ECOHYDROLOGY
Ecohydrol. **7**, 1–20 (2014)

Ecohydrology Bearings — Invited Commentary

Hydraulic redistribution by plants and nutrient stoichiometry: Shifts under global change

Jordi Sardans[1]* and Josep Peñuelas[2]

[1] *CSIC, Global Ecology Unit CREAF-CEAB-UAB, Cerdanyola del Vallès, Barcelona, Catalonia, Spain*
[2] *CREAF, Barcelona, Catalonia, Spain*

ABSTRACT

Hydraulic lift, water movement from deep to upper soil layers by roots, is a widespread process in temperate and semi-arid environments. It can contribute 17–81% of total water transpired and favour the uptake of nutrients available mainly from soil organic matter decomposition (e.g. N). Downward siphoning, water movement from upper to deep soil layers, can represent 10–60% of total transpired water, favouring the uptake of nutrients supplied mainly from the leaching of bedrock minerals (e.g. P and K). These vertical water movements also can affect the N : P ratio of runoff waters when, in the case of hydraulic lift, they open the possibility for a given pulse of water to circulate multiple times across the N-rich upper soil layers. Plants, thus, affect the stoichiometry of nutrients in soils and groundwater not only through the physical protection of the soil and through the water uptake but also through water redistribution. Soil water redistribution can also play an outstanding role in the ecosystem responses to global change drivers. The increase in soil patchiness in current and future arid lands modifies runoff fluxes, hydraulic lift and downward siphoning, allowing plants to dispose of higher water and nutrient availabilities. The higher use of hydraulic lift and/or downward siphoning by alien species is a possible cause of alien plant success. Further mechanistic and quantitative research is thus warranted to discern the plant role in water and nutrient cycling and in the responses to global change. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS plant water redistribution; drought; warming; phosphorus; nitrogen; nitrogen deposition; invasive species; water uptake; nutrient uptake, downward siphoning, hydraulic lift

Received 13 March 2013; Revised 10 October 2013; Accepted 16 November 2013

INTRODUCTION

The use and redistribution of water by plants affect the availability and stoichiometry of soil nutrients

One of the most important processes linking hydrology with the availability of soil nutrients through plant function is the capacity of plants to redistribute water from deep to shallow soil layers and vice versa.

Hydraulic lift (HL) involves the redistribution of soil moisture by the root systems of plants from deep, wet soil layers to the drier surface layers, mainly at night. HL is a passive process driven by gradients in water potentials and is thought to benefit plants by increasing the availability of soil moisture for use the next day (Caldwell *et al.*, 1998; Filella and Peñuelas, 2003, Zou *et al.*, 2005). HL is advantageous in resisting drought, the capacity of which is variable among plant species (Huang 1999), and some studies suggest that HL could play an important role in global water circulation and the seasonal cycles of temperature, mainly in areas with dry seasons (Lee *et al.*, 2005). Epigeous ectomycorrhizal fungi have been shown to lift water from deep to shallow soil layers during periods of drought in a montane pine forest (Lilleskov *et al.*, 2009). HL can enhance water use in entire plant communities. The water raised by deep-rooted species can benefit shallow-rooted species (Burgess, 2011), thus enhancing the survival not only of the lifting but also of the neighbouring plants (Liste and White, 2008; Katul and Siqueira, 2010; Prieto *et al.*, 2011).

The quantity of water lifted can vary between 17% and 81% of the water transpired (Caldwell and Richards, 1989; Kurz-Benson *et al.*, 2006; Bayala *et al.*, 2008; Bleby *et al.*, 2010; Domec *et al.*, 2010; Brooksbank *et al.*, 2011a, 2011b) with a mean value among the different studies of approximately 40% of total water transpired by vegetation (Table I). HL can result in an increase of water content in the upper soil layers of between 28% and 102% (Emerman and Dawson, 1996; Brooks *et al.*, 2002, 2006; Hao *et al.*, 2010; Brooksbank *et al.*, 2011a, 2011b; Warren *et al.*, 2011)

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*Correspondence to: Jordi Sardans, CSIC, Global Ecology Unit CREAF-CEAB-UAB, Cerdanyola del Vallès, Barcelona 08913, Catalonia, Spain. E-mail: j.sardans@creaf.uab.cat

Table I. Effects of the redistribution of water in soil by plant roots [hydraulic lift (HL) and downward siphoning (DS)] on the hydrology, nutrient cycle and stoichiometry in plant–soil–water systems.

Site and species	Results	Reference
	Hydraulic lift	
Vitis vinifera × *Vitis rupestris*; field study and greenhouse experiment	Observation of HL and lateral water redistribution	Bauerle *et al.* (2008)
African agroforestry system with tree species *Vitellaria paradoxa* and *Parkia biglobosa*; field study	Observation of HL, which was more intense under higher nutrient availability in the upper soil layers; lifted water represents 53–60% of total water transpired	Bayala *et al.* (2008)
Semi-arid woodland, *Quercus fusiformis*, *Bumelia lanuginosa* and *Prosopis glandulosa*; field study	Observation of HL and lateral water redistribution; lifted water represents 22% of total water transpired	Bleby *et al.* (2010)
Temperate forest of *Pinus ponderosa* and *Pseudotsuga menziesii*; field study	28% and 35% of the water removed daily from the upper 2 m were replaced by nocturnal HL in stands of *P. menziesii* and *P. ponderosa*, respectively	Brooks *et al.* (2002)
P. menziesii forest; field study	Observation of HL; in the most active periods, HL replenished approximately 40% of the water depleted from the upper soil on a daily basis	Brooks *et al.* (2006)
Eucalyptus kochii stands in Australia; field study	Observation of HL; lifted water represents 27% of total water transpired, increasing water in the upper soil layer by 30%	Brooksbank *et al.* (2011a, 2011b)
Artemisia tridentate, *Agropyron desertorum*	Observation of HL; lifted water represents 25–50% of total water transpired	Caldwell and Richards (1989)
Semi-arid shrubland; field study	No evidence of HL contributing to smoothing spatial soil nutrient heterogeneity	Caldwell and Manwaring (1994)
Medicago sativa; pot experiment	Observation of HL	Corak *et al.* (1987)
Seasonal Amazonian rainforest; field study	Observation of HL during dry season	Da Rocha *et al.* (2004)
Quercus ilex and *Quercus suber* mixed forest; field experiment	Observation of HL in both species in summer	David *et al.* (2007)
Acer saccharum; field study	Observation of HL; between 3% and 60% of lifted water by trees was uptaken by understorey	Dawson (1993)
P. menziesii and *P. ponderosa* stands; field study	Observation of HL	Domec *et al.* (2004)
Blepharocalyx salicifolius, *Kielmeyera coriacea*, *Qualea parviflora*, *Byrsonima crassa*, dry tropical woodland; field experiment	Observation of HL	Domec *et al.* (2006)
Pinus taeda forest; field study	Observation of HL; lifted water represents 30–50% of total water transpired	Domec *et al.* (2010)
Quercus agrifolia; pot experiment	Observational HL and posterior transfer of hydraulically lifted water between plants by the action of mycorrhizae	Egerton-Warburton *et al.* (2007)
A. saccharum stand; field study	Observation of HL; HL replenished approximately 102% of the water depleted from the upper soil on a daily basis	Emerman and Dawson (1996), Dawson (1996)

Continues

Table I. (*Continued*)

