

The Role of Plants in the Effects of Global Change on Nutrient Availability and Stoichiometry in the Plant-Soil System^{1[W]}

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CYCLES ALTERED BY HUMAN ACTIVITY: IMPACTS ON THE AVAILABILITY AND STOICHIOMETRY OF NUTRIENTS

The impact on nitrogen (N) and phosphorus (P) cycles of human activity is a growing concern and has several causes and consequences (MacDonald et al., 2011; Peñuelas et al., 2012; Sardans et al., 2012b). Carbon (C) inputs by human CO₂ emissions and N inputs from diverse human-driven sources are continuously increasing (Peters et al., 2011; Peñuelas et al., 2012). On the other hand, anthropogenic biospheric inputs of P are increasing much less than emissions of N and P (Peñuelas et al., 2012). These changes impact all ecosystems, including cropland (MacDonald et al., 2011), and seem to lead to shifts in C-N-P ratios and balances (Mackenzie et al., 2002; Peñuelas et al., 2012), with significant impacts on the structures and functions of ecosystems through effects on growth rates and on the competitive abilities of different species (Sterner and Elser, 2002; Peñuelas et al., 2012). Furthermore, increased warming, drought, and concentrations of atmospheric CO₂ also change the N and P contents and stoichiometry of plants (Reich et al., 2006; Funk and Vitousek, 2007; Elser et al., 2010; Rivas-Ubach et al., 2012) and, therefore, can indirectly impact soil processes and nutrient availability and stoichiometry. These increases also influence ecosystemic structures and functions and the capacity of Earth to balance its levels of CO₂, given the importance of nutrients in the efficiency of plants to take up CO₂ (Vicca et al., 2012).

Invasion by plant species, another driver of global change, is also strongly related to the availability and stoichiometry of soil nutrients in most cases (Davis et al., 2000; Chun et al., 2007; Dassonville et al., 2007, 2008; González et al., 2010) and exerts an additional

effect on the availability and stoichiometry of N and P in ecosystems and frequently interacts significantly with other drivers of global change, such as N deposition (Huebner et al., 2009; He et al., 2011).

Plants respond to drivers of global change by several metabolic and physiological shifts that frequently alter, among several other functions, a plant's capacity to take up and reallocate nutrients and, consequently, the elemental composition and stoichiometry of plants. Plants are thus the main factor underlying the links between global change and the status of N and P in ecosystems. This role of plants is critical to Earth's N and P biogeochemical cycles and to the changes occurring in these cycles. We urgently need to review our knowledge of the role that plant responses to global change plays in changing and/or buffering the availability and stoichiometry of nutrients in ecosystems.

In this Update, we discuss (1) the effects of plants on the availability and stoichiometry of nutrients in ecosystems through their responses to drivers of global change at the individual, population, and community levels, (2) the consequences and feedback mechanisms occurring from changes in the availability and stoichiometry of nutrients in terrestrial ecosystems, and (3) the key aspects we need to investigate to reach a global understanding of the links among drivers of global change, plant responses, and the availability and stoichiometry of nutrients.

INCREASED CONCENTRATIONS OF ATMOSPHERIC CO₂

Meta-analyses of herbaria studies and field experiments have observed that elevated concentrations of atmospheric CO₂ tend to decrease N (Peñuelas and Matamala, 1990; Sardans et al., 2012b) and P (Peñuelas and Matamala, 1990, 1993; Sardans et al., 2012b) in plant tissues. Foliar C-N and C-P ratios have usually increased as a consequence (Gifford et al., 2000; Tognetti and Peñuelas, 2003; Sardans et al., 2012b). Under high concentrations of atmospheric CO₂, the most commonly observed plant response, especially in C3 plants, is an increase in C uptake that frequently

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leads to an increase in growth (Newton et al., 1995; Reich et al., 2006). Increased concentrations of atmospheric CO₂ also lead to reduced transpiration (Niklaus et al., 2001; Del Pozo et al., 2007), because the uptake of CO₂ is possible with higher stomatal closure (Samarakoon and Gifford, 1995), which can further limit the capacity to take up N (Berntson, 1994; Pritchard and Rogers, 2000; BassiriRad et al., 2001) and can lead to a progressive limitation of nutrients that can quickly limit the initial increase in plant production under elevated concentrations of atmospheric CO₂ (Murray et al., 2000; Zak et al., 2003; Luo et al., 2004; Newton et al., 2010; Norby et al., 2010).

The capacity to enhance plant growth can be further increased by external inputs of nutrients. The current increases in N deposition in several regions of North America and Europe increase the capacity of further plant growth (Finzi et al., 2007). In this case, the increase in plant growth is fundamentally due to an increase in N uptake but not to an improvement in the efficiency of use of N (Finzi et al., 2007). Some experiments of N fertilization have not observed significant increases of plant growth and nutrient cycling under increased atmospheric CO₂ concentrations (Lagomarsino et al., 2008).

Plants also tend to take up more N, which can reduce the availability of soil N (Norby et al., 1999; Hovenden et al., 2008; Garten et al., 2011), an effect further enhanced by the frequent increase in N uptake by microbes in response to increased levels of CO₂ (Zak et al., 2000; Dijkstra et al., 2010a). The large uptake of N by plants and the decrease of N in soil can prevent losses of N from ecosystems by preventing leaching (Johnson et al., 2004). Plants, however, respond with a series of metabolic and physiological mechanisms for increasing their capacity to take up N in a scenario of high levels of atmospheric CO₂. Changes in the structure of mycorrhizal communities and/or increases in mycorrhizal biomass frequently occur (Díaz, 1995; Treseder, 2004; Gamper et al., 2005; Olsrud et al., 2010; Fransson, 2012). Plants also increase their allocation of N to root structures (Norby et al., 1999; Arnone et al., 2000; Norby and Iversen, 2006), including the increase of root exudates that increase the capacity for nutrient chelation (Phillips et al., 2011; Fransson, 2012). An increase in the efficiency of N use is generally observed (Taub and Wang, 2008; Dijkstra et al., 2010a, 2010b) due to these mechanisms, which include an increase in internal plant remobilization (Peñuelas and Estiarte, 1997). An increase in nitrogen fixation is also observed as a short-term response to increases in concentrations of atmospheric CO₂ (Reich et al., 2006), but the limitation of other elements such as P and potassium (K) limit the increase in the capacity of ecosystems to fix N₂ (Reich et al., 2006; Tobita et al., 2010). The possibility of community invasion by fixers of N₂ can increase if levels of atmospheric CO₂ rise (Zanetti et al., 1996; Polley et al., 1997).

A follow-on consequence of all these processes is a progressive change in the proportions of individuals of different species of the plant community due to variable

capacities of the various species with different ecological strategies, phylogenies, successional stages (Arnone et al., 2000; Handa et al., 2008), or life stages (Shimono and Bunce, 2009). Young plants have a higher capacity to improve uptake than plants in reproductive stages (Shimono and Bunce, 2009). All these mechanisms of increases in nutrient use efficiency and/or uptake in response to higher concentrations of atmospheric CO₂ are strongly dependent on soil nutrients and water sources and resources. Nutrient-poor soils may limit the capacity of plants to increase their root production in response to atmospheric concentrations of CO₂ and, consequently, limit the capacity to absorb nutrients (Johnson et al., 2006). The capacity to invest to increase nutrient uptake is also limited in arid environments. Clark et al. (2009) observed no changes in mycorrhizal infection in plants growing in the Mojave Desert in response to increased atmospheric CO₂ concentration. The capacity of plants to increase their growth by a higher uptake or use efficiency of N is very dependent on the chemical form of the source of N. In general, NH₄⁺ is preferable to NO₃⁻ because the allocation of N in plants to nitrate reductase activity must compete with the allocation of other factors (Bauer and Berntson, 2001; Cruz et al., 2003). If most of the N uptake is in the NH₄⁺ form, plants do not need to allocate N to nitrate reductase. A negative feedback can be produced, because increased concentrations of CO₂ can increase soil nitrification (Azam et al., 2005). On the other hand, higher levels of soil moisture from reduced transpiration should prevent soil nitrification, as observed in some studies (Cheng et al., 2012), contributing to diminished uptake of NO₃⁻ by plants and favoring NH₄⁺ uptake. These processes appear to contribute to a better use of N in the ecosystem.

