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

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## 1 **Abstract**

2 Potassium (K) is essential for a wide range of physiological functions in plants, and a limiting  
3 element for wood productivity in numerous forest ecosystems. However, the contribution of  
4 each of the K-sensitive physiological processes to the limitation of wood productivity is  
5 poorly known. In trees, K deficiency acts both on the source and the sinks of carbon making  
6 it difficult to disentangle its effects on wood productivity. Here, we review the literature  
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  
13 towards the process-based modelling of the influence of K on the carbon and water cycles in  
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.

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

18

## 19 **Introduction**

20 Plants are autotrophic organisms that require energy, water, CO<sub>2</sub>, macro- and micronutrients  
21 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  
28 ecosystems are principally C-limited. This hypothesis is important for climate change  
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.

32 To test the validity of this C-centric view, Free Air CO<sub>2</sub> Enrichment experiments have been  
33 used over the past three decades. Elevated CO<sub>2</sub> concentrations do lead to a positive effect on  
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  
40 that nutritional stresses are currently increasing (Jonard et al., 2014, 2009; Penuelas et al.,  
41 2020). This could negatively impact the assimilation of C by plant leaves, since the  
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  
45 studied (Crous et al., 2017; Kattge et al., 2009; Reich, 2012; Reich et al., 2009; Walker et al.,  
46 2014). With the aim of a better representation of the C cycle, the effect of N (e.g. Corbeels et  
47 al., 2005; Dezi et al., 2010; Vuichard et al., 2019) and more recently P (Goll et al., 2017; Thum  
48 et al., 2019; Yang et al., 2014) on ecosystem processes has been implemented in many  
49 vegetation models. In simulations, representation of N and P limitations can lead to a 25%  
50 decrease in the land carbon sink between 1860 and 2100 under a climate change scenario  
51 (SRES A1B) (Goll et al., 2012).

52 A mounting body of evidence has made apparent that liebigian limitation ("one factor limits  
53 growth") does not hold in forest ecosystems (Elser et al., 2007; Fanin et al., 2015; Kaspari et  
54 al., 2008; Santiago et al., 2012; Townsend et al., 2011; Wurzbürger et al., 2012). It has thus  
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.

60 Contrary to N and P, K is present exclusively in its ionic form ( $K^+$ ) in the plants and in the  
61 soil.  $K^+$  is the most important cation in terms of mass in the plant biomass, and the second  
62 nutrient after N. There are two main pools of K in plant cells: the cytosol and the vacuole.  
63 While the concentration of K in the vacuole is variable and depends on K availability,  
64 cytosolic K concentration remains relatively constant (Walker et al., 1996). In plant cells  $K^+$  is  
65 essential for enzyme activation, charge balance and osmoregulatory functions (Wakeel et al.,  
66 2011).

67 While evidence of K limitation of forest productivity is scarce in temperate and boreal  
68 regions (Bonneau, 1972; Ouimet and Moore, 2015; Wang et al., 2016), K is co-limiting or  
69 limiting productivity in many tropical and subtropical forests (Baribault et al., 2012; Bond,  
70 2010; Epron et al., 2012; Laclau et al., 2009; Lloyd et al., 2015; Rocha et al., 2019; Sardans and  
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  
74 resources (a so-called 'source-limitation' of productivity) or the formation of new tissues  
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  
84 organs, (3) modifications of C partitioning, and (4) direct limitation (e.g. stoichiometric  
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.  
88 The rationale for the choice of this biological model is that *Eucalyptus* trees have been grown  
89 in field experiments manipulating tree nutrition for a long time. The effects of nutrient

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).

93 In section 1 of this review, we describe the main processes governing the K biogeochemical  
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  
96 the trees. In section 2, we review the processes related to the uptake and circulation of K  
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

