



The role of cover crops in improving soil fertility and plant nutritional status in temperate climates. A review

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Abstract

Cover crops (CCs) are a promising and sustainable agronomic practice to ameliorate soil health and crop performances. However, the complex of relationships between CCs, the soil, and the plant nutritional status has been little investigated. In this article, for the first time, we critically review, under a holistic approach, the reciprocal relationships between CCs and the soil physical and hydraulic properties, microbial, and faunal communities, soil nutrient availability, and plant nutritional status in temperate climates. For each of these topics, we report the current state of understanding, the influence of CC management options and suggested strategies, thus including both fundamental and applied aspects. In addition, we provide a detailed focus on the history of CCs and a list of the main temperate CCs. Cover cropping is a helpful practice in improving the physical, chemical, and biological soil properties, optimizing nutrient use efficiency and reducing the dependency of crops on external supplies of nutrients. The interactions between CCs and the nutritional status of soil and plants are complex and dynamic. Their understanding could be useful to set up an appropriate and site-specific management of fertilization. Management options play a key role in developing an effective and context-specific cover cropping.

Keywords Cover cropping · Soil health · Crop nutritional status · Cover crop management · Soil microorganisms

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1 Introduction

Global human population is continuously growing and it is esteemed to reach 9.2 billion in 2050, thus exacerbating the climate change and the loss of natural resources and biodiversity, especially in developing countries (Maja and Ayano 2021). Until today, agriculture was called on to maximize yields by dramatically enhancing the use of auxiliary inputs (tillage, mineral fertilizers, and pesticides) to feed the population growth. Among auxiliary inputs, mineral fertilizers and especially nitrogen ones have provided an important contribution to yield increase since World War II. The intensification of agricultural processes, however, has led to the exhaustion of soils (caused by erosion, the depletion of organic matter and nutrients, since cultivated plants have higher nutrient requirements) and to environmental problems such as water pollution and trace gas emissions (Ludwig et al. 2011). The loss of soil organic matter (SOM) in agroecosystems, in particular, which is a key factor in affecting the physical, chemical, and biological soil properties, has determined a massive decrease in soil quality. The magnitude of this scenario has reached a critical point in Europe, Northern America, and other temperate climates, where cropping systems have been spatially and temporally simplified in terms of biodiversity to facilitate management operations. According to Rasmussen et al. (1998), to make the agricultural activity sustainable for future generations, soil quality has to be maintained and improved. For these reasons, in recent years, there has been an increasing interest towards environmentally friendly agricultural practices, as evidenced by the United Nations (UN) Sustainable Development Goals and the strategies of the European Commission (EC) *Green Deal* (EC 2019; United Nation (UN) 2015).

The inclusion of cover crops (CCs) into farming systems is well-recognized to ensure many ecosystem services including soil erosion control, carbon sequestration, regulation of water infiltration, reduction of nutrient leaching and improvement of nutrient availability, degradation of agrochemicals, increase of biodiversity, pollinator attraction, limitation of pests, weeds, etc. (Adetunji et al. 2020; Blanco-Canqui et al. 2015; Sharma et al. 2018;). Cover crops are broadly defined as non-harvested crops grown in addition to the primary cash crop with the aim of improving soil fertility and enhancing yields. According to the Soil Science Society of America (SSSA), CCs are “close-growing crops that provide soil protection, and soil improvement between periods of normal crop production, or between trees and vines in vineyard” (Fageria et al. 2005). The agronomic technique to realize a CC is known as cover cropping (Fig. 1).