The decrease in plant transpiration is frequently related to higher soil-water contents (Ebersberger et al., 2003; Staddon et al., 2004). Higher soil-water content, litter production, and root allocation are related to the higher activities of soil enzymes frequently observed under high concentrations of atmospheric CO₂ (Ebersberger et al., 2003; Lipson et al., 2006; Jin and Evans, 2007). Higher fungal biomass is also a trait related to higher decomposition rates of soil organic carbon observed in some soils subjected to elevated concentrations of atmospheric CO₂ (Lipson et al., 2006). Despite the frequent lower quality of litter resulting from higher C-N ratios and higher concentrations of C-based secondary compounds (Peñuelas et al., 1997; Aerts et al., 2012), these litter changes do not decrease soil organic matter (SOM) or litter decomposition (Zak et al., 2003; Hyvönen et al., 2007; Aerts et al., 2012), which have even been found to increase in several studies (Billings and Ziegler, 2005; Cotrufo et al., 2005; Jin and Evans, 2007). Changes in mineralization under high concentrations of atmospheric CO₂ are very dependent on the species of plant (Finzi et al., 2006; Austin et al., 2009).

Thus, increased levels of CO₂ concentration lead to high plant production capacity (C3 plants) and lower

transpiration. Plants respond by increasing the resource allocation to mechanisms involved in N and P uptake. Nevertheless, plant C-N and C-P ratios tend to increase (Table I). At the end, however, an acclimation effect of plants is observed at medium and long terms, thus diminishing the previous trends. Further research is necessary to reach a more conclusive view of the impacts on N-P ratios of plants and soils.

WARMING

The Contrast between Cold/Wet and Hot/Dry Ecosystems

An overview of the information currently available leads to the general conclusion that the responses of plants to warming strongly depend on the indirect effect of warming on soil moisture (Schmidt et al., 2004; Aerts, 2006; Sardans et al., 2012b). In cold and temperate ecosystems, especially in wet conditions, the reduction of soil moisture by warming is insufficient to counteract the enhancement of plant activity in response to rises in temperature. In these conditions, plants increase their biological activity by several mechanisms, such as lengthening the growth and active annual periods (Farnsworth et al., 1995; Peñuelas et al., 2004) and increasing photosynthetic rates (Wookey et al., 1995), vegetative growth (Wookey et al., 1995; Hobbie and Chapin, 1998; Suzuki and Kudo, 2000; Cole et al., 2002; Peñuelas et al., 2004; Day et al., 2008; Olsrud et al., 2010; Melillo et al., 2011; Dreesen et al., 2012), reproductive output (Wookey et al., 1995), and seed reservoirs (Blödner et al., 2007). These increases in photosynthesis activity can be further enhanced under increased atmospheric CO₂ concentrations such as observed in some experiments coupling field manipulations of temperature and atmospheric CO₂ concentrations (Albert et al., 2011). However, the effects of warming and elevated atmospheric CO₂ on other ecosystem processes can be different. For example, Dijkstra et al. (2010a) observed an increase in soil N availability under warming and a decrease in N content (due to the enhancement of N uptake by microbes) that, when acting together, tend to compensate their effects on soil N. On the other hand, nutrient mineralization, cycling rates, and availability frequently increase under warming (Fig. 1). Despite these increases, the enhancement of plant activity and growth involves a dilution of nutrients that leads to frequent decreases in N concentrations in leaves and litter (Suzuki and Kudo, 2000; Shen et al., 2009) and increased C-nutrient ratios in plant tissues and litter (Hyvönen et al., 2007; Sardans et al., 2012b, 2012c). At the individual and community levels, plants respond by increasing nutrient uptake, mycorrhizal symbiosis (Clemmensen et al., 2006; Olsrud et al., 2010), root growth (Volder et al., 2007), and N₂ fixation (Sorensen and Michelsen, 2011). These plant responses lead to an increase in nutrient uptake under warming (Wookey et al., 1995; Dijkstra et al., 2010a; Olsrud

et al., 2010). The responses of plants to continuous warming generally tend to be limited by the availability of N (Jonasson et al., 2004; Majdi and Öhrvik, 2004) and/or P (Jonasson et al., 2004) in cold and temperate regions (Jarvis and Linder, 2000).

These limitations can be reduced by N deposition, as observed in regions of Europe and North America (Aerts et al., 1992; Majdi and Öhrvik, 2004; Clemmensen et al., 2006). The most direct consequence of the rapid response of plants to warming is the change in competitive relationships among plant species of a community (De Valpine and Harte, 2001). Plant species adapt differently to the new conditions by species-specific differences in metabolism (Schuster and Monson, 1990), phenology (Dreesen et al., 2012), or reproductive strategy (Moulton and Gough, 2011). Reductions in the rates of photorespiration in C3-C4 intermediate-metabolism plants create advantages in photosynthetic capacities at warmer foliar temperatures than in C3 plants, which can only enhance photosynthetic efficiency under warming at substantial costs in water and nutrient use efficiency (Schuster and Monson, 1990). In cold environments, increases in the availability of soil nutrients through enhanced decomposition of SOM and the capacity for plant production favor plants that mainly reproduce sexually (Moulton and Gough, 2011), which frequently leads to a competitive advantage of higher plants over lichens (Moulton and Gough, 2011).

Plants can sometimes respond negatively to warming even in cold and temperate environments. During warming events, an extreme winter snow cover in the Arctic can disappear, and freezing temperatures can reduce a plant's potential to grow and reproduce the following summer (Bokhorst et al., 2011). In temperate grassland, the large frequency of freeze-thaw cycles has proved to increase the N leaching effect linked to higher water penetration and leaching capacity (Joseph and Henry, 2008). This loss of N can be associated with the increases of plant C-N ratios and growth decreases associated with the increased frequency of freeze-thaw cycles (Kreyling et al., 2010). Moreover, some Alpine plants have roots that grow upward to the snow cover to acquire nitrogen, thereby compensating for the very short season for nutrient uptake (Onipchenko et al., 2009). Plants highly dependent on this strategy can be particularly threatened under a scenario of rapid warming that shortens the period of snow cover. All these sources point at the importance of single events and, by the impacts of extreme warming events, impacts on snow cover and temperature variability in winter.

In contrast, warming in dry environments, such as those of continental, Mediterranean, and dry tropical biomes, can increase soil drought, exacerbating limitations of water and nutrients (Link et al., 2003; Allison and Treseder, 2008). Plants respond by activating mechanisms for water conservation, which can frequently increase C-nutrient ratios in photosynthetic tissues (Sardans et al., 2008b, 2008c, 2012a).