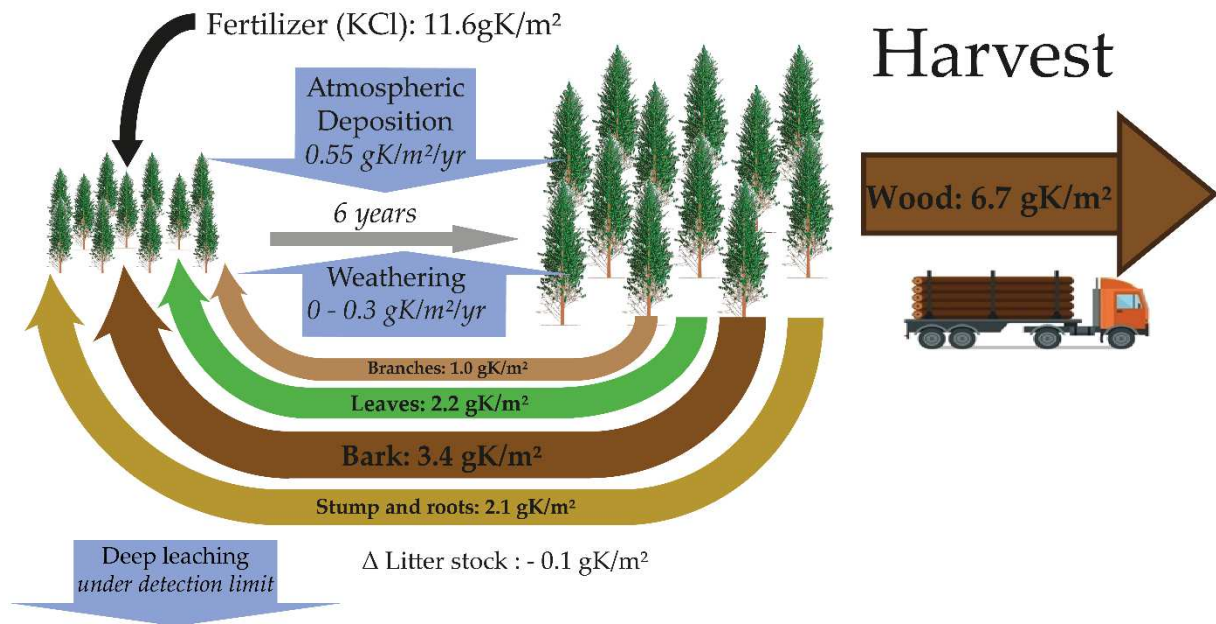


113 regions belong to species *Eucalyptus grandis*, *E. urophylla* (ST Blake) or are hybrids including  
114 *E. grandis*. The vulnerability of *Eucalyptus* plantations to climate change is of concern (Booth,  
115 2013) and process-based models could be useful tools to help improve management practices  
116 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  
118 deficiency is common, with a very strong limitation of wood productivity (up to 50% in  
119 absence of K fertilisation) in some tropical areas ( Gonçalves et al., 2008; Laclau et al., 2009;  
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).

129 Experimental designs have been set up in *Eucalyptus* plantations with a positive control fully  
130 fertilized (tree growth not limited by the availability of micro- and macro-nutrients)  
131 compared to other treatments with the same full fertilization except a single nutrient  
132 (omission trials), and a negative control without any fertilization (Laclau et al., 2009). Such  
133 experiments made it possible to assess which processes are affected by the deficiency of each  
134 nutrient, with or without the confounding interactions with other nutrients (Christina et al.,  
135 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).



138

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

153 In highly weathered tropical soils, K availability is low due to small amounts of K-bearing  
154 primary minerals (e.g., illite and vermiculite) likely to release K in the soil solution. The  
155 replenishment of the pool of exchangeable K<sup>+</sup> in highly weathered tropical soils comes  
156 mainly from atmospheric depositions and from the biological cycle in natural ecosystems, as  
157 well as fertilization in agroecosystems. Only a fraction of the total stock of K in the soil is  
158 directly available to the plants and sorption as well as diffusion speed may limit the access of  
159 the trees to the pool of K.

