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Stoichiometry constraints challenge the potential of agroecological practices for the soil C storage. A review

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Abstract

To date, the stoichiometry concept has been poorly used to explore C, N, and P cycles in agroecosystems. As agriculture is now under pressure to reduce the use of synthetic inputs, ecological processes and alternative agricultural practices will become the main regulators of the relationships between C, N, and P and thereby of nutrient availability and C storage in soils. In this paper, we review the ecological theories underpinning the concepts of homeostasis and stoichiometric flexibility, their application to agroecosystems, and how stoichiometry could constraint agroecological practices related to nutrient availability and soil C storage. Our main findings are (1) optimal C:N:P ratios exist at the species level, reflecting a range of ecological strategies and representing a keystone constraint for the coupling of C, N, and P cycles, resulting in canonical ratios at the community level. Stoichiometric flexibility nevertheless exists from the organism level—autotrophs having higher flexibility than heterotrophs—to the community level, depending on assembly rules. (2) Agroecosystems are stoichiometrically constrained especially in the soil compartment, due to the low stoichiometric flexibility of microorganisms at the community level. (3) Agricultural practices such as fertilization decrease N:P ratios in soil surface when total P is considered, while C:N ratios remained constant. (4) Stoichiometry homeostasis constraints for soil C storage require the availability of N and P. They can be supported by agroecological practices that promote nutrient recycling (organic fertilization, permanent soil cover, N fixation). The 45-Tg N and 4.8-Tg P needed to increase the C stock of cropped soils by “4 per mille per year” can be also provided by suppressing nutrient losses. We conclude that two soil compartments should be more investigated to evaluate their potential to bypass stoichiometric constraints and foster C storage while reducing chemical inputs: deep soil horizons and particulate organic matter fraction.

Keywords Agricultural soils · Carbon · Nitrogen · Organic matter · Phosphorus · Plants

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1 Introduction

Elemental stoichiometry provides a powerful framework for understanding the complex relationships between ecosystem functioning and biogeochemical cycles (Manzoni et al. 2010; Sardans et al. 2012; Sterner and Elser 2002). Although this concept was developed and has been widely used in marine and freshwater ecosystems since 1958 with the well-known Redfield ratio (Redfield 1958), it was only recently applied to terrestrial ecosystems (Cleveland and Liptzin 2007; McGroddy et al. 2004; Reich and Oleksyn 2004; Xu et al. 2013). Ecological stoichiometry is thus a relatively new branch of terrestrial ecology and provides a relevant conceptual framework to predict the effects of global change on ecosystems at several embedded scales (Zechmeister-Boltenstern et al. 2015). Until now, this concept was mainly applied to natural or semi-natural terrestrial ecosystems.

Although C:N:P ratios are often measured in key compartments of agroecosystems, the overarching concept of stoichiometry is far less frequently used by agronomists. One likely reason is that inputs of fertilizers have to some extent reduced interactions among nutrients by altering their potential limiting effects on biological processes. For example, there is very little evidence to support P limitation of processes of C and N transformations in soils since agricultural soils in developed countries have been enriched by P fertilization for decades (Ringeval et al. 2014). A “decoupling” of N and P cycles was thus reported for fertilized agroecosystems (Yuan and Chen 2015). The decoupling is characterized by a decrease in biological interactions and may consequently increase N and/or P losses to the environment (air, soil, water, etc.) and negatively influence the ecosystems services associated with agricultural land.

The urgent need for more sustainable farming systems requires overall a drastic reduction in nutrient losses, meaning an increase efficiency of nutrient recycling, or reduction in the use of synthetic fertilizers, while at the same time additional ecosystem services are expected from farming systems (Fig. 1) (Duru et al. 2015). The overuse of N fertilizers reduces the potability of drinking water and facilitates the eutrophication of aquatic ecosystems because of nitrate leaching. It also alters air quality through the volatilization of ammonia and contributes to climatic change through emissions of nitrous oxide. P losses from agricultural soils contribute to marine and freshwater eutrophication, and there is increasing concern about the depletion of phosphate reserves at the world level (Cordell and Neset 2014). Incentives for less intensive farming systems are expected to promote the reduced use of mineral fertilizers in the near future, while



Fig. 1 Intercropping and agroforestry as examples of agroecological cropping systems aiming at increasing crop diversity, reducing N fertilization and providing several ecosystem services

enabling interactions among nutrients that are crucial to agroecosystem functioning.

Here we address the question of the relevance of applying stoichiometry concepts to agricultural land, particularly to anticipate the future effects of the agroecological transition on soil ecosystem services. A related question is to what extent the C:N:P ratio in agricultural soils could be altered by agricultural management practices. To address these questions, we first present a synthesis of the theories underpinning the concepts of homeostasis and flexibility in stoichiometry. Based on these theories, we argue that the potential flexibility of C:N:P ratios has important consequences for agroecosystem functioning. Second, we present a literature review focused on C:N:P relationships in agroecosystems. Finally, we discuss the possibility that fostering ratio flexibility in crop fields, both in plants and in soil communities, could be important to insure optimal production and ecosystem services, such as C storage.

2 Stoichiometry theory: importance of homeostasis and flexibility from individuals to ecosystems

Organisms require specific ratios of C, N, and P to survive and function optimally. Sterner and Elser (2002) proposed the concept of stoichiometric homeostasis, i.e., the degree to which an organism or a community maintains its elemental ratios when the elemental ratios of its resource vary (Fig. 2). The homeostasis of ratios at species and community scales has important consequences for ecosystem functioning, from food web dynamics (Andersen 1997; Gusewell and Gessner 2009; Manzoni et al. 2010) to global limitation of primary and secondary production (Andersen 1997; Penuelas et al. 2013; Tyrrell 1999). It is thus a keystone constraint for the coupling of biogeochemical cycles. Stoichiometric flexibility is the extent to which elemental ratios can switch from strict homeostasis to nonhomeostasis behavior (Fig. 2). It is regulated by the intensity and nature of the perturbation and exists across scales (Sistla and Schimel 2012).

2.1 Optimal elemental ratios: from species to communities to ecosystems

Species have evolved different strategies to maintain their metabolism and optimize their fitness. These strategies require different biological structures and hence different optimal ratios of chemical elements (Reiners 1986; Sterner and Elser 2002). As a consequence, the stoichiometric diversity (i.e., the diversity of ratios observed) in nature reflects the diversity of ecological strategies.