Site and species	Results	Reference
Temperate oak forest dominated by *Quercus incana*, *Quercus margaretta*, *Pinus palustris* and *Quercus laevis*, with an understorey with the C4 grasses *Aristida stricta* and *Schizachyrium scoparium*; field study	HL was observed in three tree species and in the C4 *A. stricta*	Espeleta *et al.* (2004)
Ambrosia dumosa, *Encelia farinosa*; pot experiment	No HL observed	Espino and Schenk (2009)
P. ponderosa, *Festuca pallescens*; field experiment	Observation of HL	Fernández *et al.* (2008)
Mediterranean shrubland, *Pinus halepensis*; field study	Observation of HL	Filella and Peñuelas (2003)
Prunus persica; greenhouse experiment	Observation of HL	Glenn and Welker (1993)
Populus euphratica stands; field study	Observation of HL; HL replenished approximately 28–38% of the water depleted from the upper soil on a daily basis	Hao *et al.* (2010)
Mediterranean fynbos; field study	HL observed in *Proteaceae* shrubs that facilitate water uptake by understorey grasses and shrubs	Hawkins *et al.* (2009)
Markhamia lutea, *Oryza sativa*; pot experiment	Observation of HL	Hirota *et al.* (2004)
Q. laevis, *Helianthus anomalus*, *A. tridentate*; greenhouse experiment	Observation of HL	Howard *et al.* (2009)
Buchloe dactyloides and *Zoysia japonica*; greenhouse experiment	Observation of HL	Huang (1999)
California blue oak (*Quercus douglasii*) forest; field study	Observation of HL	Ishikawa and Bledsoe (2000)
Sahelian agroecosystem with the shrubs *Guiera senegalensis* and *Piliostigma reticulatum*; field study	Observation of HL	Kizito *et al.* (2012)
Q. suber Mediterranean savanna; field study	HL was estimated to account for 17–81% of the water used during the following day by trees at the peak of the drought season	Kurz-Benson *et al.* (2006)
Montane *Pinus contorta* forest; field study.	Epigeous ectomycorrhizal fungi derived a significant proportion of their water (25–80%) from deep to shallow surface soils (HL)	Lilleskov *et al.* (2009)
African savanna with *Acacia tortilis*; field study	Observation of HL	Ludwig *et al.* (2003)
African savanna with *Acacia* sp.; field study	Observation of HL	Ludwig *et al.* (2004)
Gossypium hirsutum; pot experiment	Observation of HL	McMichael and Lascano (2010)
Three North American temperate forests and three Brazilian ‘cerrado’ forests; field study	HL was observed in all studied forests	Meinzer *et al.* (2004)
Tropical Brazilian ‘cerrado’ savanna; field study	Observation of HL	Moreira *et al.* (2003)
Chilean coastal desert with *Porlieria chilensis*, *Adesmia bedwellii* and *Proustia cuneifolia*; field study	HL was observed in all three species	Muñoz *et al.* (2008)
Q. suber forest; field study	Observation of HL	Nadezhdina *et al.* (2008)
A. saccharum, *Chamaecytisus proliferus*, *Eucalyptus globules*, *Banksia prionotes*; field study	Observation of HL	Pate and Dawson (1999)

Continues

Table I. (*Continued*)

Site and species	Results	Reference
Semi-arid Mediterranean ecosystem with *Retama sphaerocarpa*; field study	Observation of HL	Prieto *et al.* (2010a)
Semi-arid Mediterranean shrubland of Chile and Spain; field study	HL was observed and was higher in loamy than in sandy soils	Prieto *et al.* (2010b)
R. sphaerocarpa and seedlings of *Marrubium vulgare* in a patchy Mediterranean shrubland; field study	Seedling survival increased by the HL of adult plants of *R. sphaerocarpa*	Prieto *et al.* (2011)
Mycorrhized *Q. agrifolia* saplings; pot experiment	Nocturnal water translocation from plant to mycorrhizal fungi occurred in association with HL	Prieto *et al.* (2012b)
Q. agrifolia; mesocosm experiment	Nocturnal HL from plants to mycorrhizal fungi	Querejeta *et al.* (2003)
Mediterranean forest, *Quercus engelmannii*, *Q. agrifolia* and *Bromus* sp.; field study	HL was observed in trees, enhancing moisture in upper soil layers and improving survival of mycorrhizal hyphae	Querejeta *et al.* (2007)
Q. agrifolia; mesocosm experiment	HL was observed with and without the presence of mycorrhizae	Querejeta *et al.* (2012)
Semi-arid shrubland with *A. tridentate*; field study	Observation of HL	Richards and Caldwell (1987)
Sesbania rostrata; field study	Observation of HL	Sakuratani *et al.* (1999)
Eight woody species of Brazilian ‘cerrado’ savanna; field study	HL was observed in all species	Scholz *et al.* (2002)
Nine tree species of Brazilian ‘cerrado’ savanna; field study	HL was observed in deciduous and brevideciduous tree species, but not evergreen trees, in summer	Scholz *et al.* (2008)
Grasses and shrubs of Brazilian ‘cerrado’ savanna; field study	HL was observed in all species, but with higher intensity in grasses	Scholz *et al.* (2010)
P. menziesii stands; field study	The seedlings of *P. menziesii* took up more than 21·6% of the water supplied by the HL of nearby adult trees	Schoonmaker *et al.* (2007)
Grassland communities with *Cajanus cajan*, *Crotalaria juncea*, *Panicum maximum*, *Bromus inermis*, *Trifolium repens* and *Festuca arundinacea*; pot experiment	HL was observed with different intensities depending on community species composition	Sekiya *et al.* (2011)
Different genotypes of *Zea mays*; pot experiment	Observation of HL, but with different intensity depending on the genotypes	Wan *et al.* (2000)
P. ponderosa and *P. menziesii* forest; field study	HL accounted for 3–9% of the estimated total site water depletion seasonally	Warren *et al.* (2007)
P. ponderosa and *P. menziesii* forest; field study	HL was observed, representing 60–80% of the water extracted in the upper soil (15–60 cm) each day at the end of drought	Warren *et al.* (2005)
P. ponderosa stands; field study	HL accounted for 80% of daily recovery of soil water content in the upper soil layers in the dry season	Warren *et al.* (2011)
P. ponderosa; field experiment	Observation of HL of water from *P. ponderosa* trees to seedlings	Warren *et al.* (2008)
Sagebrush/bunchgrass steppe of North American Great Basin; field study	Observation of HL	Williams *et al.* (1993)
Artemisia ordosica; greenhouse study	Observation of HL	Xu *et al.* (2007)

Continues

Table I. (*Continued*)