Table 1. Summary of the main results of the studies on plant responses to global change drivers and the flow-on effects on soil fertility and stoichiometry

The necessary future research to advance in a global overview of this topic is highlighted in the last column.

| Global Change Drivers | Plant Responses | Changes in Soil Nutrient Availability and Stoichiometry | Further Research |
|--|--|---|--|
| Increased atmospheric CO ₂ concentrations | <p>↑Plant production capacity at short term (C3 plants), and acclimation capacity at medium and long term</p> <p>↓Transpiration</p> <p>↑Plant C-N and C-P ratio</p> <p>↑Plant investment of resources in N and P uptake</p> | <p>Habitually no observed changes in soil fertility</p> <p>↑Soil C-N and C-P ratios</p> | Effects on N-P stoichiometry |
| Warming (cold/wet environments) | <p>↑Plant production and growth (but the effects can be negative in short, extreme warming events)</p> <p>↑Plant C-N and C-P ratios</p> <p>↑Plant investment of resources in N and P uptake</p> | ↑Of nutrient cycling, by higher mineralization rates and soil enzyme activity counteracting the negative effect of litter production with high C-N and C-P ratios | <p>Study of the possible different effects on N than on P cycling</p> <p>Study of the effects of increasing frequency of warming events during winter in temperate and cold ecosystems</p> |
| Warming (hot/dry environments) and drought | <p>↑Growth</p> <p>↑Investment in increasing WUE and in N and P uptake</p> <p>↑Plant C-N and C-P ratios by increase in the presence of C-rich structures and compounds linked to water stress avoidance</p> <p>No significant effects on plant N-P ratios</p> | <p>↓Soil enzyme activity and nutrient cycling</p> <p>↑C-N and C-P ratios</p> <p>↓Decrease of N and P availability</p> <p>↑N and P occluded fractions</p> <p>↑Risk of N and P losses by torrential rainfalls</p> | The role of plant roots in the mechanism of water transport from deep soil layers to upper soil layers |
| N eutrophication | <p>↑Aboveground growth and plant competition intensity</p> <p>↑Investment in P uptake</p> <p>↑N-P ratios</p> <p>↓Root uptake capacity under high levels of N saturation</p> | <p>↑P availability, increasing P-limiting role</p> <p>↑N-P ratio</p> <p>↑Soil phosphatase activity and soil respiration</p> <p>↑Accumulation of recalcitrant C</p> <p>↑N leaching</p> | The impacts of N deposition through its role by increasing plant and soil N-P ratios |
| Species invasion | <p>In nutrient-rich soils, high invasive success of species with higher growth rates, low C-N and C-P ratios, fast plasticity in resource acquisition capacity, and high reproductive investment</p> <p>In nutrient-poor soils, high invasive success related to conservative use of resources, including nutrients</p> <p>Communities dominated by legumes growing in soils with limited availabilities of soil P or water are vulnerable to competition by nonfixing plants with high capacities of P uptake or stomatal control, and low availabilities of P reduce the probability of successful invasion by N₂-fixing plants</p> | ↑Of N and P soil concentrations and availability as well as cycling, particularly in rich nutrient soils | The role of N-P ratios (of plant and soil) in invasive success |

In response to warming, leaves and litter of plants thus tend to increase C-nutrient ratios by the dilution effect and/or by increases in nutrient use efficiency (An et al., 2005) in temperate and cold ecosystems not limited by water and by conservative mechanisms related to the avoidance of water stress in dry areas (Sardans et al., 2012b). Nevertheless, these increased C-nutrient ratios may not be observed in the short and

medium terms in cold and temperate sites, because the higher temperatures can increase respiration and enhance soil activity, thus releasing more nutrients, although respiration subsequently tends to acclimate to the new situation (Atkin et al., 2000; Hartley et al., 2006). Anyway, climate-manipulation studies in high-latitude ecosystems report increases (12% on average) in the C-N ratio of litter under warmings ranging from

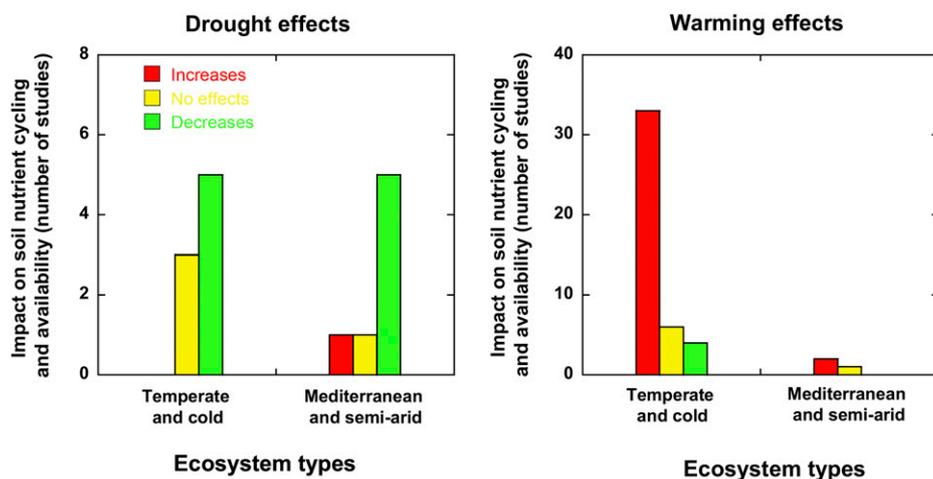


Figure 1. Impact of drought and warming on rates of soil nutrient cycling and availability. Detailed results and bibliographic references are provided in Supplemental Table S1.

1°C to 4°C (Cornelissen et al., 2007; Aerts et al., 2012), showing that increases of C-N ratios can be a frequent effect of warming.

Effects on the Availability and Stoichiometry of Soil Nutrients

Along with the responses of plants to warming, soil enzyme activity, SOM decomposition, and rates of nutrient cycling and mineralization tend to change in a direction mainly determined by the impact of warming on soil moisture (Peñuelas et al., 2004; Aerts, 2006; Allison and Treseder, 2008), changes in litter quantity, and the composition and activity of soil microorganisms.

In cold and temperate ecosystems not limited by water, warming also tends to increase nutrient release and availability for plants, despite frequent increases in C-nutrient ratios in litter (Luo, 2007; Fig. 1). Warming frequently increases soil enzyme activities (Bell et al., 2010; Dreesen et al., 2012), soil respiration (Updegraff et al., 2001; Biasi et al., 2008), nutrient mineralization, soil-cycle rates (Fig. 1), and SOM decomposition (Aerts, 2006; Hyvönen et al., 2007; Von Lützow and Kögel-Knabner, 2009). Plants, though, must compete more strongly with microbes for nutrients (Jonasson et al., 2004; Dijkstra et al., 2010b), because the warmer temperatures enhance the activities of the microbes (Von Lützow and Kögel-Knabner, 2009). Nonetheless, plants frequently enhance their uptake of nutrients (Cole et al., 2002). In the long term, when vegetation has a large capacity to take up nutrients, for example in a young forest in its growing stage, this increase in the source of nutrients can imply an increase in leaf concentrations of N (Butler et al., 2012). On the other hand, this increase in the release of soil nutrients can increase leaching to streams (Schmidt et al., 2004). Fewer studies have investigated the effects of warming on soil processes in dry areas than in temperate and cold environments not limited

by water. In boreal and dry mountainous and tropical dry areas, the effects of warming are opposite to those in areas not limited by water; soil enzyme activities (Allison and Treseder, 2008), soil respiration (Lellei-Kovacs et al., 2008), and N availability are decreased (Fig. 1).

Some studies have observed that N mineralization is enhanced more rapidly than P mineralization under warming (Rinnan et al., 2007), observing that warming increases more in the N cycle than the P cycle (Sardans et al., 2012b). These results support studies of foliar stoichiometry under natural gradients that have observed positive correlations between temperature and foliar N-P ratios (De Frenne et al., 2011; Kang et al., 2011). In scenarios of rapid rises in temperature, plants in particular and ecosystems in general can respond more quickly and strongly to increases in N availability than to enhanced P availability due to increases in N₂ fixation or decreases in denitrification resulting from enhanced evapotranspiration, among other factors. This possibility of increases in soil N-P ratios in the short term can lead to a more persistent rise in N-P ratios if warming continues to increase. Experimentation to specifically study and respond to this question is warranted, because the soil N-P ratio is a key factor in the structures and functions of ecosystems (Sardans et al., 2012c).

