Potassium: a neglected nutrient in global change

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Running title: Potassium stoichiometry and global change

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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
conservative biogeochemical cycle are underlying the maintenance of K supply to plants (Nowak et al., 1991; Jobbáry & 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, hence 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 immediate available-water soluble and the exchangeable fraction are 1-2%, and the soil unavailable fractions are 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, Figure 1).

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

However, soil-plant system has a notable control on the ecosystem K-cycle they contribute in its retention. Current available data show a notable plant capacity to retain K by resorption. Diverse results have been reported in the studies comparing N, P, and K resorption efficiency (RE). Some researchers have observed N=P<K RE (van den Driessche, 1985; Nieminen & Helmisaari, 1996; Sardans et al., 2005), others have observed P<N=K RE (Ozbuacak et al. 2008), N<K=P RE (Chuyong et al., 2000), N>K>P RE (Yin et al., 2009), P>K>N RE (Sahehi et al., 2013), K<N=P RE (Helmisaari, 1992; Duchesne et al., 2001; Tartachnyk & Blanke, 2004; Hagen-Thorn et al., 2006), and N=P=K RE (Gallardo et al., 1999; Trémolières et al., 1999). A recent review of a global dataset has observed that K RE on a global scale (70.1%) seems to be higher than the RE of 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 to know the role of K foliar leaching in the studies that have calculated RE of these three nutrients, and some of these studies might be biased. Nieminen & Helmisaari (1996) observed in Pinus sylvestris that after correcting RE for nutrient losses by net throughfall, K RE was higher than N and P RE. Some results add even more complexity in the interpretation of the comparison of RE among these three nutrients. Some studies showed that the RE of N, P and K varied considerably depending on the phase of RE, and that this variance depended of each studied species,
but that this K RE was generally higher than N and P RE (Niemenen & Helmisaari, 1996; Fife & Nambiar, 1997; Fife et al., 2008). In summary, the available data allow 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 by atmospheric deposition (Table 2), which can vary from 0.07 to more than 100 kg ha\(^{-1}\) yr\(^{-1}\) (with a mean of the total, dry plus wet, atmospheric K deposition of 4.1 kg ha\(^{-1}\) yr\(^{-1}\) for the available studies, Table 2). The available data suggest that the current levels of K fertilization (0.025 \(\times 10^9\) t yr\(^{-1}\)) and K atmospheric deposition (0.066 \(\times 10^9\) t yr\(^{-1}\)) are very low compared with the global amount of available soil K (57.7 \(\times 10^9\) t). The current data for atmospheric K deposition also suggest that the amounts of K from atmospheric deposition in some areas of the world could have a large impact on soil K concentrations and on the stoichiometric relationships 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 K deposition by analyzing rainfall of 237 plots throughout North-America; the data show a great variability depending on the site (from 0.022 to 3.0 kg K ha\(^{-1}\) yr\(^{-1}\)). In this regard, we must highlight that the data of wet K deposition from precipitation have been collected for some world areas, the data of total K deposition are scarce despite the current knowledge suggest that K dry deposition could also be important (Table 2). It is surprising that studies on the potential effects of high amounts of K in terrestrial ecosystems have been apparently neglected,
though there are so many on the causes and consequences of N- and, even, P depositions.

The atmospheric deposition of K originates from natural processes, such as sea spray (Table 2) but also from agricultural activities and human industrial activities such as fertilizer and cement production, petrochemistry, steel industry, and coal combustion (Klumpp et al., 2002; Walker et al., 2003; Urban et al., 2012). Human activities can represent a higher proportion than the natural processes (Ferm & Hultberg, 1999; Golobocanin et al., 2008). We are, however, far from understanding the K fluxes between the atmosphere and the land and the role of anthropogenic activities in these fluxes (Quennehen 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, 2013b).

There is an increase in number of reports that highlight 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 study, we aim to demonstrate the urgent necessity to include K in the studies of biogeochemistry and stoichiometry in terrestrial ecosystems, and of the consequences of 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 Ca²⁺ (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
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 to 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 (Figure 2, Table 3). Tripler et al. (2006) conducted a review and metadata analysis of K limitation in forest ecosystems with all the data available until 2004. This meta-analysis, including 38 articles (a subset that is included in Figure 2 and Table 3), showed an overall limiting effect of K in 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 (Figure 2, Table 3).

K stoichiometry and water availability in terrestrial ecosystems

Most of the studies on 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 few others observed contrary relationships (Sardans et al., 2011; 2012a). On the other hand, some studies positively related plant K uptake capacity with 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 commented, K is specially determinant to increase water use efficiency and to limit water losses. Therefore, at a global scale in wet and more productive environments, we should expect that plants are able to uptake more K than in dry environments, but, on the other hand, in drier environments plants can also increase their K concentrations by conservative mechanisms, such as increasing K resorption. Thus, current data suggest not only that K uptake is strongly determined by water availability but also that K is crucial to the strategies of water economy, leading to the paradox that the more necessary K is (under drought), the more difficult is its uptake.