Site and species	Results	Reference
C3, C4 and CAM species of the Mojave desert; field study	HL was observed in all groups, but whereas C3 and C4 species transported water from deep to upper soil layers at night, CAM plants did so during the day	Yoder and Nowak (1999)
Fagus sylvatica and *Quercus petraea* mixed forest; field study	HL was clearly observed in *Q. petraea*, but not in *F. sylvatica*	Zapater *et al.* (2011)
Diverse crop species; pot experiment	Evidence of HL in 16 crop species, seven of which increased HL under drought	Zegada-Lizarazu and Iijima (2004)
Arid region of China, *Elaeagnus angustifolia*, *Alhagi sparsifolia*, *Karelina caspica*, *Tamarix ramosissima* and *Calligonum caput medusae*; field study	No HL observed.	Zeng *et al.* (2006)
Subtropical savanna of Texas with *P. glandulosa* as dominant tree species; field study	HL was observed in the dominant *P. glandulosa* and in some species of understorey shrubs	Zou *et al.* (2005)
	Downward siphoning	
Juglans major (phreatophyte) in Chihuahuan desert; field study	DS was observed after moderate rainfall during summer	Hultine *et al.* (2003)
Semi-arid shrubland in Utah with *A. tridentate*; field study	Rainwater was moved rapidly downward (DS) after summer rains and continued the process over a few days; after a rainfall, between 87% and 100% of rainwater can be moved downwards bellow 0·3 m by roots	Ryel *et al.* (2003)
Semi-arid shrubland with *A. tridentate*; field study	DS was observed following pulses of water availability in the upper soil layers	Ryel *et al.* (2004)
Dry savanna dominated by *Acacia haematoxylon* and *Acacia erioloba*; field study	DS was observed after pulses of precipitation	Schulze *et al.* (1998)
Grevillea robusta; common garden experiment	Observation of DS	Smith *et al.* (1999)
	Hydraulic lift plus downward siphoning	
Semi-arid tropical (Kenya) and Mediterranean (Australia) areas with *G. robusta* and *Eucalyptus camaldulensis*; field study	Observation of HL and DS	Burgess *et al.* (1998)
Semi-arid *Eucalyptus* woodland; field study	Observation of HL and DS, which were associated with the horizontal transfer of water between roots on opposite sides of the stem	Burgess and Bleby (2006)
Mediterranean forest, *E. camaldulensis* and *Eucalyptus platypus*; field study	Observation of HL and DS; the water moved below by roots is 26% of total transpired water	Burgess *et al.* (2001)
Rhizophora mangle	Observation of HL and DS	Hao *et al.* (2009)
Semi-arid forest of Arizona dominated by *Prosopis velutina*; field study	Observation of HL and DS; the water moved below by roots is 10–60% of total transpired water	Hultine *et al.* (2004)
Several Amazonian trees; field study	Observation of HL and DS	Lee *et al.* (2005)
A. tridentate, Chrysothamnus nauseosus; glasshouse experiment	Observation of HL and DS	Leffler *et al.* (2004)
Semi-arid grassland with *Bromus tectorum*; field study	*B. tectorum* promoted both HL and DS throughout roots; the amount of water redistributed represented	Leffler *et al.* (2005)

Continues

Table I. (*Continued*)

Site and species	Results	Reference
	a significant proportion of what can be stored in the rooted zone	
Picea abies; field experiment	Observation of HL and DS	Nadezhdina *et al.* (2006)
Pseudotsuga menziesii; field experiment	Observation of HL and DS	Nadezhdina *et al.* (2009)
Three tree species, *Coussarea racemosa*, *Manilkara huberi* and *Protium robustum*, of the Amazonian forest; field study	The three species showed both HL and DS	Oliveira *et al.* (2005)
Semi-arid forest; *P. velutina*; field study	Observation of HL and DS	Scott *et al.* (2008)
V. vinifera × *Vitis berlandieri*; common garden experiment	Observation of HL and DS	Smart *et al.* (2005)
	HL and SD effect on soil nutrient cycling	
A. tridentate ssp. *tridentate*, *Sarcobatus vermiculatus*; field manipulation experiment	Observational evidences that HL can accelerate organic matter decomposition and nutrient cycling rates	Aanderud and Richards (2009)
Bouteloua dactyloides; pot study	Observational evidences that HL can accelerate organic matter decomposition and nutrient cycling rates	Armas *et al.* (2012)
Carex flacca; greenhouse experiment	HL increased N acquisition	De Kroon *et al.* (1998)
Q. agrifolia with mycorrhizal fungal hyphae; mesocosm experiment	Observation of HL by mycorrhizal fungal hyphae, and evidence that HL improved N uptake and soil enzyme activities in the upper soil layers	Egerton-Warburton *et al.* (2008)
Semi-arid shrubland, *A. tridentate*; pot experiment	Observation of HL related to increased N and P uptake	Matzner and Richards (1996)
Temperate grassland, *Bouteloua eriopoda*, *Bouteloua gracilis*, *Stipa* sp. and *S. scoparium*; field study	Observation of DS linked to high uptake of P, Ca^{2+} and Mg^{2+}	McCulley *et al.* (2004)
Semi-arid shrubland, *R. sphaerocarpa*; field experiment	Observation of HL related to the selective placement of roots in nutrient-rich soil patches and to high nutrient capture under drought	Prieto *et al.* (2012b)
Brassica napus; common garden experiment	HL has no clear effect on P and K uptake from dry topsoil	Rose *et al.* (2008)
S. vermiculatus; field study	Observation of HL, but no clear effects on plant N uptake	Snyder *et al.* (2008)
Triticum aestivum; greenhouse experiment	Observation that the levels of HL are higher when upper soil layers have higher amounts of N and P	Shen *et al.* (2011)
G. hirsutum; pot experiment	Observation of HL, which did not aid P uptake from surface soil by *G. hirsutum* plants	Wang *et al.* (2009)
P. ponderosa; pot experiment	Observation of HL in trees that enhanced mycorrhizal survival and facilitated nutrient uptake under drying conditions	Warren *et al.* (2008)

with a mean value among the different studies of approximately 53%. Moreover, an outstanding consequence of HL is that a significant part of water lifted (3–60%) can be used by other species, normally understorey species, rather than the species that have lifted the water, normally trees (Dawson, 1993; Schoonmaker *et al.*, 2007). Even though most studies have reported HL in woody plants growing in semi-arid and arid areas (Filella and Peñuelas, 2003; Huxman *et al.*, 2004; Neumann and Cardon, 2012), other studies have shown that HL is not uniquely restricted to these areas (Caldwell *et al.*, 1998; Horton and Hart, 1998; Neumann and Cardon, 2012). This capacity of plants to move water along positive gradients of osmotic pressure is related to the existence of water channel proteins (aquaporins) that facilitate water movement (Kaldenhoff *et al.*, 1998; Kjellbom *et al.*, 1999; Jackson *et al.*, 2000). Moreover, shallow roots also redistribute water to other shallow roots (lateral hydrological redistribution). Much fewer studies have reported a lack of HL in arid areas (e.g. Zeng *et al.*, 2006; Espino and Schenk, 2009).

The reverse of HL, called *downward siphoning* (DS) (Smith *et al.*, 1999), has been observed when the topsoil is wetter than the subsoil. By transferring water beyond the reach of shallow-rooted neighbours, DS may enhance the competitiveness of deep-rooted perennials over shallow-rooted annuals when drought returns (Smith *et al*., 1999). This mechanism is especially useful in soils with shallow layers of low permeability (Burgess *et al*., 2001) and in semi-arid environments where woody plants transport water from upper to deeper layers during wet winters and where a deep reservoir of water in dry springs allows growth without competition from herbaceous plants (Hultine *et al*., 2004). DS thus prolongs the availability of water during periods of drought (Schulze *et al*., 1998; Huxman *et al*., 2004; Ryel *et al*., 2004), allows a higher annual transpiration and capacity for plant production (Scott *et al*., 2008; Katul and Siqueira, 2010) and contributes to the islands of fertility in semi-arid areas (Pugnaire *et al*., 1996; Huxman *et al*., 2004; Archer *et al*., 2012). The roots of some plant species, however, can redistribute water from deeper to upper soil layers during drought and can transport water from the soil surface to deeper soil layers after rewetting of the soil (Burgess *et al*., 1998; Bayala *et al*., 2008) (Figure 1). Burgess and Bleby (2006) monitored the flow of sap in *Eucalyptus wandoo* trees and observed that after a rainfall, water is rapidly moved vertically and laterally among roots. These authors observed large axial flows moving vertically up or down the stem; these movements were associated with the horizontal transfer of water between roots on opposite sides of the stem. Considerable portions of the stem axis become involved in the redistribution of water between lateral roots because of the partial sectoring of the xylem around the circumference of these trees (Burgess and Bleby, 2006). The capacity to rapidly redistribute water throughout the entire root system may thus be an important mechanism in plants growing where the availability of water is spatially heterogeneous (Smart *et al*., 2005; Peñuelas *et al*., 2011).