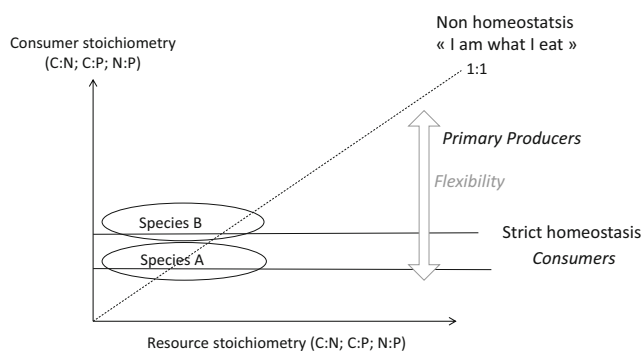


Fig. 2 Relationships between consumer and resource stoichiometry. Horizontal and vertical axes are stoichiometric measure such as C:N, N:P, or C:P ratios. The dashed line (1:1 line) represents identical stoichiometry for consumer and resource, i.e., a nonhomeostasis behavior. The solid lines represent two types of consumers (species A and B) with strict homeostasis behavior meaning that consumers do not adapt their own stoichiometry to that of their environments. Between the dashed and solid lines, the domain of flexibility represents consumers that perform constant differential nutrient retention. Adapted from Sterner and Elser (2002)

Addressing the causes underlying this diversity requires case by case analysis. Yet, some general trends have captured the attention of ecologists. Perhaps the most famous example is the growth rate hypothesis sensu Elser et al. (1996). In short, species that allocate more matter to biological structures that guarantee a high growth rate (biosynthesis) have higher P requirements because these biosynthesis structures (in particular, ribosomes) are rich in P. Although we did not find any evidence in the literature, we can muse that plant species that have been domesticated for agriculture may have lower optimal N:P ratios than their wild ancestor, since they have been selected for higher growth rate.

At higher levels of organization, e.g., at the scale of communities (primary producers, for instance), the diversity of species ratios is spread around an average that seems to be canonical in the ocean, Redfield's ratio extended to microelements (Quigg et al. 2003). In terrestrial biomes, the study by McGroddy et al. (2004) on forest ecosystems suggests that, despite significant differences between biomes, elemental ratios in tree leaves tend to be constrained within a biome, as observed in the ocean. Similarly, C, N, and P concentrations of soil microbial biomass in nonagricultural soils vary over several orders of magnitude at the global scale, while C:N:P ratios are constrained (C:N average = 8.6 ± 0.3 and N:P average = 6.9 ± 0.4 determined on 132 and 150 samples, respectively) (Cleveland and Liptzin 2007). Modeling has been used to better understand the determinism of these diagnostic ratios in communities. The current paradigm is that these ratios result from some general rules regarding the optimization of competitive ability (Klausmeier et al. 2004) or growth rate (Loladze and Elser 2011). The underlying hypothesis is that species with better competitive ability dominate the community and thus leave their imprint on the average community ratio. However, for the soil and its different components (soil microbial biomass, fauna, soil organic matter, etc.), the meaning and mostly the characteristics of "better competitive species" remain to be determined.

At the scale of ecosystems, to our knowledge, no available dataset or paradigm addresses the existence and the causes of potential canonical ratios. Ecosystem biomass is the sum of community biomasses with different elemental ratios. At this point in our knowledge, we can only reflect on how elemental ratios in ecosystems depend on the biomass ratios of communities. For instance, communities of primary producers have higher C:N, C:P, and N:P ratios than communities of heterotrophs (Elser et al. 2000). Thus, elemental ratios in the biomass at ecosystem scale could reflect the biomass ratio of primary producers over heterotrophs. According to the ecosystem development theory (Loreau 1998), competition within and between material cycles during ecosystem development

may lead to higher productivity and better retention of limiting nutrients. Thus, observed elemental ratios in mature ecosystems may reflect the biomass ratio of primary producer over heterotrophs that guarantees high productivity and nutrient retention.

2.2 Ratio homeostasis and flexibility: from individuals to communities to ecosystems

Heterotrophs generally show stricter ratio homeostasis than autotrophs, although in bacteria, strict homeostasis has been questioned. For instance, Makino et al. (2003) showed that elemental ratios in *Escherichia coli* cells could vary by two-folds. The lack of homeostasis in autotrophs is mainly caused by the storage capacity of the autotrophic cell and was originally introduced in growth models by Droop (1974). Some authors even used deviations from optimal ratios in autotrophs as a proxy for nutrient limitation. For instance, a N:P ratio higher than 16 in plant leaves is considered by some authors to be evidence for P limitation (Gusewell 2004; Vitousek et al. 2010).

At higher levels of organization, homeostasis depends to some extent on homeostasis at organismal level, but also on community assembly rules. According to some authors, homeostasis at the organismal level does not guarantee homeostasis at the community level. Indeed, modeling approaches based on the classic competition theory suggest that species sorting may prevent homeostasis, and that instead, elemental ratios in the biomass at community scale may adjust on the ratios available in the food (Schade et al. 2005; Danger et al. 2008). Yet, such a flexible, “bottom-up” stoichiometry is bounded by the most extreme strategies of the species with regard to elemental ratios. For instance, Danger et al. (2008) argue that a bacterial community feeding on a gradient of C:P ratios may adjust to the elemental ratio of the food. This adjustment may operate through species sorting until a threshold C:P ratio is reached beyond which a “boundary species”, the one with the most extreme elemental ratio, dominates the community. Once this state is reached, homeostasis processes at organismal level dominate and the community becomes more homeostatic (Danger et al. 2008). A particular case arises if some species have access to sources of nutrients that are not accessible to other species. For instance, N fixers in a community of primary producers have the capacity to fix N from the atmosphere and to inject it into the ecosystem in the form of organic N and partly transfer it to non-fixing primary producers. In such a case, modeling shows that species sorting leads to the dominance of fixers when the ecosystem is limited by inorganic N. By fixing inorganic N, fixers maintain homeostasis of C:N and N:P ratios at ecosystem level (Tyrrell 1999; Schade et al. 2005).

2.3 Consequences of homeostasis or flexibility for ecosystem functioning

The consequences of ratio homeostasis across functional groups have been widely addressed by ecologists, in both theoretical and experimental studies. Most results suggest that food web dynamics are highly dependent on the homeostasis of these ratios, and on the ratio mismatches between trophic levels. In particular mismatches between primary producers and herbivores, and between primary producers and decomposers (Sterner 1990; Andersen 1997; Daufresne and Loreau 2001; Cherif and Loreau 2013; Manzoni et al. 2010; Mooshammer et al. 2014; Spohn 2015) challenge the transfer of energy and matter through trophic levels, and affect the recycling of elements, a key process that guarantees primary production in the long term. Generally, these mismatches appear to be deleterious to productivity and stability. They may generate instability, leading to oscillatory dynamics (Andersen 1997), chaos (Andersen 1997), or even ecosystem crash (Daufresne and Loreau 2001). In short, homeostasis at community level constrains ecosystem functioning and reduces ecosystem resilience. On the other hand, ratio flexibility tends to ease these constraints. For instance, Danger et al. (2008) showed that a community of bacteria had much higher resilience in terms of total biomass than a single species when facing changes in the C:P ratio of their food, due to ratio flexibility. This argument can be rephrased in terms of the insurance hypothesis (Yachi and Loreau 1999) for ratio diversity, more specifically the width of the range of ratios in a community insures ratio flexibility and hence ecosystem resilience to changes in nutrient inputs.

