
Potassium: a neglected nutrient in global change
Jordi Sardans1,2* and Josep Peñuelas1,2

ABSTRACT

Aim Potassium (K) is the second most abundant nutrient in plant photosynthetic tissues after nitrogen (N). 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 content, stoichiometry and roles of K in the soil–plant system and in terrestrial ecosystems. We have also reviewed the impacts of global change drivers on K content, stoichiometry 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. Some degree of K limitation has been seen in up to 70% of all studied terrestrial ecosystems. However, in some areas atmospheric K deposition from human activities is greater than that from natural sources. 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 drivers of global change, such as increasing atmospheric CO2 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 semi-arid ecosystems.

Keywords Climate change, drought, ecological stoichiometry, eutrophication, global change, invasiveness, N:K, plant growth.

INTRODUCTION: POTASSIUM IN THE 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, 2011, 2012a; Zheng & Shangguan, 2007). 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 p.p.m. 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 P availability and low N availability (Houlton et al., 2008). N gradually accumulates in soils as they age (Hedin et al., 2003), while they become more depleted in P (Walker & Syers, 1976; Vitousek & Howarth, 1991). K can be more easily leached than N or P (Boxman et al., 1994; Neiryck et al., 1998). However, terrestrial ecosystems, such as forests and shrublands, have a great biological capacity for retention of K by several processes, such as plant ‘pumping’ and resorption of K (Nowak et al., 1991; Jobbágy & Jackson, 2001).

K ‘pumping’ describes the uptake of K by plants from deep soil layers (with K provided in part by mineral weathering

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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 high levels of available K in the surface of most of the world’s soils (Jobbágy & Jackson, 2001). This biological control of the ecosystem K cycle strongly suggests a great evolutionary pressure to retain K in terrestrial ecosystems. Moreover, this ‘pumping’ capacity can allow long-term conservation of K in soils (Stone & Kszystyniak, 1977). The potential of parent material together with a conservative biogeochemical cycle underlie maintenance of the supply of K to plants (Nowak et al., 1991; Jobbágy & Jackson, 2001).

K in soil can be allocated to three pools of availability for uptake by roots. It is dissolved in soil water, adsorbed onto particles of clay and organic matter and held within the crystal structures of feldspar and mica. The organic matter in soils contains a negligible amount of K because it is not a constituent of biomolecules, and hence is easily and quickly leached from leaves due to its high solubility. However, the fraction of soil K directly available to plants (i.e. in soil solution) is usually a small proportion (0.1–0.2%) of the total soil K, whereas both the immediately available water-soluble fraction and the exchangeable fraction comprise 1–2% and the soil-unavailable fractions 96–99% (Wang et al., 2010; Britzke et al., 2012). The soil-available K pool is easily leached by runoff. Soil plant-available K concentrations can thus frequently be lower than the soil plant-available N and P concentrations, even though the total soil K concentrations are generally higher than those of N and, especially, P (Sardans & Peñuelas, 2007; Sardans et al., 2008). We have estimated the global K contents of the various K fractions in soil from the data in Soil taxonomy (Soil Survey Staff, 1999) and other bibliographic sources (Table 1, Fig. 1).

On the other hand, in terrestrial ecosystems, K shows a greater loss from the plant canopy by foliar leaching than other nutrients such as N and P (Duchesne et al., 2001; Kopacek et al., 2009). Thus, this poses the question that if K is potentially limiting, why has there not been a greater natural selection to minimize leaching losses from leaves? We must take into account that, unlike N and P that mostly constitute complex molecular structures, K occurs exclusively in soluble K⁺ form. For this reason, from a physical point of view, K can be more easily leached through cell membranes due to its smaller size. Probably, the need to maintain its cationic soluble form for its function has not allowed any improvement in plants’ capacity to retain it. Moreover, mechanisms such as reduction of stomatal density or thickening of the cuticle, which could help to preventing loss of K, very probably have several evolutionary trade-offs with other important plant functions such as gas exchange and water economy.