These mechanisms for moving water through the soil profile support the hypothesis of hydrological niche segregation (Araya *et al*., 2011), which claims that coexisting plants tend to occupy different spaces in fine-scale gradients of soil moisture and to partition water by different strategies of acquisition, such as different phenologies or rooting depths that prevent direct competition for water. In this context, by moving water in time and space in a way favourable to the plant, the redistribution of soil water could be a mechanism for avoiding interspecific competition for water. Moreover, the redistribution of water constitutes a plant mechanism, which, without involving changes in plant cover or in species composition, significantly influences water movement in soil–plant–water (runoff) systems, with important implications for the concentration, availability and stoichiometry of nutrients.

Because HL is directed to dry, upper soil layers, the lifted water provides moisture that facilitates favourable biogeochemical conditions for enhancing soil organic matter decomposition (Aanderud and Richards, 2009; Armas *et al*., 2012) and plant nutrient uptake (Matzner and Richards, 1996; Allen, 2011). In fact, the observed HL from the deep roots of trees in dry environments to the upper soil layers could easily result in the evaporation of water, which would not be a good mechanism for conserving water in the soil. We thus hypothesize that the main positive role of HL is to improve nutrient uptake, because nutrients are frequently more abundant in the upper soil layers. Some studies have also suggested that HL could be a strategy for enhancing nutrient uptake from surface soil layers (Matzner and Richards, 1996; Scholz *et al*., 2008), and some evidence supports enhanced capacities of nutrient (especially N) uptake by HL (Table I). This hypothesis could be extended to the bidirectional movement of water that would allow the optimization of available water for preventing stomatal closure and for facilitating nutrient acquisition and cycling (Horton and Hart, 1998; Bayala *et al*., 2008). Supporting this, several studies have associated HL with the decomposition of soil organic matter (Querejeta *et al*., 2007; Warren *et al*., 2008; Aanderud and Richards 2009), the maintenance of mycorrhizal symbiosis (Querejeta *et al*., 2003), increased nutrient cycling rates (Armas *et al*., 2012) and plant nutrient uptake, mainly of N (De Kroon *et al*., 1998; Egerton-Warburton *et al*., 2008). Prieto *et al*. (2012a) observed that HL promoted selective root placement in nutrient-rich soil patches. Moreover, some evidence indicates that HL enhances the nutrient supply in upper

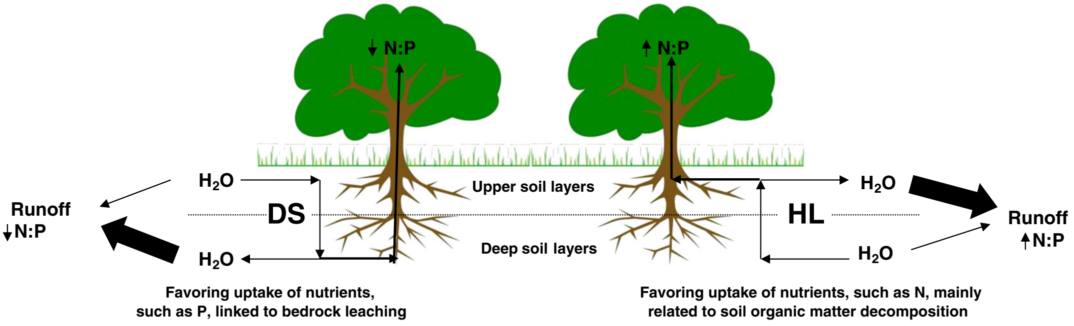

Figure 1. Diagram of the impacts on N : P ratios of redistribution of soil water by plants. HL, hydraulic lift; DS, downward siphoning.

soil layers (Shen *et al*., 2011). Mycorrhizal fungi are also able to utilize HL water from plants to obtain nutrients in dry surface soils (Allen, 2011). Caldwell and Manwaring (1994), though, reported that HL did not change the heterogeneity of soil nutrients in a dry shrubland, and Snyder *et al*. (2008) were unable to find a clear relationship between HL and plant N uptake. On the other hand, nutrients other than N, such as P, Ca^{2+} and Mg^{2+}, are more available in deeper than in upper layers, and DS may be a mechanism through which deep-soil nutrients are mobilized and taken up by plants (McCulley *et al*., 2004) and also a mechanism contributing to the increase in bedrock leaching of nutrients (Burgess *et al*., 2001). The water moved by DS can be 10–60% of the total transpired water (Burgess *et al*., 2001; Hultine *et al*., 2003), and the water moved downwards below 0·3 m by DS after rain events can be between 87% and 100% of total rainfall water (Ryel *et al*., 2003).

The impact of soil water redistribution by plants on the stoichiometry of soil nutrients is not clearly understood, but some general trends emerge from the review of the literature. Nitrogen tends to enter the soil by mechanisms driven by litter, mostly in the upper soil layers, and by the vegetation and not by the leaching of bedrock (because most rocks have a very low N content). On the other hand, P and most metals enter the soil by the leaching of parental bedrock materials. HL could thereby favour the asymmetrical absorption of N over other elements, whereas DS could favour the uptake of other nutrients, thus affecting the N : P ratio of runoff in different ways (Figure 1). In support of this hypothesis of the asymmetrical effects of HL and DS, some studies have observed that HL did not increase the acquisition of P from dry surface soil (Rose *et al*., 2008; Wang *et al*., 2009), whereas McCulley *et al*. (2004) observed that DS was correlated with higher uptakes of P and metals from deep soil in a semi-arid region. Several studies have observed positive relationships between HL and N uptake (Table I), but such relationships are not always found (Snyder *et al*., 2008). HL may decrease the concentrations of soil nutrients, leading to a possible reduction in nutrient uptake (Horton and Hart, 1998). In semi-arid land during drier seasons, nutrient runoff is low and tends to have higher N : P ratios (Green and Finlay, 2010), which may, at least in part, be due to an increase in HL and consequently in water losses from the N-rich upper soil layers and/or lower water losses from the P-rich deeper layers during these dry periods.

The global importance of the redistribution of soil water on nutrient cycles and availabilities, mainly on N : P ratios, in soil and runoff is poorly known. This unresolved question can impact ecosystemic structure and function, because the stoichiometry of the nutrients taken up by plant communities depends on the species composition of the community (Price *et al*., 2012), and in turn because the N : P ratios of soil and fresh water have a determinant role on community species production, composition and function (Sterner and Elser, 2002; Sardans *et al*., 2012a).

Thus, the current data suggest that HL and DS are very widespread phenomena that favour water recirculation and efficiency of use by the soil–plant system and in doing so favour the capacity of plant nutrient uptake. In drier periods when water should only be available in deep soil layers, HL favours the uptake of N. Contrarily, in wetter periods and mainly in more impermeable soils, DS improves the capacity of taking up nutrients coming from bedrock minerals. Thus, HL and DS contribute to a more equilibrated uptake of different nutrients and consequently favour the stoichiometrical balance of plants.