3 The case of agroecosystems

As mentioned earlier, ecological stoichiometry approaches have rarely been applied to agroecosystems up to now. The question is whether the above mentioned ecological theories are relevant in agroecosystems and what are the implications for an agroecosystem facing changes in agricultural management. Hereafter, we discuss this question in the light of our current knowledge of the biogeochemistry of C, N, and P in agricultural soils. Based on a request using ISI Web of knowledge from 1975 to present, over 10699 articles addressing soil biogeochemistry of C, N or P, we found 6374 papers focusing on C and N only, 4137 focusing on N and P, 994 focusing on C and P, and only 418 focusing on C, N and P. These numbers highlight the relative rarity of studies addressing more than two chemical elements in a study site. As pointed out in former studies, this rarity is not to be specific to agricultural soils. For instance, most studies of forest ecosystems focus on the cycles of C and N, and ignore the cycle of P (Bol et al. 2016).

3.1 Agroecosystems characteristics: from intensive to agroecological transition

An agroecosystem is an area of agricultural production understood as an ecosystem. Even if some authors question the relevance of the ecosystem concept for cultivated areas (Tassin 2012), simplified structures and characteristics of natural ecosystems can be observed in agroecosystems (Gliessman 2006): an individual plant (organism level), single-species plant cover (population), mixed-species crops or ensemble of crops at the farm level (community), a farm in its biophysical context (ecosystem). Therefore, the ecosystem concept may provide a framework to analyze the complexity of energy flows among the components of agricultural systems and the cycling of nutrients.

However, the anthropization of ecosystems for the purpose of establishing agricultural production makes agroecosystems very specific in some key respects (Altieri et al. 1983; Odum 1969):

-The prime aim of agriculture is to manage those processes and resources to export biomass from the system and to maximize yields, minimize year-to-year instability in production, and prevent the long-term degradation of the productive capacity of the agricultural system, particularly soils. In agroecosystems in which natural communities have been replaced by single plant species in pluri-annual rotation, species, genetic diversity and hence the diversity of stoichiometric ratios are expected to be lower than in natural ecosystems (Fig. 3). Biodiversity loss has been extended by the intensification of agriculture and population regulating mechanisms altered with simplified trophic structure and reduced interactions (Gliessman 2006).

-Agroecosystems are also highly dynamic. The temporal changes and vegetation succession they undergo are mainly driven by human decisions and do not result from self-organization of the system. For instance, annual crop rotations induce high variability over time at the field scale, and the agroecosystem undergoes regular and frequent changes in the form of soil tillage, planting, and harvest. The question arises if these agricultural practices modify the stoichiometric ratios of soil heterotrophic communities, for instance, and if these ratios are more prone to rapid change or are rather constrained.

-Nutrient cycling is greatly altered by human interference in agroecosystems. Agroecosystems are open systems (Fig. 4). Nutrients are directed out of the system at the time of harvest rather than stored in the biomass, which prevents their accumulation within the system (Loucks 1977). External nutrient inputs are added to the system in the form of inorganic or organic fertilizers. Because of the frequent lack of efficient synchronization between plant requirement and nutrients released by the soil, large quantities are lost from the system during the growing cycle and after harvest, as the result of

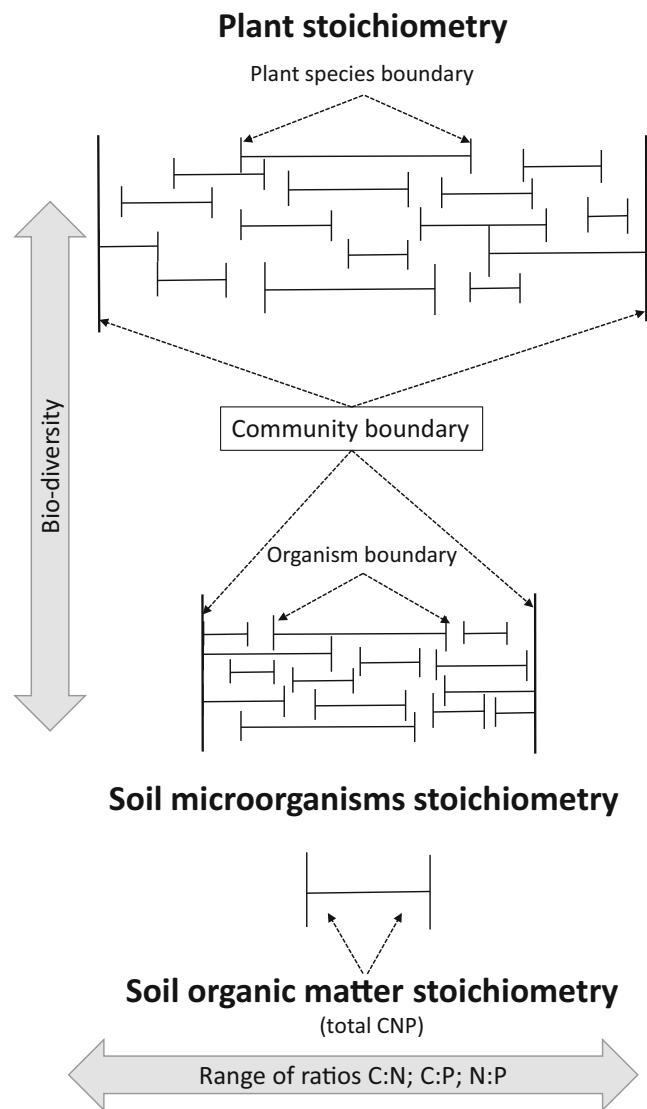


Fig. 3 Schematic representation of the impact of “bottom-up” plant stoichiometry on soil microorganisms and soil organic matter stoichiometry. Autotroph represented by plants exhibited a larger range of stoichiometric ratios (i.e., C:N; C:P; N:P) than heterotrophs such as soil microorganism. Stoichiometry is bounded by the most extreme strategies of the species present with regard to the elemental ratio. After passing through the prism of microorganisms, the ratios are highly constrained

increased erosion, leaching, gas emissions (Dinnes et al. 2002). This is favored by the reduction in permanent plant biomass held within the system, as the result of soil tillage, and by overall loss of plant and soil diversity. The effect of permanent plant cover on soil stoichiometry was more investigated in grassland (Vertes et al. 2019; Poeplau et al. 2018) and demonstrates the relationships between fertilization strategies and C storage in soils while it was less studied in arable lands. Agriculture is now under pressure to design sustainable agroecological systems, i.e., to achieve natural ecosystem-like characteristics while maintaining qualitative and quantitative harvest outputs. The farming practices expected to develop in

