1 **Potassium: a neglected nutrient in global change**

2

3 Jordi Sardans[1,2*] & Josep Peñuelas[1,2]

4 [1]CSIC, Global Ecology Unit CREAF-CEAB-CSIC-UAB. 08913 Cerdanyola del Vallès.

5 Catalonia. Spain.

6 [2]CREAF. 08913 Cerdanyola del Vallès. Catalonia. Spain.

7 Running title: Potassium stoichiometry and global change

8 *Corresponding author. Email: j.sardans@creaf.uab.es Tel: 34 93 851 2934 Fax: 34 93

9 581 4151

10

11

12 Keywords: climate change, drought, ecological stoichiometry, eutrophication, global

13 change, invasiveness, N:K, plant growth

14

15

16

17

18

19

20

21

22

23

24

25

ABSTRACT

Aim: Potassium (K) is the second most abundant nutrient after nitrogen (N) in plant photosynthetic tissues. Thousands of physiological and metabolic studies in recent decades have established the fundamental role of K in plant function, especially in water use efficiency and economy, and yet macroecological studies have mostly overlooked this nutrient.

Methods: We have reviewed available studies on the contents, stoichiometries and roles of potassium in the soil-plant system and in terrestrial ecosystems. We have also reviewed the impacts of global change drivers on K contents, stoichiometries, and roles.

Conclusions: The current literature indicates that K, at a global level, is as limiting as N and phosphorus (P) for plant productivity in terrestrial ecosystems. K limitation has been seen up to some degree in 70% of all studied terrestrial ecosystems. However, atmospheric K deposition from human activities represents higher amounts than that from natural sources in some areas. We are far from understanding the K fluxes between the atmosphere and land, and the role of anthropogenic activities in these fluxes. The increasing aridity expected in wide areas of the world makes K more critical through its role in water use efficiency. N deposition exerts a strong impact on the ecosystem K-cycle, decreasing K availability and increasing K limitation. Plant invasive success is enhanced by higher soil K availability, especially in environments without strong abiotic stresses. The impacts of other global change drivers, such as increasing atmospheric CO_2 or changes in land use remain to be elucidated. Current models of the responses of ecosystems and carbon storage to projected global climatic and atmospheric changes are now starting to consider N and P, but they should also consider K, mostly in arid and semiarid ecosystems.

Introduction: Potassium in plant-soil system

Potassium (K) is the most abundant cation in plant cells and is the second most abundant nutrient after nitrogen (N) in leaves. K is thus more abundant than phosphorus (P) (Leigh & Jones, 1984; Sardans *et al*., 2006; Zheng & Shangguan, 2007; Sardans *et al*., 2011, 2012a). K represents 2.6% of the weight of the Earth's crust. The concentrations of P and N in rocks are lower; P represents only 0.1% of the weight of the Earth's crust, and N is only present in trace amounts in magmatic rocks (< 200 ppm in granite). The most N-rich sedimentary rocks have only 0.1% N (Greenwood & Earnshaw, 1997; Holloway & Dahlgren, 2002). Young soils tend to have high phosphorus availability and low nitrogen availability (Houlton *et al*., 2008). However, as soils age, nitrogen gradually accumulates in the soils (Hedin *et al*., 2003), while they become more depleted in phosphorus (Walker & Syers, 1976; Vitousek & Howarth, 1991). K can be more easily leached than N or P (Boxman *et al*., 1994; Neirynck *et al*., 1998). However, terrestrial ecosystems, such as forests and shrublands, have a great biological capacity for K-retention by several processes, such as plant "pumping" and resorption of K (Nowak *et al*., 1991; Jobbáry & Jackson, 2001).

K "pumping" describes the plant K uptake from deep soil layers (with K provided in part by mineral weathering release) to upper soil layers. This can imply higher K losses by runoff (Barré *et al*., 2009), but despite this runoff the pumping activity allows maintenance of the high levels of available-K in the surface of most soils of the globe (Jobbáry & Jackson, 2001). This biological control of ecosystem K-cycle strongly suggests a great evolutionary pressure to retain K in terrestrial ecosystems. Moreover, this "pumping" capacity can allow a long-term conservation of K in soils (Stone & Kszystyniak, 1977). The potential of parent material together with a

76 conservative biogeochemical cycle are underlying the maintenance of K supply to

77 plants (Nowak *et al*., 1991; Jobbáry & Jackson, 2001).

78   K in soil can be allocated to three pools of availability for uptake by roots. It is

79 dissolved in soil water, adsorbed onto particles of clay and organic matter and held

80 within the crystal structures of feldspar and mica. The organic matter in soils contains a

81 negligible amount of K because it is not a constituent of biomolecules, hence easily and

82 quickly leached from leaves due to its high solubility. However, the fraction of soil K

83 directly available to plants (i.e., in soil solution) is usually a small proportion (0.1-0.2%)

84 of the total soil K, whereas both the immediate available-water soluble and the

85 exchangeable fraction are 1-2%, and the soil unavailable fractions are 96-99% (Wang *et*

86 *al*., 2010; Britzke *et al*., 2012). The soil available-K pool is easily leached by runoff.

87 Soil-plant available K concentrations can thus frequently be lower than the soil-plant

88 available N and P concentrations, even though the total soil K concentrations are

89 generally higher than those of N and, especially, P (Sardans & Peñuelas, 2007; Sardans

90 *et al*., 2008). We have estimated the global K contents of the various K fractions in soil

91 from the data in Soil Taxonomy (Soil Survey Staff, 1999) and other bibliographic

92 sources (Table 1, Figure 1).

93   On the other hand, in terrestrial ecosystems, K shows a greater loss from the

94 plant canopy than other nutrients such as N and P by foliar leaching (Duchesne *et al*.,

95 2001; Kopacek *et al*., 2009). Thus, this poses the question that if K is potentially

96 limiting, why there has not been a greater natural selection to minimize leaching losses

97 from leaves?. We must take into account that differently from N and P, that mostly

98 constitute complex molecular structures, K occurs exclusively in soluble K^+ form. For

99 this reason, from a physical point-of-view perspective, K can be more easily leached

100 through cell membranes due to its smaller size. Probably, the need of maintaining its

101   cationic soluble form for its function has not allowed to improve the plant capacity to

102   retain it. Moreover, mechanisms, such as reduction of stomatal density or thickening of

103   the cuticle, which could help in preventing K losses, very probably present several

104   evolutionary trade-offs with other important plant functions such as gas exchanges and

105   water economy.

106   However, soil-plant system has a notable control on the ecosystem K-cycle they

107   contribute in its retention. Current available data show a notable plant capacity to retain

108   K by resorption. Diverse results have been reported in the studies comparing N, P, and

109   K resorption efficiency (RE). Some researchers have observed N=P<K RE (van den

110   Driessche, 1985; Nieminen & Helmisaari, 1996; Sardans *et al*., 2005), others have

111   observed P<N=K RE (Ozbucak *et al*. 2008), N<K=P RE (Chuyong *et al*., 2000),

112   N>K>P RE (Yin *et al*., 2009), P>K>N RE (Sahehi et al., 2013), K<N=P RE

113   (Helmisaari, 1992; Duchesne *et al*., 2001; Tartachnyk & Blanke, 2004; Hagen-Thorn *et*

114   *al*., 2006), and N=P=K RE (Gallardo *et al*., 1999; Trémolières *et al*., 1999). A recent

115   review of a global dataset has observed that K RE on a global scale (70.1%) seems to be

116   higher than the RE of N (62.1%) and P (64.9%) (Vergutz *et al*., 2012), although most of

117   the studies reviewed by these authors did not take into account the role of leaf leaching

118   when calculating RE. In fact, K leaches more easily from leaves than N and P; hence it

119   is difficult to know the role of K foliar leaching in the studies that have calculated RE of

120   these three nutrients, and some of these studies might be biased. Nieminen &

121   Helmisaari (1996) observed in *Pinus sylvestris* that after correcting RE for nutrient

122   losses by net throughfall, K RE was higher than N and P RE. Some results add even

123   more complexity in the interpretation of the comparison of RE among these three

124   nutrients. Some studies showed that the RE of N, P and K varied considerably

125   depending on the phase of RE, and that this variance depended of each studied species,

126   but that this K RE was generally higher than N and P RE (Nieminen & Helmisaari,

127   1996; Fife & Nambiar, 1997; Fife et al., 2008). . In summary, the available data allow to

128   deduce that the internal plant RE of K is important, and similar, on average, to the REs

129   of N and P.

130   The availability of K in several terrestrial ecosystems can also strongly depends

131   on the input of K by atmospheric deposition (Table 2), which can vary from 0.07 to

132   more than 100 kg ha^{-1} yr^{-1} (with a mean of the total, dry plus wet, atmospheric K

133   deposition of 4.1 kg ha^{-1} yr^{-1} for the available studies, Table 2). The available data

134   suggest that the current levels of K fertilization (0.025×10^9 t yr^{-1}) and K atmospheric

135   deposition (0.066×10^9 t yr^{-1}) are very low compared with the global amount of

136   available soil K (57.7×10^9 t). The current data for atmospheric K deposition also

137   suggest that the amounts of K from atmospheric deposition in some areas of the world

138   could have a large impact on soil K concentrations and on the stoichiometric

139   relationships between K and other elements. For example, the deposition of 281 kg K

140   ha^{-1} reported for southern Nigeria (Muoghalu & Oakhumen, 2000) or the 6-23 kg K ha^{-1}

141   of wet deposition observed in some areas of India (Prathibha *et al*., 2010) are notable. In

142   the last few decades, the National Atmospheric Deposition Program database

143   (http://nadp.sws.uiuc.edu/) has determined wet K deposition by analyzing rainfall of

144   237 plots throughout North-America; the data show a great variability depending on the

145   site (from 0.022 to 3.0 kg K ha^{-1} yr^{-1}). In this regard, we must highlight that the data of

146   wet K deposition from precipitation have been collected for some world areas, the data

147   of total K deposition are scarce despite the current knowledge suggest that K dry

148   deposition could also be important (Table 2). It is surprising that studies on the potential

149   effects of high amounts of K in terrestrial ecosystems have been apparently neglected,

150 though there are so many on the causes and consequences of N- and, even, P

151 depositions.

152   The atmospheric deposition of K originates from natural processes, such as sea

153 spray (Table 2) but also from agricultural activities and human industrial activities such

154 as fertilizer and cement production, petrochemistry, steel industry, and coal combustion

155 (Klumpp *et al*., 2002; Walker *et al*., 2003; Urban *et al*., 2012). Human activities can

156 represent a higher proportion than the natural processes (Ferm & Hultberg, 1999;

157 Golobocanin *et al*., 2008). We are, however, far from understanding the K fluxes

158 between the atmosphere and the land and the role of anthropogenic activities in these

159 fluxes (Quennehen *et al*., 2012).

160   Ecological stoichiometric studies of terrestrial ecosystems have focused mostly

161 on N and P (Vitousek & Howarth 1991; Elser *et al*., 2000; Sterner & Elser, 2002;

162 Sardans *et al*., 2012b). Similarly, studies on the impacts of the drivers of global change

163 on terrestrial biogeochemical cycles have focused mainly on these two elements

164 (Vitousek *et al*., 2010; Sardans *et al*., 2012c; Peñuelas *et al*., 2013a,b). Models of global

165 carbon (C) circulation frequently do not include the role of nutrients in the

166 establishment of C balances and the capacity of sinks to store C (Lé Quére *et al*., 2009).

167 However, those that do, usually include only N (Schimel *et al*., 2001; Mack *et al*., 2004;

168 Langley & Megonigal, 2010) or more recently P (Peñuelas *et al*., 2012, 2013a, 2013b).

169   There is an increase in number of reports that highlight the importance of K in

170 plant functions (Box 1) and responses to environmental changes, and its frequent

171 limiting role for plant growth and C storage in terrestrial ecosystems. In the present

172 study, we aim to demonstrate the urgent necessity to include K in the studies of

173 biogeochemistry and stoichiometry in terrestrial ecosystems, and of the consequences of

174 global change on nutrient cycles and their mutual feedbacks.

Plant K uptake

The importance of K in terrestrial plants is reflected by the sophisticated mechanisms of K uptake, redistribution, and homeostasis involving several families of cell-wall and membrane proteins (Hirsch *et al*., 1998; Armengaud *et al*., 2004; Szczerba *et al*., 2009; Pyo *et al*., 2010). Several regulatory mechanisms have been identified for K transporters, which are activated by various environmental factors such as water availability and soil concentrations of K^+, Na^+ or Ca^{2+} (Zhang *et al*., 2006; Szczerba *et al*., 2009; Pyo *et al*., 2010). Low-affinity and high-affinity K-transport systems have been identified. Briefly, the low-affinity transport system, believed to be channel mediated, acts at high external K concentrations and is isothermodynamically passive (Leigh, 2001; Szczerba *et al*., 2009). The high-affinity transport system is a saturable system, which catalyzes the thermodynamically active uptake of K at low external K concentrations (< 1 mM) (Schachtman & Schroeder, 1994; Szczerba *et al*., 2009; Cuéllar *et al*., 2010). The high-affinity transport system, as opposed to the low-affinity transport system, is down-regulated at high external K concentrations and up-regulated at low external K concentrations (Schroeder & Fang, 1991; Maathuis & Sanders, 1994; Hirsch *et al*., 1998; Szczerba *et al*., 2009). Both the systems, though, represent an electrogenic entry of net positive charge, which requires the active removal of protons to maintain electrical neutrality (Leigh, 2001; Szczerba *et al*., 2009).

