sup>+</sup>'s osmotic 392 properties (Hermans et al., 2006). The accumulation of sucrose in leaves accompanied by a 393 decrease in sucrose stem content has been observed in K-deficient cotton plants (Zhao et al., 394 2001) and supports the hypothesis of a lower loading of sucrose into the phloem. In palm 395 trees, both very high K supply (toxic) and low K supply lead to higher leaf dark respiration 396 compared to the control treatment (Cui et al., 2019).. This is a symptom of sucrose 397 accumulation in the leaf because a relationship exists between the leaves' carbohydrate 398 content and dark respiration. Further studies are needed to explain the underlying processes.

399

## 400 3.1.3 Symptoms of K deficiency at the leaf level

401 K deficiency manifests in leaves through discoloration (e.g. yellowing, or turning purple in

402 Eucalyptus trees) and progressive leaf margin necrosis (Ericsson and Kähr, 1993; Battie-

403 Laclau et al., 2013; Silveira et al., 2000). The purple colour is related to the accumulation of

404 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).

410

#### 411 3.1.4 Leaf Lifespan

Leaf lifespan (LL) can greatly influence the carbon, water, and nutrient cycles through e.g., 412 modifications of leaf area index as well as a faster cycling of nutrients in the system. The 413 414 changes in LL are central in the response of Eucalyptus stands to K availability. While the 415 mean LL of K fertilized E. grandis trees was 149 days at the Itatinga site, the LL of K-deficient 416 trees was only 25% to 50% shorter (75 to 111 days) (Battie-Laclau et al., 2013; Laclau et al., 417 2009). This is consistent with observations of reduced LL under K deficiency in other species 418 such as sugar Maple (Acer saccharum; Wilmot et al. (1996)) and north American spruces 419 (Driessche and Ponsford, 2011). Declining photosynthetic capacities over the ageing of K-420 deficient leaves, leads to a decline in nutrient use efficiency (the ratio of assimilated carbon to 421 K present in the leaf). This in turn could lead to accelerated senescence that would allow K to 422 be reallocated to newly formed leaves.

423

#### 424 3.1.5 Consequences for GPP

Leaf biomass production (leaves produced per unit time) is similar in K-deficient and Kfertilized *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

428	development, morphology and lifespan described in section 3.1, the total leaf surface is lower
429	under K deficiency. Combined with a lower photosynthetic capacity per unit of surface leaf,
430	the GPP is lower in K-deficient stands.
431	
432	3.2 Potassium-induced changes to the water cycle
433	3.2.1 Influence at the ecosystem scale
434	Characterizing the water economy of the plant is essential to understand C-source
435	limitations. Both water and carbon cycles are interdependent (Law et al., 2002) and water
436	availability has a strong impact on GPP through its effects on stomatal opening. K is a central
437	element for the water cycle as it is necessary for stomatal function, but it also plays a role in
438	osmotic adjustment and xylem conductivity as described below.
439	
440	3.2.1 Effect of K on tree hydraulic conductance
441	Leaf and xylem hydraulic conductance is essential when considering the water cycle since, in
442	combination with evaporative demand and soil water availability, it influences tree
443	transpiration. Ultimately, this impacts carbon assimilation through the closing or opening of
444	the stomata.
445	A higher K content in the xylem sap is associated with a higher xylem hydraulic conductivity
446	(Oddo et al. (2020) in grapevine; Gascó et al. (2006) in laurel). The exact mechanism is still
447	unknown, but $K^{+}$ concentrations influence the conductivity of the xylem pits, possibly

