

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

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26 **ABSTRACT**

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

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

35 **Conclusions:** The current literature indicates that K, at a global level, is as limiting as N
36 and phosphorus (P) for plant productivity in terrestrial ecosystems. K limitation has
37 been seen up to some degree in 70% of all studied terrestrial ecosystems. However,
38 atmospheric K deposition from human activities represents higher amounts than that
39 from natural sources in some areas. We are far from understanding the K fluxes
40 between the atmosphere and land, and the role of anthropogenic activities in these
41 fluxes. The increasing aridity expected in wide areas of the world makes K more critical
42 through its role in water use efficiency. N deposition exerts a strong impact on the
43 ecosystem K-cycle, decreasing K availability and increasing K limitation. Plant invasive
44 success is enhanced by higher soil K availability, especially in environments without
45 strong abiotic stresses. The impacts of other global change drivers, such as increasing
46 atmospheric CO₂ or changes in land use remain to be elucidated. Current models of the
47 responses of ecosystems and carbon storage to projected global climatic and
48 atmospheric changes are now starting to consider N and P, but they should also consider
49 K, mostly in arid and semiarid ecosystems.

50

51 **Introduction: Potassium in plant-soil system**

52

53 Potassium (K) is the most abundant cation in plant cells and is the second most
54 abundant nutrient after nitrogen (N) in leaves. K is thus more abundant than phosphorus
55 (P) (Leigh & Jones, 1984; Sardans *et al.*, 2006; Zheng & Shangguan, 2007; Sardans *et*
56 *al.*, 2011, 2012a). K represents 2.6% of the weight of the Earth's crust. The
57 concentrations of P and N in rocks are lower; P represents only 0.1% of the weight of
58 the Earth's crust, and N is only present in trace amounts in magmatic rocks (< 200 ppm
59 in granite). The most N-rich sedimentary rocks have only 0.1% N (Greenwood &
60 Earnshaw, 1997; Holloway & Dahlgren, 2002). Young soils tend to have high
61 phosphorus availability and low nitrogen availability (Houlton *et al.*, 2008). However,
62 as soils age, nitrogen gradually accumulates in the soils (Hedin *et al.*, 2003), while they
63 become more depleted in phosphorus (Walker & Syers, 1976; Vitousek & Howarth,
64 1991). K can be more easily leached than N or P (Boxman *et al.*, 1994; Neiryneck *et al.*,
65 1998). However, terrestrial ecosystems, such as forests and shrublands, have a great
66 biological capacity for K-retention by several processes, such as plant "pumping" and
67 resorption of K (Nowak *et al.*, 1991; Jobbáry & Jackson, 2001).

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

175

176 **Plant K uptake**

177 The importance of K in terrestrial plants is reflected by the sophisticated mechanisms of
178 K uptake, redistribution, and homeostasis involving several families of cell-wall and
179 membrane proteins (Hirsch *et al.*, 1998; Armengaud *et al.*, 2004; Szczerba *et al.*, 2009;
180 Pyo *et al.*, 2010). Several regulatory mechanisms have been identified for K transporters,
181 which are activated by various environmental factors such as water availability and soil
182 concentrations of K⁺, Na⁺ or Ca²⁺ (Zhang *et al.*, 2006; Szczerba *et al.*, 2009; Pyo *et al.*,
183 2010). Low-affinity and high-affinity K-transport systems have been identified. Briefly,
184 the low-affinity transport system, believed to be channel mediated, acts at high external
185 K concentrations and is isothermodynamically passive (Leigh, 2001; Szczerba *et al.*,
186 2009). The high-affinity transport system is a saturable system, which catalyzes the
187 thermodynamically active uptake of K at low external K concentrations (< 1 mM)
188 (Schachtman & Schroeder, 1994; Szczerba *et al.*, 2009; Cuéllar *et al.*, 2010). The high-
189 affinity transport system, as opposed to the low-affinity transport system, is down-
190 regulated at high external K concentrations and up-regulated at low external K
191 concentrations (Schroeder & Fang, 1991; Maathuis & Sanders, 1994; Hirsch *et al.*, 1998;
192 Szczerba *et al.*, 2009). Both the systems, though, represent an electrogenic entry of net
193 positive charge, which requires the active removal of protons to maintain electrical
194 neutrality (Leigh, 2001; Szczerba *et al.*, 2009).