The capacity of terrestrial plants to take up K and to maintain their homeostatic properties is determined by sophisticated mechanisms of genetic expression (Armengaud *et al*., 2004; Yin *et al*., 2011; El-Mesbahi *et al*., 2012). Moreover, K uptake is closely linked to water economy. Some studies have observed that transmembrane channels for K and water are likely to be co-regulated and may function

200 in a coordinated manner to maintain the appropriate cytosolic osmolarity (Patrick *et al*.,

201 2001; Liu *et al*., 2006; Osakabe *et al*., 2013). Reports on the co-regulation of K and

202 water channels in plants, however, are still scarce.

203

204 **A widespread limiting role of K in plant growth and ecosystem productivity**

205 In contrast to the many physiological studies demonstrating the importance of K in

206 terrestrial plants, few ecological studies have investigated the possible role of K

207 limitation in terrestrial plant productivity, particularly in comparison to the studies on N

208 and P limitation. The existing studies suggest that the fraction of vegetation that is K

209 limited or K co-limited with N and/or P is high (Figure 2, Table 3). Tripler *et al*. (2006)

210 conducted a review and metadata analysis of K limitation in forest ecosystems with all

211 the data available until 2004. This meta-analysis, including 38 articles (a subset that is

212 included in Figure 2 and Table 3), showed an overall limiting effect of K in tree growth,

213 with 69% of the studies showing some level of K limitation. We have now also included

214 data from studies published up to July 2013 and from other terrestrial ecosystems such

215 as grasslands, observing that 69% of 56 studies have detected at least some significant

216 limiting role of K (Figure 2, Table 3).

217

218 **K stoichiometry and water availability in terrestrial ecosystems**

219 Most of the studies on relationship between terrestrial plant stoichiometry and climatic

220 gradients exclusively focused on N and P and their ratio (Reich & Oleksyn, 2004;

221 Kerkhoff *et al*., 2005). Some recent studies observed that foliar K concentrations are

222 negatively correlated with mean annual precipitation (MAP) (Fyllas *et al*., 2009; Zhang

223 *et al*., 2012), whereas few others observed contrary relationships (Sardans *et al*., 2011;

224 2012a). On the other hand, some studies positively related plant K uptake capacity with

225 soil water availability (Fernandez *et al*., 2011; Ge *et al*., 2012); Tomlinson *et al*. (2013),

9

226 while comparing leaf traits of different plant species growing in wet and arid

227 environments, observed that leaves of species adapted to arid sites are small with high K

228 concentrations. Furthermore, it was observed that tree species at the driest sites, such as

229 in Mediterranean evergreen and dry tropical forests, have a higher capacity to change

230 their seasonal internal allocation of K, with a higher allocation of K to leaves during

231 summer (the driest season) than the species at wetter sites (Milla *et al*., 2005; Rivas-

232 Ubach *et al*., 2012; Sardans *et al*., 2012a).

233   Thus a trade-off is expected because K uptake is strongly related to soil water

234 content (Watson *et al*., 2001; Oliveira *et al*., 2004), while, as previously commented, K

235 is specially determinant to increase water use efficiency and to limit water losses.

236 Therefore, at a global scale in wet and more productive environments, we should expect

237 that plants are able to uptake more K than in dry environments, but, on the other hand,

238 in drier environments plants can also increase their K concentrations by conservative

239 mechanisms, such as increasing K resorption. Thus, current data suggest not only that K

240 uptake is strongly determined by water availability but also that K is crucial to the

241 strategies of water economy, leading to the paradox that the more necessary K is (under

242 drought), the more difficult is its uptake.

243   Some studies have observed that K accumulation in soil is greatest in arid

244 ecosystems rather than in mesic ecosystems (Singer, 1989), despite studies of natural

245 gradients have observed that K accumulates and concentrates more in biomass with

246 increasing annual mean precipitation (Sardans *et al*., 2011). However, RE of K remains

247 considerable and could be expected to be higher in dry ecosystems, compensating the

248 low capacity of K uptake in dry conditions (in comparison with plants at wetter sites as

249 reported in some studies, see e.g. Fayyaz *et al*., 2013; Tomlinson *et al*., 2013).

250 Moreover, the K retention capacity in plants in arid environments could be improved by

251   lower leaching (Singer, 1989). Thus at this moment, given all these previous results, it

252   is difficult to reach any consistent conclusion on whether K is more actively retained in

253   dry or wet ecosystems.

254   Recent stoichiometric studies have observed that K is even more variable among

255   dry plant ecotypes than N and P (Sardans *et al*., 2011) and is also more responsive to

256   environmental pressure such as drought or herbivore attack (Sardans *et al*., 2013; Rivas-

257   Ubach *et al*., 2012; 2014). Foliar K concentrations have been found to co-vary with the

258   entire metabolome, suggesting the importance of K in global plant function, despite its

259   absence from biomolecules (Rivas-Ubach *et al*., 2012; 2014). The strong link between

260   plant K concentrations and water availability justifies the study of K and its

261   stoichiometric relationships with other nutrients. Focusing on K would more strongly

262   integrate the dimension of water availability in the study of terrestrial ecological

263   stoichiometry. Recent ecological stoichiometric studies have observed that K plays a

264   more fundamental role than does N or P in the differences in elemental composition

265   among and within species in response to different water availability.

266   Some studies have shown that different grass species have different optimal N:K

267   ratios of supply (Lawniczak *et al*., 2009). A reduction in soil K availability is frequently

268   observed as a consequence of N deposition. As commented below, this is due to large

269   losses of K by leaching that causes nutrient imbalances. Moreover, other studies have

270   observed that K concentrations in the soil solution and in runoff are more sensitive to

271   changes in land use and fertilization than N or P concentrations (Watmough *et al*., 2005;

272   Anguelov *et al*., 2011), and also that K is more quickly leached from litter than N or P,

273   and it has a much shorter residence time in soil organic matter (Schreeg *et al*., 2013;

274   Florez-Florez *et al*., 2013).

275

Anthropogenic impacts on the K cycle

K fertilizers: K is required in large amounts for growing crops, but farmers in poor countries often do not fertilize with K due to high costs, which leads to K deficiencies in large areas of farmland (Hoa *et al*., 2006; Andrist-Rangel *et al*., 2007). The situation is especially critical in Africa. Many African croplands are dramatically under-fertilized, especially with K. Despite covering 25% of global potential cropland area (FAO 2003, 2011), the African share of global fertilizer consumption is 2.7% for N, 2.4% for P and 1.7% for K (FAO, 2011). The fertilizer nutrient supply/demand balance indicates that Africa will remain as an exporter of phosphate and nitrogen, but for potash, the region would continue to depend solely on import (FAO, 2011). This fact, along with the great economical deficits in most African states, makes K a critical limiting factor for food production in this continent.

Croplands in China, Egypt, Bulgaria and parts of southeastern Asia also have negative balances of K, mainly due to socio-economic factors that decrease crop productivity (Magen, 2008; Ryan & Sommer, 2012; Ryan *et al*., 2012). This negative balance leads to an increasing impoverishment of K in cropland soils (Vanderpol & Traore, 1993; Singh & Bansai, 2009). Moreover, the increasing demand for food and increasing aridity in several areas of the world, such as the Mediterranean Basin (mainly the Maghreb) and the Sahel, make K fertilization more critical given the important role of K in water use efficiency (Ruan *et al*., 1997; Römheld & Kirkby, 2010). A recent study has concluded that K is currently the most important limiting nutrient in Mediterranean croplands (Ryan & Sommer, 2012). Agriculture practices that decrease soil pH favor K leaching and thus decrease availability for plants (Sharifi *et al*., 2013). For example, despite that sometimes N fertilization can enhance soil K-availability in a short term by decreasing soil pH (Mitchell & Smethurst, 2008), but in absence of K

301   fertilization, it finally leads to a decrease in soil K-availability because of leaching (He

302   *et al*., 1999; Mitchell & Smethurst, 2008; Yavitt *et al*., 2011; Glab & Gondek, 2014).

303   Demands and uses of fertilizers are expected to increase in the coming decades

304   (Roberts, 2008). Mineable reserves of K are sufficient to meet the projected demand for

305   centuries (Roberts, 2008). Some results suggest that the increasing use of K fertilizer in

306   some regions in recent decades has increased the atmospheric deposition of K in areas

307   adjacent to cropland (Gélinas *et al*., 2000). The deposition of K from agricultural

308   activities is very high in some developing countries such as Brazil, reaching 55% of

309   total K deposition (Allen *et al*., 2010). In contrast, the deposition of K from energy

310   production and industrial plants has decreased in some European countries (Ruoho-

311   Airola & Salminen, 2003). Some studies have observed that K deposition, linked to

312   industrial and, frequently, agricultural activities as well, can represent a higher

313   proportion than that from natural processes (Ferm & Hultberg, 1999; Golobocanin *et al*.,

314   2008) such as sea spray (Poor *et al*., 2006; Prathibha *et al*., 2010).

315   Inputs of K from atmospheric deposition have a determinant role in K balances

316   of forests, counteracting, such as observed in some areas, the loss of K from leaching,

317   which is favored by N deposition (Friedland & Miller, 1999; Watmough & Dillon,

318   2004). These inputs of K contribute to K availability in tropical forest ecosystems

319   (Vitousek & Sanford, 1986; Muoghalu & Oakhumen, 2000). All these findings justify

320   the study of the impacts of an increased use of K fertilizers on the rates of K

321   atmospheric deposition and thereafter on ecosystem function at least in some parts of

322   the world.

323

324   **K in a drier world:** Climate models project an increase in the extent of drought over

325   large areas of the world that are already dry such as the Mediterranean Basin and the

326   Sahel (IPCC, 2007). Despite the intensive study of drought resistance under field

327   conditions, only a few field studies have tested the impacts of drier conditions on the

328   status of K in terrestrial plant communities (Table 4). These studies show that drought

329   increases total soil K but decreases its soluble soil fraction. Moreover, drought increases

330   the retention of K in the wood of some species and the concentration of K in the

331   photosynthetic tissues of others (Table 4). The effects of drought are usually

332   asymmetrical in different plant organs, because plants tend to allocate and retain more

333   K in stems, and a fraction of this K is transported to leaves during the driest seasons

334   (Table 4). These few studies suggest a possible increase in biomass K concentrations in

335   dry areas but also a possible decrease in total biomass K content as a result of reduced

336   growth. This decrease of K in biomass and total soil K increases could enhance the risk

337   of higher losses of K from soil.

338   As previously stated, the availability and uptake of K are essential for

339   improving drought resistance in various types of plant communities (Harvey & van den

340   Driessche, 1999; Ashraf *et al*., 2002; Egilla *et al*., 2005; Sardans & Peñuelas, 2012c).

341   Globally, plant K uptake, however, appears to be associated with water availability

342   (Sardans *et al*., 2011; 2012a; Ge *et al*., 2012), wherein less K uptake in turn negatively

343   affects water uptake by reducing the activity of aquaporins (Kanai *et al*., 2011). All

344   these interconnected relationships strongly suggest a cascade of higher water deficit,

345   lower K uptake and a reduced capacity to avoid drought, which could become a serious

346   problem in currently dry areas that are threatened by future drier scenarios. These

347   scenarios could even be more negative if torrential rain increases and MAP decreases,

348   as projected for areas such as the Mediterranean Basin and the Sahel (ICPP, 2007).

349   Moreover, the capacity of different plant species to use and remobilize K can be crucial

350   in their competitive relationships (Dunlop *et al*., 1979; Tilman *et al*., 1999). Thus, due

351   to the high relevance of K under conditions of water stress, we can expect that K will

352   become an important factor in the shifts in species composition of plant communities

353   under drought. Plants can also respond to drought by improving efficiencies of K and

354   water uptake. Some phenomena linked to an improved resistance to drought stress, such

355   as soil patchiness or the capacity to redistribute water, can favor K uptake. Plants under

356   drought can improve the use of water for the uptake of nutrients by their capacity to

357   redistribute soil water (Sardans & Peñuelas, 2013b). Hydraulic lift and its opposite,

358   downward siphoning (Smith *et al*., 1999), can favor water recirculation, efficiency of

359   water use and the capacity of plants to take up nutrients (Sardans & Peñuelas, 2013b). A

360   higher capacity to redistribute water to increase K uptake can be a key factor for the

361   survival of plants in drier conditions. In this context, due to the lack of studies, it is not

362   possible to assess the importance of water redistribution in enhancing not only water use

363   efficiency but also the capacity of nutrient uptake.