Summarizing, in wet/cold ecosystems, warming enhances plant production and growth, increasing the investment in N and P uptake and generally increasing plant C-N and C-P ratios. In spite of the higher litter C-N and C-P ratios, increases in mineralization and nutrient release from soil organic matter are observed as a result of the increases in soil biological activity and, frequently, the higher water availability by increasing defrost. The possible different effects of warming in N and P cycles remain to be clarified. There are some reports suggesting that warming can have an additional impact by the increases of warming periods during winter in cold and temperate ecosystems. All these aspects warrant future research. Contrarily, in hot/dry

environments, the effects of warming are determined by the impacts of changing water availability.

DROUGHT

Shifts in Elemental Composition

Prolonged water stress frequently translates into a reduction of aboveground plant growth (Inclán et al., 2005; Xu and Zhou, 2006; Ogaya and Peñuelas, 2007; Prieto et al., 2009; Jyske et al., 2010; Wu et al., 2011b), but plants respond by trying to increase water uptake and enhancing conservative mechanisms to improve water use efficiency (WUE). Single drought events also initiate plant physiological responses that frequently result in changes in soil activity, affecting ecosystem nutrient cycling that allows the survival of the plant community and thereafter the return to initial conditions (Jentsch et al., 2011; Lloret et al., 2012).

Drought increases the production of abscisic acid, the accumulation of water in plant tissues (Radin and Ackerson, 1981; Wittenmayer and Merbach, 2005; Planchet et al., 2011), and mechanisms to protect the PSII enzymatic system based on pigments and anti-stress enzymes (Munné-Bosch and Lalueza, 2007; Zhang et al., 2011). All these changes tend to reduce photosynthetic efficiency (Munné-Bosch and Lalueza, 2007). Abscisic acid coordinates the protective responses of plants to drought, mainly by increasing stomatal closure, decreasing foliar surface areas, and increasing root-shoot ratios through the allocation of more resources to the root system (Bahrun et al., 2002; Wittenmayer and Merbach, 2005). Increased synthesis of antioxidant enzymes such as superoxide dismutase is characteristic of plants under drought (Ruiz-Lozano et al., 1996). Proteomic and metabolomic analyses have discerned the stepwise changes in N use and allocation in plants responding to drought. Rubisco is hydrolyzed, and N is further allocated to the synthesis of amino acids with osmoprotective functions (Aranjuelo et al., 2011). These “omic” techniques should be used to study shifts in the metabolic use of other nutrients, such as P.

Coinciding with these general physiological responses, an increase of mycorrhizal symbiosis under drought is frequently observed in field studies (Ruiz-Lozano et al., 1995; Davies et al., 1996; Al-Karaki and Al-Raddad, 1997; Shi et al., 2002; Roldán et al., 2008). The enhancement of mycorrhizal symbiosis improves the capacity of plants to take up both water and nutrients (Ruiz-Lozano et al., 1995; Alvarez et al., 2009; Wu et al., 2011a). Drought can also increase the allocation of resources to roots (Huang, 2001; Wittenmayer and Merbach, 2005; Suralta, 2010), the acceleration of turnover of fine roots (Meier and Leuschner, 2008), and an increased production of root exudates, contributing to increased chelation and uptake of nutrients (Henry et al., 2007; Kohli et al., 2012). Mycorrhization is positively correlated with an enhanced antioxidant metabolism in plants (Ruiz-Lozano et al., 1996).

In addition to activating mechanisms for improving the capacity to take up water, plants respond to drought by enhancing mechanisms for conserving water and nutrients, such as the retranslocation of nutrients prior to tissue senescence (Heckathorn and DeLucia, 1994, 1996; Correia and Martins-Loução, 1997; Milla et al., 2005) and the internal remobilization of nutrients dependent on the availability of water (Sardans and Peñuelas 2012a). As observed in plants adapted to severe periods of drought, P tends to remobilize from leaves to roots, whereas K has the opposite movement, as observed in Mediterranean trees during summer drought (Milla et al., 2005; Sanz-Pérez et al., 2009; Sardans et al., 2012a). Plants with the genotypic capacity to maintain N, P, and K concentrations and contents under drought have a competitive advantage if drought persists or becomes more severe (Ghandilyan et al., 2009). Plants adapted to drought are able to raise the concentration of N in leaves (Inclán et al., 2005; Weih et al., 2011).

Different metabolic systems of CO₂ uptake can provide differences among plants competing under drought. C₄ plants maintain higher photosynthetic rates than C₃ plants under drought conditions (Taylor et al., 2011). Plants with Crassulacean acid metabolism respond very efficiently to drought even in nutrient-poor soils (Maiquetía et al., 2009).

Drought reduces net photosynthesis and growth as well as the capacity to take up N and P from soil (Chidumayo, 1994), but these effects are ameliorated if N, P, and/or K availability is high, leading to higher root proliferation, water uptake, and WUE (Radin and Ackerson, 1981; DeLucia and Schlesinger, 1991; Borch et al., 2003; Garg et al., 2004; Waraich et al., 2011). Higher concentrations of P in plants improve WUE because they allow a minor suppression of photosynthesis per unit of water transpired (Singh et al., 2000; Jones et al., 2005) and improve the capacity of stomatal control (Waraich et al., 2011). Enzymes of N metabolism play an important role in the acclimation to drought (Xu and Zhou, 2006). Most studies show that decreases in soil moisture also reduce N and/or P uptake by plants (Jupp and Newman, 1987; Sardans et al., 2005; Sardans and Peñuelas, 2007; Cramer et al., 2009; Waraich et al., 2011), suggesting a negative feedback of less water and fewer nutrients on the production capacity and fitness of plants when drought persists or becomes more severe. As a result, plants under drought tend to produce leaves and litter with high C-nutrient ratios (Yarie and Vancleve, 1996; Sardans et al., 2008b; Limousin et al., 2010). The few studies of the specific effects of drought on the N-P ratio in plants, however, have not provided a clear conclusion (Sardans and Peñuelas, 2008; Sardans et al., 2008c, 2012b), in spite of studies in gradients of water availability in Mediterranean regions that have observed a negative correlation between water supply and leaf N-P ratio (Sardans et al., 2011), an effect linked to higher growth capacity in plants with lower N-P ratios (Sardans and Peñuelas, 2012b). Moreover,

drought limits the capacity to fix N_2 by limiting the metabolic capacity of bacteria and by generating oxidative damage (Streeter, 2003; Naya et al., 2007; Franzini et al., 2010; Aranjuelo et al., 2011), which further decrease the N content of ecosystems. The responses of plants to drought in cold ecosystems, where temperature, light irradiation, and soil nutrients are the main limiting resources, cannot always be detected and may even have effects opposite to those discussed above (Yarie and van Cleve, 1996; Nilsen et al., 1998).

Effects on the Availability and Stoichiometry of Nutrients and on Primary Production and Community Structure

Drought can affect soil activity and fertility as a direct effect of low soil water content and changes in plants. The most common effect of drought is a decrease in soil biological activity, including decreases in soil enzyme activity (Lorenz et al., 2001; Yavitt et al., 2004; Henry et al., 2005; Sardans and Peñuelas, 2005, 2010; Sardans et al., 2006, 2008a, 2008d), mineralization (Fig. 1), and SOM decomposition (Van Meeteren et al., 2008; Sanaullah et al., 2012) that frequently decrease the availability of soil nutrients (Fig. 1). These effects are due most frequently to the decrease in soil moisture (Sardans et al., 2008a; Sardans and Peñuelas, 2010) but also to decreases in food quality and the nutrient contents of leaves and litter (Sardans et al., 2008d; Matías et al., 2011). These effects frequently lead to increases in recalcitrant forms of soil nutrients and decreases in forms available to plants (Sardans and Peñuelas, 2004; Sardans et al., 2006, 2008d, 2008e). As far as we know, only one study has detected increases in soil mineralization under drought (White et al., 2004).