Some studies have observed that K accumulation in soil is greatest in arid ecosystems rather than in mesic ecosystems (Singer, 1989), despite studies of natural gradients have observed that K accumulates and concentrates more in biomass with increasing annual mean precipitation (Sardans et al., 2011). However, RE of K remains considerable and could be expected to be higher in dry ecosystems, compensating the low capacity of K uptake in dry conditions (in comparison with plants at wetter sites as reported in some studies, see e.g. Fayyaz et al., 2013; Tomlinson et al., 2013). Moreover, the K retention capacity in plants in arid environments could be improved by
lower leaching (Singer, 1989). Thus at this moment, given all these previous results, it is difficult to reach any consistent conclusion on whether K is more actively retained in dry or wet ecosystems.

Recent stoichiometric studies have observed that K is even more variable among dry plant ecotypes than N and P (Sardans et al., 2011) and is also more responsive to environmental pressure such as drought or herbivore attack (Sardans et al., 2013; Rivas-Ubach et al., 2012; 2014). Foliar K concentrations have been found to co-vary with the entire metabolome, suggesting 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 availability justifies the study of K and its stoichiometric relationships 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 fundamental role than does N or P in the differences in elemental composition among and within species in response to different water availability.

Some studies have shown that different grass species have different optimal N:K ratios of supply (Lawniczak et al., 2009). A reduction in soil K availability is frequently observed as a consequence of N deposition. As commented below, this is due to large losses of K by leaching that causes nutrient imbalances. Moreover, 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 it has a much shorter residence time in soil organic matter (Schreeg et al., 2013; Florez-Florez 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 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
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).

Demands and uses 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 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 as well, can represent a higher proportion than that from natural processes (Ferm & Hultberg, 1999; Golobocanin et al., 2008) 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 & Oakhumen, 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 (Table 4). 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 (Table 4). 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 (Table 4). 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 total soil K increases 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 & Peñuelas, 2012c). Globally, plant K uptake, however, appears to be associated with water availability (Sardans et al., 2011; 2012a; Ge et al., 2012), wherein less 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 (ICPP, 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 high relevance of K under conditions of water stress, we can expect that K will become an important factor in the shifts in species composition of plant communities under drought. Plants can also respond to drought by improving efficiencies of K and water uptake. Some phenomena linked to an improved resistance to drought stress, such as soil patchiness or the capacity to redistribute water, can favor 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, 2013b). Hydraulic lift and its opposite, downward siphoning (Smith et al., 1999), can favor water recirculation, efficiency of water use and the capacity of plants to take up nutrients (Sardans & Peñuelas, 2013b). 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 of 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, 2013c). This effect of patches is crucial in 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 the 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 proportion of the studies on the impacts of N deposition on terrestrial ecosystems stoichiometry have taken K into account (Figure 3). Our review of current literature shows that atmospheric N deposition increases the leaching of K from soils, thus decreases K concentrations in the soils (and decreases K concentrations and increases N:K ratios in plants. Despite that plants respond to increasing K uptake, an ultimate enhancement of K limitation is frequently observed. This loss of K under N deposition is frequently related to K deficiencies in trees (Tzvetkova & Haddjiivanova, 2006). Moreover, atmospheric S deposition has also contributed to K leaching 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) areas. However, this 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, after the reduction of coal combustions and the implementation of policies to improve air quality (Eurostat, 2009; Navratil et al., 2010; Robinson et al., 2013).

The N eutrophication effects on the K cycle and N:K ratios may have large flow-on impacts (Figure 3). Decreases in soil K contents and increases in soil N:K ratios are associated with the loss of species richness (Huang et al., 2013). Moreover, P:K soil ratios can increase because the solubility and mobility of K are higher than those of P, therefore K leaches more easily than P (Olde Venterink et al., 2009). Changes in N:K and P:K ratios can favor species tolerance to water stress or competitively faster-growing species, depending on the circumstances. For example, a decrease in N:K ratio under increasing drought would probably favor the stress-tolerant species, which are
better adapted to allocate K to their leaves and to use it to improve drought avoidance, more than favoring the faster-growing competitors.

**K and success of plant invasion:** Most studies have focused on the roles of N and P in the success of species invasion (Sardans & Peñuelas, 2012). The few studies investigating relationships between invasive success and the K availability of soils have found the relationships to be important. In most cases, the success of alien plants depends on a high availability of soil K (Figure 4) and on a higher capacity of K uptake by the invasive species compare to the native plants (Pieters & Baruch, 1997), but it has also been associated with low soil K availability after the establishment of invasive species (Figure 4). Other studies, however, have observed an opposite pattern. The invasive success of *Taraxacum officinalis* 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 low number of studies precludes formulation of a definitive conclusion on 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 most threatened areas by plant invasive success (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), 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 nearest continent (Traveset et al., 2014), and climate change (Yamashita et al., 2000).