364   Moreover, the variability of water and nutrient availability on slopes in the drier

365   areas of the Mediterranean Basin is related to the distribution of patches of vegetation

366   relative to the patches of bare soil that can be considered as runoff sinks and sources,

367   respectively (Gabarrón-Galeote *et al*., 2012; Merino-Martin *et al*., 2012; Sardans &

368   Peñuelas, 2013c). This effect of patches is crucial in the conservation of vegetation at

369   drier sites. Gómez-Aparicio *et al*. (2005) have observed that the presence of large

370   woody plants improves the availability of soil nutrients and in particular of K in

371   Mediterranean ecosystems. The role of soil patches in the changes in the complete K

372   cycle has not been specifically studied, despite the possibility that in patches the higher

373   availability of water, the better soil texture and the horizontal redistribution of water

374   could strongly affect the K cycle.

375

376 **Impacts of N and acid atmospheric deposition on the K cycle:** The impacts of N

377 deposition on decreasing C:N in plants and soils have been extensively reported

378 (Mulder *et al.*, 2013). However, only a relatively small proportion of the studies on the

379 impacts of N deposition on terrestrial ecosystems stoichiometry have taken K into

380 account (Figure 3). Our review of current literature shows that atmospheric N

381 deposition increases the leaching of K from soils, thus decreases K concentrations in the

382 soils (and decreases K concentrations and increases N:K ratios in plants. Despite that

383 plants respond to increasing K uptake, an ultimate enhancement of K limitation is

384 frequently observed. This loss of K under N deposition is frequently related to K

385 deficiencies in trees (Tzvetkova & Haddjiivanova, 2006). Moreover, atmospheric S

386 deposition has also contributed to K leaching thus decreasing soil K availability in

387 several European (Britton *et al.*, 2008; Sutton *et al.*, 2011) and North-American

388 (Mitchell *et al.*, 1996; Navratil *et al.*, 2010) areas. However, this K leaching has been

389 reduced in the last decades as a result of the dramatic reduction of S emissions in

390 Europe since the early 1980s, after the reduction of coal combustions and the

391 implementation of policies to improve air quality (Eurostat, 2009; Navratil *et al.*, 2010;

392 Robinson *et al.*, 2013).

393 The N eutrophication effects on the K cycle and N:K ratios may have large flow-

394 on impacts (Figure 3). Decreases in soil K contents and increases in soil N:K ratios are

395 associated with the loss of species richness (Huang *et al.*, 2013). Moreover, P:K soil

396 ratios can increase because the solubility and mobility of K are higher than those of P,

397 therefore K leaches more easily than P (Olde Venterink *et al.*, 2009). Changes in N:K

398 and P:K ratios can favor species tolerance to water stress or competitively faster-

399 growing species, depending on the circumstances. For example, a decrease in N:K ratio

400 under increasing drought would probably favor the stress-tolerant species, which are

401   better adapted to allocate K to their leaves and to use it to improve drought avoidance,

402   more than favoring the faster-growing competitors.

403

404   **K and success of plant invasion:** Most studies have focused on the roles of N and P in

405   the success of species invasion (Sardans & Peñuelas, 2012). The few studies

406   investigating relationships between invasive success and the K availability of soils have

407   found the relationships to be important. In most cases, the success of alien plants

408   depends on a high availability of soil K (Figure 4) and on a higher capacity of K uptake

409   by the invasive species compare to the native plants (Pieters & Baruch, 1997), but it has

410   also been associated with low soil K availability after the establishment of invasive

411   species (Figure 4). Other studies, however, have observed an opposite pattern. The

412   invasive success of *Taraxacum officinalis* in the Andes has been linked to low soil K

413   availability (Cavieres *et al*. 2008). By examining the impacts of seven widespread

414   invasive plant species in northern Europe, Dassonville *et al*. (2008) observed that

415   invasive species reduced soil K availability in K-rich soils, but increased soil K

416   availability in K-poor soils. The success of alien plants thus appears to depend on high

417   K availability in productive environments and on low K availability in less productive

418   environments; however, the low number of studies precludes formulation of a definitive

419   conclusion on this dependence (Funk & Vitousek, 2007; Peng *et al*., 2011; Sardans &

420   Peñuelas, 2012). Alien plants with a more efficient use of K may be able to increase

421   their spread in arid areas. Islands are among the most threatened areas by plant invasive

422   success (Denslow et al., 2009; Atwood & Meyerson, 2011). Current literature relates

423   alien success in islands to several variables linked to humans, such as population

424   density (Atwood & Meyerson, 2011; Traveset *et al*., 2014), level of human impact

425   (MacDonald *et al*., 1991; Monty *et al*., 2013), ecological traits such as genetic diversity

426 (Hardman *et al*., 2012; Traveset *et al*., 2014), differences in phylogeny with native

427 species (Bezeng *et al*., 2013), island area (Traveset *et al*., 2014), isolation and distance

428 to nearest continent (Traveset *et al*., 2014), and climate change (Yamashita *et al*., 2000).

429 The possible relationship between bedrock K_2O concentrations and plant alien success

430 remains mostly unexplored. However, Denslow *et al*. (2009) observed a significant

431 relationship between the main substrate of the island (coralline limestone islands,

432 basaltic with metamorphic, ultrabasic, and continental plutonic islands) and the number

433 of invasive plants.

434
435 **Final remarks**

436 1. The data available from current studies on the role of K availability in the growth of

437 plants indicate that K is frequently a limiting factor for plant productivity in terrestrial

438 ecosystems.

439 2. Apart from the well-known physiological processes linked to water economy, such as

440 enzymatic function, internal transport systems and cell-membrane integrity, K has

441 recently been associated with an increasing number of plant ecological processes, such

442 as resistance to diseases, herbivory, salinity, cold, frost or waterlogging, with large

443 implications on ecosystem function and capacity of global crop production.

444 3. Recent ecological stoichiometric studies of terrestrial ecosystems that have included

445 K with the classically considered C, N and P have shown that the stoichiometric

446 changes involving K are even larger than those involving N and P in plant responses to

447 the environmental changes. These findings justify the inclusion of K in ecological

448 stoichiometric studies.

449 4. Drought can be more intense in current arid areas. Given the importance of K in

450 water use efficiency and the difficulty of K uptake under drought conditions, K is

451 expected to have an increasingly important role in determining the function and survival

452 of plant communities.

453 5. N deposition has been linked to several processes, such as forest decline and soil

454 imbalances, but the impacts on K are not well known.

455 6. Current studies suggest that the success of invasive species in environments that are

456 not strongly limited by nutrients is associated with a high capacity of K uptake and with

457 the consequent decrease in K availability of soils.

458

459

460 **Acknowledgements**

464

465

466

467

468

469

470

471

472

473

474

475

476   BOX 1. Main Ecophysiological roles of K

477   **Water economy**: K is involved in many mechanisms that mitigate drought stress.

478   Studies in greenhouses and with potted plants have demonstrated the importance of K

479   supply in the resistance of plants toward drought. K plays many fundamental

480   physiological and metabolic roles in terrestrial plants related to water economy and

481   osmotic homeostasis such as maintenance of cellular turgor and osmotic pressure

482   (Ashraf *et al.*, 2002; Levi *et al.*, 2011), control of water conductance and transpiration

483   (Harvey & van Driessche, 1999; Arquero *et al.*, 2006; Benloch-González *et al.*, 2010),

484   improvement of root hydraulic conductivity (El-Mesbahi *et al.*, 2012), regulation of sap

485   flow (Oddo *et al.*, 2011), regulation of membrane potentials (Schroeder & Fang, 1991),

486   stomatal control (Talbott & Zeiger, 1996; Benlloch-González *et al.*, 2010), and

487   maintenance of ionic homeostasis or transmembrane potential (Su *et al.*, 2001; Waraich

488   *et al.*, 2011). Moreover, field studies have observed that K, apart from its role in

489   stomatal control and water conductance, can further affect water economy as an

490   osmolyte (Babita *et al.*, 2010; Levi *et al.*, 2011) directly linked to improving the

491   capacity to retain water (Nandwal et al., 1998; Rao *et al.*, 2012).

492   In support of these physiological observations, some recent metabolomic studies

493   have observed that K concentrations are related to increases in molecular osmolytes

494   under drought (Talbott & Zeiger, 1996; Levi *et al.*, 2011; Rivas-Ubach *et al.*, 2012).

495   The Mediterranean evergreen *Olea europea* decreases its capacity to regulate stomatal

496   control when growing under moderate K deficiency (Arquero *et al.*, 2006); this suggests

497   that even drought-resistant tree species can suffer detrimental effects in their growth

498   capacity and survival under drought conditions through a reduction in their capacity to

499   take up K. A few studies, though, have observed no effects of K availability on drought

500   avoidance (e.g., Ashraf *et al.*, 2002).

501   K also contributes to the detoxification of reactive oxygen species (ROS) (Wang

502 *et al.*, 2013). The impairment of stomatal regulation in K-deficient plants under drought

503 stress produces a consequent impairment of CO_2 fixation, and molecular oxygen is

504 activated leading to the generation of ROS (Cakmak, 2000). Under drought conditions,

505 an increase of extrachloroplastic K^+ concentrations in plant cells with an adequate K

506 supply prevents the inhibition of photosynthesis (Egilla *et al.*, 2005). This effect is

507 related to the role K plays in enhancing photosynthetic CO_2 fixation, improving the

508 transport of photosynthates into sink organs and inhibiting the transfer of photosynthetic

509 electrons to O_2, thereby reducing ROS production (Cakmak, 2005). Many field studies

510 have thus observed correlations between K concentrations in plants and soils with

511 mechanisms of drought avoidance (Nandwal *et al.*, 1998; Arquero *et al.*, 2006; Teixeira

512 *et al.*, 2008; Fayyaz *et al.*, 2013; Tomlinson *et al.*, 2013).

513   Many physiological and metabolomic studies in garden and potted plants (Babita

514 *et al.*, 2010; Cuéllar *et al.*, 2010) and in crops (Römheld & Kirkby, 2010; Waraich *et al.*,

515 2011; Wang *et al.*, 2013), and some studies across environmental gradients under field

516 conditions (Kadar & Foldesi, 2001), have observed a strong link between K

517 concentrations and the resistance and adaptation of plants to drought. Under drought K

518 deficiency, plant defoliation (Harvey & van den Driessche, 1999) and mortality (Del

519 Campo *et al.*, 2011; El-Mesbahi *et al.*, 2012) increases. A few studies, though, have

520 observed no effects of K availability on drought avoidance (e.g., Ashraf *et al.*, 2002).

521

522 **Other physiological functions**: Many plant functions that are not directly related to

523 water economy have recently been associated with K, such as enzymatic activity and

524 protein synthesis (Armengaud *et al.*, 2004; 2009), internal transport and allocation of

525 amino acids and nitrates (Jarvis *et al.*, 1989), photosynthetic activity and retranslocation

526 of fixed C (Zhao *et al*., 2001; Teixeira *et al*., 2008), signal transduction and energy

527 transport (Gajdanowicz et al., 2011), cellular, foliar and root expansion (Elumalai *et al*.,

528 2002; Yin *et al*., 2011) and foliar movement (Travlos *et al*., 2008), among several other

529 metabolic and physiological functions essential for plant life. Evidences, moreover, are

530 increasing that adequate K fertilization plays an important role in defending crops not

531 only against drought but also against many other biotic and abiotic stresses such as

532 diseases, pests, salinity, cold, frost, and waterlogging (see recent review of Wang *et al*.,

533 2013). Gajdanowicz *et al*. (2011) recently observed that K^+ circulating in the phloem

534 creates a mobile gradient serving as a decentralized energy store that can be used to

535 overcome local energy limitations through the activation of diverse membrane proteins.

536 The authors observed that posttranscriptional modification of the phloem-expressed

537 *Arabidopsis* K^+ channel AKT2 taps this "potassium battery", which then efficiently

538 assists the plasma membrane H^+-ATPase in energizing the transmembrane phloem

539 reloading processes. Thus K^+ will be loaded into the phloem from source tissues where

540 sufficient chemical energy is available. The established transmembrane K^+ gradient is

541 then transported with the phloem stream to other parts of the plant. The energy stored in

542 the K^+ membrane gradient can be harvested to fuel transport processes by opening a

543 gateway (for example the AKT2-like channels) for the passage of K^+ ions through the

544 membrane being this process related to sucrose leakage from the phloem that enhances

545 energy status.