Impact of the hydrological cycle on the availability and stoichiometry of soil nutrients

The hydrological cycle in terrestrial ecosystems is strongly coupled to nutrient cycles. Different nutrients, though, have different chemical traits, and their cycles are differently connected to the hydrological cycle. Despite the importance of soil type (Elsenberg, 2001), precipitation is the most important factor determining the nitrate content of runoff (Weih, 1998; Ohte *et al*., 2001; Bhat *et al*., 2007). Several studies have observed a large capacity of N mobilization by hydrological processes (subsuperficial and superficial runoff) from neighbouring ecosystems, observing that up to 74% of the total N needed in one ecosystem comes from neighbouring ecosystems (Lisuzzo *et al*., 2008). In contrast, soils have a large capacity of P sorption and retention (Chang *et al*., 2005; Vadas *et al*., 2005). The higher solubility of N compared with that of P can lead to proportionately higher exports of N than P from soil by runoff, which can thus mitigate the tendency towards increasing soil N : P ratios along soil chronosequences (Vitousek *et al*., 2010). The N : P ratios observed in runoff and streams in temperate grassland and forests range from 9 to 670 (on a molar basis), with most ratios being over 20 (Inoue and Ebise, 1991; Binkley *et al*., 2004; Kleinman *et al*., 2006; Kortelainen *et al*., 2006; Shen and Liu, 2009; Yang *et al*., 2009; Guo *et al*., 2012; Varol, 2012). These values are mostly above the global average of 13 for soils (Cleveland and Liptzin, 2007). The N : P ratios of global loads from rivers to oceans are 18–24 (Smith *et al*., 2003). Green and Finlay (2010) observed a positive correlation between N : P ratios and the amount of runoff in 57 watersheds in the United States. This correlation is observed when the analysed N and P are dissolved fractions (Guo *et al*., 2012). The positive relationship between the amount of runoff and the runoff N : P ratio, however, cannot be universal, because lower N : P ratios are observed in runoff when heavy rainfall is accompanied by high levels of soil erosion, caused by the mobilization of particulates rich in P by the high water forces able to carry them (Kim *et al.*, 2006; Green and Wang, 2008). Negative relationships between the level of runoff and the runoff N : P ratio are observed in semi-arid climates, whereas positive relationships are found in humid climates (Green and Finlay, 2010). These relationships may be very important for the asymmetrical evolution of N : P stoichiometries of soils and freshwater ecosystems in dry compared with wet climates and may have large implications under climate change. The available studies thus suggest that the loss of N from soil to fresh water is proportionately higher than the loss of P in most wet areas, and the opposite occurs in semi-arid areas, mainly if erosion is high (high frequency of torrential rainfall and low soil protection by vegetation; Figure 1). These relationships may be importantly connected to the tendency of increased soil N : P ratios in semi-arid environments and of decreased soil N : P ratios in wet environments, which should favour slow-growing, resource-conservative species in semi-arid areas and fast-growing species in wet areas, as expected by the growth rate hypothesis (Sterner and Elser, 2002).

In support of the high N : P ratios of runoff from soils observed in most studies, Craft and Casey (2000) observed on average N : P ratios of 34·7 in sediments from runoff in freshwater wetlands. The accumulation of N over time has been frequently observed in chronosequences of riparian forests (Adair *et al.*, 2004). Riparian areas retain N by trapping sediments and organic matter and by uptake by plants and microbes from groundwater and river water (Ambus *et al.*, 1992; Vought *et al.*, 1994; Groffman *et al.*, 1998). These high levels of N and high N : P ratios observed in several riparian sediments could be even higher, but the removal of N in these zones by denitrification may be generally greater (Vought *et al.*, 1994), reducing the store of N.

IMPACTS OF GLOBAL CHANGE ON NUTRIENT CYCLES IN PLANT–SOIL–WATER SYSTEMS

The strong relationships between plants and hydrology with nutrient cycling, availability and stoichiometry are now additionally being impacted by all those drivers of global change, such as land-use changes, drought, warming, eutrophication or invasive plant species, that alter plant structure and functioning, the hydrological cycle and nutrient availability itself.

Land-use changes and water pollution related to urban and agricultural loadings (Mulholland *et al.*, 1997; Sobota *et al.*, 2009), increases in livestock (Chartier *et al.*, 2011), changes in species distribution and the frequency of fire (Engel *et al.*, 2005; Jacobs *et al.*, 2007; Alexander and Arthur, 2010; Smith *et al.*, 2012), forest management (Webb and Kathuria, 2012), land abandonment (Fu *et al.*, 2009) and the intensification of agriculture followed, in most cases, by increases in N in runoff (Sobota *et al.*, 2009) have been the key drivers of global change most studied in relation to shifts in biogeohydrology. We here focus on the impacts from climate change, eutrophication and invasive species on runoff and water redistribution by plants.

Climate change

The specific effects of climate change on nutrient cycles and the availability and stoichiometry of nutrients in soil through alterations of the plant–soil–water system have been studied less than the effects of land-use changes. The large impact of land-use changes on the hydrology of terrestrial ecosystems hinders the study of the effects of climate change on watershed hydrology, which are frequently subtle compared with the strong seasonal cycles of drought and wet periods and which are difficult to separate from the effects of land-use changes. Tomer and Schilling (2009) have observed, in four watersheds of Midwestern North America, that land-use changes and climate change together have increased the susceptibility of nutrients to be exported by water.

Drought. Several studies have projected an enhancement of drought in many areas of the world, including Europe, China and other Asian countries, northern Africa, north-eastern United States and Australia (van Tol *et al.*, 1998; Huntington *et al.*, 2009; Sheffield *et al.*, 2009; Burke *et al.*, 2010; Ryu *et al.*, 2011; Wang *et al.*, 2011). This enhancement of drought can be accompanied by more frequent torrential rainfall in some areas (Wetherald, 2009; Rodríguez-Blanco *et al.*, 2012). The consequent changes of P in runoff in natural gradients, in different climatic situations and under climate change are highly uncertain because of insufficient observational and experimental data for calculations and modelling and are based more on assumptions than on established knowledge (Kovács and Clement, 2009). Until now, studies that have investigated the effects of an enhancement of drought at the level projected by most climate models suggest a high probability for P losses through erosion from torrential rainfall because of the high accumulation of P as organic P in the upper soil layers. Drought decreases soil and root-phosphatase activity (Sardans and Peñuelas, 2005; Sardans *et al.*, 2007) and the labile P fraction (Sardans and Peñuelas, 2004) in the soil of Mediterranean forests. An increase of the most recalcitrant soil fractions (Sardans and Peñuelas, 2004) and a reduction of P content in stand biomass (Sardans and Peñuelas, 2007) have also been observed. More studies on different soil and vegetation types with different levels of N : P ratio in soil are warranted in semi-arid areas to discern the possible role of HL and SD in soil P cycle, i.e. whether the observed low P availability under drought in upper soil layers could be compensated by P uptake from deep soil layers by increasing DS or not.

In contrast, more data are available on the mineralization, immobilization and loadings of soil N in runoff along natural gradients and under different climatic situations. The effects of drought can be different if drought increases in a currently dry area or in an area that is not currently water limited and if drought does not cause drastic changes in these situations. Drought tends to increase mineralization and nitrification in the UK, probably because of an increase of oxygen in soils and because of increases in nitrate loads in runoff (Morecroft *et al*., 2000). The most frequent effect observed after droughts in temperate forests is an increase of nitrate concentrations in runoff after the first rain following a drought, with the nitrates coming mainly from superficial runoff, but from subsurface runoff after subsequent rainfall (Lange and Haensler, 2012). Model projections of drought and increased warming in semi-arid regions, though, suggest a significant reduction in soil water content and a decrease of nitrate losses by runoff despite the large nitrate concentrations in the runoff due to a concentration effect (Wu *et al*., 2012).