However, the soil–plant system has a notable control on the ecosystem K cycle by contributing to its retention. Currently available data show the capacity of plants to retain K by resorption. Diverse results have been reported in studies comparing the resorption efficiency (RE) for N, P and K. A number of different REs have been observed by researchers: N > P < K (van den Driessche, 1985; Nieminen & Helmsaari, 1996; Sardans et al., 2005), P < N = K (Ozbuçak et al., 2008), N < K = P (Chuyong et al., 2000), N > K > P (Yin et al., 2009), P > K > N (Salehi et al., 2013), K < N = P (Helmsaari, 1992; Duchesne et al., 2001; Tartachnyk & Blanke, 2004; Hagen-Thorn et al., 2006) and N = P = K (Gallardo et al., 1999; Trémolières et al., 1999). A recent review of a global dataset has observed that the RE for K on a global scale (70.1%) seems to be higher than the RE for N (62.1%) and P (64.9%) (Vergutz et al., 2012), although most of the studies reviewed by these authors did not take into account the role of leaf leaching when calculating RE. In fact, K leaches more easily from leaves than N and P; hence it is difficult

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

<table>
<thead>
<tr>
<th>Soil type</th>
<th>Global surface area (×10⁶ km²)</th>
<th>Average available K in soil profile (mg g⁻¹) (range of soil depth, cm)</th>
<th>Average bulk density (g cm⁻³)</th>
<th>Global total available K (×10⁹ t)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alfisols</td>
<td>12.62</td>
<td>0.123 (0–130)</td>
<td>1.73</td>
<td>3.51</td>
</tr>
<tr>
<td>Andisols</td>
<td>0.91</td>
<td>0.119 (0–200)</td>
<td>0.80</td>
<td>0.17</td>
</tr>
<tr>
<td>Aridisols</td>
<td>15.73</td>
<td>0.620 (0–279)</td>
<td>1.50*</td>
<td>40.10</td>
</tr>
<tr>
<td>Entisols</td>
<td>21.14</td>
<td>0.040 (0–152)</td>
<td>1.50*</td>
<td>1.70</td>
</tr>
<tr>
<td>Gelisols</td>
<td>11.30</td>
<td>0.072 (0–110)</td>
<td>1.41</td>
<td>1.57</td>
</tr>
<tr>
<td>Histisols</td>
<td>1.53</td>
<td>0.147 (0–100)</td>
<td>1.50*</td>
<td>0.34</td>
</tr>
<tr>
<td>Inceptisols</td>
<td>12.83</td>
<td>0.005 (0–73)</td>
<td>1.20</td>
<td>0.06</td>
</tr>
<tr>
<td>Mollisols</td>
<td>9.00</td>
<td>0.706 (0–165)</td>
<td>1.48</td>
<td>21.8</td>
</tr>
<tr>
<td>Oxisols</td>
<td>9.81</td>
<td>0.024 (0–100)</td>
<td>1.32</td>
<td>0.31</td>
</tr>
<tr>
<td>Spodosols</td>
<td>3.35</td>
<td>0.125 (0–100)</td>
<td>1.50*</td>
<td>0.21</td>
</tr>
<tr>
<td>Ultisols</td>
<td>11.05</td>
<td>0.064 (0–280)</td>
<td>1.65</td>
<td>3.25</td>
</tr>
<tr>
<td>Vertisols</td>
<td>3.35</td>
<td>0.311 (0–234)</td>
<td>1.95</td>
<td>4.69</td>
</tr>
<tr>
<td>Global total (continental areas covered by rocks or ice)</td>
<td>130.80</td>
<td></td>
<td></td>
<td>57.70</td>
</tr>
</tbody>
</table>

*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-Vilarrubia et al. (2010).
to ascertain the role of foliar leaching of K in the studies that have calculated the RE of these three nutrients, and some of these studies might be biased. Nieminen & Helmisaaari (1996) observed in Pinus sylvestris that after correcting RE for nutrient losses by net throughfall, the RE for K was higher than for N and P. Some results add even more complexity to interpretations comparing the RE among these three nutrients. Some studies showed that the RE for N, P and K varied considerably depending on the phase of RE, and that this depended on each studied species, but that the RE for K was generally higher than that for N and P (Nieminen & Helmisaaari, 1996; Fife & Nambiar, 1997; Fife et al., 2008). In summary, the available data allow us to deduce that the internal plant RE of K is important, and similar on average to the REs of N and P.