Fertilization is commonly adopted to improve plant nutrition and crop productivity. Organic fertilizers typically enhance the soil nutrient status and the SOM content, while mineral fertilizers mainly aim at improving the crop

nutritional status (Francioli et al. 2016). Mineral fertilization has indirect and negative long-term effects on soil quality deriving from soil pH modification, enhanced soil nutrient unavailability, and decrease of soil physical fertility (Barak et al. 1997). On the contrary, other field trials indicate that mineral fertilization may increase microbial biomass in agroecosystems depending on pedo-climatic conditions and crop management (Geisseler and Scow 2014). Francioli et al. (2016) found that organic fertilizers, thanks to their composition in terms of macro- and micro-nutrients, different from that of mineral fertilizers, not only greatly increase the biomass and diversity of soil microorganisms, but also favor some beneficial taxa while hindering the harmful ones. Plant nutritional status is closely linked to soil quality and crop fertilization. For many crops, especially arboreal plants, the nutritional status is considered as a guide for fertilization (Menesatti et al. 2010). Hence, knowing the nutritional status allows identifying possible nutrient disorders and serves to manage fertilization programmes.

In order to use CCs as an effective tool for improving crop nutrition, it is necessary to clearly understand their interactions with the nutritional properties of both the soil and plants. Among other things, CCs are a pillar of the “Rethinking the management paradigm,” aimed at avoiding chronic surplus additions of inorganic nutrients directly to crops for improving yield performances. This perspective change is in favor of an ecosystem-based approach at multiple scales founded on plant diversity and their associated microorganisms, which can regulate the biogeochemical cycling of nutrients, thus reducing the need for surplus nutrient supply (Drinkwater and Snapp 2007). The interactions between CCs, soil quality, and the crop nutritional status are complex and dynamic. Understanding these relationships in the field is difficult, but their prediction could be useful to set up an appropriate and site-specific management of fertilization, especially in low-input and conservative agricultural systems. This review collects and discusses published papers on CCs and their influence on the soil and plant nutritional status, with the aim of helping farmers and stakeholders in optimizing a context-specific cover cropping and fertilization management. The role of cover cropping typology (single vs mixed, seeding period, intercropping, mulching, green manure, termination method and termination stage) has been also investigated in order to suggest context-specific criteria for CC choice and management options for maximizing the benefits. Moreover, a detailed section on the history of CCs is provided for the first time. The literature review was performed using a systematic bibliographic search on the Scopus, Web of Science, PubMed, and Google Scholar databases with the topic keywords. The bibliographic search on the history of CCs was conducted by directly consulting historical sources and documents. Overall, 158 items were

Fig. 1 Experimental field with *Trifolium subterraneum* L. cover cropping in central Sicily (Italy). Photograph by S. Fontanazza.



examined, of which 106 research papers, 31 reviews (including meta-analyses), 2 websites, and 20 books or book chapters. Only case studies of temperate zones have been selected due to their high consistency with cover cropping. To be included in the review, papers had to be written in English and involve at least three replications.