In temperate regions, the N : P ratio in runoff can decrease when the climate is drier, favouring P with losses of N (Green and Wang, 2008; Lutz *et al*., 2012). This decrease agrees with the observations of Green and Finlay (2010), who reported that the amount of runoff was positively correlated with the N : P ratio of the runoff. Runoff from soils during a drought is mainly sustained by groundwater close to the bedrock; leaching from bedrock is frequently the main source of inorganic soluble P (Luxmoore and Huff, 1989). The availability of N is usually higher in the upper soil layers, whereas the availability of P is proportionately higher towards the deeper soil layers, and more P than N is lost in runoff (Figure 2). But the effect of drought in semi-arid areas could be opposite, and an increase in N : P ratios in runoff can occur. Studies have found a wide range of N : P ratios in runoff in semi-arid catchments, but the ratios are generally considered high or very high: 17–1150 (on a molar basis) (Alvarez-Cobelas *et al*., 2010). The features of the soil in semi-arid catchments, however, are much better descriptors of runoff N : P ratios than are features of soils in wetter ecosystems (Alvarez-Cobelas *et al*., 2010). As mentioned earlier, the capacity of roots to redistribute water can increase under drought by the transport of water from deeper to upper soil layers favoured by large potential

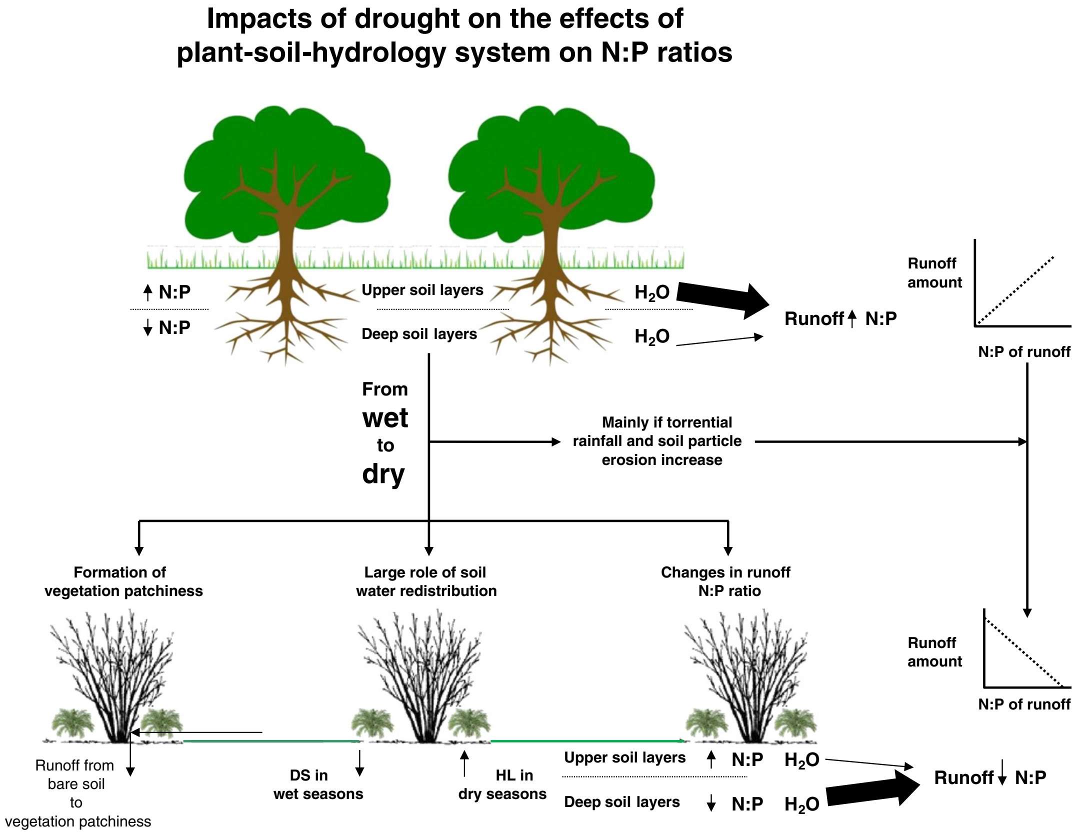

Figure 2. Diagram of the effects of drought on the plant–soil–water system and N : P ratios.

gradients in the soil. N can consequently be lost from the upper soil layers. A higher prevalence of deep-rooted species and more HL should thus prevent the loss of P and increase the probability of losing N. Vegetation, therefore, plays a very important role, through its influence on hydrology, in controlling the concentration and stoichiometry of nutrients in soils and runoff and should become a relevant subject of research in the study of the impacts of global change on terrestrial ecosystems.

The nocturnal flux of water in plants has been shown to decrease under drought in some studies (Dawnson *et al.*, 2007; Howard and Donovan, 2007; Barbeta *et al.*, 2012) and to increase in others (Zeepel *et al.*, 2011). Anyway, the capacity to maintain the flow of sap under drought differs among species in semi-arid plant communities (Barbeta *et al.*, 2012). This finding suggests that species better able to exploit wet periods by taking up more water while maintaining higher rates of flow of sap during dry periods could replace species with lower rates of flow during drought if the climate evolves towards drier conditions (Figure 2). This scenario would constitute a community-level change representing an increased capacity to take up water, which would decrease runoff and increase the global efficiency of water and nutrient capture if drought increases. Thus, under different water availability conditions, the impacts of drought on the N : P ratios of plant–soil systems could be different and remain uncertain (Sardans *et al.*, 2012b).

In semi-arid areas such as those of the Mediterranean basin and North America, drought has been frequently related with the increase of soil patchiness that implies changes in runoff and in vertical water redistribution in soils. Variations in the availability of water and nutrients in these arid areas are due to the patchy distribution of vegetation and bare soil, with vegetation acting as runoff sink and bare soil acting as runoff source (Boix-Fayos *et al.*, 1998; Wainwright *et al.*, 2002; Gabarrón-Galeote *et al.*, 2012; Merino-Martin *et al.*, 2012) changing the erosion behaviour of the slopes (Ruiz-Sinoga *et al.*, 2011) (Figure 2). This effect of patches is crucial to the maintenance of vegetation at drier sites. Soil–plant interactions in patchiness exert strong effects enhancing vertical water movements that favour water and nutrient recycling and efficiency of use and uptake, altogether contributing to decreased erosion and water and nutrient losses from runoff. Patches of vegetation influence infiltration capacity and maintain higher soil water content and fertility (Maestre and Cortina, 2002; Agra and Ne'eman, 2012). Moreover, the presence of large trees in the patches plays an important role in maintaining a high richness of herbaceous species by affecting light, water, nutrient availability and the intensity of nutrient competition (Blank and Carmel, 2012). HL by tall trees frequently creates a nursery effect for the understorey vegetation (Zou *et al.*, 2005). Tree patches constitute true islands of fertility (Wainwright *et al.*, 2002). On the other hand, DS after rainfall can also contribute to further improve water and nutrient uptake capacity (Pugnaire *et al.*, 1996; Huxman *et al.*, 2004; Archer *et al.*, 2012). Two important questions, though, remain to be solved. First, is vegetation patchiness a convergent trend that maximizes the conservation of water and nutrients on slopes when climate becomes severely dry? Second, what are the shifts, if any, in soil N : P ratio produced by HR associated to plant patchiness?