The availability of K in several terrestrial ecosystems can also strongly depend on the input of K from atmospheric deposition (Appendix S1 in Supporting Information), which can vary from 0.07 to more than 100 kg ha\(^{-1}\) year\(^{-1}\) (with a mean of the total, dry plus wet, atmospheric K deposition of 4.1 kg ha\(^{-1}\) year\(^{-1}\) from the available studies; Appendix S1). The available data suggest that the current levels of K fertilization (0.025 x 10\(^{9}\) t year\(^{-1}\)) and atmospheric deposition of K (0.066 x 10\(^{9}\) t year\(^{-1}\) ) are very low compared with the global amount of available soil K (57.7 x 10\(^{9}\) t). The current data for atmospheric K deposition also suggest that the amount of K from deposited from the atmospheric in some areas of the world could have a large impact on soil K concentration and on the stoichiometric relationship between K and other elements. For example, the deposition of 281 kg K ha\(^{-1}\) reported for southern Nigeria (Muoghalu & Oakhumen, 2000) or the 6–23 kg K ha\(^{-1}\) of wet deposition observed in some areas of India (Prathibha et al., 2010) are notable. In the last few decades, the National Atmospheric Deposition Program database (http://nadp.sws.uiuc.edu/) has determined wet deposition of K by analysing rainfall on 237 plots throughout North America; the data show a great variability depending on the site (from 0.022 to 3.0 kg K ha\(^{-1}\) year\(^{-1}\)). In this regard, we must highlight that data on wet deposition of K from precipitation have been collected for some areas of the world, but data on total K deposition are scarce despite the current knowledge suggesting that dry deposition of K could also be important (Appendix S1). It is surprising that studies on the potential effects of high amounts of K in terrestrial ecosystems have apparently been neglected, though there are many on the causes and consequences of N and even P deposition.

The atmospheric deposition of K originates from natural processes such as sea spray (Appendix S1) but also from agricultural activities and human industrial activities such as fertilizer and cement production, petrochemicals, the steel industry, and coal combustion (Klumpp et al., 2002; Walker et al., 2003; Urban et al., 2012). In some areas human activities can contribute a higher proportion of K deposition than natural processes (Fern & Hultberg, 1999; Golobocanin et al., 2009). However, we are far
from understanding the K fluxes between the atmosphere and the land and the role of anthropogenic activities in these fluxes (Quenneneh et al., 2012).

Ecological stoichiometric studies of terrestrial ecosystems have focused mostly on N and P (Vitousek & Howarth, 1991; Elser et al., 2000; Sterner & Elser, 2002; Sardans et al., 2012b). Similarly, studies on the impacts of the drivers of global change on terrestrial biogeochemical cycles have focused mainly on these two elements (Vitousek et al., 2010; Sardans et al., 2012c; Peñuelas et al., 2013a, b). Models of global carbon (C) circulation frequently do not include the role of nutrients in the establishment of C balances and the capacity of sinks to store C (Lé Quére et al., 2009). However, those that do usually include only N (Schimel et al., 2001; Mack et al., 2004; Langley & Megonigal, 2010) or more recently P (Peñuelas et al., 2012, 2013a,b).

There is an increase in the number of reports highlighting the importance of K in plant functions (Box 1) and responses to environmental changes, and its frequent limiting role for plant growth and C storage in terrestrial ecosystems. In the present review we aim to demonstrate the urgent need to include K in studies of biogeochemistry and stoichiometry in terrestrial ecosystems, and the consequences of global change on nutrient cycles and their mutual feedbacks.