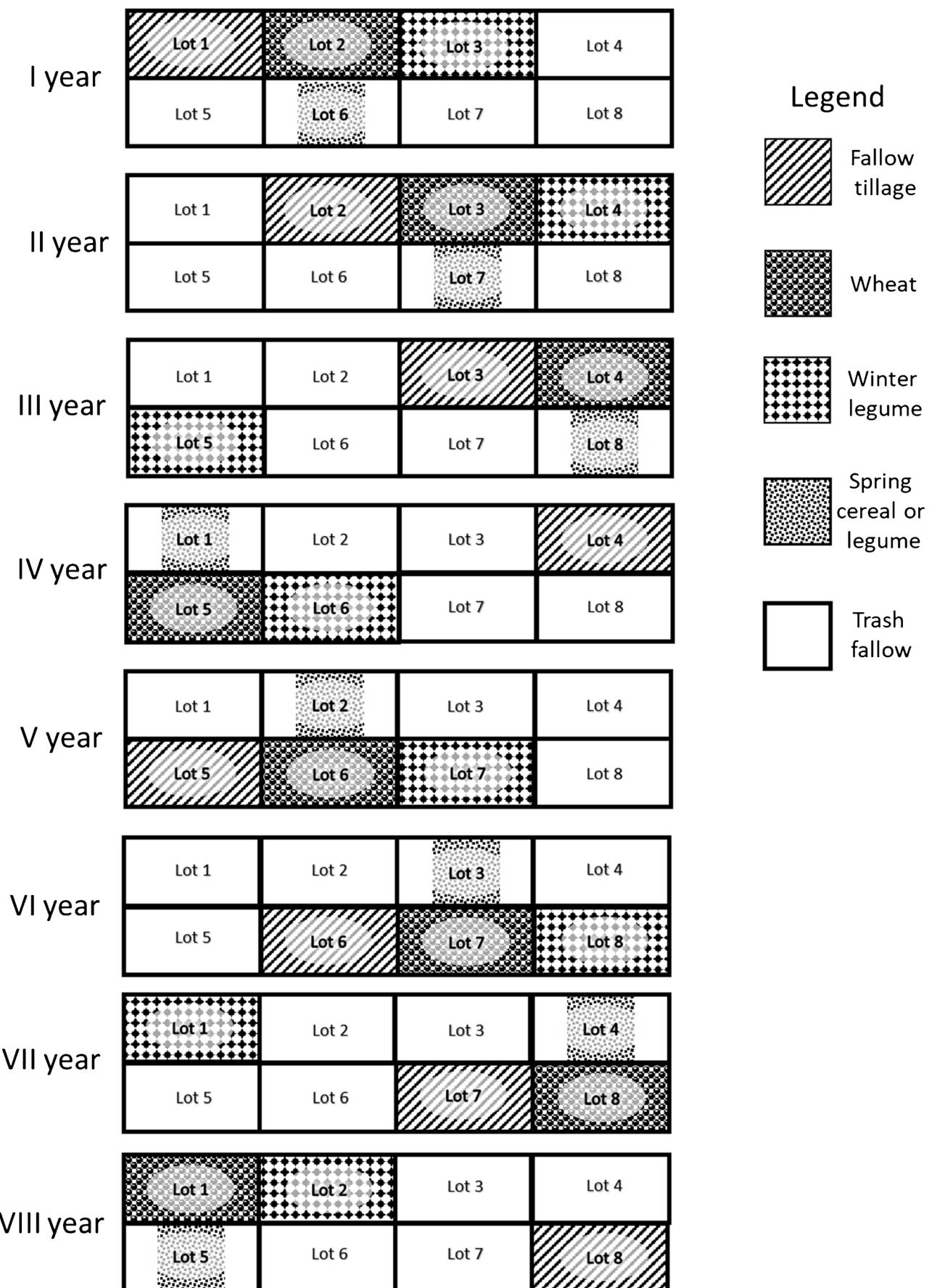
2 History of cover crops

Although the concept of CCs, as we understand it today, was probably initially coined at the end of the 19th century, cover cropping, in several undertones and meanings, has deep roots in the past history and can be found in civilizations distant from each other both in space and time.

2.1 Ancient Mediterranean agriculture is anchored in bare fallow

In ancient Mediterranean agriculture, physical soil fertility was ensured by tillage, while chemical fertility was generally improved with manure. At that time, fallow was a widespread agronomic practice aimed at improving physical and chemical soil fertility and at restoring soil moisture (Semple 1928a). The uncultivated fields were constantly tilled to remove weeds and make the soil softer and wetter (Semple 1928a). The fields