449	However, the positive effect of K fertilization on LAI, caused by both an increase of the leaf
450	individual sizes and leaf lifespan, results in decreased sapwood-to-leaf area ratio (i.e., Huber
451	value) throughout the rotation in K-fertilized <i>E. grandis</i> stands (unpublished data). Hence,
452	the whole-tree leaf-specific hydraulic conductance at the end of the rotation (i.e., 6 years after
453	planting) is higher in K-deficient than in K-fertilized stands (unpublished data). K
454	fertilization thus increases the hydraulic constraint on water use in <i>E. grandis</i> .
455	
456	3.2.2 Influence on stomatal conductance and stand transpiration
457	K deficiency has a negative impact on leaf stomatal conductance. This is explained by the
458	central role K <sup>+</sup> ions play in stomata mobility (Marschner, 2011; Nieves-Cordones et al., 2019).
459	K deficiency impairs the normal functioning of stomatal opening, with, in Eucalyptus, a much
460	lower sensitivity of stomatal conductance ( $g_s$ ) to vapor pressure deficit (VPD) and predawn
461	water potential ( $\psi_{Pdw}$ ) in K deficient trees (Battie-Laclau et al. (2014b)). Reference $g_s$ corrected
462	for daily variations in VPD and seasonal variations in $\psi_{\text{Pdw}}$ was 2 to 5 times higher in the
463	fertilised (500-1100 mmolH <sub>2</sub> O.m <sup>-2</sup> .s <sup>-1</sup> ) than in the non-fertilised trees (200 mmolH <sub>2</sub> O.m <sup>-2</sup> .s <sup>-1</sup> )
464	(Battie-Laclau et al., 2014b).
465	K-fertilized <i>E. grandis</i> stands transpire 1.7 times more than K-deficient stands (Battie-Laclau
466	et al., 2016). A lower LAI explains most of this strong transpiration decrease in K-deficient
467	stands (Battie-Laclau et al., 2014b; Christina et al., 2018). A consequence is that K-deficient
468	stands tap less in the deep soil profile and water table (which follows rooting depth), which
469	is decisive for the stand functioning during droughts (Christina et al. 2018). Hence, the K-

470 deficient stands are less water-stressed than K-fertilized stands. Indeed, both predawn and

471 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).

#### 478 3.3 Transport limitations

The carbon fixed by the leaves is exported to fuel the growth and metabolic activity of other 479 organs and tissues. Here K also plays a role as it is necessary for the loading of sugars in the 480 phloem. A low availability of K can lead leaves to store C, principally as soluble sugars 481 482 (Cakmak et al., 1994; Marschner et al., 1996) which in turn downregulates photosynthesis. In 483 Eucalyptus stands, while concentration of sugars in the phloem is invariant between Kdeficient and K-fertilized trees (Battie-Laclau et al., 2016; Epron et al., 2016), a field study 484 based on <sup>13</sup>C labelling showed a strong negative effect of K deficiency on the transport 485 486 velocity of sugars through the phloem (Epron et al., 2016). This might be a result of changes 487 in phloem anatomy (sieve tubes) that impedes the phloem flow. This low rate of phloem 488 transport could lead in turn to a low rate of sugar export from leaves (Cakmak, 2005), which 489 might lead to degraded photosynthetic capacity of leaves (Battie-Laclau et al., 2014a). This is 490 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). 491

492

493 3.4 Changes in Carbon Partitioning

494 The impacts of soil K availability on wood production depend directly on Gross Primary 495 Productivity (GPP) as described above in detail, but also greatly on the partitioning of C 496 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 497 evidence in the literature of a direct influence of soil K availability on the respiration of 498 499 organs per unit of organ mass, except for dark leaf respiration (Christina et al., 2015). 500 However, an indirect effect through the reduced living biomass under K deficiency leads to a 501 reduction in stand-scale maintenance respiration. Some authors have also suggested that 502 carbohydrates are retained in shoots and more specifically in leaves (Hermans et al., 2006), 503 which could also impact allocation patterns.