### 160 1.2.1 K inputs and outputs in the soil

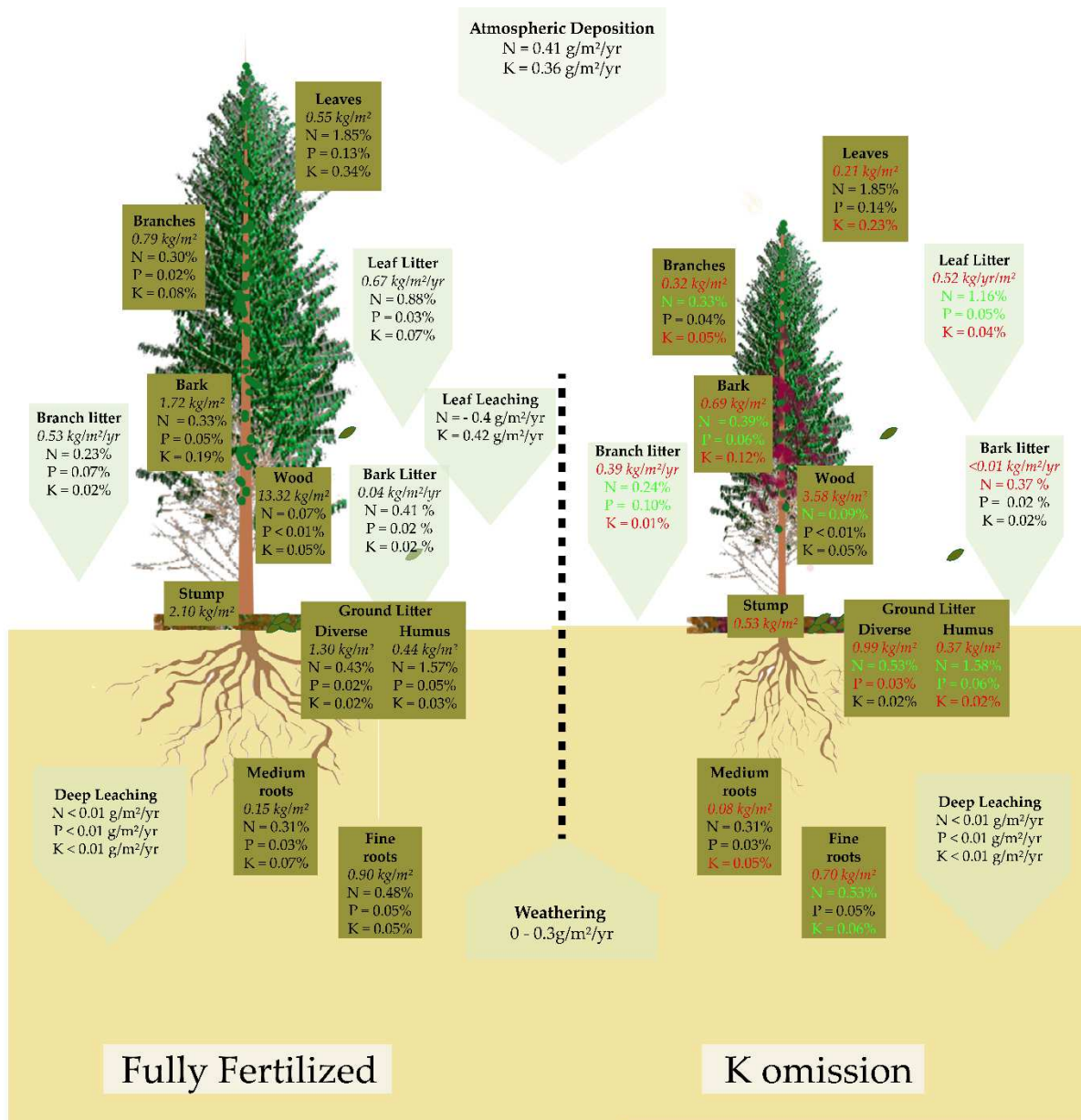
161 Atmospheric deposition is an external source of K to *Eucalyptus* plantations. It amounts to  
162 about 0.55 gK/m<sup>2</sup>/yr in *Eucalyptus* plantations at Itatinga (Fig. 1 and 2; Laclau et al. 2010). This  
163 flux is comparable to the global average of 0.41gK/m<sup>2</sup>/yr (Sardans and Peñuelas, 2015). This  
164 atmospheric deposition flux is higher than mineral weathering, that was considered  
165 negligible by Maquère (2008) at the same site based on quantitative mineralogical work.  
166 However, a recent study considering the rhizosphere of eucalypt trees suggested that the  
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

174 these highly productive *Eucalyptus* plantations where biomass export (mostly tree trunks) is  
175 massive (Fig. 1). Highly productive plantations are therefore fertilized, with typical amounts  
176 of about 12 gK/m<sup>2</sup> before canopy closure (Fig. 1), which is enough to cover the requirements  
177 of the tree throughout the rotation (Almeida et al., 2010). We note that the cycling of K is fast  
178 in those plantations, with annual inputs to the soil surface of about 1.0 gK/m<sup>2</sup>/yr mostly  
179 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  
182 range from 0.09 to 0.13 (change in exchangeable K (mg/100g) / change in soil-solution K  
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. The Biological cycle of K in the ecosystem



193  
 194

**Figure 2. Main stocks (boxes) and fluxes (arrows) of Carbon, Nitrogen, Phosphorus and**

195

**Potassium in a Eucalypt plantation of 72 months of age (before harvest). A fully fertilised stand**

196

is represented on the left. A K-omission stand is represented on the right. Concentrations or dry

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

202

at 72 months).