MECHANISMS OF PLANT K UPTAKE

The importance of K in terrestrial plants is reflected by the sophisticated mechanisms of uptake, redistribution and homeostasis of K involving several families of cell wall and membrane proteins (Hirsch et al., 1998; Armengaud et al., 2004; Szczepańska 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 Ca2+ (Zhang et al., 2006; Szczepańska 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; Szczepańska et al., 2009). The high-affinity transport system is a saturable system, which catalyses the thermodynamically active uptake of K at low external K concentrations (< 1 mm) (Schachtman & Schroeder, 1994; Szczepańska 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; Szczepańska et al., 2009). Both systems, though, represent the entry of net positive electric charge, which requires the active removal of protons to maintain electrical neutrality (Leigh, 2001; Szczepańska 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-Mesbah 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 in a coordinated manner to maintain the appropriate cytosolic osmolarity (Patrick et al., 2001; Liu et al., 2006; Osakabe et al., 2013). Reports on the co-regulation of K and water channels in plants, however, are still scarce.

A WIDESPREAD LIMITING ROLE OF K IN PLANT GROWTH AND ECOSYSTEM PRODUCTIVITY

In contrast to the many physiological studies demonstrating the importance of K in terrestrial plants, few ecological studies have investigated the possible role of K limitation in terrestrial plant productivity, particularly in comparison with the studies on N and P limitation. The existing studies suggest that the fraction of vegetation that is K limited or K co-limited with N and/or P is high (Fig. 2, Appendix S2). Tripler et al. (2006) conducted a review and meta-analysis of K limitation in forest ecosystems with all the data available up to 2004. This meta-analysis, including 38 articles (a subset that is included in Fig. 2 and Appendix S2), showed an overall limiting effect of K on tree growth, with 69% of the studies showing some level of K limitation. We have now also included data from studies published up to July 2013 and from other terrestrial ecosystems such as grasslands, observing that 69% of 56 studies have detected at least some significant limiting role of K (Fig. 2, Appendix S2).

K STOICHIOMETRY AND WATER AVAILABILITY IN TERRESTRIAL ECOSYSTEMS

Most of the studies on the relationship between terrestrial plant stoichiometry and climatic gradients exclusively focused on N and P and their ratio (Reich & Oleksyn, 2004; Kerkhoff et al., 2005). Some recent studies observed that foliar K concentrations are negatively correlated with mean annual precipitation (MAP) (Fyllas et al., 2009; Zhang et al., 2012), whereas a few others observed contrary relationships (Sardans et al., 2011, 2012a). On the other hand, some studies positively related the capacity of plants to take up K to soil water availability (Fernandez et al., 2011; Ge et al., 2012). Tomlinson et al. (2013), while comparing leaf traits of different plant species growing in wet and arid environments, observed that leaves of species adapted to arid sites are small with high K concentrations. Furthermore, it was observed that tree species at the driest sites, such as in Mediterranean evergreen and dry tropical forests, have a higher capacity to change their seasonal internal allocation of K, with a higher allocation of K to leaves during summer (the driest season) than the species at wetter sites (Milla et al., 2005; Rivas-Ubach et al., 2012; Sardans et al., 2012a).

Thus a trade-off is expected because K uptake is strongly related to soil water content (Watson et al., 2001; Oliveira et al., 2004) while, as previously noted, K has a particular role in increasing water use efficiency and limiting water loss. Therefore, at a global scale in wet and more productive environments we should expect that plants are able to take up more K than in dry environments, but, on the other hand, in drier environments
Box 1

Main ecophysiological roles of K

**Water economy:** K is involved in many mechanisms that mitigate drought stress. Studies in greenhouses and with potted plants have demonstrated the importance of K supply in the resistance of plants to drought. K plays many fundamental physiological and metabolic roles in terrestrial plants in relation to water economy and osmotic homeostasis, such as maintenance of cellular turgor and osmotic pressure (Ashraf et al., 2002; Levi et al., 2011), control of water conductance and transpiration (Harvey & van den Driessche, 1999; Arquero et al., 2006; Benlloch-González et al., 2010), improvement of root hydraulic conductivity (El-Mesbahi et al., 2012), regulation of sap flow (Oddo et al., 2011), regulation of membrane potentials (Schroeder & Fang, 1991), stomatal control (Talbott & Zeiger, 1996; Benlloch-González et al., 2010) and maintenance of ionic homeostasis or transmembrane potential (Su et al., 2001; Waraich et al., 2011). Moreover, field studies have observed that K, apart from its role in stomatal control and water conductance, can further affect water economy as an osmolyte (Babita et al., 2010; Levi et al., 2011) directly linked to improving the capacity to retain water (Nandwal et al., 1998; Rao et al., 2012).