195 The capacity of terrestrial plants to take up K and to maintain their homeostatic
196 properties is determined by sophisticated mechanisms of genetic expression
197 (Armengaud *et al.*, 2004; Yin *et al.*, 2011; El-Mesbahi *et al.*, 2012). Moreover, K
198 uptake is closely linked to water economy. Some studies have observed that
199 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),

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

276 **Anthropogenic impacts on the K cycle**

277 **K fertilizers:** K is required in large amounts for growing crops, but farmers in poor
278 countries often do not fertilize with K due to high costs, which leads to K deficiencies in
279 large areas of farmland (Hoa *et al.*, 2006; Andrist-Rangel *et al.*, 2007). The situation is
280 especially critical in Africa. Many African croplands are dramatically under-fertilized,
281 especially with K. Despite covering 25% of global potential cropland area (FAO 2003,
282 2011), the African share of global fertilizer consumption is 2.7% for N, 2.4% for P and
283 1.7% for K (FAO, 2011). The fertilizer nutrient supply/demand balance indicates that
284 Africa will remain as an exporter of phosphate and nitrogen, but for potash, the region
285 would continue to depend solely on import (FAO, 2011). This fact, along with the great
286 economical deficits in most African states, makes K a critical limiting factor for food
287 production in this continent.

288 Croplands in China, Egypt, Bulgaria and parts of southeastern Asia also have
289 negative balances of K, mainly due to socio-economic factors that decrease crop
290 productivity (Magen, 2008; Ryan & Sommer, 2012; Ryan *et al.*, 2012). This negative
291 balance leads to an increasing impoverishment of K in cropland soils (Vanderpol &
292 Traore, 1993; Singh & Bansai, 2009). Moreover, the increasing demand for food and
293 increasing aridity in several areas of the world, such as the Mediterranean Basin (mainly
294 the Maghreb) and the Sahel, make K fertilization more critical given the important role
295 of K in water use efficiency (Ruan *et al.*, 1997; Römheld & Kirkby, 2010). A recent
296 study has concluded that K is currently the most important limiting nutrient in
297 Mediterranean croplands (Ryan & Sommer, 2012). Agriculture practices that decrease
298 soil pH favor K leaching and thus decrease availability for plants (Sharifi *et al.*, 2013).
299 For example, despite that sometimes N fertilization can enhance soil K-availability in a
300 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 K₂O 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.

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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 (Talbot & Zeiger, 1996; Benloch-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 (Talbot & 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 CO₂ 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 CO₂ fixation, improving the
508 transport of photosynthates into sink organs and inhibiting the transfer of photosynthetic
509 electrons to O₂, 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.

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552 **References**

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1129 Additional references to data sources can be found in Appendix S5 at [URL].

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1134 **SUPPORTING INFORMATION**

1135 Additional supporting information may be found in the online version of this article at
 1136 publisher's website.

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

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.

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

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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)
Alfisol	12.62	0.123 (0-130)	1.73	3.51
Andisol	0.91	0.119 (0-200)	0.8	0.17
Aridisol	15.73	0.620 (0-279)	1.5*	40.1
Entisol	21.14	0.040 (0-152)	1.5*	1.70
Gelisol	11.3	0.072 (0-110)	1.41	1.57
Histosol	1.53	0.147 (0-100)***	1.5*	0.337
Inceptisol	12.83	0.005 (0-73)	1.2	0.059
Mollisol	9.0	0.706 (0-165)	1.48	21.8
Oxisol	9.81	0.024 (0-100)**	1.32	0.310
Spodosol	3.35	0.125 (0-100)	1.5*	0.210
Ultisol	11.05	0.064 (0-280)	1.65	3.25
Vertisol	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.