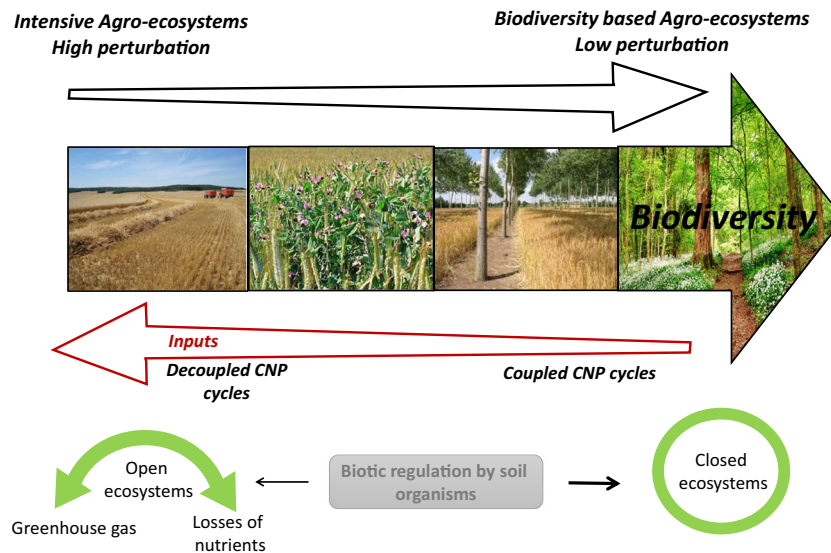


Fig. 4 Illustration of intensive versus biodiversity-based agroecosystems and their impact on nutrient cycles. Intensive agroecosystems (such as monocropping) are highly disturbed and lead to open agroecosystems with higher nutrient losses than in less disturbed biodiversity-based

agroecosystems (such as intercropping, agroforestry). In the latter, biotic regulations play a greater role in maximizing nutrient recycling, thereby leading to more closed ecosystems

this context include mixed cropping, greater introduction of N-fixing crops in rotations, fewer inputs of synthetic fertilizers, and the selection and use of crop varieties that are adapted to such conditions (Duru et al. 2015). Considering the processes that underpin the coupling of biogeochemical cycles, and the resistance of ecosystems to the changes discussed above, the question arises as to the capacity of the promoted agroecological practices to direct currently "open" cultivated systems towards more "closed" agroecosystems. Answering this question is difficult and beyond the objective of this paper, but we propose that the framework of stoichiometry flexibility could help agronomists better understand the boundaries of agroecosystems, and to apply this framework in particular to the objective of increasing the storage of organic C in soils. Under these specific conditions, we define the domain of stoichiometric flexibility of agroecosystems as the possible change in stoichiometric ratios before an economically unacceptable decrease in crop production has occurred.

3.2 Ratio homeostasis and flexibility in agroecosystems

3.2.1 Plant stoichiometry in agroecosystems

As discussed in the theory section, the difference in ratios between plant species within a community defines the extent to which the community is likely to be flexible. As autotrophs are more flexible due to their storage capacity, stoichiometry in an ecosystem may be imposed by primary producers i.e. plant stoichiometry at the top of the trophic food web (Fig. 3). Plants respond to environmental and anthropic changes by several

metabolic and physiological shifts that alter their capacity to take up and reallocate nutrients and consequently their elemental composition and stoichiometry, which, in turn, affects the C cycle (Peng et al. 2017). Plants are thus the main actors underlying the links between environmental conditions (in the broadest sense) and the status of N and P, in (agro) ecosystems.

The single or few species present in a field and facing a change in nutrient availability, can only modify their own growth by either higher/lower uptake of nutrients or by a change in their nutrient use efficiency and through phenomena such as complementarity, facilitation and competition that occur through the diversification of farming systems by increasing the number of cultivated species and introducing more legumes (Bedoussac et al. 2015; Malezieux et al. 2009). Despite a rather constant C fraction of plant dry matter (40–50%), the shoot C:N ratio is highly variable both within and between crop species: Soussana and Lemaire (2014) estimate that C:N ratio of leaf dry matter varies between 17 and 37 in temperate grasslands; Justes et al. (2009) measured C:N ratios ranging from 10.9 to 31.6 in 25 catch crop residues of white mustard, radish, and Italian ryegrass collected from fields with different sowing dates, N fertilization and irrigation rates. Within a species, this variability can be ascribed to a decrease in the critical shoot N concentration with increasing aboveground biomass, and, at a given shoot biomass, to the effects of N deficiency or saturation (Justes et al. 2009; Lemaire et al. 2008). Changes in the root:shoot ratio also strongly affect the stoichiometry of the whole plant, as roots and rhizomes have, on average, a higher C:N ratio than shoots (Amougou et al. 2011).

Crop species therefore have an optimal level of N and P supply for growth and plant function, but also notable phenotypic plasticity for adapting to changes in nutrient supply. For

instance, when the availability of N becomes limiting, high-affinity nitrate and ammonium transport systems are up-regulated and lateral root growth is stimulated (Sardans and Penuelas 2012). N deficiency reduces foliar area and chlorophyll content, which negatively affects photosynthetic capacity and growth. An increase in the concentration of N in the plant increases plant activity and uptake of other nutrients, such as P, which may become progressively limiting, leading to increasing N:P ratio of living biomass and non-living OM compartments (Sardans and Penuelas 2012; Penuelas et al. 2013).

Plant storage capacity is also used to determine the critical P or N curves for cereals based on Liebig's law of the minimum (Gusewell 2004). Across a large range of ecosystems plants with high growth rates typically have higher leaf N and P concentrations and lower C:N, C:P and N:P ratios than slow growing species, which supports the growth rate hypothesis (Elser et al. 2000; Yu et al. 2011). Changes in N:P ratios reported in various vegetation types across the world vary from 11.9 for forbs to 17.8 for Graminoids (Gusewell 2004). However, the question arises if this hypothesis applied for all species encountered in agroecosystems. For instance, legumes have high N and P contents while slower growth rates relative to annual grass and C4 species have high growth rates with lower leaf N content than C3 species. Critical P curves are rare and depend on the site due to the strong affinity between P and soil mineral phases. Some authors have determined critical P concentrations in the shoot from N concentrations assuming constant N:P ratios (Ziadi et al. 2007). However, these ratios are prone to change due to the storage capacity of plants and to the different levels of N and P availability in soils. When N and P are limiting, plants can reduce their growth, their biomass and their grain production thus going beyond the boundaries of the flexibility domain. However, plants are more flexible in their elemental composition than their consumers. Their varying capacity of resorption of nutrients from senescent leaves is an important pathway that explains the alteration in the C:N:P ratio of plant debris (McGroddy et al. 2004).