Warming. Warming is expected to disproportionately affect regions of high latitude by increasing temperature, precipitation and the availability of water. In ecosystems currently dominated by fluxes of snowmelt-derived water, a higher frequency of rainfall and a change in the thickness of seasonally active soils can change the hydrology and nutrient cycling by changes to both runoff and vertical movement of water in the soil profile. The thawing of permafrost in cold areas such as the Arctic implies that freshwater systems are likely to experience a transition from runoff loaded mainly by surface-soil water to runoff dominated by groundwater, with several consequent impacts on the entire biological system of the region (Frey and McCelland, 2009). Moreover, increases in the mineralization of litter under warming, together with higher soil runoff, can increase the export of nutrients to lakes and streams (Hobbie and Chapin, 1996; Lükewille and Wright, 1997; Harms and Jones, 2012), as observed in some Arctic rivers (McClelland *et al.*, 2007). An increase of nutrients, particularly N, transported from soil to fresh water has been observed as an effect of warming on hydrology and nutrient fluxes, apart from the significant effects on precipitation and drought (Whitehead *et al.*, 2006; Li *et al.*, 2011). The impacts of warming increasing the depth of active no-frost soil open the possibility of having HL and DS dynamics, a possibility that remains to be investigated.

Eutrophication

The study of the effects of the human-driven eutrophication on the stoichiometry of plant–soil–water systems requires the distinction of cropland areas with intense human use of animal slurry for land fertilization from the natural and semi-natural terrestrial ecosystems (Peñuelas *et al.*, 2012, 2013). Areas of cropland strongly and continuously fertilized with livestock wastes, which have N : P ratios of about 3:1 (by mass) when crop requirements are generally 10:1 or more, end up with lower N : P ratios over time (Gilliam, 1995; McFarland and Hauck, 2004). In fact, studies of cropland with a high, extended use of livestock manure as fertilizer have observed large accumulations of P in soils (Chang *et al*., 2005; Némery and Garnier, 2007), which decrease soil N : P ratios over time (Cech *et al*., 2008; Peñuelas *et al*., 2009) and increase the amount of P but not N in the runoff (Sprague and Lorenz, 2009), leading to low runoff N : P ratios (Kim *et al*., 2006; Ramos and Martínez-Casasnovas, 2006; Stork and Lyons, 2012) (Figure 3). In areas with intensive pastoral activity and a high use of animal slurry for land fertilization, decreases in the N : P ratio also occur in the water of soil, lakes and streams (Arbuckle and Downing, 2001; Peñuelas *et al*., 2009). This problem is the result of too high a concentration of animals in a small area where the amount of applied waste exceeds the P-fixing capacity of the soil (Gilliam, 1995). In this scenario, there is no information of the role of plants in the nutrient distribution by HL and DS. This information is warranted to figure out whether the negative effects of the N limitation resulting from low N : P in upper soil layers could be compensated by crop plants with low optimal N : P ratio or with plants with more active HL that favours higher N uptake.

The decrease of N : P ratios in soil, runoff and streams from the application of livestock manure in some areas of the world, though, is not the most widespread phenomenon. On a global scale, the anthropogenic application of P in fertilizers, livestock slurry and manure has reached 22–26 Tg P year^{-1} and has been nearly constant since 1989 (see detailed information in Peñuelas *et al*., 2012, 2013). In comparison, the global anthropogenic input of N from the combustion of fossil fuels, industrial fertilizers and the biological fixation of atmospheric N_2 by cultivated leguminous crops and rice is 208–216 Tg N year^{-1} and is continuously increasing (Peñuelas *et al*., 2012). Streams and lakes in areas dominated by crops fertilized solely with industrial fertilizers have systematically high N : P ratios (Arbuckle and Downing, 2001). N is more mobile than P and consequently tends to leach easily from crop soils to water (Lerman *et al*., 2004; Gundersen *et al*., 2006), but P from fertilizers tends to remain and accumulate in crop soils (Cech *et al*., 2008; Peñuelas *et al*., 2009). Unlike N, P is not volatile, so that very little P is redistributed from cropland to nearby natural terrestrial ecosystems.

In contrast to P deposition (~3–4 Tg P year^{-1}) (Mahowald *et al*., 2008), atmospheric N deposition is geographically widespread; it mostly impacts northern ecosystems but is continuously increasing on a global scale and will likely extend to the tropics during this century (Galloway *et al*., 2004). Moreover, only approximately 22% of all these anthropogenic inputs of N end up accumulating in soils and biomass. Most is dispersed by the atmosphere or leached by runoff to rivers (UNESCO, 2007). Most studies of natural ecosystems under high, long-term levels of N deposition show that soil is the major sink for N inputs. The consequences of continuous inputs of N on several world ecosystems have been widely studied, and several consequences of the nutrient movements by runoff have been observed. As the concentration of N in the soil increases and soils become saturated, though, less N is immobilized in the soil but enters the runoff (Stein and van Breemen, 1993; Moldan and Wright, 1998; Wright *et al*., 1998; Kahl *et al*., 1999; Kaste and Skjelvale, 2002; Mitchell *et al*., 2003; Fang *et al*., 2008). The loss of nitrates can continue for several years even if N deposition decreases (Hill *et al*., 2002). Furthermore, N deposition, mainly when accompanied by sulfur deposition, can acidify soil and water and can export cations in the runoff (Nodvin *et al*., 1995). As a result, the N : P ratio of inputs into the biosphere and the N : P ratio of atmospheric deposits, although extremely variable geographically, have continuously increased in the Northern Hemisphere since pre-industrial times (Peñuelas *et al*., 2012). Future projections of N emissions suggest an expansion of the area with high anthropogenic N deposition and high deposited N : P ratios from the populated temperate regions of the Northern Hemisphere

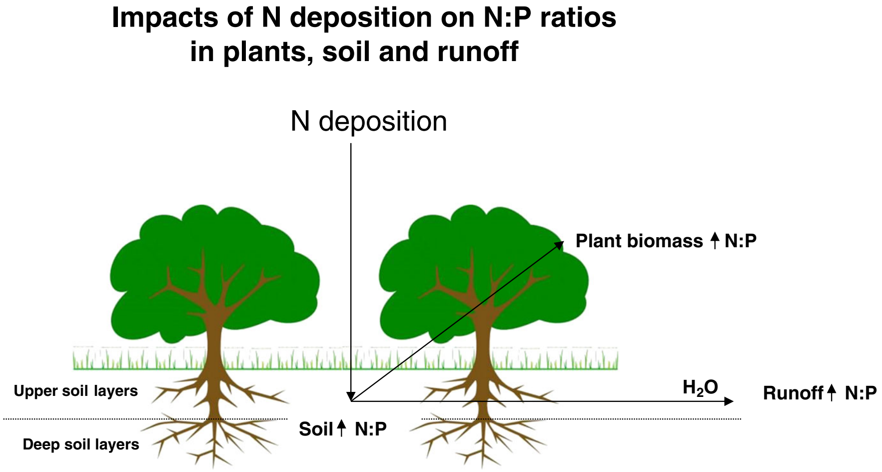

Figure 3. Diagram of the impacts of N deposition on N : P ratios in plants, soil and runoff.

into tropical regions (Lamarque *et al.*, 2010). The stoichiometry of these deposits currently presents a molar N : P deposition ratio of 44–47 over land, more than twice the current molar ratio in terrestrial plants (22–30), and of 114–370 over the oceans, a much larger proportion than the Redfield ratio (Peñuelas *et al.*, 2013). These unbalanced inputs of nutrients are very likely to alter the environment and the life it supports. Altered N : P balances have already been reported for terrestrial ecosystems in the temperate zone, and several lakes in northern and central Europe and in North America have shifted from a N-limited to P-limited environment (Elser *et al.*, 2009). The higher solubility of N compared with P increases the probability that streams, rivers, lakes and estuaries around the world will tend to increase their N : P ratios by acting as the main sinks of reactive anthropogenic N. In a scenario of higher N : P ratio in upper soil layers in most terrestrial ecosystems, the species with higher optimum N : P ratio can be favoured, and also the species with higher DS capacity by increasing the potential to uptake P from the deep soil layers.