The increase in SOM and nutrient stocks in soils under drought can increase the risk of nutrient losses from the ecosystem, mainly if drought is accompanied by more frequent and intense torrential rainfall, as expected in some areas such as the Mediterranean basin (Sardans and Peñuelas, 2012a; Zaimes et al., 2012). Field studies that experimentally manipulate climate have observed that decreases in soil-water content at a level projected by most climatic models have led to the loss of N from the ecosystem (Ogaya and Peñuelas, 2009). Furthermore, rewetting events in a scenario of increasing drought can further increase the loss of nutrients from the ecosystem; sudden increases of more soluble forms of N in soil have been observed after rewetting events (Ryan et al., 1998). Prolonged drought coupled to less predictable and intense torrential rainfall (Frei et al., 1998) opens a scenario of shifts in the feedbacks and equilibria within the plant-soil system in some semiarid areas such as the Mediterranean region. The most threatening phenomenon for Mediterranean soils, especially in the most xeric areas, is desertification linked to a continual positive feedback: higher frequency and intensity of torrential rainfall and longer, more severe drought

periods (both associated with climatic change) with increased soil erosion, which in turn leads to a loss of soil fertility and thus plant cover (Garcia et al., 2002; Moreno-de las Heras et al., 2011; Ruiz-Sinoga et al., 2011, 2012), a phenomenon that finally drives desertification. In this process, the most drought-resistant plants are selected and constitute patches in the middle of bare soil (Ochoa-Hueso et al., 2011; Ruiz-Sinoga et al., 2011). The soil variability of water and nutrient availability are related to the distribution of vegetation patches with respect to bare soil patches, which can be considered as runoff sinks and sources, respectively (Boix-Fayos et al., 1998; Kutiel et al., 1998; Mayor et al., 2009; Ruiz-Sinoga and Martínez Murillo, 2009; Gabarrón-Galeote et al., 2012; Mayor and Bautista, 2012; Merino-Martin et al., 2012). Thus, soil nutrients and water availability are higher in soils with higher infiltration capacity and biological activity that coincides with vegetation patches throughout the slopes (Maestre and Cortina, 2003; Agra and Ne'eman 2012).

In summary, drought reduces net photosynthesis and growth, but these effects are ameliorated if N, P, and/or K availability is high, which allows improving plant WUE by enhancing the capacity of stomatal control (Waraich et al., 2011). Most studies show that decreases in soil moisture also reduce N and/or P uptake by plants; as a result, plants under drought tend to produce leaves and litter with high C-nutrient ratios, with further consequences on litter decomposition by decreasing litter quality. These effects frequently lead to increases in recalcitrant forms of soil nutrients and to decreases of the forms available to plants (Table I). Moreover, deep root systems transfer water from deep to upper soil layers, potentially favoring the mineralization of leaf litter and improving the water status of the community species with superficial root systems (Filella and Peñuelas, 2003), which merits future research.

N EUTROPHICATION

Impacts on Plant Function, Chemical Composition, and Stoichiometry

Human activities have more than doubled the nitrogen inputs in terrestrial ecosystems (Matson et al., 1999; Peñuelas et al., 2012). Individual plants respond to N availability at metabolic and physiological levels. Plant species have an optimal level of N supply for growth and plant function (Baghour et al., 2000; Horchani et al., 2010). Plants also have a notable phenotypic plasticity for adapting to changes in N supply. For example, when the availability of N becomes limiting, high-affinity nitrate and ammonium transport systems are up-regulated and lateral root growth is stimulated (Quaggiotti et al., 2003; Remans et al., 2006; Engineer and Kranz, 2007; Krapp et al., 2011). About 3,000 genes in *Medicago truncatula* are up-regulated under N starvation (Ruffel et al., 2008), and

the main enzymes of the N cycle (nitrite and nitrate reductases, Gln synthetase and dehydrogenase) are very sensitive to N supply (Horchani et al., 2010), indicating the importance that N uptake has for plants. N deficiency reduces foliar area and chlorophyll content, which negatively affect photosynthetic capacity and growth (Zhao et al., 2005).

Increases in N availability due to enhanced N deposition should have a rapid positive effect on plant growth and metabolism. The increases in plant growth under N deposition (Eisenlord and Zak, 2010; Bontemps et al., 2011) enhance the intensity of competition among plants (Friedrich et al., 2012). Ecological responses to increases in N supply, though, are more complex. Several other processes, such as plant competition, plant-herbivore and plant-fungus relationships, and plant-soil feedbacks, among others, are involved in the responses of plants to N deposition in field conditions (Gilliam, 2006). Increased concentrations of N in plants further raise plant respiration (Reich et al., 2008), along with increases in plant activity and the need for resources. Although increases in N supply and uptake result in increases in the uptake of other nutrients such as P, these other nutrients eventually tend to become progressively limiting (Fujita et al., 2010). An increase in phosphate activity in roots is a general plant response to increased P limitation under N deposition (Fujita et al., 2010). The availability and uptake capacity of P is thus a critical factor in the capacities of communities and individual plants to respond to N deposition (Johnson et al., 1999; Phoenix et al., 2003; Menge and Field, 2007; Blanes et al., 2012). Another observed plant response to enhanced P uptake under N deposition is the change of the mycorrhizal community from being specialists in N uptake to being specialists in P uptake (Lilleskov et al., 2002), although some studies have not observed clear changes in plant mycorrhizal infections (Wallenda and Kottke, 1998). In most cases, though, the increases in N availability under N deposition are associated with increases in concentrations of N in plants (Fenn et al., 1998; Baron et al., 2000; Peñuelas and Filella, 2001) and decreases in concentrations of P (Duquesnay et al., 2000; Kowalenko, 2006). Increases in the N-P ratio in plant tissues (Sardans et al., 2012c) and decreases in the C-N ratio (Sardans et al., 2012c) are consequently widely observed in most areas of North America and Europe under prolonged increases in N deposition. This increase in the plant N-P ratio further limits plant growth (Güsewell, 2005; Granath et al., 2012) and photosynthetic rates (Güsewell, 2005). Another frequent effect accompanying N deposition is an increase of root growth (Brunner and Godbold, 2007), but some studies have observed a reduction in root growth (Gundersen et al., 1998; Nadelhoffer 2000) and increases in fine-root turnover (Nadelhoffer 2000) and very frequently a lower root-shoot ratio (Leith et al., 1999).

All these responses are species specific and lead to varying capacities of adaptation to N deposition in the

different species. Species with traits that enable better adaptation to P limitation are thus favored (Leith et al., 1999; Fujita et al., 2010; Blanes et al., 2012). The chemical form of the N supply is also important in plant responses. NH_4^+ generally has a larger effect than NO_3^- on plant responses (Sas et al., 2003; Cárdenas-Navarro et al., 2006; Horchani et al., 2010). Several species, such as Norway spruce (*Picea excelsa*), prefer ammonia to nitrate as a source of N (Kronzucker et al., 1997). Increases in the $\text{NH}_4^+:\text{NO}_3^-$ ratio under N deposition have been observed in soils (Stevens et al., 2006; Sparrius et al., 2012). A recent review provides some evidence that the efficiency of carbon use by soil microbes increases with N deposition (Manzoni et al., 2012), suggesting that soil mineralization increases and microbes improve their uptake of nutrients, which, in turn, would increase the competition for nutrients between microbes and plants.