546

547

548

549

550
551

552 **References**
553

554 Allen, A.G., Cardoso, A.A., Wiate, A.G., Machado, C.M.D., Paterlini, W.C. & Baker, J.
555   (2010) Influence of intensive agriculture on dry deposition of aerosol nutrients.
556   *Journal of the Brazilian Chemical Society*, **21**, 87-97.
557 Andrist-Randgel, Y., Edwards, A.C., Hillier, S. & Oborn, I. (2007) Long-term K
558   dynamics in organic and conventional mixed cropping systems as related to
559   management and soil properties. *Agriculture Ecosystems and Environment*, **122**,
560   413-426.
561 Anguelov, G., Anguelova, I. & Bailey, N.O. (2011) Land-use impact on soil solution
562   constituents from an Ultisol of North Florida. *Nutrient Cycling in Agroecosystems*,
563   **90**, 171-187.
564 Armengaud, P., Breiting, R. & Amtmann, A. (2004) The potassium-dependent
565   transcriptome of *Arabidopsis* reveals a prominent role of Jasmonic acid in nutrient
566   signaling. *Plant Physiology*, **136**, 2556-2576.
567 Armengaud, P., Sulpice, R., Miller, A.J., Stitt, M., Amtmann, A. & Gibon, Y. (2009)
568   Multilevel analysis of primary metabolism provides new insights into the role of
569   potassium nutrition for glycolysis and nitrogen assimilation in *Arabidopsis* roots.
570   *Plant Physiology*, **150**, 772-785.
571 Arquero, O., Barranco, D. & Benlloch, M. (2006) Potassium starvation increases
572   stomatal conductance in olive trees. *HortScience*, **41**, 433-436.
573 Ashraf, M., Ashfaq, M. & Ashraf, M.Y. (2002) Effects of increased supply of
574   potassium on growth and nutrient content in pearl millet under water stress.
575   *Biologia Plantarum*, **45**, 141-144.
576 Atwood, J.P. & Meyerson, L.A. (2011) Island biogeography extends to small-scale
577   habitats: low competitor density and richness on islands may drive trait in
578   nonnative plants. *Biological Invasions*, **13**, 2035-2043.
579 Babita, M., Maheswari, M., Rao, L.M., Shanker, A.K. & Rao, D.G. (2010) Osmotic
580   adjustment, drought tolerance and yield in castor (*Ricinus communis*) L.) hybrids.
581   *Environmental and Experimental Botany*, **69**, 243-249.
582 Barré, P., Berger, G. & Velde, B. (2009) How element translocation by plants may
583   stabilize illitic clays in the surface of temperate soils. *Geoderma*, **151**, 22-30.
584 Becker, D., Hoth, S., Ache, P., Wenkel, S., Roelfsema, M.R.G., Meyerhoff, O., Hartung,
585   W. & Hedrich, R. (2003) Regulation of the ABA-sensitive Arabidopsis potassium
586   channel gene GORK in response to water stress. *FEMS Letters*, **554**, 119-126.
587 Benlloch-González, M., Romera, J., Cristescu, S., Harren, F., Fournier, J.M. & Benlloch,
588   M. (2010) K^+ starvation inhibits water-stress-induced stomatal closure via
589   ethylene synthesis in sunflower plants. *Journal of Experimental Botany*, **61**, 1139-
590   1145.
591 Bezeng, B.S., Savolainen, V., Yessoufou, K., Papadopoulos, A.S.T., Maurin, O. & van
592   der Bank, M. (2013) A phylogenetic approach towards understanding the drivers
593   of plant invasiveness on Robben island, South Africa. *Botanical Journal of the
594   Linnean Siciety*, **172**, 142-152.
595 Boxman, A.W., Cobben, P.L.W. & Roelofs, J.G.M. (1994) Does (K+Mg+Ca+P)
596   fertilization lead to recovery of tree health in a nitrogen stressed *Quercus rubra* L.
597   stand? *Environmental Pollution*, **85**, 297-303.
598 Britton, A.J., Helliwell, R.C., Fisher, J.M. & Gibbs, F.S. (2008) Interactive effects of
599   nitrogen deposition and fire on plant and soil chemistry in an alpine heathland.
600   *Environmental Pollution*, **156**, 409-416.

Britzke, D., da Silva, L.S., Moterle, D.F., dos Santos Rheinheimer, D. & Bortoluzzi, E.C. (2012) A study of potassium dynamics and mineralogy in soils from subtropical Brazilian lowlands. *Journal of Soils and Sediments*, **12**, 185-197.

Cakmak, I. (2000) Possible roles of zinc in protecting plant cells from damage by reactive oxygen species. *New Phytologist*, **146**, 185-205.

Cakmak, I. (2005) The role of potassium in alleviating detrimental effects of abiotic stresses in plants. *Journal of Plant Nutrition and Soil Science*, **168**, 521-530.

Cavieres, L.A., Quiroz, C.L. & Molina-Montenegro, M.A. (2008) Facilitation of the non-native *Taraxacum officinale* by native nurse cushion species in the high Andes of central Chile: are there differences between nurses? *Functional Ecology*, **22**, 148-156.

Chuyong, G.B., Newbery, D.M. & Songwe, N.C. (2000) Litter nutrients and retranslocation in a central African rain forest dominated by ectomycorrhizal trees. *New Phytologist*, **148**, 493-510.

Cuéllar, T., Pascaud, F., Verdeil, J.L., Torregrosa, L., Adam-Blondon, A.F.A., Thibaud, J.B., Santenac, H. & Gaillard, I. (2010) A grapevine shaker inward K+ channel activated by the calcineurin B-like calcium sensor 1-protein kinase CIPK23 network is expressed in grape berries under drought stress conditions. *The Plant Journal*, **61**, 58-69.

Da Silva, I.R., Furtini, Neto, A.E., Fernandes, L.A., Curi, N. & Do Vale, F.B. (2000) Formas, relaçao quantidade/intensidade e biodisponibilidade de potassio em diferentes latossolos. *Pesquisa agropecuaria brasileira*, **35**, 2065-2073.

Dassonville, N., Vanderhoeven, S., Vanparys, V., Hayez, M., Gruber, W. & Meerts, P. (2008) Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. *Oecologia*, **157**, 131-140.

Del Campo, A.D., Hermoso, J., Flors, J., Lidón, A. & Navarro-Cerrillo, R.M. (2011) Nursey location and potassium enrichment in Aleppo pine stock 2. Performance under real and hydrogel-mediated drought conditions. *Forestry*, **84**, 235-245.

Denslow, J.S., Space, J.C. & Thomas, P.A. (2009) Invasive Exotic Plants in the Tropical Pacific Islands: Patterns of Diversity. *Biotropica*, **41**, 162-170.

Duchesne, L., Ouimet, R., Camire, C. & Houle, D. (2001) Seasonal nutrient transfers by foliar resorption, leaching, and litter fall in a northern hardwood forest at Lake Clair watershed, Quebec, Canada. *Canadian Journal of Forest Research*, **31**, 333-344.

Dunlop, J., Glass, A.D.M. & Tomkins, B.D. (1979) Regulation of K+ uptake by ryegrass and white clover roots in relation to their competition for potassium. *New Phytologist*, **83**, 365-370.

Egilla, J.N., Davies, Jr F.T. & Boutton, T.W. (2005) Drought stress influences leaf water content, photosynthesis, and water-use efficiency of *Hibiscus rosa-sinensis* at three potassium concentrations. *Photosynthetica*, **43**, 135-140.

El-Mesbahi, M.N., Azcón, R., Ruiz-Lozano, J.M. & Aroca, R. (2012) Plant potassium content modifies the effects of arbuscular mycorrhizal symbiosis on root hydraulic properties in maize plants. *Mycorrhiza*, **22**, 555-564.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R. Folarin, A., Huberty, A., Interlandi, S., Kilham, S.S., McCauley, E., Schulz, K.L., Siemann, E.H. & Sterner, R.W. (2000) Nutritional constraints in terrestrial and freshwater ecosystems. *Nature*, **408**, 578-580.

Elumalai, R.P., Nagpal, P. & Reed, J.W. (2002) A mutation in the Arabidopsis KTA/KUP2 potassium transporter gene affects shoot cell expansion. *The Plant Cell*, **14**, 119-131.

Eurostat (2009) Statistical books. Panorama of Energy. Energy statistics to support EU policies and solutions. Edited by: Office for Official Publications of the European Communities, Luxembourg.

FAO (2011) Current word fertilizer trends and outlook to 2015. Roma.

Fayyaz, P., Etemadi, E., Julaiee-Manesh, N. & Zolfaghari, R. (2013) Sodium and potassium allocation under drought stress in Atlas mastic tree (*Pistacia atlantica* subsp. *mutica*). *Forest-Biogeosciences and Forestry*, **6**, 90-94.

Ferm, M. & Hultberg, H. (1999) Dry deposition and internal circulation of nitrogen, sulphur and base cations to a coniferous forest. *Atmospheric Deposition*, **33**, 4421-4430.

Fernandez, F.G., Brouder, S.M., Volenec, J.J., Beyrouty, C.A. & Hoyum, R. (2011) Soybean shoot and root response to localized water and potassium in a split-pot study. *Plant and Soil*, **344**, 197-212.

Fife, D.N., Nambiar, E.K.S. & Saur, E. (2008) Retranslocation of foliar nutrients in evergreen tree species planted in a Mediterranean environment. *Tree Physiology*, **28**, 187-196.

Filella, I. & Peñuelas, J. (2003) Indications of hydraulic lift by *Pinus halepensis* and its effects on the water relations of neighbour shrubs. *Biologia Plantarum*, **47**, 209-214.

Florez-Florez, C.P., Leon-Pelaez, J.D., Osorio-Vega, N.W. & Restrepo-Llano, M.F. (2013) Nutrient dynamics in forest plantations of *Azadirachta indica* (Meliaceae) established for restoration of degraded lands in Colombia. *Revista de Biologia Tropical*, **61**, 515-529.

Friedland, A.J. & Miller, E.K. (1999) Major-element cycling in a high-elevation Adirondack forest: patterns and changes, 1986-1996. *Ecological Applications*, **9**, 958-967.

Funk, J.L. & Vitousek, P.M. (2007) Resource-use efficiency and plant invasion in low-resource systems. *Nature*, **446**, 1079-1081.

Fyllas, N.M., Patino, S., Baker, T.R., Nardoto, G.B., Martinelli, L.A., Quesada, C.A., Paiva, R., Schwarz, M., Horna, V., Mercado, L.M., Santos, A., Arroyo, L., Jimenez, E.M., Luizao, F.J., Neill, D.A., Silva, N., Prieto, A., Rudas, A., Silveira, M., Vieira, I.C.G., Lopez-Gonzalez, G., Malhi, Y., Phillips, O.L. & Lloyd, J. (2009) Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences*, **6**, 2677-2708.

Gabarrón-Galeote, M.A., Martínez-Murillo, J.F. & Ruiz-Sinoga, J.D. (2012) Relevant effects of vegetal cover and litter on the soil hydrological response of two contrasting Mediterranean hill slopes at the end of the dry season (south of Spain). *Hydrological Proceedings*, **26**, 1729-1738.

Gajdanowicz, P., Michard, E., Sandmann, M., Rocha, M., Correa, L.G.G., Ramirez-Aguilar, S.J., Gomez-Porras, J.L., Gonzalez. W., Thibaud, J.B., van Dongen, J.T. & Dreyer, I. (2011) Potassium (K^+) gradients serve as a mobile energy source in plant vascular tissues. *Proceedings of the National Academy of Sciences USA*, **108**, 864-869.

Gallardo, J.F., Martín, A. & Moreno, G. (1999) Nutrient efficiency and resorption in *Quercus pyrenaica* oak coppices under different rainfall regimes of the Sierra de gata mountains (central western Spain). *Annals of Forest Sciences*, **56**, 321-331.

Ge, T.D., Sun, N.B., Bai, L.P., Tong, C.L. & Sui, F.G. (2012) Effects of drought stress on phosphorus and potassium uptake dynamics in summer maize (*Zea mays*) through the growth cycle. *Acta Physiologiae Plantarum*, **34**, 2179-2186.