203

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

209 *2.1 Potassium absorption by plant roots and mycorrhizae*

210 The uptake of K from the soil by plants is needed to maintain suitable  $K^+$  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)  
213 (Sardans and Peñuelas, 2015). Yet roots seem able to mobilize a fraction of the non-  
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  
222 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 *Eucalyptus* 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<sup>+</sup> (Bordron et al., 2019; Göransson et al., 2008; Silva et al., 2011).

234 Depending on the K<sup>+</sup> concentration in the rhizosphere, K<sup>+</sup> 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  
245 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<sup>+</sup>/H<sup>+</sup>  
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  $\text{NO}_3^-$  and  $\text{K}^+$ , which could participate in maintaining a charge balance in the  
250 xylem sap (Raddatz et al., 2020). Sodium ( $\text{Na}^+$ ) can act as a substitute to  $\text{K}^+$  for some osmotic  
251 functions, as shown by Na supplementation experiments for *Eucalyptus* in the field (Almeida  
252 et al., 2010; Battie-Laclau et al., 2014b) as well as in nutritive solution (de Souza Mateus et al.,  
253 2019), even though high Na concentrations are detrimental. There is also a need for the plant  
254 to maintain a balanced  $\text{K}^+/\text{Na}^+$  ratio (Cuin et al., 2008). In this context,  $\text{K}^+$  HATS can be Na -  
255 induced (Glass, 2005), notably at low  $\text{Na}^+$  concentrations in the soil solution (Chérel et al.,  
256 2014).

257 It is not straightforward to assess which of the “active” or “passive” absorption processes are  
258 mostly operating in highly fertilized tropical *Eucalyptus* plantations. They grow on severely  
259 K-deficient soils but are highly supplemented by fertilizer inputs, delivered at the beginning  
260 of the rotation (ref; Fig. 1). A shift from LATS- to HATS-dominated  $\text{K}^+$  absorption is thus  
261 likely along the rotation and down the vertical root profile, correlating with changes in K  
262 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*

271   Once K has been absorbed by the roots, it can be translocated to newly forming organs. This  
272   happens through an upward xylem flux. As for K absorption by roots, a channel for K  
273   loading in the xylem is activated by ROS (mainly H<sub>2</sub>O<sub>2</sub>) that are downregulated in case of  
274   high K<sup>+</sup> concentrations (Chérel et al., 2014). K<sup>+</sup> in the xylem ascending flux serves as a  
275   counter-ion to the anions and plays a role in electrical neutralization (Maathuis, 2009), as it  
276   does in plant cells (Chérel et al., 2014).

277

278                   2.3 *Foliar Leaching, Resorption and Remobilisation from stemwood*

279   Foliar leaching (also known as “recretion” in some sources) is the passive loss of nutrients by  
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,  
282   foliar leaching brings, via throughfall and stemflow, a non-negligible flux of K to the soil in  
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  
295 1.9 gK/m<sup>2</sup>/yr in our fertilized *Eucalyptus* plantations (Fig. 2). K resorption from leaves  
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  
299 inner rings in stem wood shows that K is strongly remobilized during wood ageing (Ortega  
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