Invasive species

The current information thus suggests that the most general effects of alien success in soils richer in resources will be an increase in nutrient and water uptake and the retention of nutrients in the biomass and a decrease in soil nutrient content, soil moisture and runoff yield, whereas the opposite is more likely in soils poor in resources (Figure 4). Supporting this hypothesis, Pysek *et al.* (2012) in a recent review reported that of 436 case studies on the effects of invasive plants on soil nutrient content, 192 found increases, 72 found decreases and 158 were inconclusive. Similarly, a metadata analysis by Sardans and Peñuelas (2012) of 65 studies conducted in environments with unclear limitations of nutrients (except some conducted mainly in arid and semi-arid areas of the United States) found that 48 reported increases in the availability of soil nutrients, 14 reported decreases and three were inconclusive. Most of the 14 studies reporting decreases in soil nutrients were studies in semi-arid areas, providing strong support for the hypothesis discussed earlier.

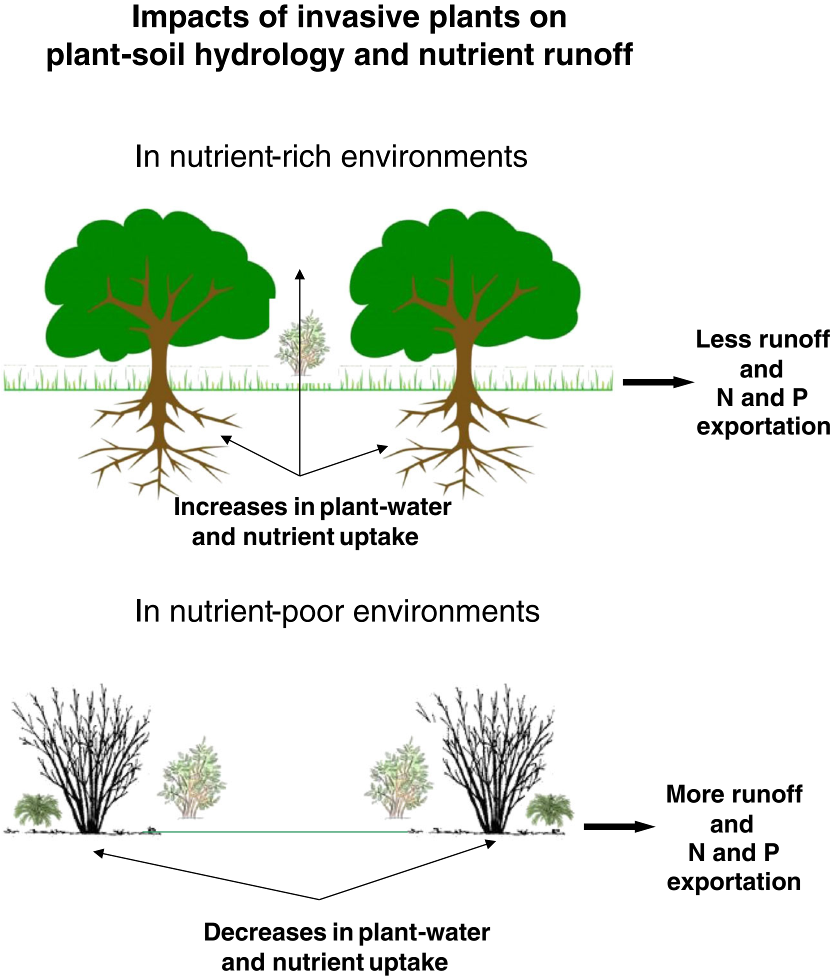

Figure 4. Diagram of the impacts of invasive plants on plant–soil hydrology and nutrient runoff.

Alien success frequently coincides with the higher uptake of water and nutrient in nutrient-rich environments (Sardans and Peñuelas, 2012). Plant invasion can greatly change hydrology and nutrient cycling (Mack *et al*., 2000). The higher levels of growth and water uptake by alien tree species decrease runoff such as observed in several studies (Le Maitre *et al*., 1996; Gerlach, 2000; Zavaleta, 2000; Dye and Jarmain, 2004; Gorgens and van Wilgen, 2004; Richardson and van Wilgen, 2004; Holmes *et al*., 2005; Darrouzet-Nardi *et al*., 2006; van Wilgen *et al*., 2008). The strong impact on nutrient and water uptake at ecosystem level suggests that alien species are capable of altering vertical water movements into soil in a favourable way for them, but this possibility remains to be investigated. In fact, conversely, most studies suggest that the success of invasive plants in nutrient-poor soils depends on more conservative strategies such as a higher nutrient-use efficiency than autochthonous plants (Funk and Vitousek, 2007; Matzek, 2011). The success of alien grass invading shrublands seems due less to the use of deep water reserves than to a higher uptake of water from the upper soil layers in Mediterranean areas (Dyer and Rice, 1999; Figueroa *et al*., 2004; Wood *et al*., 2006) and in other semi-arid regions (Schachtschneider and February, 2013). The uptake of water by the global community is thereby reduced, and yields from runoff are increased (Cline *et al*., 1977; Dukes and Mooney, 2004).

MAIN CONCLUSIONS

The capacity of plants to take up water and to change the runoff and the vertical redistribution of soil water can exert relevant effects on the cycling, availability and stoichiometry of soil nutrients and on the yield and nutrient content of runoff.

HL and DS can exert a driving role in the N : P ratio of the nutrient uptake of plants because HL favours N uptake both directly and by increasing soil organic matter decomposition, whereas DS favours the uptake of nutrients such as P, Ca^{2+} or K^+ related to the leaching from bedrock minerals.

HL can have a significant effect on N : P ratio of runoff. For example, in semi-arid environments under drought, HL can increase the runoff from upper soil layers richer in N, favouring higher N : P ratios in runoff.

Apart from land-use changes, anthropogenically driven N and P eutrophication is the current driver of global change that is most intensively affecting the N and P cycles and stoichiometry in plant–soil–water systems on a global scale and is threatening to generate global N : P imbalances.

SOME REMAINING QUESTIONS

Some results suggest that the role of plant soil water redistribution could be significant in several global change processes such as N eutrophication or plant invasiveness, but this likely role remains to be specifically investigated. Several other questions remain unsolved and warrant investigation. Do HL and DS have general effects on the cycling of soil nutrients? Do HL and DS have different effects on the cycling of soil N and P? Are the N : P ratios of runoff generally different in semi-arid and wet areas? Does a relationship exist between a decrease of N : P ratios in runoff and an increase in N : P ratios in soil that favours species with higher N : P ratios and consequently with lower growth rates under drought? Can changes in hydrology and the associated changes in the status of soil nutrients determine the success of alien plants?

Our level of knowledge is still insufficient for a good understanding of the effects of global change on P cycles throughout plant–soil–water systems. Our ignorance is even greater in the case of potassium. Potassium plays a paramount role in the ecological stoichiometry of terrestrial ecosystems (Rivas-Ubach *et al*., 2012; Sardans *et al*., 2012c), which is linked to its decisive role in the economy and use efficiency of water by plants (Babita *et al*., 2010; Oddo *et al*., 2011). There is a lack of information of how HL and SD can affect K cycle in plant–soil systems. Moreover, fertilization and land use seem to strongly impact the loss of potassium in runoff in temperate grassland (Alfaro *et al*., 2004), but studies on the effects of potassium on plant–soil–water systems in the scenario of global change are mostly lacking.

ACKNOWLEDGEMENTS

The development of this manuscript was supported by the Spanish Government grants CGL2010-17172/BOS and Consolider-Ingenio Montes CSD2008-00040 and by the Catalan Government grant SGR 2009-458.

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