700　Gélinas, Y., Lucotte, M. & Schmit, J.P. (2000) History of the atmospheric deposition of
701　　　major and trace elements in the industrialized St. Lawrence Valley, Quebec,
702　　　Canada. *Atmospheric Environment*, **34**, 1797-1810.
703　Glab, T. & Gondek, K. (2014) The influence of soil compactation and fertilization on
704　　　physic-chemical properties of mollic fluvisol under red clover/grass mixture.
705　　　*Geoderma*, **226**, 204-212.
706　Golobocanin, D., Zujic, A., Milenkovie, A. & Miljevic, N. (2009) Precipitation
707　　　composition and wet deposition temporal pattern in Central Serbia for the period
708　　　from 1998 to 2004. *Environmental Monitoring and Assessment*, **142**, 185-198.
709　Gómez-Aparicio, L., Gómez, J.M., Zamora, R. & Boettinger, J.L. (2003) Canopy vs.
710　　　soil effects of shrubs facilitating tree seedlings in Mediterranean montane
711　　　ecosystems. *Journal of Vegetation Science*, **16**, 191-198.
712　Greenwood, N.N. & Earnshaw, A. (1997) *Chemistry of The Elements*. (Second Edition).
713　　　Butterworth-Heinemann, Oxford.
714　Hagen-Thorn, A., Varmagiryte, I., Nihlgard, B. & Armolatis, K. (2006) Autumn
715　　　nutrient resorption and losses in four deciduous forest tree species. *Forest
716　　　Ecology and Management*, **228**, 33-39.
717　Hardman, C.J., Williams, S., Manco, B.N. & Hamilton, M.A. (2012) Predicting the
718　　　potential threat of Casuarina equisetifolia to three endemic plant species on the
719　　　Turks and Caicos Islands. *Oryx*, **46**, 204-212.
720　Harvey, H.P. & van den Driessche, R. (1999) Nitrogen and potassium effects on xylem
721　　　cavitation and water-use efficiency in poplars. *Tree Physiology*, **19**, 943-950.
722　He, Z.L., Alva, A.K., Calvert, D.V., Li, Y.C. & Banks, D.J. (1999) Effects of nitrogen
723　　　fertilization of grapefruit trees on soil acidification and nutrient availability in a
724　　　Rivera fine sand. *Plant and Soil*, **206**, 11-19.
725　Hedin, L.O., Vitousek, P.M. & Matson, P.A. (2003) Nutrient losses over four million
726　　　years of tropical forest development. *Ecology*, **84**, 2231-2255.
727　Hemmisaari, H.S. (1992) Nutrient retranslocation in three *Pinus sylvestris* stands.
728　　　*Forest Ecology and Management*, **51**, 347-367.
729　Hirsch, R.E., Lewis, B.D., Spalding, E.P. & Sussman, M.R. (1998) A role for the AKT1
730　　　potassium channel in plant nutrition. *Science*, **280**, 918-921.
731　Hoa, N.M., Janssen, B.H., Oenema, O. & Dobermann, A. (2006) Comparison of partial
732　　　and complete soil K budgets under intensive rice cropping in the Mekong Delta,
733　　　Vietnam. *Agriculture Ecosystems and Environment*, **116**, 121-131.
734　Holloway, J.A.M. & Dahlgren, R.A. (2002) Nitrogen in rock: Occurrences and
735　　　biogeochemical implications. *Global Biogeochemical Cycles*, **16**, 1118.
736　Houlton, B.Z., Wang, Y.P., Vitousek, P.M., Christopher, B. & Field, C.B. (2008) A
737　　　unifying framework for dinitrogen fixation in the terrestrial biosphere. *Nature*,
738　　　**454**, 327-330.
739　Hultine, K.R., Scott, R.L., Cable, W.L., Goodrich, D.C. & Williams, D.G. (2004)
740　　　Hydraulic redistribution by a dominant, warm-desert phreatophyte: seasonal
741　　　patterns and response to precipitation pulses. *Functional Ecology*, **18**, 530-538.
742　Huang, S., Pan, X.H., Sun, Y.N., Zhang, Y., Hang, X.N., Yu, X.C. & Zhang, W.J.
743　　　(2013) Effects of long-term fertilization on the weed growth and community
744　　　composition in a double-rice ecosystem during the fallow period. *Weed Biology
745　　　and Management*, **13**: 10-18.
746　http://nadp.sws.uiuc.edu/ (2012) National Atmospheric Deposition Program. U.S.
747　　　Department of Agriculture.
748　IPCC (2007) Climate Change 2007: The Physical Science Basis. Contribution of
749　　　Working Group I. p. 1-32 In: S. Solomon, et al.. (ed.). Fourth Assessment Report

750   of the Intergovernmental Panel on Climate Change. Cambridge University Press,
751   Cambridge, United Kingdom and New York, NY, USA.

752   Jobbágy, E.G. & Jackson, R.B. (2001) The distribution of soil nutrients with depth:
753   global patterns and the imprint of plants. *Biogeochemistry*, **53**, 51-77.

754   Kadar, I. & Foldesi, D. (2001) Mineral fertilization of poppy (*Papaver somniferum* L.)
755   on calcareous loamy chernozem soil. I. *Nevenytermeles*, **50**, 453-465.

756   Kanai, S., Moghaieb, R.E., El-Shemy, H.A., Panigrahi, R., Mohapatra, P.K., Ito, J.,
757   Nguyen, N.T., Saneoka, H. & Fujita, K (2011) Potassium deficiency affects water
758   status and photosynthetic rate of the vegetative sink in green house tomato prior to
759   its effects on source activity. *Plant Science*, **180**, 368-374.

760   Kerkhoff, A.J., Enquist, B.J., Elser, J.J. & Fagan, W.F. (2005) Plant allometry,
761   stoichiometry and the temperature-dependence of primary productivity. *Global
762   Ecology and Biogeography*, **14**, 585-598.

763   Kopacek, J., Turek, J., Hejzlar, J. & Santruckova, H. (2009) Canopy leaching of
764   nutrients and metals in a mountain spruce forest. *Atmospheric Environment*, **43**,
765   5443-5453.

766   Klumpp, A., Domingos, M. & Klumpp, G. (2002) Foliar nutrient contents in tree
767   species of the Atlantic rain forest as influenced by air piollution from the
768   industrial complex of Cubatao, SE-Brazil. *Water Air and Soil Pollution*, **133**, 315-
769   333.

770   Langley, J.A. & Megonigal, J.P. (2010) Ecosystem response to elevated CO2 levels
771   limited by nitrogen-induced plant species shift. *Nature*, **466**, 96-99.

772   Lawniczak, A.E., Güsewell, S. & Verhoeven, J.T.A. (2009) Effect of N:K supply ratios
773   on the performance of three grass species from herbaceous wetlands. *Basic and
774   Applied Ecology*, **10**, 715-725.

775   Lee, J.A. & Caporn, S.J.M. (1998) Ecological effects of atmospheric reactive nitrógeno
776   deposition on seminatural terrestrial ecosystems. *New Phytologist*, **139**, 127-134.

777   Lee, J.E., Oliveira, R.S., Dawson, T.E. & Fung, I. (2005) Root functioning modifies
778   seasonal climate. *Proceedings of the National Academy of Sciences USA*, **102**,
779   17576-17581.

780   Leigh, R.A. & Jones, R.G.W. (1984) A hypothesis relating critical potassium
781   concentrations for growth to the distribution and functions of this ion in the plant-
782   cell. *New Phytologist*, **97**, 1-13.

783   Leigh, R.A. (2001) Potassium homeostasis and membrane transport. *Journal of Plant
784   Nutrition and Soil Science*, **164**, 193-198.

785   Lé Quére, C., Raupach, M.R., Canadell, J.G., Marland, G., Bopp, L., Ciais, P., Conway,
786   T.J., Doney, S.C., Feely, R.A., Foster, P., Friedlingstein, P., Gurney, K.,
787   Houghton, R.A., House, J.I., Huntingford, C., Levy, P.E., Lomas, M.R., Majkut,
788   J., Metzl, N,., Ometto, J.P., Peters, G.P., Prentice, I.C., Randerson, J.T., Running,
789   S.W., Sarmiento, J.L., Schuster, U., Sitch, S., Takahashi, T., Viovy, N., van der
790   Werf, G.R. & Eoodward, F.I. (2009) Trends in the sources and sinks of carbon
791   dioxide. *Nature Geoscience*, **2**, 831-836.

792   Levi, A., Paterson, A.H., Cakmak, I. & Saranga, Y. (2011) Metabolite and mineral
793   analyses of cotton near-isogenic lines introgressed with QTLs for productivity and
794   drought-related traits. *Physiologia Plantarum*, **141**, 265-275.

795   Liu, H.Y., Sun, W.N., Su, W.A. & Tang, Z.C. (2006) Co-regulation of water channels
796   and potassium channels in rice. *Physiologia Plantarum*, **128**, 58-69.

797   Lucas, R.W., Klaminder, J., Futter, M.N., Bishop, K.H., Egnell, G., Laudon, H. &
798   Högberg, P. (2011) A meta-analysis of the effects of nitrogen additions on base

799   cations: implications for plants, soils, and streams. *Forest Ecology and*
800   *Management*, **262**, 95-104.
801 Maathuis, F.J.M. & Sanders, D. (1994) Mechanism of high-affinity potassium uptake in
802   roots of *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences*
803   *USA*, **91**, 9272-9276.
804 MacDonald, I.A.W., Thebaud, C., Strahm, W.A. & Strasberg, D. (1991) Effects of alien
805   plant invasions on native vegetation remmants on La Reunion (Mascarene-Islands,
806   Indian-Ocean). *Environmental Conservation*, **18**, 51-61.
807 Mack, M.C., Schuur, E.A.G., Bret-Harte, M.S., Shaver, G.R. & Chapin III, F.S. (2004)
808   Ecosystem carbon storage in arctic tundra reduced by long-term nutrient
809   fertilization. *Nature*, **431**, 440-443.
810 Magen, H. (2008) Balanced crop nutrition: fertilizing for crop and food quality. *Turkish*
811   *Journal of Agriculture*, **32**, 183-193.
812 Marchi, G., Silva, V.A., Guilherme, L.R.G., Lima, J.M., Nogueira, F.D. & Guimaraes,
813   P.T.G. (2012) Potassium extractability from soils of Brazilian coffee regions.
814   *Bioscience Journal*, **28**, 913-919.
815 Merino-Martin, L., Moreno-de las Heras, M., Pérez-Domingo, S., Espigarea, T. &
816   Nicolau, J.M. (2012) Hydrological heterogeneity in Mediterranean reclaimed
817   slopes: runoff and sediment yield at the patch and slope scales along a gradient of
818   overland flow. *Hydrological Earth Systems Science*, **16**, 1305-1320.
819 Milla, R., Castro-Díaz, P., Maestro-Martínez, M. & Montserrat-Martí, G. (2005)
820   Relationships between phenology and the remobilization of nitrogen, phosphorus
821   and potassium in branches of eight Mediterranean evergreens. *New Phytologist*,
822   **168**, 167-178.
823 Mitchell, M.J., Raynal, D.J. & Driscoll, C.T. (1996) Biogeochemistry of a forested
824   watershed in the central Adirondack Mountains: Temporal changes and mass
825   balances. *Water, Air and Soil Pollution*, **88**, 355-369.
826 Mitchell, A.D. & Smethurst, P.J. (2008) Base cation availability and leaching after
827   nitrogen fertilization of a eucalypt plantation. *Australian Journal of Soil*
828   *Research*, **46**, 445-454.
829 Monty, M.L.F., Florens, F.B.V. & Baider, C. (2013) Invasive alien plants elicit reduced
830   production of flowers and fruits in various native forest species on the tropical
831   island of Mauritius (Mascarenes, Indian Ocean). *Tropical Conservation Science*, **6**,
832   35-49.
833 More, J.D., Camiré, C. & Ouimet, R. (2000) Effects of liming on the nutrition, vigor,
834   and growth of sugar maple at the Lake Clair watershed, Québec, Canada.
835   *Canadian Journal of Forest Research*, **30**, 725-732.
836 Mulder, C., Ahrestani, F.S., Bahn, M., Bohan, D.A., Bonkowski, M., Griffiths, B.S.,
837   Guicharnaud, R.A., Kattge, J., Krogh, P.H., Lavorel, S., Lewis, O.T., Mancinelli,
838   G., Naeem, S., Peñuelas, J., Poorter H., Reich, P.B., Rossi, L., Rusch, G.M.,
839   Sardans, J. & Wright, I.J. (2013) Connecting the green and brown worlds:
840   allometric and stoichiometric predictability of above- and below-ground networks.
841   *Advances in Ecological Research*, **49**, 69-175.
842 Muoghalu, J.I. & Oakhumen, A. (2000) Nutrient content of incident rainfall, throughfall
843   and stemflow in a Nigerian secondary lowland rainforest. *Applied Vegetation*
844   *Science*, **3**, 181-188.
845 Nandwal, A.S., Hooda, A. & Datta, D. (1998) Effect of substrate moisture and
846   potassium on water relations and C, N and K distribution in *Vigna radiate*.
847   *Biologia Plantarum*, **41**, 149-153.