In support of these physiological observations, some recent metabolomic studies have observed that K concentrations are related to increases in molecular osmolytes under drought (Talbott & Zeiger, 1996; Levi et al., 2011; Rivas-Ubach et al., 2012). The mediterranean evergreen *Olea europea* decreases its capacity to regulate stomatal control when growing under moderate K deficiency (Arquero et al., 2006); this suggests that even drought-resistant tree species can suffer detrimental effects in their growth capacity and survival under drought conditions through a reduction in their capacity to take up K. A few studies, though, have observed no effects of K availability on drought avoidance (e.g. Ashraf et al., 2002).

K also contributes to the detoxification of reactive oxygen species (ROS) (Wang et al., 2013). The impairment of stomatal regulation in K-deficient plants under drought stress produces a consequent impairment of CO₂ fixation, and molecular oxygen is activated leading to the generation of ROS (Cakmak, 2000). Under drought conditions, an increase in extrachloroplastic K⁺ concentrations in plant cells with an adequate K supply prevents the inhibition of photosynthesis (Egilla et al., 2005). This effect is related to the role K plays in enhancing photosynthetic CO₂ fixation, improving the transport of photosynthates into sink organs and inhibiting the transfer of photosynthetic electrons to O₂, thereby reducing ROS production (Cakmak, 2005). Many field studies have thus observed correlations between K concentrations in plants and soils and mechanisms of drought avoidance (Nandwal et al., 1998; Arquero et al., 2006; Teixeira et al., 2008; Fayyaz et al., 2013; Tomlinson et al., 2013).

Many physiological and metabolomic studies in garden and potted plants (Babita et al., 2010; Cuéllar et al., 2010) and in crops (Römheld & Kirkby, 2010; Waraich et al., 2011; Wang et al., 2013), and some studies across environmental conditions under field-conditions (Kadar & Foldesi, 2001), have observed a strong link between K concentrations and the resistance and adaptation of plants to drought. Under drought K deficiency, plant defoliation (Harvey & van den Driessche, 1999) and mortality (Del Campo et al., 2011; El-Mesbahi et al., 2012) increase. A few studies, though, have observed no effects of K availability on drought avoidance (e.g. Ashraf et al., 2002).