were regularly left fallow in alternate years, but, according to Theophrastus (371–287 BCE) and Varro (116–27 BCE), the exception to this fallow system was only when a cereal crop was followed by a legume, which was ploughed after early harvest. Varro, in *De re rustica* (37 BCE), touched on the notion of cover cropping, writing that legumes should be seeded in light soil for their positive effects on succeeding crops. Virgil (70–19 BCE) seemed to be against the idea of a crop aimed at covering the soil. In fact, in the *Georgica* (29 BCE), he advised against the planting of other crops between the rows of vines, as they would interfere with soil tillage. According to the author, the vines would have had more soil moisture and more nutrients available by frequent tillage and, thus, without the competition of other plants (Semple 1928b). Columella (4–70 CE) did not specifically debate the fallow, but from his writings its importance in the 1st century Roman agriculture emerges. Reading the work of the Iberian agronomist, Saltini (1984) deduced an eight-year cultivation cycle characterized by the alternation of cereals, leguminous plants, and trash fallow covering an area of 200 *jugera* (about 50 hectares) (Fig. 2). What is relevant, for the purposes of this discussion, is that a long period of trash fallow is contemplated (today we would say "natural cover cropping") in this cultivation method. The lengthy period of the trash fallow (5 years), however, is not only linked to the restoration of soil fertility, but also and above all to the breeding of livestock.



◀ **Fig. 2** Eight-year rotation scheme taken from Columella's *De agri cultura*. An area of 200 *jugera* is divided into 8 lots of 25 *jugera*. In each lot, the cultivation of wheat is preceded by a tilled fallow. A winter legume comes after wheat. After the winter legume, on each lot, there are 5 years of fallow, interrupted only by a spring cycle crop grown on about half of the lot (12 *jugera*).

2.2 Green manuring in ancient times

Yueh Ling or fourth book of *Liji* or *Book of Rites*, a kind of encyclopedia written during the Han dynasty (206 BCE–220 CE), reports that using weeds and grasses as green manure was known in China under the Zhou dynasty (from 12th to 3rd century BCE). Chia Szu Hsieh, a Chinese writer who lived sometime in the 5th century BCE, talked about green manuring by using plants belonging to the genus *Vigna* (Pieters 1927). Starting from 400 BCE or even earlier, the ancient Mediterranean farmers developed systems of green manure crops, which represented an improvement in the older fallow system (Semple 1928a). Xenophon (430–355 BCE), in his *Oeconomicus*, stated that green manure enriches the soil just as manure does, although he did not specify the green manure plant. In the *Historia Plantarum*, Theophrastus reported that the peasants of Thessaly and Macedonia cultivated the broad bean (*Vicia faba* var. *major*) to bury it at blooming. Again Theophrastus, in the *Causa Plantarum*, attributes to almost all legumes the capacity of reinvigorating the soil. Picking up from Theophrastus, Cato in his *De agri cultura* (160 BCE), indicated the field bean (*V. faba* var. *minor*), lupine, and vetch as the best green manure plants for cereals. Columella, in *De re rustica*, indicated the importance of intercropping a short-lived green manure crop to be ploughed in vineyards. Columella considered lupines, faba beans, vetches, lentils, chickpeas, and peas as renewing crops when they were buried immediately after the forage was cut. The same author wrote that clover and alfalfa, after producing forage for an adequate number of years, had to be buried when their productivity started to decline. Many authors considered lupine as the best green manure crop due to its numerous benefits: (i) adaptability on dry, sandy, or gravelly soil; (ii) dual purpose food for humans and animals; (iii) rapid growth and prolonged flowering. More generally, the ancients, through a long experience, exploited legumes to make the soil softer and more porous, thanks to their thick and deep roots. Furthermore, they understood that incorporating legumes into the soil leaves more nutrients than removing their residues, and their cultivation represented an economically viable alternative to fallow. Pliny the Elder, in the *Naturalis Historia* (77 CE), reported the practice of planting garlic and onion in the middle of snail medick, anticipating the intercropping between legumes and vegetables.

2.3 Middle Ages

In the Middle Ages, biennial crop rotations were widespread in southern Europe, whereas northern Europe largely adopted three-year rotations. In both systems, a one-year fallow with repeated ploughing was expected and the meadows and pastures were out of the rotation. In this period, the common pastures outside the villages were the scene of the most important manifestations of civil life: fairs, gatherings, and even duels (Grand and Delatouche 1968). Here, the use of a green cover not only for income purposes — for providing food for livestock — but also for the lift that turf gives to the soil, is evident.