1164 ** Data from Marchi *et al.* (2012), Silva *et al.* (2008) and Da Silva *et al.* (2000).
1165 *** Data from Vegas-Vilarrúbia *et al.* (2010).
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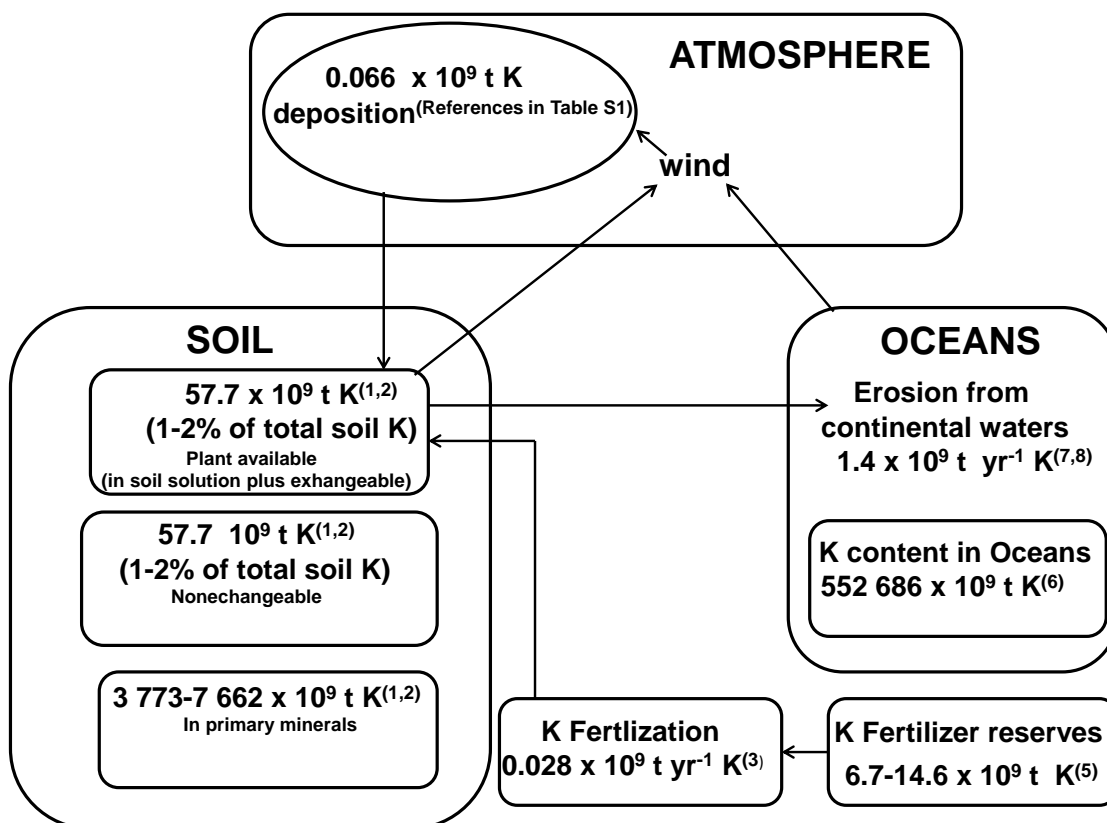
Figure legends

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).



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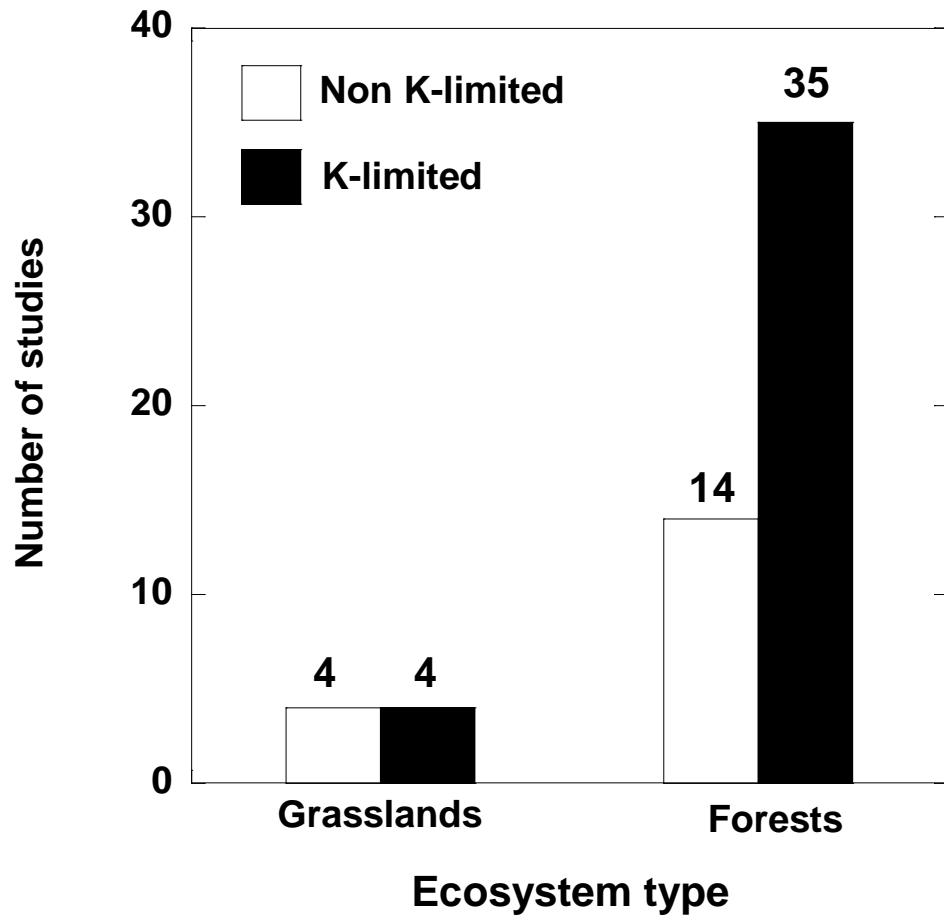