848 Neirynck, J., Maddelein, D., de Keersmaeker, L., Lust, N. & Muys, B. (1998) Biomass
849   and nutrient cycling of a highly productive Corsican pine stand on former
850   heathland in northern Belgium. *Annales des Sciences Forestieres*, **55**, 389-405.
851 Nieminen, T. & Helmisaari, H.S. (1996) Nutrient retranslocation in the foliage of *Pinus*
852   *sylvestris* L. growing along a heavy metal pollution gradient. *Tree Physiology*, **16**,
853   825-831.
854 Navratil, T., Norton, S.A., Fernandez, I.J. & Nelson, S.J. (2010) Twenty-year inter-
855   annual trends and seasonal variations in precipitation and stream water chemistry
856   at the Bear Brook Watershed in Maine, USA. *Environmental Monitoring and*
857   *Assessment*, **171**, 23-45.
858 Nowak, C.A., Downard, R.B. & White, E.H. (1991) Potassium trends in red pine
859   plantations at pack-forest, New York. *Soil Science Society of America Journal*, **55**,
860   847-850.
861 Oddo, E., Inzerillo, S., La Bella, F., Grisafi, F., Salleo, S. & Nardini, A. (2011) Short-
862   term effects of potassium fertilization on the hydraulic conductance of *Laurus*
863   *nobilis* L. *Tree Physiology*, **31**, 131-138.
864 Olde Venterink, H., Kardel, I., Kotowski, W., Peeters, W. & Wassen, M.J. (2009)
865   Long-term effects of drainage and hay-removal on nutrient dynamics and
866   limitation in the Biebrza mires, Poland. *Biogeochemistry*, **93**, 235-252.
867 Osakabe, Y., Arinaga, N., Umezawa, T., Katsura, S., Nagamachi, K., Tanaka, H.,
868   Ohiraki, H., Yamada, K., Seo, S.U., Abo, M., Yoshimura, E., Shinozaki, K. &
869   Yamaguchi-Shinozaki, K. (2013) Osmotic stress responses and plant growth
870   controlled by potassium transporters in *Arabidopsis*. *Plant Cell*, **25**, 609-624
871 Ozbucak, T.B., Kutbay, H.G., Killic, D., Korkmaz, H., Bilgin, A., Yalcin, E. & Apaydin,
872   Z. (2008) Foliar resorption of nutrients in selected sympatric tree species in
873   gallery forest (Black Sea region). *Polish Journal of Ecology*, **56**, 227-237.
874 Peng, R.H., Fang, C.M., Li, B. & Chen, J.K. (2011) *Spartina alterniflora* invasion
875   increases soil inorganic nitrogen pools through interactions with tidal subsides in
876   the Yangtze Estuary, China. *Oecologia*, **165**, 797-807.
877 Peñuelas, J., Sardans, J., Rivas-Ubach, A. & Jansens, I. (2012) The human induced
878   imbalance between C, N and P in Earth's life-system. *Global Change Biology*,
879   **189**, 5-8.
880 Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M., Barbeta, A.,
881   Rivas-Ubach, A., Llusià, J., Garbuslsky, M., Filalla, I. & Jump, A.S. (2013a)
882   Evidence of current impact of climate change on life: a walk from genes to the
883   biosphere. *Global Change Biology*, **19**, 2303-2338.
884 Peñuelas, J., Poulter, B., Sardans, J.,Ciais, P., van der Velde, M., Bopp, L., Boucher, O.,
885   Godderis, Y., Hinsinger, P., Llusia, J., Nardin, E., Vicca, S., Obersteiner, M. &
886   Janssens, I.A. (2013b) Human-induced nitrogen-phosphorus imbalances alter
887   natural and managed ecosystems across the globe. *Nature Communications*, **4**,
888   3934.
889 Pieters, A. & Baruch, Z. (1997) Soil depth and fertility effects on biomass and nutrient
890   allocation in jaragua grass. *Journal of Range Management*, **50**, 268-273.
891 Poor, N., Pollman, C., Tate, P., Begum, M., Evans, M. & Campbell, S. (2006) Nature
892   and magnitude of atmospheric fluxes of total inorganic nitrogen and other
893   inorganic species to the Tampa Bay watershed, FL, USA. *Water Air and Soil*
894   *Pollution*, **170**, 267-283.
895 Potter, C.S., Ragsdale, H.L. & Swank, W.T. (1991) Atmospheric deposition and foliar
896   leaching in a regenerating southern Appalachian forest canopy. *Journal of*
897   *Ecology*, **79**, 97-115.

898 Prathibha, P., Kothai, P., Saradhi, I.V., Pandit, G.G. & Puranik, V.D. (2010) Chemical
899   characterization of precipitation at a coastal site in Trombay, Mumbai, India.
900   *Environmental Monitoring and Assessment*, **168**, 45-53.
901 Pyo, Y.J., Gierth, M., Schroeder, J.I. & Cho, M.H. (2010) High-affinity K^+ transport in
902   *Arabidopsis*: AtHAK5 and AKT1 are vital for seedling establishment and post
903   germination growth under low-potassium conditions. *Plant Physiology*, **153**, 863-
904   875.
905 Quennehen, B., Schwarzenboeck, A., Matsuki, A., Burkhart, J.F., Stohl, A., Ancellet, G.
906   & Law, K.S. (2012) Anthropogenic and forest fire pollution aerosol transported to
907   the Arctic: observations from the POLARCAT-France spring campaign.
908   *Atmospheric Chemistry and Physics*, **12**, 6437–6454.
909 Rao, S.R., Qayyum, A., Razzaq, A., Ahmad, M., Mahmood, I. & Sher, A. (2012) Role
910   of foliar application of salicylic acid and L-tryptophan in drought tolerance of
911   maize. *Journal of Animal and Plant Sciences,* **22**, 768-772.
912 Reich, P.B. & Oleksyn, J. (2004) Global patterns of plant leaf N and P in relation to
913   temperature and latitude. *Proceedings National Academy of Sciences USA*, **101**,
914   11001-1106.
915 Rivas-Ubach, A., Sardans, J., Pérez-Trujillo, M., Estiarte, M. & Peñuelas, J. (2012)
916   Strong relationship between elemental stoichiometry and metabolome in plants.
917   *Proceedings of the National Academy of Sciences USA*, **109**, 4181-4186.
918 Rivas-Ubach, A., Gargallo-Garriga, A., Sardans, J., Oravec, M., Pérez-Trujillo, M.,
919   Ogaya, R., Urban, O. & Peñuelas, J. (2014) Drought stress enhances folivory rates
920   by shifting foliar metabolomes. *New Phytologist*, **202**, 874-885..
921 Roberts, T.L. (2008) Global potassium reserves and potassium fertilizer use. IPNI
922   (International Plant Nutrition Institute). Symposium-Global Nutrient Cycling.
923   Georgia. USA.
924 Robinson, A.L., Scanlon, T.M., Cosby, B.J., Webb, J.R. & Galloway, J.N. (2013) Roles
925   of sulfate adsorption and base cation supply in controlling the chemical response
926   of streams of western Virginia to reduced acid deposition. *Biogeochemistry*, **116**,
927   119-130.
928 Römheld, V. & Kirkby, E.S. (2010) Research on potassium in agriculture: needs and
929   prospects. *Plant and Soil*, **335**, 155-180.
930 Ruan, J., Wu, X. & Härdter, R. (1997) The interaction between soil water regime and
931   potassium availability on the growth of tea. *Communications in Soil Science and
932   Plant Analysis*, **28**, 89-98.
933 Ruoho-Airola, T. & Salminen, K. (2003) Trends in the base cation deposition in Finland.
934   *Air Pollution XI. Advances in Air Pollution Series*, **13**, 273-282.
935 Ryan, J. & Sommer, R. (2012) Soil fertility and crop nutrition research at an
936   international center in the Mediterranean region: achievements and future
937   perspective. *Archives of Agronomy and Soil Science*, **58**, S41-S54.
938 Ryan, J., Sommer, R. & Ibrikci, H. (2012) Fertilizer best management practices: a
939   perspective from the dryland west Asia-North Africa region. *Journal of Agronomy
940   and Crop Science*, **198**, 57-67.
941 Ryel, R.J., Leffler, A.J., Peek, M.S., Ivans, C.Y. & Caldwell, M.M. (2004) Water
942   conservation in *Artemisis tridentate* through redistribution of precipitation.
943   *Oecologia*, **141**, 335-345.
944 Salehi, A., Ghorbanzadeh, N. & Salehi, M. (2013) Soil nutrient status, nutrient return
945   and retranslocation in poplar species and clones in northern Iran. *Forest-
946   Biogeosciences and Forestry*, **6**, 336-341.

947 Sardans, J. & Peñuelas, J. (2007) Drought changes phosphorus and potassium
948   accumulation patterns in an evergreen Mediterranean forest. *Functional Ecology*,
949   **21**, 191-201.
950 Sardans, J. & Peñuelas, J. (2012) The role of plants in the effects of global change on
951   nutrient availability and stoichiometry in the Plant-Soil system. *Plant Physiology*,
952   **160**, 1741-1761.
953 Sardans, J., Peñuelas, J. & Rodà, F. (2005) Changes in nutrient use efficiency, status
954   and retranslocation in young post-fire regeneration *Pinus halepensis* in response
955   to sudden N and P input, irrigation and removal of competing vegetation. *Trees*
956   *Structure and Function*, **19**, 233-250.
957 Sardans, J., Rodà, F. & Peñuelas, J. (2006) Effects of a nutrient pulse supply on nutrient
958   status of the Mediterranean trees *Quercus ilex* subsp. *ballota* and *Pinus halepensis*
959   on different soils and under different competitive pressure. *Trees Structure and*
960   *Function*, **20**, 619-632.
961 Sardans, J., Peñuelas, J., Prieto, P. & Estiarte, M. (2008) Drought and warming induced
962   changes in P and K concentration and accumulation in plant biomass and soil in a
963   Mediterranean shrubland. *Plant Soil*, **306**, 261-271.
964 Sardans, J., Rivas-Ubach, A. & Peñuelas, J. (2011) Factors affecting nutrient
965   concentration and stoichiometry of forest trees in Catalonia (NE Spain). *Forest*
966   *Ecology and Management*, **262**, 2024-2034.
967 Sardans, J., Peñuelas, J., Coll, M., Vayreda, J. & Rivas-Ubach, A. (2012a)
968   Stoichiometry of potassium is largely determined by water availability and growth
969   in Catalonian forests. *Functional Ecology*, **26**, 1077-1089.
970 Sardans, J., Rivas-Ubach, A. & Peñuelas, J. (2012b) The elemental stoichiometry of
971   aquatic and terrestrial ecosystems and its relationships with organismic lifestyle
972   and ecosystem structure and function: a review and perspectives. *Biogeochemistry*,
973   **111**, 1-39.
974 Sardans, J., Rivas-Ubach, A. & Peñuelas, J. (2012c) The C:N:P stoichiometry of
975   organisms and ecosystems in a changing world: A review and perspectives.
976   *Perspectives in Plant Ecology, Evolution and Systematics*, **14**, 33-47.
977 Sardans, J. & Peñuelas, J. (2013) Plant-soil interactions in Mediterranean forest and
978   shrublands: impacts of climatic change. *Plant and Soil*, **365**, 1-33.
979 Sardans, J. & Peñuelas, J. (2014) Hydraulic redistribution by plants and nutrient
980   stoichiometry. Shifts under global change. *Ecohydrology*, **7**, 1-20.
981 Schachtman, D.P. & Schroeder, J.I. (1994) Structure and transport mechanism of a
982   high-affinity potassium uptake transporter from higher plants. *Nature*, **370**, 655-
983   658.
984 Schimel, D.S., House, J.I., Hibbard, K.A. Bousquet, P., Ciais, P., Peylin, P., Braswell,
985   B.H., Apps, M.J., Baker, D., Bondeau, A., Canadell, J., Churkina, G., Cramer, W.,
986   Denning, A.S., Field, C.B., Friedlingstein, P., Goodale, C., Heimann, M.,
987   Houghton, R.A., Melillo, J.M., Moore III, B., Murdiyarso, D., Noble, I., Pacala,
988   S.W., Prentice, I.C., Raupach, M.R., Rayner, P.J., Scholes, R.J., Steffen, W.L., &
989   Wirth, C. (2001) Recent patterns and mechanisms of carbon exchange by
990   terrestrial ecosystems. *Nature*, **414**, 169-172.
991 Schreeg, L.A., Mack, M.C. & Turner, B.L. (2013) Nutrient-specific patterns of leaf
992   litter across 41 lowland tropical woody species. *Ecology*, **94**, 94-105.
993 Schroeder, J.I. & Fang, H.H. (1991) Inward-rectifying K^+ channels in guard cells
994   provide a mechanism for low-affinity K^+ uptake. *Proceedings of the National*
995   *Academy of Sciences USA*, **88**, 11583-11587.