2.4 Use of cultivated plants to control biotic adversities in pre-modern agriculture

Nowadays, CCs are also grown for weed control. The ancients observed that some cultivated plants such as legumes have a particular ability to compete with weeds. Indeed, Theophrastus, in the *Historia Plantarum*, reported how chick-pea destroys weeds ($\pi\omega\chi\ \varepsilon\xi\alpha\pi\lambda\lambda\omega\sigma\tau$), in particular the tribulus (*Tribulus terrestris* L.). Palladius (4th century CE), in his *Opus Agriculturae*, referred to the benefits of lupine in controlling weeds without the intervention of a worker. In *Geponics* (10th century CE), it is recommended to sow lupines in soils pervaded by many roots, then to mow and bury them at blooming. It would appear that the buried biomass of lupine was thought to be useful in containing weeds (Zadoks 2013). Pietro de' Crescenzi (1233–1320), in the *Ruralium Commodorum libri XII*, recommended sowing broad beans or lupines for ferns control. The ability of some plants to act as repellents or baits for the parasitic insects of food plants did not go unnoticed. Here then is what Theophrastus had suggested, namely sowing vetch among radishes to save them from parasite attacks. This concept is reiterated in the *Geponics*, where it is possible to read about the use of rocket among cabbages as a trap plant.

2.5 Modern Age

In the 18th century, the idea of using meadows and pastures instead of fallow as a means of conserving and restoring soil fertility began to spread. In one of the largest English treatises of the 18th century, *The whole Art of Husbandry*, John Mortimer (1656–1736) attested to the great importance of forage crops, and in particular clover, in English agriculture. Mortimer recognized an important agronomic significance to the clover, but did not take the next step, that is towards conceiving the replacement of the bare fallow with forage. It would be precisely the costs of the frequent work entailed by fallow to push Mortimer's successors to consider the possibility of replacing the fallow forage to restore fertility. Jethro

Tull (1674-1741), although starting from an erroneous postulate, in his *Horse-hoeing husbandry*, proposed the surmounting of fallow as a means of restoring soil fertility. The same did the Hungarian scholar Mitterpacher (1734-1814), who clearly took a stand against fallow. Arthur Young (1741-1820), in his *A Course of Experimental Agriculture*, observed that clover produces more if cut and hay, rather than left to graze freely. The explanation provided by the English agronomist was that the vegetation cover forming between one mowing and the other protects the soil from the sun, helping to conserve its humidity. In this use of plant cover to conserve soil moisture, it is possible to see the concept of cover cropping. François Rozier (1734-1793), in the wake of Weston (1591-1652), Tull, Young, Duhamel (1700-1782), in the entry “alterner” of his *Cours complet*, summarized the reasons why the alternation of crops improves the soil, thus setting the basis for the theory of rotations. However, the three-year rotation typical of the Middle Ages, characterized by a bare fallow year, was difficult to surmount. Albrecht Thaer (1752-1828) was aware of this and identified the various stages of evolution from three-year cultivation to continuous succession, in which the soil is never left bare. Thaer focused on the covering function of some species such as peas, vetches, and clovers, stating that one of the reasons why they are considered enhancers is the shade created by their leaves. A striking example of soil erosion due to its indiscriminate exploitation is represented by the so-called Dust Bowl, a series of huge sandstorms that swept the central part of the USA in the 1930s. A few years earlier, the United States Department of Agriculture had sounded an alarm — which went unheard — about the dangers related to the massive adoption of deep tillage and the non-use of crop rotation. However, farmers and the public opinion became sensitive to the issue of soil conservation and related practices, including the use of CCs (Hartwig and Ammon 2002), only once the “Dust Bowl” had occurred. Between the 1950s and 1960s of the last century, agricultural productivity increased considerably thanks to mineral fertilizers, pesticides, and fossil fuels. Conservative practices, therefore, were increasingly abandoned, until the energy crisis of 1973, which required reflection on a more careful use of inputs in agriculture. Today, the considerable attention paid by the public and decision-makers to the environmental issue has sparked interest in the use of CCs as a means of conserving soil fertility while respecting the environment.