#### 504 3.4.1 Aboveground partitioning of GPP

505 Potassium has a strong effect on carbon partitioning among the different organs of trees. As 506 developed in the section 3.1, the total GPP is lower in K-deficient than in fertilized tropical 507 *Eucalyptus* plantations. On the same species, *in* situ measurements along a full rotation 508 further showed that a lower proportion of GPP was allocated aboveground in K-deficient 509 stands compared to fertilized stands (Epron et al., 2012). Root-shoot ratio was also increased 510 in the mature K deficient stands (Fig. 2, -K: 0.27, +K: 0.19), in contradiction with decreases in 511 R/S ratio under K deficiency observed in other plant species (Gerardeaux et al., 2010). 512 While the cumulated biomass of leaves produced was similar along a Eucalyptus rotation 513 when comparing K-deficient and K-fertilized stands, the ratio of this biomass to cumulated 514 GPP, which is a proxy of the fraction of carbon allocated to leaves, was doubled in K-

- 515 deficient trees because of the lower GPP (Epron et al., 2012).
- 516

517 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.

529 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 530 531 al., 2020). Fine root biomass, specific root tip number and specific root length were shown to 532 increase in the mineral soil in response to K fertilisation in spruce stands (Wang et al. 2016). 533 In Eucalyptus plantations, fine root biomass in K-deficient stands was lower than in K-534 supplied stands, but precise measurements of this compartment remain challenging 535 (Bordron et al., 2019; Christina et al., 2015). The lack of influence of K fertilization on total 536 belowground carbon flux while fine root biomass increased in E. grandis plantations (Epron 537 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. 538

#### 540 3.5. Stoichiometric limitations of wood growth

542 Langer et al., 2002; Wind et al., 2004) through modulating cell expansion and vessel size 543 (Fromm, 2010). K fertilization influences wood physiological characteristics, with positive 544 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 545 Fig. 2 with similar K concentration in the wood between K-fertilized and K-deficient trees 546 547 (Sette et al., 2013). This contrasts with all the other tree organs (except fine roots; Fig. 2) 548 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 549 550 soils where K is rare: (1) directly (K-sink limitation of wood growth) because an absence of 551 stoichiometric flexibility sets a limit to the amount of wood that can be grown by trees, (2) 552 indirectly because the inflexible investment of K in wood restricts its investment in others, 553 stoichiometrically flexible organs and notably leaves (Fig. 2), thereby biomass and thus their 554 photosynthetic activity.

Potassium has a direct effect on cambial activity and wood formation (Ache et al., 2010;

555

541

#### 556 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 ecophysiological 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,

563	the modelling options retained are based on mechanistic formulations. We address: (1)
564	Processes linked to the canopy (influencing GPP), (2) Processes linked to the water cycle, (3)
565	Processes of organ sink activity, (4) Processes of K cycling in the soil and in the plant.
566	The effects of K availability on leaf biomass and photosynthetic capacity need to be
567	explicitly considered, as experimental observations suggest a strong effect, especially in fast
568	growing species such as <i>Eucalyptus grandis</i> . While leaf production in terms of the number of
569	new leaves per unit of time does not change in K-deficient stands, the maximum leaf surface
570	of developed leaves and leaf lifespan were strongly reduced under low K availability
571	(section 3.1). A leaf-cohort model, such as the one developed for <i>Eucalyptus</i> (SLCD; Sainte-
572	Marie et al., 2014) is ideal to this respect. This type of model allows for fine control over leaf
573	development and senescence through functions linking leaf expansion and leaf aging to K
574	availability in the plant, e.g., considered as a function of the xylem K stock (see below).
575	The impact of K availability on the photosynthetic capacity of leaves can be modelled in two
576	ways: (1) through a direct relationship between the cohort K content and the photosynthetic
577	parameters (e.g. Vcmax, Jmax in the Farquhar et al. (1980) model), (2) through the modelling
578	of the proportion of leaf surface discoloured ("symptoms", section 3.1.3) in K-deficient leaves
579	and the direct link observed between the symptom surface and the leaf -scale photosynthetic
580	parameters (Battie-Laclau et al., 2014a). Datasets allowing to evaluate the link between leaf K
581	concentration and photosynthetic parameters are scarce for trees, while leaf symptom
582	surface might be easier to measure and implement, and the relationship between leaf
583	symptom surface and leaf photosynthetic capacity is supposedly more generic, advocating
584	for the second option. Whatever modelling options, a modulation of Farquhar
585	photosynthetic parameters should be implemented to represent the direct biochemical