In sites with N saturation after long-term N deposition, plants can reduce the uptake capacity of roots. Lipson et al. (1996) observed that the Alpine herb *Bistorta bistortoides* decreases the capacity of its roots to take up N when the N stored in amino acids in rhizomes reaches certain levels. Despite the mechanisms of plants that increase the uptake of other resources or reduce the uptake of N under conditions of N deposition, most studies have observed a decrease in the C-N ratio of leaves and litter under N deposition (Aerts et al., 2012; Sardans et al., 2012b).

The plasticity of plants in reducing their uptake of N under high availabilities of N coupled with enhanced uptake of other resources, such as CO_2 , P, or K, should be studied. Metabolomic and transcriptomic techniques applied to field experiments are promising tools for advancing our understanding of these responses.

Effects on the Availability and Stoichiometry of Soil Nutrients

As a consequence of the increases in P uptake, the concentration of P in soils tends to decrease (Kowalenko, 2006), and increases in P limitation in plants are observed after long-term N deposition (Bragazza et al., 2004; Güsewell, 2004; Menge and Field, 2007; Lund et al., 2009; Sardans et al., 2012b) and in experiments simulating N deposition (Braun et al., 2010; Sardans et al., 2012b), which can lead to high N-P ratios in soils (Fenn et al., 1998; Manning et al., 2006; Braun et al., 2010). This P limitation can scale up through trophic webs and affect herbivores (Tao and Hunter, 2012). Despite these general trends of increased P limitation when N deposition strongly increases ecosystemic activity, including soil decomposition, ecosystems have large immobilized stocks of P in their soils, which can imply an increase in P availability, as observed in some European heathland (Jones and Power, 2012). Moreover, increases in the activities of soil phosphatases under N deposition have been observed in some

studies (Johnson et al., 1998; Turner et al., 2002; Papanikolaou et al., 2010), where an increase in the allocation of P uptake by soil organisms further favors the uptake of P by plants. Increases in the P cycle in soil (Marklein and Houlton, 2012) and the uptake of P by plants, although generally insufficient to prevent the rise of plant and soil N-P ratios, can contribute to the retention of P in the ecosystem (Perring et al., 2008). The effects of N deposition on P limitation in areas with very N-poor soils can remain undetected, as in forests of the northeastern United States (Finzi, 2009; Groffman and Fisk, 2011) and some areas of Europe (Binkley and Högberg, 1997; Stevens et al., 2011). In these situations, an increase in C-N ratios in litter and soil can be observed (Jones et al., 2004; Stevens et al., 2011).

N deposition, in addition to frequently enhancing plant growth and N uptake, also increases the concentration of N in soil (Bobbink et al., 1998; Nissinen and Hari, 1998; Falkegren-Grerup and Diekmann, 2003; Robinson et al., 2004; Manning et al., 2006) and decreases soil C-N ratios, as observed in soil subjected to long-term N deposition (Vourlitis and Zorba, 2007; Vourlitis et al., 2007; Fang et al., 2009; Fahey et al., 2011; Sardans et al., 2012b) or to N fertilization that simulates N deposition (Britton et al., 2008; Esmeijer-Liu et al., 2009; Sardans et al., 2012b). A widely observed feedback effect is the increase in N mineralization in soil observed under N deposition (Carroll et al., 2003; Vourlitis and Zorba, 2007; Vourlitis et al., 2007; Holub and Záhora, 2008; Manning et al., 2008; Duprè et al., 2010), an effect related to the lower C-N ratio in litter under N deposition (Bergkvist and Folkeson, 1992; Tietema, 1998) that leads to an increase in N cycling (Mansson and Falkengren-Grerup, 2003; Michopoulos et al., 2004), nitrification (Nilsson et al., 2006), and N availability of soil (Manning et al., 2008; Duprè et al., 2010; Jones and Power, 2012; Phoenix et al., 2012). This increase in N availability is related to the loss of species diversity observed in some areas of Europe (Duprè et al., 2010) and is probably linked to the homogenization of N availability in soils with the loss of soil diversity in terms of fertility.

A general increase in soil respiration (Tietema, 1998; Allen and Schlesinger, 2004) and SOM decomposition is observed under N deposition (Waldrop et al., 2004a; Dalmonech et al., 2010), but a decrease in the mineralization of the most recalcitrant organic matter, such as lignin and phenolics, is also frequently observed (Magill et al., 1997; Saiya-Cork et al., 2002; Dijkstra et al., 2004; Sinsabaugh et al., 2005), together with a more rapid decomposition of litter (Saiya-Cork et al., 2002). All these effects strongly depend on the type of vegetation; N deposition increases the storage of C in soils when the vegetation's litter has a natural low nutritional quality and decreases the storage when the nutritional quality is high (Waldrop et al., 2004b). Under N deposition, soil generally tends to accumulate highly recalcitrant forms of soil organic carbon, such as lignin, that are incompatible with high soil activity

(Zeglin et al., 2007; Grandi et al., 2008). If the inputs of N are very high, however, soil activities can decay (Waldrop and Zak, 2006; Dalmonech et al., 2010). An increased P limitation can lead to a very high N-P ratio in litter. Güsewell and Freeman (2005) observed that N-P ratios over 22 can limit the decomposition of litter.

By increasing the N-P ratio of plants and soil, N deposition can favor species with slow rates of growth in the long term. Despite a possible initial enhancement of photosynthetic activity, the increasing stoichiometric mismatches, especially high N-P ratios, can lead to slow rates of growth and shifts in species composition (Granath et al., 2012; Sardans et al., 2012b, 2012c).

Some processes can contribute to the buffering of N saturation. Ecosystems saturated with N by N deposition frequently lose N through leaching to streams (Kristensen et al., 2004; Brookshire et al., 2007) and through denitrification (Chen et al., 2012). N deposition also tends to decrease N₂ fixation (Compton et al., 2004; Jin et al., 2012), an effect probably associated with the increase in P limitation.

This overview of the current literature thus indicates that long-term N deposition in terrestrial ecosystems, despite general increases of N and P mineralization, leads to larger increases of N in soils than of other elements, to nutrient mismatches, and mainly to increases in N-P ratios in soils and plant tissues that threaten to decrease species diversity by favoring species adapted to P limitation and high N-P ratios (Table I). However, the further possible impacts of N deposition by changing N-P ratios of plants and soil remain mostly ignored.

SPECIES INVASION

The Role of Soil Nutrients in Alien Success

Invasions of alien plant species are currently increasing and are a serious threat to global plant diversity (Vitousek et al., 1987; Vitousek, 1990; Funk and Vitousek, 2007). Most studies that have investigated alien success have identified nutrient availability and the competitive capacities for nutrient uptake and for coping with low levels of nutrients as the key factors in explaining alien success (Fig. 2), factors that can be less important in dry environments as a result of the more limiting role of water (Drenovsky et al., 2012).

The physiological traits linked to alien success have also been widely studied, and some underlie the changes in nutrient stoichiometries of the plant community and soil (Levine et al., 2002; Daehler, 2003; Leger et al., 2007; González et al., 2010; van Kleunen et al., 2010; Scharfy et al., 2011). Several mechanisms involved in the uptake and use efficiency of nutrients are involved in alien success (Daehler, 2003; González et al., 2010). Low costs of foliar construction and higher phenotypic plasticity in taking up available nutrients frequently contribute to alien success (Daehler, 2003;

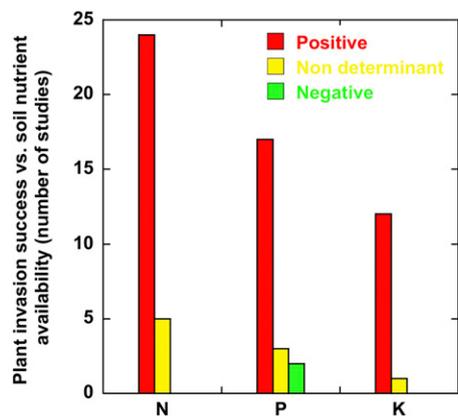


Figure 2. Studies reporting information on the dependence of plant-invasion success on soil nutrient availability. Detailed results and bibliographic references are provided in Supplemental Table S2.