3.2.2 The stoichiometry of soil total C, N and P pools

Impacts on soil stoichiometry have been reported following shifts from natural ecosystems (i.e., forests, savannah) to agroecosystems (grasslands, croplands) or from cropland to forest (Zhao et al. 2015). These land use changes modify the amount and nature of the organic inputs to the soil, the level of nutrient availability, particularly with N and P mineral fertilization, and soil management through tillage. These changes affect the C, N and P stocks in the soil, and in most cases, result in a marked decrease in these stocks, but the total elemental ratios in soils appear to be rather constrained, at least at the biome level (Cleveland and Liptzin 2007; Xu et al. 2013; Khan et al. 2016). In their meta-analysis, Cleveland and Liptzin (2007) quoted a C:N:P stoichiometry of 72:6:1 for

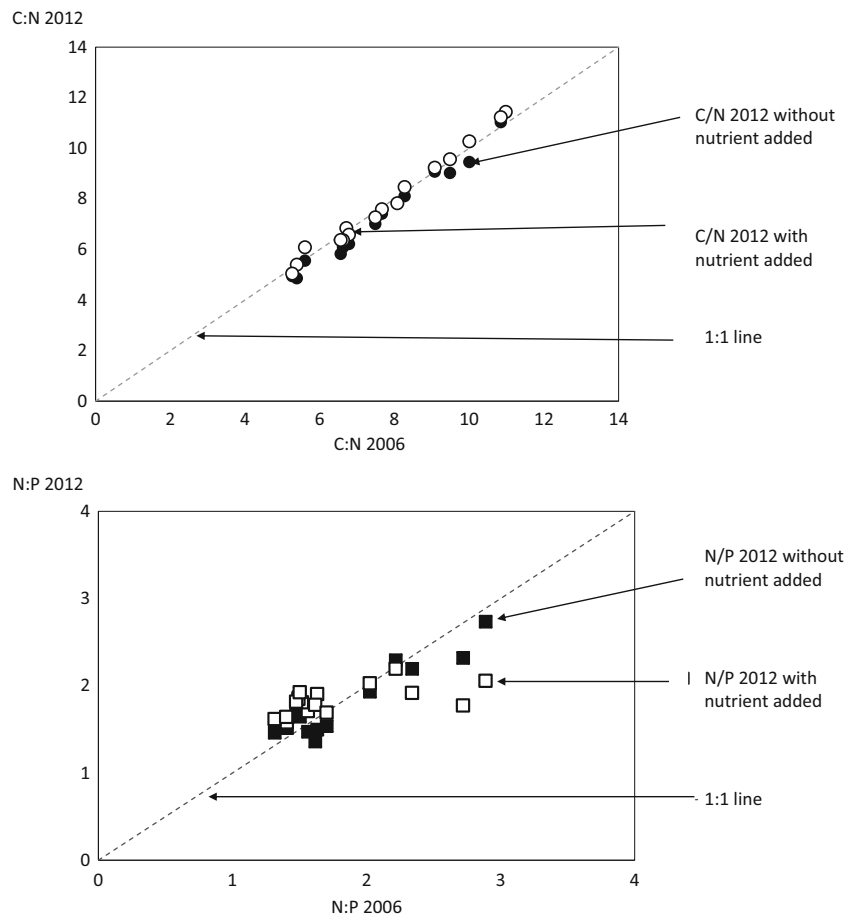
topsoils. Xu et al. (2013) found on average for cropland and pastures a C:N:P stoichiometry of 38:5:1 and 32:5:1, respectively. Comparing a broader range of soils, including arable soils, peatlands and shrubs, Tipping et al. (2016) show that C:N and C:P ratios decrease with increasing C content in SOM (soil organic matter) but for nutrient rich SOM, the average stoichiometry they found (67:7:1) is quite similar to that proposed by the previous authors. Following their study SOM can be divided into two subgroups: nutrient poor SOM and nutrient rich SOM. Nutrient rich SOM selects compounds with strong adsorption to the mineral phase which is particularly the case for P. The resulting change in N:C and P:C ratios ranged between of 0.039 and 0.0011 for nutrient poor SOM to 0.12 and 0.016 for nutrient rich SOM, mainly being related to P.

C:N ratios have also been shown to be unresponsive to several land use changes (Zinn et al. 2018). Soils with the same geochemical background but under different land uses, have construed stoichiometry. Most published studies report a decrease in the soil C:N ratio a long time after land conversion from forests or pastures to cropped soils (Murty et al. 2002; Li et al. 2016). The total P concentration in the soil increases and therefore the C:P and N:P ratios decrease due to the accumulation of inorganic P linked to higher P retention by the soil compared to N (Tiessen and Stewart 1983; Tiessen et al. 1982; Jiao et al. 2013; Schrumpf et al. 2014; Tischer et al. 2014). When analyzing the response of soil stoichiometry to changes in land use, the length of time since land conversion must be taken into consideration. When considering the transitory phase i.e., 5 to 10 years after forest conversion to cropped land, Murty et al. (2002) observed a decrease in C and N stocks of about 24% and 15% respectively, leading to a decrease in the soil C:N ratio after the shift from the native system to agriculture, but, in the longer term (more than 10 years), the C:N ratio stabilized. Frossard et al. (2016) concluded that to capture the effect of land use changes, soil stoichiometry needed to be coupled with balance (input-output) approaches and soil texture and structure indicators. These two studies stressed the relative importance of the time to equilibrium in soil stoichiometry and question whether total soil nutrients, commonly used in stoichiometry approaches in natural environments (Cleveland and Liptzin 2007), are relevant indicators of ratio flexibility in frequently disturbed soils, such as cropped land. Furthermore, the form of soil P considered impact the stoichiometric ratios. Kirkby et al. (2011) measured a stronger relationship between C and organic P than between C and total P although P always exhibited a weaker relationship with C than N and S. When considering total N, organic N could be overestimated because some N exists under inorganic forms (nitrate and ammonium mainly). However, this fraction is smaller for N than for P, which explains why P leads to the main variation in C:N:P ratios (Tipping et al. 2016). Because in agricultural soils, P is mainly added with mineral fertilization, the fraction of mineral P compared to organic P is

higher than in natural ecosystems and could lead to more variable C:P ratios.

Organic and synthetic fertilizers have a strong effect on nutrient availability in agroecosystems and may influence soil stoichiometric ratios. Few studies have investigated the effects of the form or rate of fertilization on soil stoichiometry and most of those that have, focused either on C and N, or on P dynamics. Kirkby et al. (2016) analyzed changes after five years in the C:N, C:P and N:P ratios of the fine fraction of SOM in cropped soils supplemented or not with nutrients at a rate based on the fine fraction of SOM stoichiometry and as a function of soil depth (from the surface to a depth of 1.6 m). Calculated using the Kirkby et al.'s data, we show that no change occurred in the C:N ratios, while C:P and N:P ratios decreased only in the soil surface layers (0–10 and 10 to 20 cm layers) (Fig. 5). The crop yields measured in the same plots did not significantly differ between fertilized and non-fertilized treatments, suggesting that the changes in soil N:P ratios are likely to be part of stoichiometry flexibility. In this work, total P was considered and it accumulated more rapidly than N or C (decreased in N:P ratios between 2006 and 2012) in the surface layers, which could be due to more P retained on minerals than N. The N:P ratios decreased from 2.89 to 2.06 at 0–10 cm depth and from 2.72 to 1.77 at 10 to 20 cm depth.