**Other physiological functions:** Many plant functions that are not directly related to water economy have recently been associated with K, such as enzymatic activity and protein synthesis (Armengaud et al., 2004, 2009), internal transport and allocation of amino acids and nitrates (Jarvis et al., 1990), photosynthetic activity and retranslocation of fixed C (Zhao et al., 2001; Teixeira et al., 2008), signal transduction and energy transport (Gajdanowicz et al., 2011), cellular, foliar and root expansion (Elumalai et al., 2002; Yin et al., 2011) and foliar movement (Travlos et al., 2008), among several other metabolic and physiological functions essential for plant life. Evidence, moreover, is increasing that adequate K fertilization plays an important role in defending crops not only against drought but also against many other biotic and abiotic stresses such as diseases, pests, salinity, cold, frost and waterlogging (see the recent review by Wang et al., 2013). Gajdanowicz et al. (2011) recently observed that K⁺ circulating in the phloem creates a mobile gradient serving as a decentralized energy store that can be used to overcome local energy limitations through the activation of diverse membrane proteins. The authors observed that post-transcriptional modification of the phloem-expressed *Arabidopsis* K⁺ channel AKT2 taps this ‘potassium battery’, which then efficiently assists the plasma membrane H⁺-ATPase in energizing the transmembrane phloem reloading processes. Thus K⁺ will be loaded into the phloem from source tissues where sufficient chemical energy is available. The established transmembrane K⁺ gradient is then transported with the phloem stream to other parts of the plant. The energy stored in the K⁺ membrane gradient can be harvested to fuel transport processes by opening a gateway (for example the AKT2-like channels) for the passage of K⁺ ions through the membrane, this process being related to sucrose leakage from the phloem that enhances energy status.
reported in some studies; see, e.g. Fayyaz dry ecosystems, compensating for the low capacity for K uptake K remains considerable and could be expected to be higher in insures such as drought or herbivore attack (Rivas-Ubach et al. 1989). Thus, at the moment, given all these previous results, it is more actively retained in dry or wet ecosystems. difficult to reach any consistent conclusion on whether K is have been found to co-vary with the entire metabolome, sug-gesting the importance of K in global plant function, despite its absence from biomolecules (Rivas-Ubach et al. 2012, 2014; Sardans & Peñuelas, 2012). Foliar K concentrations have been found to co-vary with the entire metabolome, suggest-ing the importance of K in global plant function, despite its absence from biomolecules (Rivas-Ubach et al., 2012, 2014). The strong link between plant K concentrations and water avail-ability justifies the study of K and its stoichiometric relation-ships with other nutrients. Focusing on K would more strongly integrate the dimension of water availability in the study of terrestrial ecological stoichiometry. Recent ecological stoichiometric studies have observed that K plays a more funda-mental role than does N or P in the differences in elemental composition among and within species in response to differen-tial availability of water.

Some studies have shown that different grass species have different optimal N:K supply ratios (Lawniczak et al., 2009). A reduction in soil K availability is frequently observed as a con-sequence of N deposition. As noted below, this is due to large losses of K by leaching that causes nutrient imbalances. More-over, other studies have observed that K concentrations in the soil solution and in runoff are more sensitive to changes in land use and fertilization than N or P concentrations (Watmough et al., 2005; Anguelov et al., 2011), and also that K is more quickly leached from litter than N or P and has a much shorter residence time in soil organic matter (Florez-Florez et al., 2013; Schreeg et al., 2013).

**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 potential global cropland area (FAO, 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 supply/demand balance for fertilizer nutrients indicates that Africa will remain an exporter of phosphate and nitrogen – but for potash the region would continue to depend solely on imports (FAO, 2011). This fact, along with the great economic deficits in most African states, makes K a critical limiting factor for food production in that continent.

Croplands in China, Egypt, Bulgaria and parts of south-eastern 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 increasing impoverishment of K in cropland soils (Vanderpol & Traore, 1993; Singh & Bansai, 2009). Moreover, the rising 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). Agricultural practices that decrease soil pH favour K leaching and thus decrease availability for plants (Sharifi et al., 2013). For example, despite N fertilization sometimes enhancing soil K availability in the short term by decreasing soil pH (Mitchell & Smethurst, 2008), in the absence of K fertilization it finally leads to a decrease in soil K availability because of leaching (He et al., 1999; Mitchell & Smethurst, 2008; Yavitt et al., 2011; Glab & Gondek, 2014).

Demand for and use of fertilizers are expected to increase in the coming decades (Roberts, 2008). Mineable reserves of K are sufficient to meet the projected demand for centuries (Roberts, 2008). Some results suggest that the increasing use of K fertilizer in some regions in recent decades has increased the atmospheric deposition of K in areas adjacent to cropland (Gélinas et al., 2000). The deposition of K from agricultural activities is very high in some developing countries such as Brazil, reaching 55% of total K deposition (Allen et al., 2010). In contrast, the

**Figure 2** The 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.)
deposition of K from energy production and industrial plants has decreased in some European countries (Ruoho-Airola & Salminen, 2003). Some studies have observed that K deposition, linked to industrial and, frequently, agricultural activities, can represent a higher proportion than that from natural processes (Ferm & Hultberg, 1999; Golobocanin et al., 2009) such as sea spray (Poor et al., 2006; Prathibha et al., 2010).