Sala et al., 2007). The success of the relationship between alien plants and the uptake and use of nutrients varies with the availability of nutrients in the soil. Further increases in nutrient availability generally favor alien success when the soils are rich in nutrients (Fig. 2). Alien invasion in nutrient-rich environments also frequently favors plant species with high rates of photosynthesis and growth (Baruch and Goldstein, 1999; Leishman et al., 2007; Feng et al., 2008; Schumacher et al., 2009; González et al., 2010; Mozdzer and Zieman, 2010; Feng et al., 2011), high reproductive outputs (González et al., 2010), large size (van Kleunen et al., 2010), low C-nutrient ratios in tissues (Monaco et al., 2003; Agrawal et al., 2005; Reed et al., 2005; Packett and Chambers, 2006; Schumacher et al., 2009; González et al., 2010; Peñuelas et al., 2010), low costs of foliar construction (Nagel and Griffin, 2001; Feng et al., 2007; González et al., 2010), large investments of N in photosynthetic production (Ehrenfeld, 2003; Xu et al., 2007; Shen et al., 2011), higher capacities of nutrient uptake (Zabinsky et al., 2002; Harrington et al., 2004; Blank and Sforza, 2007; Feng, 2008; Blank, 2010; Hewins and Hyatt, 2010; Leffler et al., 2011; Peng et al., 2011), and high levels of plasticity in the acquisition of resources as a function of pulses in nutrient availability (Leffler et al., 2011). These factors indicate that nutrient uptake and all foliar traits enabling rapid rates of growth (Zabinsky et al., 2002; Leishman et al., 2007) will help invading species to succeed when resources are not limited (Bray et al., 2003; Shah et al., 2009). Alien plants can increase their symbiotic relationships with fungi by directly increasing their capacity for nutrient uptake (Zabinsky et al., 2002; James et al., 2010) or by inhibiting the germination and growth of native plants (Rudgers and Orr, 2009), but some studies are inconclusive (Shah et al., 2009, 2010). The role of nutrient use efficiency is not clear (Scharfy et al., 2009; Aguilera et al., 2010). The resistance of native plants to alien invasion is linked to their capacity to maintain the lowest possible levels of nutrient

availability (Davis et al., 2000; James et al., 2008). Segregating the requirements of nutrient ratios from the invaders can allow native species to persist in invaded communities (James et al., 2008; Peñuelas et al., 2010), a persistence that increases plant diversity (Tilman et al., 1997) and thus helps to reduce competition between native and alien plants. Most studies suggest that increasing the availability of nutrients increases the invasive success of plants (Fig. 2). Current information is insufficient for reaching a clear understanding of whether low N-P ratios in soils favor alien success in nutrient-rich ecosystems, as expected from the growth rate hypothesis, affecting species with higher rates of growth, as is frequently the case for aliens relative to their native competitors (Sterner and Elser, 2002; Sardans et al., 2012c). Despite some studies suggesting the confirmation of this hypothesis, Neves et al. (2010) found lower N-P ratios in alien than in native competitor plants. Therefore, more studies are needed on these two elements in native and alien plants to determine whether some general relationships exist between alien plant success and N-P ratios, at least in nutrient-rich ecosystems.

A higher capacity of N uptake can have further positive consequences for invasive success through the facilitation of the synthesis of N-rich allelopathic compounds that can inhibit the growth of natives (Hewins and Hyatt, 2010). In fact, allelopathic substances in the litter of alien plants can inhibit growth (Hata et al., 2010; Cipollini et al., 2012; Rashid and Reshi, 2012), mycorrhization and the capacities of nutrient uptake (Zhang et al., 2007), and N₂ fixation in native plants (Wardle et al., 1994) and change soil nutrient decomposition rates (Chen et al., 2007a), frequently stimulating soil nutrient cycling (Chen et al., 2007b). Allelopathic compounds in the litter of native plants, however, can also inhibit the growth of alien plants (Hou et al., 2012). The “weapon hypothesis” claims that the roots of alien plants exude allelopathic substances that inhibit the growth of native plants, alter soil microbial communities, and confer a competitive advantage to alien plants in the uptake of soil nutrients (Lorenzo et al., 2010; Weidenhamer and Callaway, 2010).

N₂-fixing plants can have an advantage in N-poor soils dominated by nonfixing plants (Lonsdale et al., 1989; Yelenik et al., 2004; Hughes and Denslow, 2005; Morris et al., 2011). Communities dominated by legumes growing in soils with limited availabilities of soil P or water, however, are vulnerable to competition by nonfixing plants with high capacities of P uptake or stomatal control (Suriyagoda et al., 2011), and low availabilities of P reduce the chances of successful invasion by N₂-fixing plants (Haubensak and D’Antonio, 2011). The success of alien nonfixing plants in native communities dominated by N₂-fixing plants is reduced when P is added (Brewer and Cralle, 2003). Conversely, in soils poor in N and P, plants able to acquire extra N by a stable symbiosis with N₂-fixing bacteria can increase their allocation to P uptake and increase

their invasive success (Rout and Chrzanowski, 2009). The more limiting N is, the higher the possibility of alien invasion by N₂-fixing plants, especially if P is not so limiting.

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 (Funk and Vitousek, 2007; González et al., 2010; Matzek, 2011), especially on short time scales (Funk and Vitousek, 2007), long nutrient residence times (Laungani and Knops, 2009) with high C-nutrient ratios in tissues (González et al., 2010), high nutrient competitive ability enabling resistance to low levels of nutrients (Muth and Pigliucci, 2007; Schumacher et al., 2009; Kueffer, 2010), and high plasticity of stoichiometric ratios (González et al., 2010). In ecosystems poor in resource availability (e.g. with deficits of water and nutrients), stress-tolerant plants with efficient metabolisms, such as C4 plants, can increase their chances of invasive success (Szente et al., 1996). Interestingly, a high capacity to allocate N to photosynthesis aids invasive success in both nutrient-rich and nutrient-poor sites (Feng, 2008; Feng et al., 2008, 2009; Matzek, 2011).

Impacts of Plant Invasion on the Availability and Stoichiometry of Nutrients in Soil

Alien plants frequently alter soil conditions. Several studies report significant impacts on the availability of soil nutrients, the decomposition of organic matter, nutrient cycling, and soil stoichiometry (Fig. 3). Plant invasive success in northern Europe was related to increases in nutrient content in nutrient-poor soils and

to decreases in nutrient content in nutrient-rich soils (Dassonville et al., 2008). In a recent review, Pysek et al. (2012) reported that of 436 case studies on the effects of invasive plants on soil nutrient content, 192 found increases, 72 found decreases, and 158 found inconclusive changes. We have reviewed the effect on N and P availability, C-N-P ratios of soils, rates of soil decomposition, and mineralization and nutrient cycling (Fig. 3). Of 65 studies conducted in environments with unclear limitations of nutrients (except some conducted mainly in arid and semiarid areas of the United States), 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 with *Bromus tectorum*, an invader plant of semiarid areas of the United States (six studies) and with N₂-fixing invasive plants (three studies), showing that most invasions in nutrient-rich ecosystems tend to increase the availability of soil nutrients. This effect is related to increases in nutrient cycling. The effects on SOM decomposition and mineralization are not as clear, despite a trend of increases in most reports.