Fig. 5 Relationships between C:N and N:P ratios measured in soils in 2006 and in 2012 after the incorporation of the same amount of C-rich crop residues and with or without added nutrients. Data were taken from Kirkby et al. (2016) and represent soil depths from 0 to 160 cm



This pattern is in agreement with the results obtained by Li et al. (2013) in a paddy soil ecosystem following different P applications. Therefore, agricultural practices such as P fertilization may modify SOM stoichiometry and the observed changes in ratios suggest some flexibility. However, the impact of the forms of P (organic versus mineral) used in the ratios would deserve more investigations as most of this flexibility accounts for change in P, whereas C and N are constraints at least in the surface soil.

3.2.3 Trophic interactions and the soil microbial biomass stoichiometry

Trophic interactions are important to understand the role of soil biota during the decomposition process. However, the impact of these interactions on litter or soil stoichiometry was rarely reported. Top down regulation of microbial decomposer by the soil fauna regulates C and nutrients availability (Hedlund and Öhm 2000; Sauvadet et al. 2016). Carrillo et al. (2016) model the effect of different litter stoichiometry on the contribution of different functional groups to C and N mineralization. They conclude that litter type does not affect the litter and soil communities in the same manner, and thus the effect of populations and their trophic interactions on

mineralization are not correlated. Furthermore, change in litter stoichiometry traits impacted N cycling. Litter with intermediate N content or mixture of litters promote food webs able to cope with change in substrate stoichiometry.

Studies focusing on soil microorganisms are more abundant than those related to soil biota. Despite variation of the elemental ratios of soil microorganisms has been observed in studies considering a wide range of habitats (Manzoni et al. 2010), they are on average less variable than plants and are considered as stoichiometrically homeostatic (Cleveland and Liptzin 2007; Xu et al. 2013; Khan et al. 2016). However, published C:N:P ratios of microbial biomass should be taken with caution, as almost all data are derived from methods (e.g. fumigation-extraction) that select for a limited group of microbial biomarkers such as cytoplasmic soluble components, whose stoichiometric composition may be more stable than that of other components (e.g. cell wall components, extracellular polysaccharides) and used constant coefficients for C and N (Kallenbach et al. 2016). In cropped land, because soil nutrient contents are high compared to C contents (C:N and C:P ratios of 12.5 and 63.9 respectively in cropland soils compared to 18.9 and 253.8 in mixed forest soils as reported by Xu et al. 2013), the growth of microorganisms is considered more limited by C than by nutrients (Allison et al. 2010). Kallenbach and Grandy (2011) conducted a meta-analysis comparing microbial biomass data in which systems with organic wastes (various animal manures, crop residues) were compared to the same system with inorganic fertilizer in a wide range of agroecosystems, soil types and climates (a total of 297 comparisons). On average, microbial C (C_{mic}) increased by +36% and microbial N (N_{mic}) by +27% compared to systems without organic amendment, and the $C_{mic}:N_{mic}$ ratio was 8.58 ± 0.26 showing a relative increase of about 30% (with 70% of the observed microbial C:N between 6 and 11), with no significant correlation with the C:N ratio of manure and plant amendments (whose C:N varied between 10 and 29). The mean microbial C:N ratio at 8.58 agreed well with the value of 8.6 ± 3 reported by Cleveland and Liptzin (2007) in grasslands and forests, and all these authors assumed a strong homeostatic relationship between C_{mic} and N_{mic} , which persisted even with the intensive addition of resources and irrespective of the elemental stoichiometry of those resources (Cleveland and Liptzin 2007; Mooshammer et al. 2014). Fertilization could thus have an impact on the size of the soil microbial biomass through higher plant biomass production and degradation, but seem to not change much its average stoichiometry in the long term, although data are still scarce to definitively confirm this hypothesis. However, the variation observed (e.g. from 3 to 21 in the Kallenbach and Grandy meta-analysis) was attributed to change in microbial community composition according to nutrient availability, and not to stoichiometry flexibility of a given community. Fanin et al. (2016a, 2016b) previously demonstrated under different

land uses that enzymatic stoichiometry during litter decomposition was driven by C needs rather than by N or P needs. However, fertilization could influence the stoichiometry of available nutrients in soils (mineral N, Olsen P etc.) and future research needs to focus on the stoichiometry of such dynamic pools.

3.2.4 The vertical stratification of soil stoichiometry

The references cited above, which mainly focus on the top soil horizons, show that C:N:P ratios of bulk soils and microbial biomass are quite constrained in agroecosystems, and that fertilization practices do not appear to be a major lever of stoichiometric flexibility. In China, Tian et al. (2010), demonstrated that the C:N, C:P and N:P ratios of an organic-rich horizon (0–10 cm depth) were constrained, arguing in favor of a soil Redfield-like ratio. However, in underlying soil layers, which have a lower content in organic matter, the C:N:P ratios were less constrained, likely because of less biotic regulation and more control through edaphic conditions (geochemical background, weathering etc.) compared to the surface layer. Soil vertical stratification may therefore be important. For example, when investigating the effect of land-use changes (natural forest, pastures of different ages, secondary succession) in tropical conditions, Tischer et al. (2014) reported significant differences in soil C:N:P stoichiometry between soil layers at different depths. Particularly the “organic” layers that are often present in natural systems (forest, savannah) with residue mulches, had higher C:N and C:P ratios than the underlying “mineral” soil layers. This results from the higher accumulation of partially-degraded plant debris, whose elemental composition is closer to plant tissues than to soil stabilized organic matter. In their study, these authors did not observe any changes in the C:N ratio between 0 and 20 cm, indicating a tight coupling of C and N during microbial transformations, while soil C:P and N:P ratios decreased with soil depth, and there was no longer relationships between total P and soil organic carbon. Tischer et al. (2014) concluded that a considerable change in stoichiometry and molecular structure of resources evolves in the soil profile, and the distribution in the soil may vary strongly depending on the land use. In agroecosystems, the major impacts of reduction or suppression of tillage practices on the stratification of SOM and nutrients in the soils profile have been broadly reviewed (Luo et al. 2010). Few papers report measurements of both C, N, and P contents in soils under no-till versus full-inversion tillage, and of the resulting C:N and C:P ratios. In most cases, reduced-tillage had no significant effect on soil C:N ratio (Wander and Bidart 2000; Jacobs et al. 2009; Gregorich et al. 2009; Jagadamma and Lal 2010; Spargo et al. 2011; Dimassi et al. 2014) nor C:P (N:P) ratios of total SOM (Tracy et al. 1990; Kingery et al. 1996; Lilienfein and Wilcke 2003; Gonzalez-Chavez et al. 2010; Wyngaard et al.

2013) neither in the soil layer previously tilled (in most cases the first top 15 to 20 cm) nor in the first top 5 cm. In some studies, conversion to no-tillage resulted in a slight but nevertheless statistically significant increase in the C:N ratio of total SOM in the first 5 to 7 cm of soil (Hussain et al. 1999; Fabrizzi et al. 2003), emphasizing the importance of the stratification of the freshly added and “native” SOM, and their chemical differences in no-till systems.