Inputs of K from atmospheric deposition have a determinant role in K balances of forests, counteracting, such as observed in some areas, the loss of K from leaching, which is favored by N deposition (Friedland & Miller, 1999; Watmough & Dillon, 2004). These inputs of K contribute to K availability in tropical forest ecosystems (Vitousek & Sanford, 1986; Muoghalu & Oakhunen, 2000). All these findings justify the study of the impacts of an increased use of K fertilizers on the rates of K atmospheric deposition and thereafter on ecosystem function at least in some parts of the world.

**K in a drier world**

Climate models project an increase in the extent of drought over large areas of the world that are already dry, such as the Mediterranean Basin and the Sahel (IPCC, 2007). Despite the intensive study of drought resistance under field conditions, only a few field studies have tested the impacts of drier conditions on the status of K in terrestrial plant communities (Appendix S3). These studies show that drought increases total soil K but decreases its soluble soil fraction. Moreover, drought increases the retention of K in the wood of some species and the concentration of K in the photosynthetic tissues of others (Appendix S3). The effects of drought are usually asymmetrical in different plant organs, because plants tend to allocate and retain more K in stems and a fraction of this K is transported to leaves during the driest seasons (Appendix S3). These few studies suggest a possible increase in biomass K concentrations in dry areas but also a possible decrease in total biomass K content as a result of reduced growth. This decrease of K in biomass and increases in total soil K could enhance the risk of higher losses of K from soil.

As previously stated, the availability and uptake of K are essential for improving drought resistance in various types of plant communities (Harvey & van den Driessche, 1999; Ashraf et al., 2002; Egilla et al., 2005; Sardans et al., 2012c). Globally, however, plant K uptake appears to be associated with water availability (Sardans et al., 2011, 2012a; Ge et al., 2012), wherein a lower K uptake in turn negatively affects water uptake by reducing the activity of aquaporins (Kanai et al., 2011). All these interconnected relationships strongly suggest a cascade of higher water deficit, lower K uptake and a reduced capacity to avoid drought, which could become a serious problem in currently dry areas that are threatened by future drier scenarios. These scenarios could even be more negative if torrential rain increases and MAP decreases, as projected for areas such as the Mediterranean Basin and the Sahel (IPCC, 2007). Moreover, the capacity of different plant species to use and remobilize K can be crucial in their competitive relationships (Dunlop et al., 1979; Tilman et al., 1999). Thus, due to the importance of K in conditions of water stress, we can expect that K will become an significant factor in the shifts in species composition of plant communities under drought. Plants can also respond to drought by improving their efficiencies of K and water uptake. Some phenomena linked to improved resistance to drought stress, such as soil patchiness or the capacity to redistribute water, can favour K uptake. Plants under drought can improve the use of water for the uptake of nutrients by their capacity to redistribute soil water (Sardans & Peñuelas, 2014). Hydraulic lift and its opposite, downward siphoning (Smith et al., 1999), can favour the recirculation of water, efficiency of water use and the capacity of plants to take up nutrients (Sardans & Peñuelas, 2014). A higher capacity to redistribute water to increase K uptake can be a key factor for the survival of plants in drier conditions. In this context, due to the lack of studies, it is not possible to assess the importance of water redistribution in enhancing not only water-use efficiency but also the capacity for nutrient uptake.

Moreover, the variability of water and nutrient availability on slopes in the drier areas of the Mediterranean Basin is related to the distribution of patches of vegetation relative to the patches of bare soil that can be considered as runoff sinks and sources, respectively (Gabarrón-Galeote et al., 2012; Merino-Martin et al., 2012; Sardans & Peñuelas, 2013). This effect of patches is crucial for the conservation of vegetation at drier sites. Gómez-Aparicio et al. (2005) have observed that the presence of large woody plants improves the availability of soil nutrients, and in particular of K, in Mediterranean ecosystems. The role of soil patches in changes in the complete K cycle has not been specifically studied, despite the possibility that in patches the higher availability of water, the better soil texture and the horizontal redistribution of water could strongly affect the K cycle.