996 Sharifi, M., Cheema, M., McVicar, K., LeBlanc, L. & Fillmore, S. (2013) Evaluation of
997   liming properties and potassium bioavailability of three Atlantic Canada Wood
998   ash sources. *Canadian Journal of Plant Science*, **93**, 1209-1216.
999 Silva, V.A., Marchi, G., Guimaraes Guilherme, L.R., de Lima, J.M., Dias Nogueira, F.
1000   & Gontijo Guimaraes, P.T. (2008) Kinetics of K release from soils of Brazilian
1001   coffee regions: effect of organic acids. *Revista Brasileira de Ciencia do Solo*, **28**:
1002   597-603.
1003 Singer, A. (1989) Illite in the hot-aridic soil environment. *Soil Science*, **147**, 126-133.
1004 Singh, K. & Bansai, S.K. (2009) Potassium indexing of crops grown on eight
1005   Benchmark soil series of India. *Communications in Soil Science and Plant
1006   Analysis*, **40**, 1369-1379.
1007 Smith, D.M., Jackson, N.A., Roberts, J.M. & Ong, C.K. (1999) Reverse flow of sap in
1008   tree roots and downward siphoning of water by *Grevillea robusta*. *Functional
1009   Ecology*, **13**, 256-264.
1010 Soil Survey Staff (1999) Soil Taxonomy. A Basic System of Soil Classification for
1011   Making Classification for making and interpreting Soil Surveys.
1012 Sterner, R.W. & Elser, J.J. (2002) Ecological stoichiometry: the biology of elements
1013   from molecules to the biosphere. Princeton University Press, Princeton.
1014 Stone, E.L. & Kszystyniak, R. (1977) Conservation of potassium in the *Pinus resinosa*
1015   ecosystem. *Science*, **198**, 192-194.
1016 Su, H., Golldack, D., Katsuhara, M., Zhao, C. & Bohnert, H.J. (2001) Expression and
1017   stress-dependent induction of potassium channel transcripts in the common ice
1018   plant. *Plant Physiology*, **125**, 604-614.
1019 Sutton, M.A., Howard, C.M., Erisman, J.W., Billen, G., Bleeker, A., Grennfelt, P.,
1020   Grinsven, H.V. & Grizzetti, B. (eds) (2011) The European Nitrogen Assessment.
1021   Cambridge University Press.
1022 Szczerba, M.W., Britto, D.T. & Kronzucker, H.J. (2009) K^+ transport in plants:
1023   physiology and molecular biology. *Journal of Plant Physiology*, **166**, 447-466.
1024 Talbott, L.D. & Zeiger, E. (1996) Central roles for potassium and sucrose in guard-cell
1025   osmoregulation. *Plant physiology*, **111**, 1051-1057.
1026 Tartachnyk, I.I. & Blanke, M.M. (2004) Effect of delayed fruit harvest on
1027   photosynthesis, transpiration and nutrient remobilization of apple leaves. *New
1028   Phytologist*, **164**, 441-450.
1029 Teixeira, P.C., Gonçalves, J.L.M., Arthur, J.C. & Dezordi, C. (2008) *Eucalyptus* sp.
1030   seedling response to potassium fertilization and soil water. *Ciencia Forestal*, **18**,
1031   47-63.
1032 Tilman, E.A., Tilman, D., Crawley, M.J. & Johnston, A.E. (1999) Biological weed
1033   control via nutrient competition: potassium limitation of dandelions. *Ecological
1034   Monographs*, **9**, 103-111.
1035 Tomlinson, K.W., Pooter, L., Sterck, F.J., Borghetti, F., Ward, D., de Bie, S. & van
1036   Langevelde, F. (2013) Leaf adaptations of evergreen and deciduous trees of semi-
1037   arid and humid savannas on three continents. *Journal of Ecology*, **101**, 430-440.
1038 Traveset, A., Kueffer, C. & Daehler, C.C. (2014) Global and regional nested patterns of
1039   non-native invasive floras on tropical islands. *Journal of Biogeography*, **41**, 823-
1040   832.
1041 Travlos, I.S., Liakopoulos, G., Karabourniotis, G., Fasseas, C. & Karamanos, A.J. (2008)
1042   Ciscadian leaflet movements of *Tylosema esculetum* (Burch) A. schreib, and the
1043   abolishment of these diurnal movements by potassium deficiency. *Journal of Arid
1044   Environments*, **72**, 1745-1750.

1045 Trémolières, M., Schnitzler, A., Sánchez-Pérez, J.M. & Schmitt, D. (1999) Changes in
1046   foliar nutrient content and resorption in *Fraxinus excelsior* L., *Ulmus minor* Mill.
1047   and *Clematis vitalba* L. after prevention of floods. *Annals of Forest Science*, **56**,
1048   641-650.
1049 Tripler, C.E., Kaushal, S.S., Linkens, G.E. & Walter, M.T. (2006) Patterns in potassium
1050   dynamics in forest ecosystems. *Ecology Letters*, **9**, 451-466.
1051 Tzvetkova, N. & Hadjiivanova, C.H. (2006) Chemical composition and biochemical
1052   changes in Needles of Scots pine (*Pinus sylvestris* L.) stands at different stages of
1053   decline in Bulgaria. *Trees Structure and Function*, **20**, 405-409.
1054 Urban, R.C., Lima-Souza, M., Caetano-Silva, L., Queiroz, M.E.C., Nogueira, R.F.P.,
1055   Allen, A.G., Cardoso, A.A., Held, G. & Campos, M.L.A.M. (2012) Use of
1056   levoglucosan, potassium, and water-soluble organic carbon to characterize the
1057   origins of biomass-burning aerosols. *Atmospheric Environment*, **61**, 562-569.
1058 Van den Driessche, R. (1985) Late-season fertilization mineral nutrient reserves and
1059   retranslocation in planted douglass-fir *Pseudotsuga menziessi* seedlings. *Forest
1060   Science*, **31**, 485-496.
1061 Vanderpol, F. & Traore, B. (1993) Soil nutrient depletion by agricultural production in
1062   southern Mali. *Fertilizer Research*, **36**, 79-90.
1063 Vegas-Vilarrúbia, T., Baritto, F., López, P., Meléan, G., Ponce, M.E., Mora, L. &
1064   Gómez, O. (2010) Tropical Histosols of the lower Orinoco Delta, features and
1065   preliminary quantification of their carbon storage. *Geoderma*, **155**, 280-288.
1066 Vergutz, L., Manzoni, S., Porporato, A., Novais, R.F. & Jackson, R.B. (2012) Global
1067   resorption efficiencies and concentrations of carbon and nutrients in leaves of
1068   terrestrial plants. *Ecological Monographs*, **82**, 205-220.
1069 Vitousek, P.M. & Sanford, R.L. (1986) Nutrient cycling in moist tropical forest. *Annual
1070   Review of Ecological Systems*, **17**, 585-594.
1071 Vitousek, P.M. & Howarth, R.W. (1991) Nitrogen limitation on land and in the sea:
1072   How can it occur? *Biogeochemistry*, **13**, 87-115.
1073 Vitousek, P.M., Porder, S., Houlton, B.Z. & Chadwick, O.A. (2010) Terrestrial
1074   phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus
1075   interactions. *Ecological Applications*, **20**, 5-15.
1076 Vogt RD, Seip HM, Larssen, T., Zhao, D., Xiang, R., Xiao, J., Luo, J. & Zhao, Y.
1077   (2006) Potential acidifying capacity of deposition experiences from regions with
1078   high NH_4^+ and dry deposition in China. *Science of the Total Environment*, **367**,
1079   394-404.
1080 Walker, T.W. & Syers, J.K. (1976). The fate of phosphorus during pedogenesis.
1081   *Geoderma*, **15**, 1-19.
1082 Walker, T.R., Young, S.D., Crittenden, P.D. & Zhang, H. (2003) Anthropogenic metal
1083   enrichment of snow and soil in north-eastern European Russia. *Environmental
1084   Pollution*, **121**, 11-21.
1085 Walna, B., Drzymala, S. & Siepak, J. (2000) The impact of acid rain on potassium and
1086   sodium status in typical soils of the Wielkopolski National Park (Poland). *Water
1087   Air and Soil Pollution*, **121**, 31-41.
1088 Wang, H.Y., Zhou, J.M., Du, C.W. & Chen, X.Q. (2010) Potassium fractions in soils as
1089   affected by monocalcium phosphate, ammonium sulfate and potassium chloride
1090   application. *Pedosphere*, **20**, 368-377.
1091 Wang, M., Zheng, Q., Shen, Q. & Guo, S. (2013) The critical role of potassium in plant
1092   stress response. *International Journal of Molecular Science*, **14**, 7370-7390.

1093 Waraich, E.A., Ahmad, R., Saifullah & Ehsanullah, M.Y.A. (2011) Role of mineral
1094   nutrition in alleviation of drought stress in plants. *Australian Journal of Crop*
1095   *Science*, **5**, 764-777.
1096 Watmough, S.A. & Dillon, P.J. (2004) Major element fluxes from a coniferous
1097   catchment in central Ontario, 1983-1999. *Biogeochemistry*, **67**, 369-398.
1098 Watmough, S.A., Aherne, J., Alewell, C., Arp, P., Bailey, S., Clair, T., Dillon, P.,
1099   Duchesne, L., Eimers, C., Fernandez, I., Foster, N., Larssen, T., Miller, E.,
1100   Mitchell, M. & Page, S. (2005) Sulphate, nitrogen and base cation budgets at 21
1101   forested catchments in Canada, the United States and Europe. *Environmental*
1102   *Monitoring and Assessment*, **109**, 1-36.
1103 Yamashita, N., Ishida, A., Kushima, H. & Tanaka, N. (2000) Acclimatation to sudden
1104   increase in light favoring an invasive over native tres in subtropical islands, Japan.
1105   *Oecologia*, **125**, 412-419.
1106 Yavitt, J.B., Harms, K.E., Garcia, M.N., Mirabello, M.J. & Wright, S.J. (2011) Soil
1107   fertility and fine root dynamics in response to 4 years of nutrient (N, P, K)
1108   fertilization in a lowland tropical forest, Panama. *Austral Ecology*, **36**, 433-445.
1109 Yin, L.M., Wang, L.H. & Liu, B. (2009) Dynamics variation and resorption of nutrient
1110   elements in the leaves of *Xanthoceras sorbifolia bunge*. *Bulletin of Botanical*
1111   *Research*, **29**, 685-691.
1112 Yin, X.M., Rocha, P.S.C.F., Wang, M.L., Zhu, Y.X., Li, L.Y., Song, S.F. & Xia, X.
1113   (2011) Rice gene OsDSR-1 promotes lateral root development in *Arabidopsis*
1114   under high-potassium conditions. *Journal of Plant Biology*, **54**, 180-189.
1115 Zhang, Y., Wang, Z., Zhang, L., Cao, Y., Huang, D. & Tang, K. (2006) Molecular
1116   cloning and stress-dependent regulation of potassium channel gene in Chinese
1117   cabbage (*Brassica rapa* ssp. *pekinensis*). *Journal of Plant Physiology*, **163**, 968-
1118   978.
1119 Zhang, S.B., Zhang, J.L., Slik, J.W.F. & Cao, K.F. (2012) Leaf element concentrations
1120   of terrestrial plants across China are influenced by taxonomy and the environment.
1121   *Global Ecology and Biogeography*, **21**, 809-818.
1122 Zhao, D., Oosterhuis, D.M. & Bednarz, C.W. (2001) Influence of potassium deficiency
1123   on photosynthesis, chlorophyll content, and chloroplast ultrastructure of cotton
1124   plants. *Photosynthetica*, **39**, 103-109.
1125 Zheng, S. & Shangguan, Z. (2007) Spatial patterns of leaf nutrient traits of the plants in
1126   the Loess Plateau of China. *Trees Structure and Function*, **21**, 357-370.
1127
1128

1129 Additional references to data sources can be found in Appendix S5 at [URL].
1130
1131
1132
1133
1134 **SUPPORTING INFORMATION**

1135 Additional supporting information may be found in the online version of this article at

1136 publisher's website.

1137

1138 **Appendix S1**. Annual atmospheric rates of K deposition (kg ha^{-1} yr^{-1}).

1139

1140   **Appendix S2**. The limiting role of K on plant growth.

1141

1142   **Appendix S3**. Effects of water availability on ecosystemic K cycle.

1143

1144   **Appendix S4**. Impacts of increases of N supply on ecosystem K cycle.

1145

1146   **Appendix S5**. Plant invasion and soil K availability.

1147

1148   **Appendix S6**. References for the supporting information.

1149

1150

1151   BIOSKETCH

1152   Dr. Jordi Sardans and Prof. Josep Peñuelas are researchers focusing on the field of plant

1153   ecophysiology, biogeochemical cycles and atmosphere-biosphere interactions. JS's

1154   primary focus is on the elemental stoichiometry relationships with terrestrial ecosystems

1155   structure and function and in the metabolomic plant responses to abiotic and biotic

1156   changes. JP's research covers a wide range of ecological disciplines: chemical ecology,

1157   biogeochemistry, global change, climate change, atmospheric pollution, biogenic VOCs

1158   emissions, remote sensing, and functioning and structure of terrestrial plants and

1159   ecosystems.

1160 Table 1. Global K contents of various soils. The data, except those indicated below the table, were obtained from Soil Taxonomy (Soil Survey
1161 Staff, 1999).

Soil type	Global surface area (x 10^6 km^2)	Average available K in soil profile (mg g^{-1}) (range of soil depth, cm)	Average bulk density (g cm^{-3})	Global total available K (x 10^9 t)
Alfisols	12.62	0.123 (0-130)	1.73	3.51
Andisols	0.91	0.119 (0-200)	0.8	0.17
Aridisols	15.73	0.620 (0-279)	1.5*	40.1
Entisols	21.14	0.040 (0-152)	1.5*	1.70
Gelisols	11.3	0.072 (0-110)	1.41	1.57
Histosols	1.53	0.147 (0-100)***	1.5*	0.337
Inceptisols	12.83	0.005 (0-73)	1.2	0.059
Mollisols	9.0	0.706 (0-165)	1.48	21.8
Oxisols	9.81	0.024 (0-100)**	1.32	0.310
Spodosols	3.35	0.125 (0-100)	1.5*	0.210
Ultisols	11.05	0.064 (0-280)	1.65	3.25
Vertisols	3.35	0.311 (0-234)	1.95	4.69
Global total (continental areas covered by rocks or ice)	130.8			57.7

1162
1163 * No data provided in Soil Taxonomy; estimated from the average of other soil types.