3.2.5 The stoichiometry of particulate organic matter

In addition to considering the stoichiometry of bulk soil and soil microorganisms, considering that of particulate organic matter (POM) may be relevant. POM is indeed a physical fraction (53–2,000 μm size) of non-living SOM, not closely associated with soil minerals, and dominated by relatively fresh, undecomposed plant residues with a recognizable cellular structure. POM may also include fungal hyphae, seeds, spores and fauna skeleton (Baldock and Skjemstad 1999). This macro-organic matter decomposes faster than total SOM, meaning that POM composition changes over time with more advanced microbial alteration. POM is recognized to be a sensitive indicator of changes in SOM brought about by changes in soil management (Franzluebbers and Stuedemann 2008). Considering the plant origin of POM, as the C:N:P stoichiometry of the “bulk” soil does not resemble that of plant litter (Finn et al. 2016). POM can be found at different degrees of alteration and transformation of plant structural material, by soil decomposers having different activities at different soil depths and consequently has different stoichiometric ratios depending on the microbial processing which interacts with depth and with the time since the change in practices occurred. For example, in a comparison of decomposition in soils amended with flowering and mature pea residues varying in their initial C:N and C:P contents, and the same soil but not amended with pea residues, Ha et al. (2008) showed that the C:N and C:P ratios of the POM in the mature pea treatment decreased during decomposition, towards the values of the flowering-pea and control POM, indicating the narrowing of the stoichiometry ratio with increasing microbial alteration. POM composition may also be affected by tillage practices. Some studies that provided C and N measurements in POM reported similar C:N (Wander and Bidart 2000; Sequeira et al. 2011; Dimassi et al. 2014) and C:P ratios (Wyngaard et al. 2013) for POM under no-till and conventional tillage, whether in the very soil surface (2.5 to 5 cm) or in the tilled soil layer (15 to 20 cm). Other authors reported a decrease in the C:N ratio of the POM under no-till compared to tilled plots, either in the very soil surface (Spargo et al. 2011) or in the tilled layer (Hussain et al. 1999). Conversely, Fabrizzi et al. (2003) found an increase in the C:N ratio of POM under no-tillage in the first 7.5 cm. Differences in POM C:N:P ratios according to tillage management could arise from

different proportions of POM in different stages of decomposition present in the soil, the extreme situation being an “organic” layer of litter particles on top of the bulk soil, whose composition is quite close to that of the original plant litter (Tischer et al. 2014). Because, crop residues have contrasted stoichiometry with C:N ratios ranging from 10 to more than 150 (Trinsoutrot et al. 2000) according to species, maturity and plant parts, the C:N:P ratios of POM varied, and under no tillage, increased the soil C:N:P vertical stratification.

4 Stoichiometric constraints on agroecological practices

The theoretical basis of stoichiometry in agroecosystems and the results discussed above concerning the relationships between agricultural practices and stoichiometry flexibility raise the question of to what extent stoichiometric constraints may weigh on the implementation of some agroecological practices. Based on our literature survey, we show that crops have a greater potential for stoichiometric flexibility at the organismal level, as they can adapt to temporary shortage or imbalance of nutrients by modifying different physiological processes, finally modifying crop production and the quality of the biomass produced if the shortage persists. Their ability to modify re-sorption from senescent parts to grains and fruits is also a key property, as it directly influences the C:N:P stoichiometry of plant debris, source of fresh organic matter in soils. Conversely, the relative lack of stoichiometric flexibility of the soil microbial communities at the individual level and to a lesser extent at the soil community level, was evidenced both in natural and agricultural contexts. Between the two, SOM taken as a whole, is both a resource for heterotrophic microorganisms and a sink for microbial products. The limited stoichiometric flexibility of the stabilized organic matter, particularly for C and N, reflects the microbial physiology and the contribution of microbial biomass and microbial residues to total SOM. In situations in which the C:N ratio of the organic matter was observed to increase in comparison with other management (e.g., in no-till situations with vertical stratification of organic matter compare with tillage situations), our hypothesis is that the SOM included an increasing proportion of partially decomposed plant debris (particulate organic matter), which reflects the elemental composition of plant litter more than that of microbial products (Khan et al. 2016). These conclusions are important for implementing agroecological practices aiming to mitigate the greenhouse effect, by playing on its function as a sink for atmospheric C. This is the whole debate about the international “4 per mille” initiative (Lal 2016; Chabbi et al. 2017; Poulton et al. 2018).

Concerning the first objective, i.e., reducing the use of synthetic fertilizers and reducing nutrients losses and their impact on environment, the options proposed aim to maintain the

elemental ratio of crops and crop products by introducing (again) N by symbiotic fixation in rotations, increasing N and P recycling through organic wastes and animal manure as substitutes to synthetic fertilizers, improving synchronisms between soil supplies and crop requirements (notably through permanent soil cover by plants), and by diversifying crops both in space and time to combine their different abilities to capture resources and to produce different “after-life” plant debris (shoots and roots) (Bedoussac et al. 2015; Duru et al. 2015). All these practices are options that promote the coupling of C and nutrient cycles on the one hand through the presence of vegetation and on the other hand through the constant solicitation of the heterotrophic microbial community that ensures mineralization-immobilization turnover during the degradation of above-ground and below-ground litters, rhizodeposits and organic wastes (Hufnagl-Eichiner et al. 2011) Therefore C management combined with stoichiometry homeostasis constraints of microbial communities and SOM can be viewed as opportunity to move from open and leaky farming systems to “closed” systems with reduced losses (Recous et al. 2019).

Concerning the second objective, it is clear that the low stoichiometric flexibility of the decomposers and of the SOM calls into question the possibility of increasing C storage in soils without simultaneously storing additional amounts of N and P, as pointed out by Richardson et al. (2014) and Van Groenigen et al. (2017). A rough calculation shows that increasing the C stock of agricultural soils by “4 per mille per year” (i.e. 0.527 Pg C/y considering a current stock of 132 Pg C in the top 0.3 m of cropland soils, Zomer et al. 2016) assumes the additional annual storage of 0.045±0.003 Pg N (=45±3 Tg N) and 0.0048±0.0014 Pg P (=4.8±1.4 Tg P) (considering a C:N and C:P ratio of 11.74±0.75 and 110.5±30.5 for SOM; adapted from Kirkby et al. 2011). If this additional amount of N and P were supplied by synthetic chemical fertilizers, it would represent 46% and 24% of the current amount of mineral N and P, respectively, which are spread on cropland soils every year (97 Tg N yr⁻¹ and 20 Tg P yr⁻¹; Lassaletta et al. 2016; Chen and Graedel 2016). This would be in complete disagreement with the above-mentioned target of developing agroecological systems that are less dependent on chemical fertilizers. Moreover, the greenhouse gas emissions that occur during the industrial synthesis, transport and application of N mineral fertilizers on the fields, would seriously reduce the expected benefit of additional C storage in soils for climate change mitigation. However, comparing the additional amount of nutrients required to store the amount of carbon targeted by the 4/1000 initiative (45±3 Tg N and 4.8±1.4 Tg P) to the N and P surpluses calculated for croplands (i.e. between +85 and + 88 Tg N yr⁻¹ in 2009 according to Bouwman et al. 2017 and Lassaletta et al. 2016, respectively; and between +9 and + 14 Tg P yr⁻¹ according to Bouwman et al. 2017 and Chen

and Graedel 2016, respectively) strongly suggests that this additional N and P required to store additional C can be provided under current fertilization rates by reducing nutrient losses thanks to improved management practices like cover crops, fertilizer incorporation, etc.