**Impacts of N and acid atmospheric deposition on the K cycle**

The impacts of N deposition on decreasing C:N in plants and soils have been extensively reported (Mulder et al., 2013). However, only a relatively small number of studies on the impacts of N deposition on terrestrial ecosystems stoichiometry have taken K into account (Fig. 3, Appendix S4). Our review of current literature shows that atmospheric N deposition increases the leaching of K from soils, thus decreasing K concentrations in the soils (and decreasing K concentrations and increasing N:K ratios in plants). Despite plants responding by increasing K uptake, ultimately K limitation is often observed. This loss of K under N deposition is frequently related to K deficiencies in trees (Tzvetkova & Hadjiivanova, 2006). Moreover, atmospheric S deposition has also contributed to leaching of K, thus decreasing soil K availability in several European (Britton et al., 2008; Sutton et al., 2011) and North American (Mitchell et al., 1996; Navratil et al., 2010) regions. However, this type of K leaching has been reduced in the last decades as a result of the dramatic reduction of S emissions in Europe since the early 1980s due to reduced coal combustion and the
have observed the opposite pattern. The invasive success of *Taraxacum officinale* in the Andes has been linked to low soil K availability (Cavieres et al., 2008). By examining the impacts of seven widespread invasive plant species in northern Europe, Dassonville et al. (2008) observed that invasive species reduced soil K availability in K-rich soils, but increased soil K availability in K-poor soils. The success of alien plants thus appears to depend on high K availability in productive environments and on low K availability in less productive environments; however, the small number of studies precludes formulation of a definitive conclusion about this dependence (Funk & Vitousek, 2007; Peng et al., 2011; Sardans & Peñuelas, 2012). Alien plants with a more efficient use of K may be able to increase their spread in arid areas. Islands are among the areas most threatened by the success of invasive plants (Denslow et al., 2009; Atwood & Meyerson, 2011). Current literature relates alien success in islands to several variables linked to humans, such as population density (Atwood & Meyerson, 2011; Traveset et al., 2014), the level of human impact (MacDonald et al., 1991; Monty et al., 2013), ecological traits such as genetic diversity (Hardman et al., 2012; Traveset et al., 2014), differences in phylogeny with native species (Bezeng et al., 2013), island area (Traveset et al., 2014), isolation and distance to the nearest continent (Traveset et al., 2014) and climate change (Yamashita et al., 2000). The possible relationship between bedrock K$_2$O concentrations and alien plant success remains mostly unexplored. However, Denslow et al. (2009) observed a significant relationship between the main substrate of the island (coralline limestone islands, basaltic with metamorphic, ultrabasic, and continental plutonic islands) and the number of invasive plants.

**FINAL REMARKS**

1. The data available from current studies on the role of K availability in the growth of plants indicate that K is frequently a limiting factor for plant productivity in terrestrial ecosystems.
2. Apart from the well-known physiological processes linked to water economy, such as enzymatic function, internal transport systems and cell membrane integrity, K has recently been associated with an increasing number of plant ecological processes, such as resistance to diseases, herbivory, salinity, cold, frost or waterlogging, with large implications for ecosystem function and capacity for global crop production.
3. Recent ecological stoichiometric studies of terrestrial ecosystems that have included K with the classically considered C, N and P have shown that the stoichiometric changes involving K
are even larger than those involving N and P in the responses of plants to environmental changes. These findings justify the inclusion of K in ecological stoichiometric studies.

4. Drought can be more intense in currently arid areas. Given the importance of K in water-use efficiency and the difficulty of K uptake under drought conditions, K is expected to have an increasingly important role in determining the function and survival of plant communities.

5. Several processes, such as forest decline and soil imbalances, have been linked to N deposition but the impacts on K are not well known.

6. Current studies suggest that the success of invasive species in environments that are not strongly limited by nutrients is associated with a high capacity for K uptake and with the consequent decrease in the K availability of soils.

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**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of this article at the publisher’s web-site.

**Appendix S1** Annual atmospheric rates of K deposition (kg ha⁻¹ year⁻¹).

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

**Appendix S3** Effects of water availability on the ecosystem K cycle.

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

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

**Appendix S6** References for the Supporting Information.

**BIOSKETCHES**

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