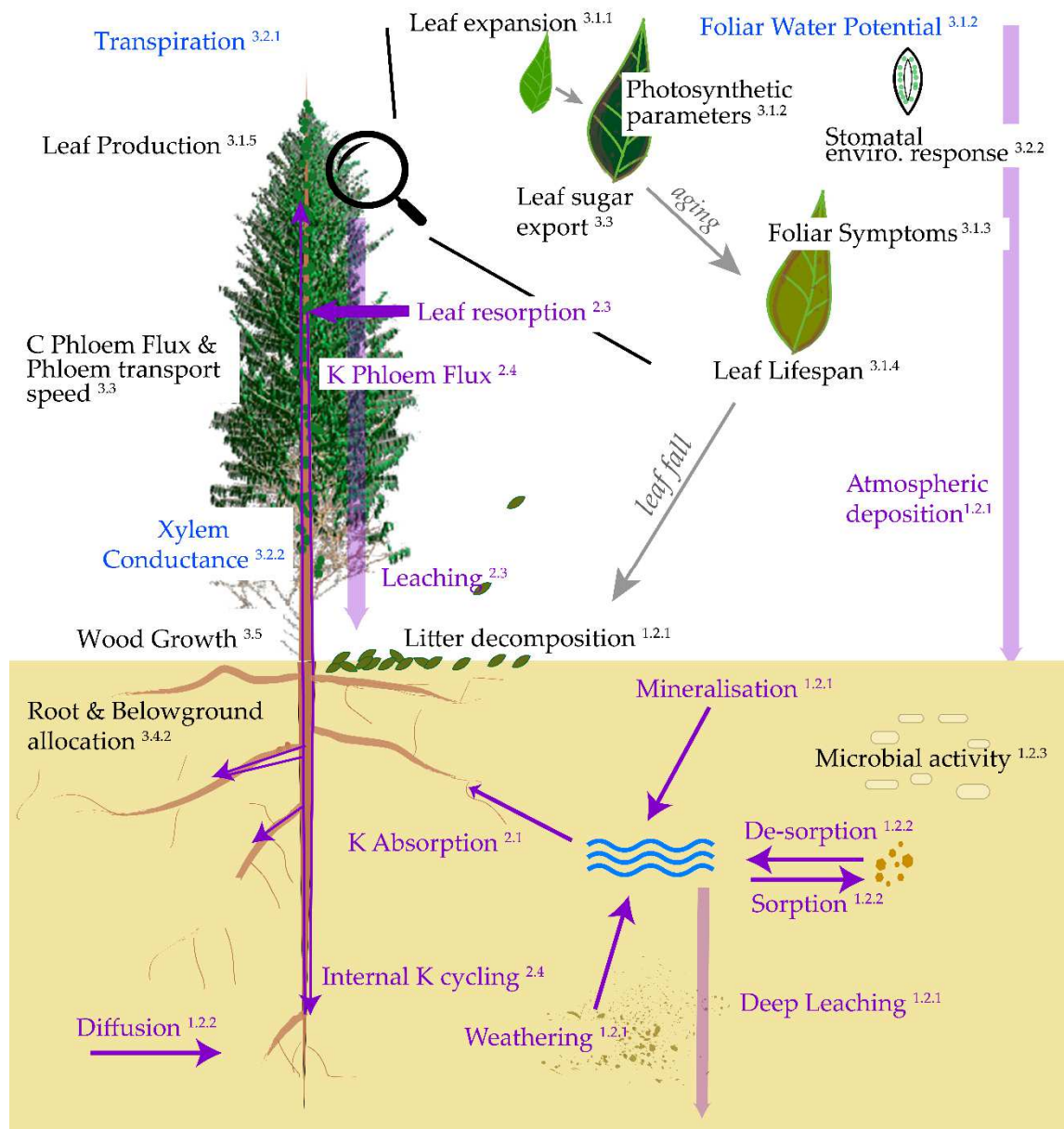
#### 304 2.4 Internal K Cycling

305 Once remobilized from leaves, K is cycled through the phloem. The downward phloem K  
306 flux has been estimated to be about 50% of the upward xylem flux (Marschner et al., 1996;  
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  
313 most likely due to higher osmotic pressure in sieve tubes (Mengel and Haeder, 1977).  
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  $K^+$  ions act as a 'mobile battery'  
322 (Dreyer et al., 2017; Gajdanowicz et al., 2011). This functioning could be useful in the case of  
323 low ATP availability for the process of sucrose loading into the phloem (that goes against a  
324 concentration gradient). Its working principle is based on the gradient between apoplastic  
325 and cytosolic  $K^+$  concentrations. Specific channels allow  $K^+$  to diffuse to the apoplast and  
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**



330

331

**Figure 3. Processes of interest for the limitation of growth by K.** The processes and fluxes

332

directly linked to the K cycle in the system are represented in purple. The processes related

333

to the water cycle are represented in blue. The processes closely linked to the C cycle are

334

represented in black. The numbers appearing in exponents beside process names refer to the

335

section describing this process in the text.