** Data from Marchi *et al*. (2012), Silva *et al*. (2008) and Da Silva *et al*. (2000).
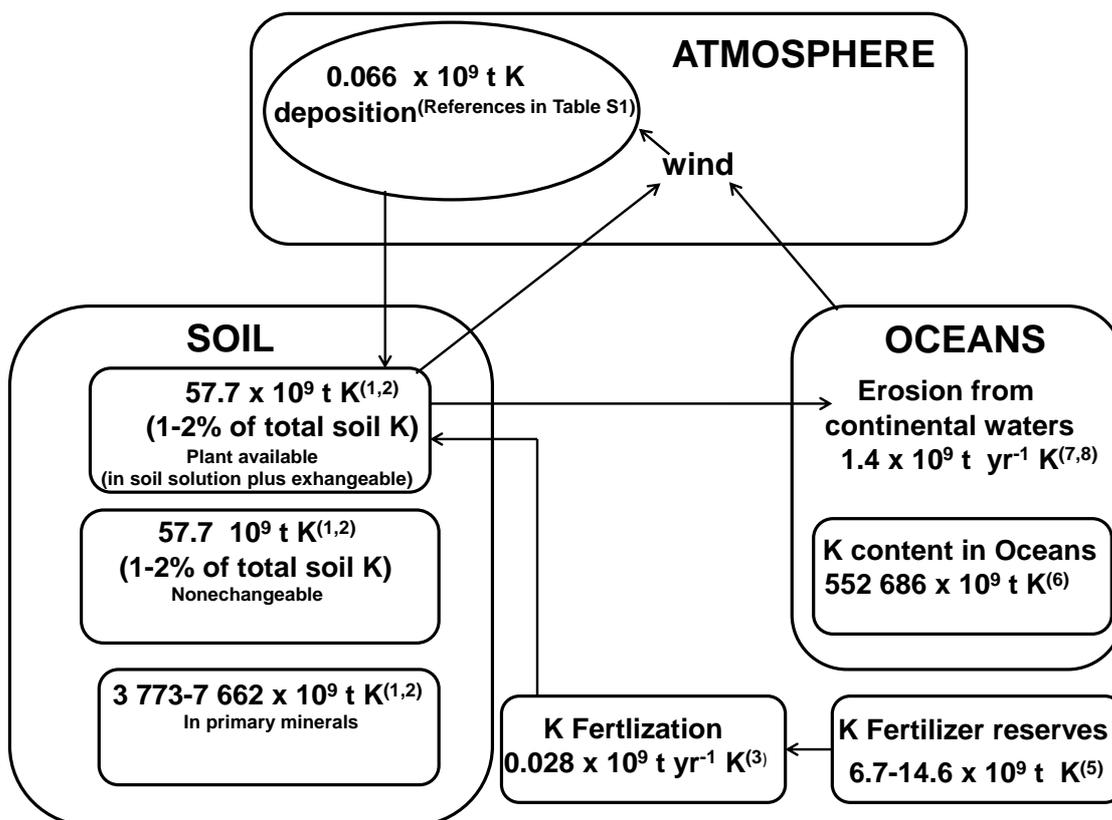
*** Data from Vegas-Vilarrúbia *et al*. (2010).

Figure legends

Figure 1. K cycle among soils, atmosphere and oceans.

Figure 2. Number of studies reporting limiting and non-limiting roles of K availabilities for plant growth under field conditions in terrestrial ecosystems. (Detailed information regarding these studies is presented in Table S2, Supplementary material).

Figure 3. The reported effects of N loadings (by N deposition or by N fertilization simulating N deposition) in field conditions. The numbers within brackets correspond to the number of the studies that have observed the corresponding effect. (Detailed information of the studies is shown in Table S4, Supplementary material).

Figure 4. The reported relationships between Soil K-availability and alien success. The numbers within brackets correspond to the number of the studies that have observed the corresponding effect (Detailed information of the studies is shown in Table S5, Supplementary material).

ATMOSPHERE

0.066 x 10^9 t K
deposition[References in Table S1]

wind

SOIL

57.7 x 10^9 t K[1,2]
(1-2% of total soil K)
Plant available
(in soil solution plus exhangeable)

57.7 10^9 t K[1,2]
(1-2% of total soil K)
Nonechangeable

3 773-7 662 x 10^9 t K[1,2]
In primary minerals

OCEANS

Erosion from
continental waters
1.4 x 10^9 t yr^{-1} K[7,8]

K content in Oceans
552 686 x 10^9 t K[6]

K Fertlization
0.028 x 10^9 t yr^{-1} K[3]

K Fertilizer reserves
6.7-14.6 x 10^9 t K[5]

1.Soil Survey Staff (1999) Soil Taxonomy. A Basic System of Soil Classification for Making and Interpreting Soil Surveys. Second Edition. 870 pages.

2.Hoeft RG, Nafziger ED, Johnson RR, Aldrich SR (2000) Modern Corn and Soybean Production. MCSP Publications. Champaign, IL. 353p.

3. FAO (2008) Current world fertilizer trends and outlook to 2014. ftp://ftp.fao.org/ag/agp/docs/cwfto14.pdf.

4. Eakins BW,, Sharman GF (2010) Volumes of the World's Oceans from ETOPO1, NOAA National Geophysical Data Center, Boulder, CO.

5. USGS (2009). Potash. U.S. Geological Survey, Mineral commodity summaries. Online at http://minerals.er.usgs.gov/minerals/pubs/mcs.

6. Pawlowicz R (2013) Key physical variables in Ocean: temperature, salinity, and density. Nature Education Knowledge 4 (4): 13.

7. Chow V, Maidment D, Mays L (2000) *Hidrología Aplicada*. Ed. Nomos, S.A. Colombia. 584 p.

8. Cole GA (1983) Textbook of Limnology. 3rd Ed. The C.V. Mosby Co., St. Louis, Toronto, London, 401 pp.
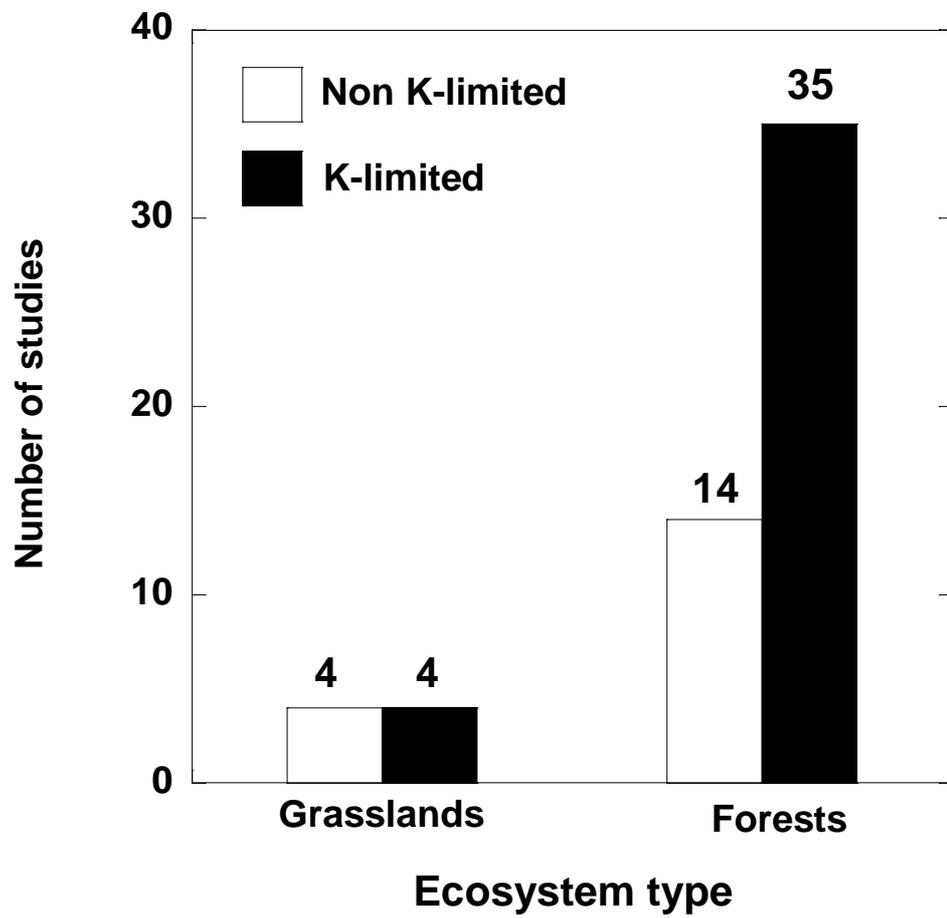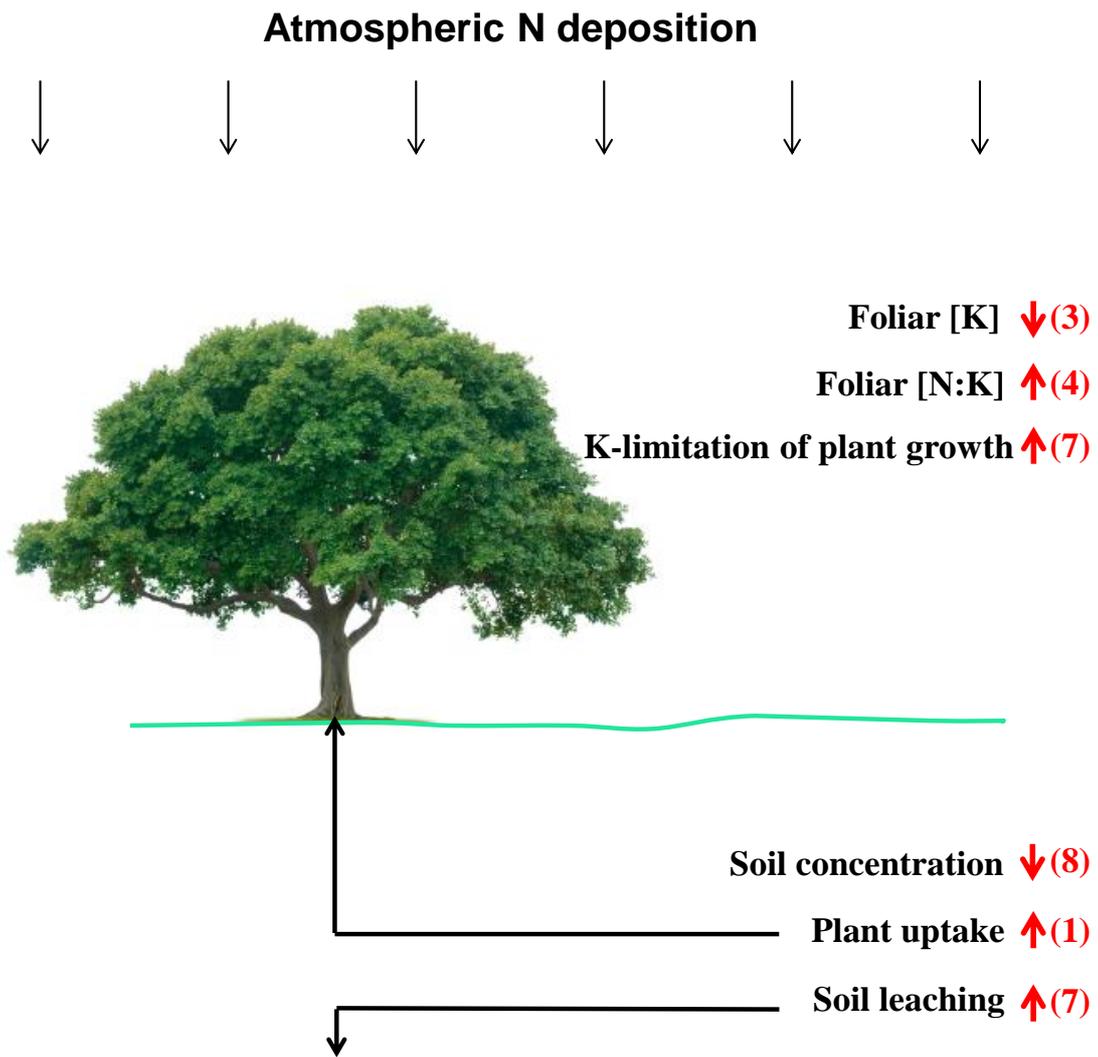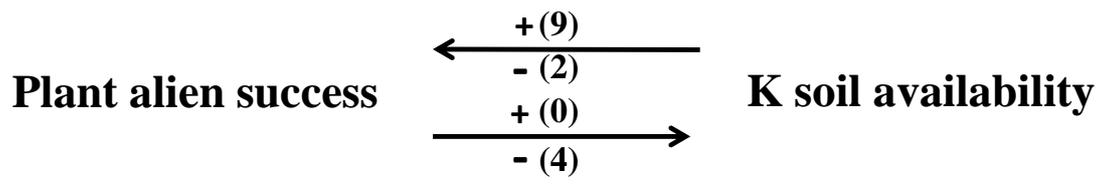
Figure 2

Atmospheric N deposition

↓   ↓   ↓   ↓   ↓   ↓

Foliar [K] ↓**(3)**
Foliar [N:K] ↑**(4)**
K-limitation of plant growth ↑**(7)**

Soil concentration ↓**(8)**
Plant uptake ↑**(1)**
Soil leaching ↑**(7)**

Figure 3

Plant alien success $\xrightleftharpoons[\substack{+ (0) \\ - (4)}]{\substack{+ (9) \\ - (2)}}$ **K soil availability**

Figure 4