This emphasizes the need for an integrated agroecological approach, not only focused on C, in which the incompressible need for additional N and P associated with C storage is fulfilled by reducing nutrient losses either directly through improved fertilization practices or by modifying cropping systems, and by other sources such as N fixation by legumes and recycling of organic resources. This review suggests that two soil compartments, which have a higher flexibility, should be specifically targeted for C storage: deep soil horizons and the POM fraction.

In addition to the longer turnover time reported for deep soil C (Balesdent et al. 2017, 2018), the C:N:P ratio in deep soil layers is less constrained, likely because of reduced biotic regulation, so that additional C storage could be achieved with lower N and P inputs. Indeed, the drivers of soil C dynamic changes from the surface to the depth with a gradient of biotic to abiotic control. At depth, less C inputs to prime microbial activity slow down the litter (mainly roots) decomposition (Gill and Burke 2002; Pries et al. 2018) thus increasing C residence time. Microbial biomass C decreased at depth and this decrease is stronger than for total organic C (Fang and Moncrieff 2005) while bioturbation does not occur, thus increasing the abiotic control of C stabilization. The less abundant biota and its adaptation lead to an increasing influence of abiotic regulations at depth, such as a larger proportion of SOM is associated to minerals (Angst et al. 2016; Rumpel and Kogel-Knabner 2011; Shahzad et al. 2018). Although physical disconnection and protection could partly be alleviated by the diffusion of root exudates which lead to loss of C through priming effect, recent studies report either no quantitative differences in priming effect between the surface and deep (80 cm depth) soil layers (Shahzad et al. 2018) or a strong decrease (72%) in deep soil layer (40-60 cm) compare to surface soil layer (0-20 cm) for 35 soils across the world (Perveen et al. 2019). Because priming effect has commonly a lower quantitative effect than litter quality on C mineralization (Fanin et al. 2016a, 2016b), the addition of root litter in deep soil layers could favor nutrient release and C storage although more C balance data including deep soil layer are needed. We argued that increasing soil C at depth without increasing nutrient could be possible to some extent because: 1) the composition and activity of soil microorganisms differed from the soil surface 2) the higher spatial heterogeneity lead to a physical disconnection between microbial activity and root litter (the main hot spots of C) 3) the biophysical environment at depth favor C protection within aggregates (Salome et al. 2010). The contribution of leaf and root litter to dissolved organic C and nutrient leaching could also foster C storage in deep soil layers (Uselman et al. 2007, 2012).

The ability of deep rooting plants to address this issue with the co-benefit of improving water and N uptake which are primary limitation to production in most agroecosystems facing climate change should be further investigated (Lynch and Wojciechowski 2015). Reviews by Kell (2011, 2012) stressed the importance of the genetic control of plant root depths and architecture and its interaction with the environment. Because root architecture between plant types or between cultivars or mutant strains varied, Kell (2012) encourages the development of breeding programs for plants with deeper rooting. However, subsoil exploration by roots must not lead to subsoil over-exploitation, such a paradigm needs to be considered before recommending practices.

Beyond the plant genetic, deep rooting is limited by soil physical properties such as compaction, low P availability, decrease in temperature, increase in acidity, low level of oxygen etc. Bypassing these physico-chemical constraints implies to adapt agronomic practices to facilitate deep rooting. For instance, pioneer species could be used to penetrate compacted subsoils such as dicots as alfalfa or lupin. Alfalfa (*Medicago sativa* L.) exhibited the deepest rooting profile amongst 11 temperate crops reaching a depth of 177 cm (Fan et al. 2016). Deep-ripping during the growing period and any root traits reducing the respiratory requirements (cortical cell number and size) or slowing down desiccation (delayed xylem maturation or suberization) would favor deep rooting (Lynch and Wojciechowski 2015). In complement of deep rooted perennial crops (e.g. alfalfa), trees (e.g. in agroforestry systems; De Stefano and Jacobson 2017) and hedges can act as C transporters towards deep soil layers in addition to providing co-benefits like N fixation, C storage in biomass, providing habitats for biodiversity, and erosion control.

Similarly, the C:N:P ratio of particulate organic matter (POM) is less constrained, because it is less a reflection of the C:N:P ratio of the soil microbial biomass than that of SOM resulting from the complete microbial alteration of organic inputs. Although the residence time of C included in POM is shorter than that of stabilized C associated with mineral particles, the amount of C in coarse-sized particulate organic matter nevertheless represents a significant proportion (>20%) of total soil C (Balesdent et al. 1998; Besnard et al. 2001). Agricultural practices that would enhance C storage in the POM fraction include the practices leading to the accumulation of less degraded plant residues, e.g. by increasing the amount and frequency of plant litters returned to soils (Autret et al. 2016) and by reducing or suppressing tillage. Reduce-tillage promotes the non-incorporation of crop residues which decomposition might be slowed down depending on the microclimate conditions (Coppens et al. 2007), such as in conservation agriculture (Chenu et al. 2019). This requires however a subtle management, and additional research is needed into balancing the stocks and flows of organic matter and thus organic C storage and nutrient and energy release for

agricultural production (Lehmann and Kleber 2015). Indeed, these practices favor the ‘microbial C pump’ whose contribution to soil C storage may have been underestimated (Lehmann and Kleber 2015; Khan et al. 2016; Liang et al. 2017). This means that agricultural management practices that are likely to increase and sustain this POM C stock, should be considered in a “4 per mille” perspective.

5 Conclusion

This synthesis has shown that the principles developed in ecology concerning the concept of stoichiometry, its flexibility or its stability against varied resources, i.e., homeostasis, and applied at different scales (organism, population, community, ecosystem) can be transposed to cultivated agrosystems. In these agroecosystems, stoichiometric homeostasis is dominant and imposes relatively constant ratios between C, N and P concentrations, especially for soil microorganisms and organic matter that are mainly derived from the microbial transformation of plant litters. Intensified agroecosystems have been able to partially overcome these constraints thanks to the use of inputs in the form of mainly mineral fertilizers. But agroecological practices based on the reduction of mineral inputs, and promoting soil C storage to mitigate greenhouse gas emissions, must necessarily take into account these stoichiometric constraints in order to be viable. This objective can be achieved by reducing the high nutrient losses usually observed in conventional agrosystems, by mobilizing other nutrient inputs such as symbiotic fixation and recycling routes, and by considering soil management options that allow C stabilization in soils without proportional stabilization of N and P.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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