336

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

### 343 **3.1 Influence of potassium availability on carbon assimilation**

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

#### 347 3.1.1 Leaf morphology and development

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

354 However, there is no difference in individual leaf area between K-supplied and Na-supplied  
355 trees in these plantations. Pressure-volume curves suggest that the differences in individual  
356 leaf area between K-deficient and fertilized trees are mainly due to higher cell turgor shared  
357 by potassium and sodium resulting from higher concentrations of osmotica increasing both  
358 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 *Eucalyptus* 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,  $V_{cmax}$ , and maximum rate of electron transport,  $J_{max}$ ),  
380 mesophyll conductance ( $g_m$ ) effects (the conductance of CO<sub>2</sub> from sub-stomatal cavities to  
381 carboxylation sites) or carbohydrate accumulation (negative feedback on photosynthesis;

382 Ainsworth and Bush, 2011). Studies investigating the influence of K deficiency on  
383 biochemical aspects of photosynthesis are contradictory (Gvozdevaite et al., 2018; Jin et al.,  
384 2011). On the other hand, the decline of mesophyll conductance in conditions of K deficiency  
385 is consistently reported, including in *Eucalyptus* trees (Battie-Laclau et al., 2014a; Lu et al.,  
386 2019, 2016; Shen et al., 2018). This decline of  $g_m$  has been attributed to a lower area of  
387 chloroplasts exposed to intercellular air space and thicker cell walls in K-deficient rice plants  
388 (Xie et al., 2020).

389 The last factor likely to explain the reduction of leaf photosynthetic capacity in K deficient  
390 leaves is the accumulation of sucrose in leaves (Cakmak et al., 1994) due to lower phloem  
391 sucrose loading (see section 4.2). Sucrose also serves as a replacement for  $K^+$ '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.,

405 2013), which could explain the decrease in photosynthetic capacity associated to symptoms  
406 (Battie-Laclau et al., 2014a). The anthocyanins may help with nutrient resorption (Duan et al.,  
407 2014; Hoch et al., 2003). They further have a photoprotective function (Close and Beadle,  
408 2003) and could help preventing the photooxidative stress caused by reduced photosynthetic  
409 capacity of K-deficient leaves (Marschner and Cakmak, 1989).

410

#### 411 3.1.4 Leaf Lifespan

412 Leaf lifespan (LL) can greatly influence the carbon, water, and nutrient cycles through e.g.,  
413 modifications of leaf area index as well as a faster cycling of nutrients in the system. The  
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

425 Leaf biomass production (leaves produced per unit time) is similar in K-deficient and K-  
426 fertilized *Eucalyptus* stands at both the stand scale (Epron et al., 2012) and at the branch  
427 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  
448 through changes in pectin volume (Nardini et al. (2011)).

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 *E. grandis* 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 *E. grandis*.

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  $K^+$  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  $\psi_{pdw}$  was 2 to 5 times higher in the  
463 fertilised (500-1100  $\text{mmolH}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) than in the non-fertilised trees (200  $\text{mmolH}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )  
464 (Battie-Laclau et al., 2014b).

465 K-fertilized *E. grandis* 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-

472 deficiency did not influence the water potential gradient (from root to shoot under  
473 transpiration) (Battie-Laclau et al., 2014b). Besides, transpiration per unit leaf area is higher  
474 in K-deficient than in K-fertilized stands throughout the rotation of *E. grandis* (Asensio et al.,  
475 2020; Battie-Laclau et al., 2016). These evidences of alleviated water stress in K-deficient  
476 stands, based on *in-situ* physiological monitoring are further corroborated by omics  
477 approaches (Favreau et al., 2019; Ployet et al., 2019).

### 478 3.3 Transport limitations

479 The carbon fixed by the leaves is exported to fuel the growth and metabolic activity of other  
480 organs and tissues. Here K also plays a role as it is necessary for the loading of sugars in the  
481 phloem. A low availability of K can lead leaves to store C, principally as soluble sugars  
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 K-  
484 deficient and K-fertilized trees (Battie-Laclau et al., 2016; Epron et al., 2016), a field study  
485 based on <sup>13</sup>C labelling showed a strong negative effect of K deficiency on the transport  
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  
491 anthocyanins could be acting as sinks for excess C in leaves (Pourtau et al., 2006).