The possible relationship between bedrock K$_2$O concentrations and plant alien 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 on ecosystem function and capacity of 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 plant responses to the environmental changes. These findings justify the inclusion of K in ecological stoichiometric studies.

4. Drought can be more intense in current 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. N deposition has been linked to several processes, such as forest decline and soil imbalances, 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 of K uptake and with the consequent decrease in K availability of soils.

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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 toward drought. K plays many fundamental physiological and metabolic roles in terrestrial plants related 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 Driessche, 1999; Arquero *et al.*, 2006; Benloch-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; Benloch-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 CO$_2$ fixation, and molecular oxygen is activated leading to the generation of ROS (Cakmak, 2000). Under drought conditions, an increase of 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 CO$_2$ fixation, improving the transport of photosynthates into sink organs and inhibiting the transfer of photosynthetic electrons to O$_2$, thereby reducing ROS production (Cakmak, 2005). Many field studies have thus observed correlations between K concentrations in plants and soils with 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 gradients 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-Mesbah et al., 2012) increases. 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., 1989), 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. Evidences, moreover, are
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 recent review of Wang et al.,
2013). Gajdanowicz et al. (2011) recently observed that K\textsuperscript{+} 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 posttranscriptional modification of the phloem-expressed
Arabidopsis K\textsuperscript{+} channel AKT2 taps this “potassium battery”, which then efficiently
assists the plasma membrane H\textsuperscript{+}-ATPase in energizing the transmembrane phloem
reloading processes. Thus K\textsuperscript{+} will be loaded into the phloem from source tissues where
sufficient chemical energy is available. The established transmembrane K\textsuperscript{+} gradient is
then transported with the phloem stream to other parts of the plant. The energy stored in
the K\textsuperscript{+} membrane gradient can be harvested to fuel transport processes by opening a
gateway (for example the AKT2-like channels) for the passage of K\textsuperscript{+} ions through the
membrane being this process related to sucrose leakage from the phloem that enhances
energy status.
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Additional references to data sources can be found in Appendix S5 at [URL].

**SUPPORTING INFORMATION**

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

**Appendix S1.** Annual atmospheric rates of K deposition (kg ha\(^{-1}\) yr\(^{-1}\)).
Appendix S2. The limiting role of K on plant growth.

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

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

Appendix S5. Plant invasion and soil K availability.

Appendix S6. References for the supporting information.

BIOSKETCH

Dr. Jordi Sardans and Prof. Josep Peñuelas are researchers focusing on the field of plant ecophysiology, biogeochemical cycles and atmosphere-biosphere interactions. JS’s primary focus is on the elemental stoichiometry relationships with terrestrial ecosystems structure and function and in the metabolomic plant responses to abiotic and biotic changes. JP’s research covers a wide range of ecological disciplines: chemical ecology, biogeochemistry, global change, climate change, atmospheric pollution, biogenic VOCs emissions, remote sensing, and functioning and structure of terrestrial plants and ecosystems.
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 (x 10^6 km^2)</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 (x 10^9 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>0.8</td>
<td>0.17</td>
</tr>
<tr>
<td>Aridisols</td>
<td>15.73</td>
<td>0.620 (0-279)</td>
<td>1.5*</td>
<td>40.1</td>
</tr>
<tr>
<td>Entisols</td>
<td>21.14</td>
<td>0.040 (0-152)</td>
<td>1.5*</td>
<td>1.70</td>
</tr>
<tr>
<td>Gelisols</td>
<td>11.3</td>
<td>0.072 (0-110)</td>
<td>1.41</td>
<td>1.57</td>
</tr>
<tr>
<td>Histosols</td>
<td>1.53</td>
<td>0.147 (0-100)**</td>
<td>1.5*</td>
<td>0.337</td>
</tr>
<tr>
<td>Inceptisols</td>
<td>12.83</td>
<td>0.005 (0-73)</td>
<td>1.2</td>
<td>0.059</td>
</tr>
<tr>
<td>Mollisols</td>
<td>9.0</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>0.310</td>
</tr>
<tr>
<td>Spodosols</td>
<td>3.35</td>
<td>0.125 (0-100)</td>
<td>1.5*</td>
<td>0.210</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><strong>Global total</strong> (continental areas covered by rocks or ice)</td>
<td>130.8</td>
<td></td>
<td></td>
<td>57.7</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-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).
0.066 x 10^9 t K
deposition (References in Table S1)

ATMOSPHERE

wind

SOIL

57.7 x 10^9 t K^{1,2}
(1-2% of total soil K)
Plant available
(in soil solution plus exchangeable)

57.7 x 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

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

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

Figure 2

<table>
<thead>
<tr>
<th>Ecosystem type</th>
<th>Non K-limited</th>
<th>K-limited</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grasslands</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>Forests</td>
<td>14</td>
<td>35</td>
</tr>
</tbody>
</table>
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 \[ \rightarrow + (9) \rightarrow K \text{ soil availability} \]
\[ \leftarrow - (2) \leftarrow + (0) \leftarrow - (4) \]

Figure 4