586	limitation of photosynthesis in function of the leaf cohort K content. Furthermore, K-
587	deficiency impacts leaf structure and explicit representation of leaf mesophyll conductance
588	(g <sup>m</sup> ) would be necessary (Knauer et al., 2019).

589 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 590 591 indirect effect of K on the water cycle (e.g., through changes in leaf area and thus 592 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 593 594 potential and stomatal conductance (e.g. Tuzet et al., 2003) is a good option for this since it 595 allows to represent the impact of K on both the xylem conductance and stomatal 596 conductance. The leaf K concentration influence on both the residual leaf conductance and 597 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. 598 599 At this stage, a mechanistic representation of the impact of K availability on the allocation of 600 carbon to the tree organs seems out of reach. For wood, as for roots, the K-limitation of sink 601 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).

604 Circulation of K in the trees is essential since, for instance, it regulates the K concentration of 605 newly formed organs, allows for a feedback on root absorption (section 2.4) and modulates 606 the xylem hydraulic conductance (section 3.2.2). An explicit xylem and phloem K circulation 607 model appears thus necessary. These types of models have already been developed for 608 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 609 610 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 611 612 stoichiometric limitation. The K phloem content would in turn allow for K tree availability to 613 be a feedback for absorption of K from the soil. Leaf K resorption can be simulated using the 614 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 615 616 important flux of K in certain systems, can be simulated using relationships that show a 617 linear relationship with throughfall quantity (Crockford et al., 1996; Lin et al., 2001). 618 Remobilisation of K from aging wood can be modelled using the framework developed by 619 Saint-Andre et al. (2002).

620 Root absorption of K will be a function of the plant demand, resulting from the concentration 621 of K in the phloem and of soil supply that can be modelled using a mass flow and diffusion 622 model (Barber, 1995; Leadley et al., 1997). Depending on the buffer power of the soil, the 623 absorption by roots will be more dependent on mass flow (low buffer power) or diffusion 624 (high buffer power). Soil K availability is determined by four main sources: fertilisation and 625 deposition, primary rock weathering, and the leaching from litter and throughfall. The 626 leaching of K from the litter is very rapid and in our opinion is not a bottleneck for K 627 availability. There is also contradicting evidence as to whether K can be limiting for the 628 decomposition processes of organic matter in the soil: this effect is most likely negligible and 629 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 630

631 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 632 633 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 634 several processes exist and could be included in carbon and water process-based models, 635 636 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 637 638 rather different from the effects of P and N. We have also found no major interactions 639 between the cycles of other nutrients and K. This indicates that is should be possible to 640 model K effects independently of other nutrients.

## 641 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.

648 With this review, we identified the major priorities for implementing the K cycle in eco-649 physiological forest models. Yet, the relative importance of each physiological process 650 influenced by K availability on the response of wood production remains unknown. The 651 mechanistic modelling of key processes is needed to quantify their relative importance. Eco-652 physiological models already incorporate most of these processes and their functioning can 653 be modulated by K availability. N and P cycles and their effects on forest functioning have 654 been successfully implemented in eco-physiological models. Since K is generally in ionic 655 form, it has a different behaviour than N and P and some new processes will need to be 656 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 657 acquisition of carbon in K-limited forest ecosystems. Leaf ontogeny has strong effects on the 658 659 canopy, which is crucial for light interception and the tree water economy. Secondly, we 660 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 661 between K availability and C export from leaves, a process that is still hard to quantify. 662 663 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 664 665 global scale, and the evolution of this limitation under future climate change in relation with 666 other nutrient limitations.

667

#### 668 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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