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  
497 partitioning, then more specifically the effects on roots biomass. We were not able to find any  
498 evidence in the literature of a direct influence of soil K availability on the respiration of  
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

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

524 The response of *Eucalyptus* trees to K fertilization is in accordance with these results: GPP  
525 was drastically increased (see section 3.1) while the total amount of carbon allocated  
526 belowground was not significantly affected by K fertilization in a field experiment at Itatinga  
527 (Epron et al., 2012). Therefore, the fraction of GPP allocated belowground was decreased by  
528 K fertilization.

529 It seems that the fine root biomass is lower in conditions of K deficiency, contrary to what  
530 usually happens in case of N and P deficiencies (Sustr, Soukup, et Tylova 2019; Fontana et  
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  
538 exudation by roots. This pattern should be confirmed by direct measurements.

539

### 540 3.5. Stoichiometric limitations of wood growth

541 Potassium has a direct effect on cambial activity and wood formation (Ache et al., 2010;  
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*  
545 plantations, wood as a tissue has apparently only little stoichiometric flexibility as shown in  
546 Fig. 2 with similar K concentration in the wood between K-fertilized and K-deficient trees  
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  
549 this lack of stoichiometric flexibility as impacting wood growth in two ways in K-deficient  
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.

555

## 556 4 Potassium-related processes in forest functioning models

557 The K-limitation of wood growth can stem from a variety of processes (Fig. 3). Here we  
558 identify the priorities when it comes to the integration of K-related processes in eco-  
559 physiological models that initially focus on the carbon and water cycles. These a priori  
560 modelling choices will need to be refined by implementation, testing and sensitivity analyses  
561 in forthcoming studies. We focus here on tropical forests, and in particular our model  
562 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 *Eucalyptus grandis*. 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 *Eucalyptus* (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.  $V_{cmax}$ ,  $J_{max}$  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 ( $g_m$ ) would be necessary (Knauer et al., 2019).

589 The water cycle in forests impacts wood productivity mainly through feedbacks between  
590 water availability, stomatal conductance, and water potential inside trees. On top of the  
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  
593 necessary. A model representing plant hydraulics, and the link between the leaf water  
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  $g_s$  and carbon assimilation should be integrated in the model. Xylem  
598 conductance for water can be modelled as a function of the xylem K concentration.

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  
602 directed to each organ, see Delpierre et al. (2016b)). Another constraint could be a direct  
603 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  
609 K stock would determine the K available for the formation of new leaves. The phloem K  
610 stock would allow for the recycling of unused xylem K and the K provided by leaf  
611 resorption. Phloem K is then available for allocation to wood and root growth, with eventual  
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  
615 species (Achat et al., 2018) and confirmed in *Eucalyptus* (see section 2.3). Leaf K leaching, an  
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  
630 follow the flow of water in the soil. We suggest that measurements and modelling

631 investigations in the future should focus on weathering fluxes. These fluxes are decisive to  
632 determine K availability in forest ecosystems. Experimental estimates vary widely (section  
633 1.2.1) and do not allow to prescribe any specific modelling options. These fluxes will vary  
634 greatly depending on the soil type and parent rock. While our review has clearly shown that  
635 several processes exist and could be included in carbon and water process-based models,  
636 their relative importance compared to other processes will need to be explored in the model  
637 through sensitivity analyses. Thankfully, we have seen that the effect K has on processes is  
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 it should be possible to  
640 model K effects independently of other nutrients.

## 641 **5 Conclusion**

642 Potassium is an essential nutrient in forest ecosystems. It can be strongly limiting tree growth  
643 in highly weathered soils, as in tropical *Eucalyptus* plantations. In this review, we have  
644 highlighted the main processes limiting K availability to the trees and the metabolic  
645 processes that are affected by low K availability. K influences with both the water cycle and  
646 the carbon cycle as it impacts light interception by the canopy, C fixation and C export from  
647 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  
657 limitation on leaf ontogeny and photosynthetic capacity are central for determining the  
658 acquisition of carbon in K-limited forest ecosystems. Leaf ontogeny has strong effects on the  
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  
661 level. If more information on phloem dynamics become available, this will allow interactions  
662 between K availability and C export from leaves, a process that is still hard to quantify.  
663 Lastly, we identify the K weathering flux to be central when considering K limitation in  
664 forest ecosystems. Simulating these processes is essential to understand K limitation at a  
665 global scale, and the evolution of this limitation under future climate change in relation with  
666 other nutrient limitations.

667

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681

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