Figure 2

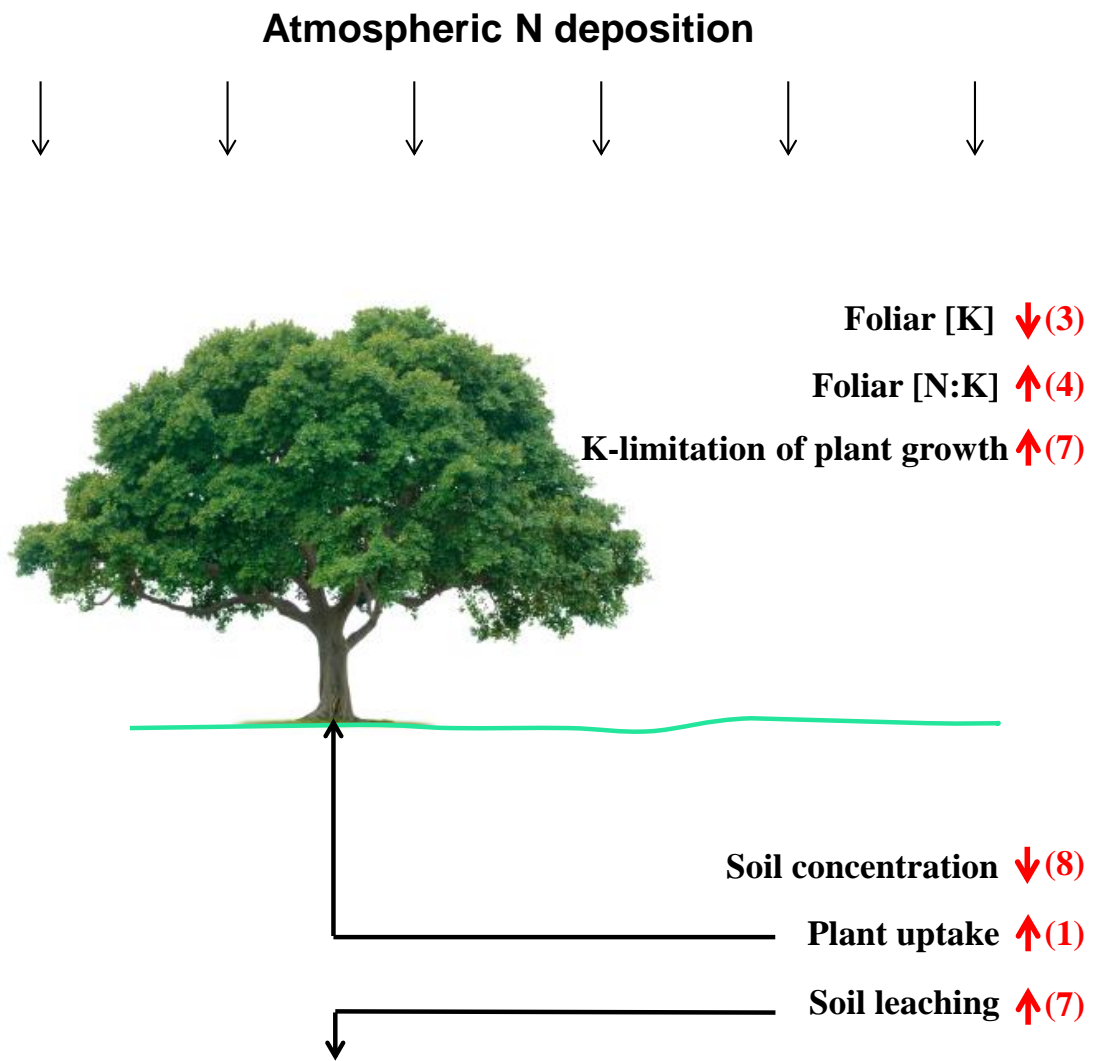


Figure 3

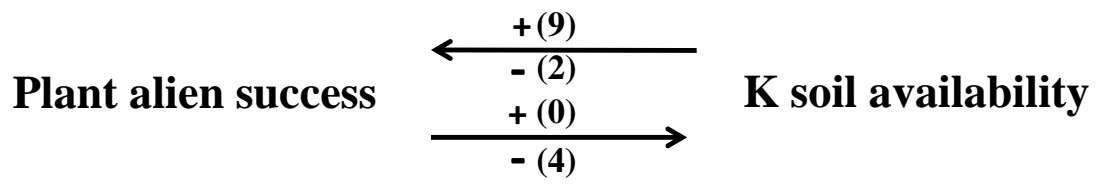


Figure 4