Results for C-nutrient and N-P ratios in soil are inconclusive and variable (Fig. 3). Increases in soil nutrient contents are accompanied by higher productions of biomass that lead to more C in the system. In the long term, more C in the soil counteracts higher stocks of soil nutrients. An insufficient number of studies are available for reaching a more solid conclusion of the impact of plant invasion on ecosystemic (plant and soil) N-P ratios. A higher rate of growth in alien species in nutrient-rich soils should be a favorable trait for invasive success, so low N-P ratios in alien species should favor their success. This important question

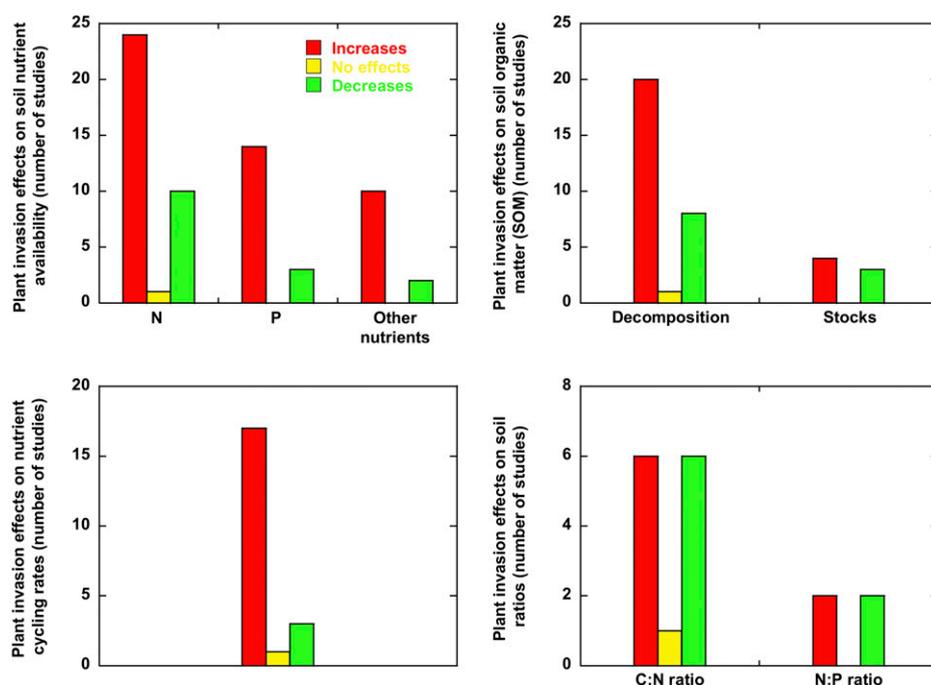


Figure 3. Studies reporting information on plant-invasion effects on soil nutrient availability, soil decomposition rates, soil nutrient cycling, soil organic matter stocks, and soil stoichiometry. Detailed results and bibliographic references are provided in Supplemental Table S3.

cannot yet be resolved due to the lack of data. N deposition, however, can favor invasion, as has been observed frequently (Tomassen et al., 2003; Bidwell et al., 2006; Dong et al., 2006; Gilliam, 2006; Huebner et al., 2009; He et al., 2011; Miki, 2012). These results thus suggest that possible increases in soil N-P ratios do not decrease alien success, but further studies are warranted to discern the role of plant invasion in ecosystemic stoichiometry. Current data suggest a decrease in C-nutrient ratios of plant communities when the number of alien plants and the availability of soil nutrients increase, but inconclusive results prevent the claim of a clear impact on soil stoichiometry. The role of N-P ratios on the invasive success of plants is thus particularly uncertain in both the invasive phase and the shifts during the invasion.

In summary, plant invasion affects soil conditions, which in turn affect plant growth and competitive relationships by plant-soil feedbacks. Invasion can further interact with other drivers of global change such as N deposition, as discussed above. Moreover, some studies have reported that the effects of plant invasion on soil facilitate further invasion by the initial invasive species or by other species (Allison and Vitousek, 2004; Sharma and Raghubanshi, 2009), although not all studies provide clear results on this topic (Yelenik and Levine, 2011). Thus, alien success in nutrient-rich soils is related to higher growth rates, low C-N and C-P ratios, fast plasticity in resource acquisition capacity and high reproductive investment; in nutrient-poor soils, high invasive success is related to conservative use of resources including nutrients. Apart from the nutrient residence time, the capacity of nutrient uptake and other previously mentioned traits, which can be more or less successful depending on the resource richness of each environment, and the capacity to exploit the resources for production and growth would be useful for alien expansion in all situations. Moreover, the role of N-P ratios (of plant and soil) in invasive success is not well known. These possibilities merit further research.

CONCLUSION AND FINAL REMARKS

Elevated concentrations of atmospheric CO₂ tend to increase foliar C-N and C-P ratios, because the initial increase in production can be quickly curtailed by limitations in the availability of N and P, despite the investment of more resources for N and P uptake by plants under high concentrations of atmospheric CO₂.

Warming tends to increase C-N and C-P stoichiometry. This effect is related to an increase in growth that progressively gives a more limiting role to nutrients in wet environments and to the enhancement of conservative strategies related to increases in soil-moisture limitation under warming in dry sites. Drought has a negative effect on SOM mineralization and plant growth in currently dry areas, where nutrient cycling slows, contributing to increased accumulations

of N and P in the soil, but mainly in recalcitrant forms. All these direct effects decrease soil fertility, increase the risk of nutrient losses caused by torrential rainfall, and have a negative feedback on the capacity of nutrient uptake, plant growth, and WUE. Plants thus frequently present higher C-nutrient ratios under drought in currently semiarid and arid regions. Clear evidence that drought can change N-P ratios in terrestrial ecosystems has not yet been reported.

N deposition can decrease C-N and increase N-P ratios of soils and plant tissues, despite the reaction of ecosystems to increasing rates of P cycling that allow higher P uptakes. The larger increases of soil N than of other elements leads to nutrient mismatches and mainly to increases in N-P ratios that threaten to reduce species diversity by favoring species adapted to P limitation and high N-P ratios. N deposition can have an interactive effect under higher concentrations of atmospheric CO₂ and under warming in wetter regions by allowing an increase in growth without C-N stoichiometric changes. However, this can further increase C-P and N-P ratios and the limiting role of P.

Most studies that have investigated the main factors underlying plant invasion have observed that nutrient availability is frequently a key factor in explaining the success of alien plants by the competitive capacity for nutrient uptake in nutrient-rich environments and for coping with low levels of nutrient availability in nutrient-poor sites.

Many unknowns remain in several of these issues, such as the effects of elevated levels of atmospheric CO₂ on the N-P ratios in plants, soils, and ecosystems. Although some current reports suggest that warming can lead to increases in N-P ratios in plants, soils, and ecosystems by asymmetrical effects on N and P cycles, more studies are necessary to gain knowledge on this topic. A sufficient number of studies is also lacking to reach a more solid conclusion of the impact of plant invasion on the N-P ratios of ecosystems (plant and soil). The higher rate of growth in alien species in nutrient-rich soils appears to be a favorable trait for invasive success. Low N-P ratios in alien species should thus favor their success being related to rapid growth. This question is very important and warrants extensive and intensive research. Moreover, some global change drivers, such as warming, increased atmospheric CO₂ concentrations, and N deposition, can actuate together at continental scales. Thus, more studies on the effects of these drivers one by one and in combination are warranted to reach a better knowledge of the particular effects of each one and the interaction effects among them.

Supplemental Data

The following materials are available in the online version of this article.

Supplemental Table S1. Studies reporting information on the relationships between drought and warming with soil-nutrient status (mineralization, content, and availability).

Supplemental Table S2. Studies reporting information on the relationships between plant invasion success and nutrient availability.

Supplemental Table S3. Studies reporting information on plant invasion effects on soil nutrient availability, soil decomposition and mineralization rates, soil nutrient cycling, soil C stocks, and soil stoichiometry.

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