3 Classification of cover crops and cover cropping

Different criteria can be adopted to classify CCs and cover cropping (Table 1). The species are commonly grouped according to the climate (temperate, sub-tropical, and tropical

species). They can also be grouped in relation to their life span cycle into annuals (winter or summer) and perennials, to the botanical family (most of the species belong to Brassicaceae, Fabaceae, and Poaceae) and cover typology (*ad hoc* seeded species and spontaneous flora, also referred to as artificial and natural cover cropping, respectively) (Mauro et al. 2013). Given that any plant could be a CC, Table 2 shows a detailed list of the most common CCs cultivated in temperate climates. Most of them are annual therophytes belonging to the Fabaceae and Poaceae families.

Cover cropping can be realized over the entire field area or localized between rows, depending mainly on the soil water availability. Moreover, a CC can be composed of a single species or a mixture of complementary species. In this regard, it is recognized that an appropriate mixture is more effective than a single species in controlling weeds (Baraibar et al. 2018). Mixtures are often used in advanced cropping systems such as fruit orchards, while self-reseeding species, together with species well adapted to the growing environment, are suitable as single CCs. Cover crops can be used as living mulches when intercropped with the cash crop, as dead mulches by leaving their plant residues on the soil surface and as green manures by incorporating their residues into the soil (Scavo and Mauromicale 2020). Generally, the management of plant residues is adopted to reduce their competition with the crop, especially in areas with low availability of natural resources (Hammermeister 2016).

4 Choice of cover crop species and management options

The choice of CC species should be based on their adaptation to local climate, soil properties, agronomic practices, expected results, and available resources. Although many CCs have been evaluated in a wide range of agroecosystems (Table 2), their performances are closely climate- and soil-dependent. Climate is the first criterion for CC choice that should be considered, especially in temperate regions characterized by four distinct seasons and marked climatic heterogeneity. According to Koppen-Geiger’s classification, in fact, warm temperate climate includes several smaller climatic zones, based on rainfall pattern: dry summer, dry winter, and fully humid (Peel et al. 2007). Most cool temperate CCs may not survive the hot dry summers and, vice versa, warm temperate CCs have a very limited winter survival in continental climates. Cover crops are generally associated to major improvements of subsequent crop yields and higher conservation of soil water in humid habitats than in semiarid and water-limited regions (Unger and Vigil 1998). Annual rainfall amount and evapotranspiration rates are the leading factors affecting CC performances. For example, cultivating oat and rye CCs across four years in a region with a mean annual rainfall of

Table 1 Classification criteria for cover crops species and cover cropping.

CLASSIFICATION CRITERIA FOR COVER CROP SPECIES			
Climate	Life span cycle	Botanical family	Cover typology
<ul style="list-style-type: none"> ● Temperate species ● Sub-tropical species ● Tropical species 	<ul style="list-style-type: none"> ● Winter or summer annual species ● Perennial species 	<ul style="list-style-type: none"> ● Brassicaceae ● Fabaceae ● Poaceae 	<ul style="list-style-type: none"> ● <i>Ad hoc</i> seeded species ● Spontaneous flora species
CLASSIFICATION CRITERIA FOR COVER CROPPING			
Occupied area	Number of species		Plant management
<ul style="list-style-type: none"> ● Total cover cropping ● Localized cover cropping 	<ul style="list-style-type: none"> ● Mixed cover cropping ● Single cover cropping 		<ul style="list-style-type: none"> ● Living mulch / intercropping ● Dead mulch ● Green manure

Table 2 List of main cover crops adopted in temperate climates and grouped according to botanical family, life span, ecophysiological group (EG), and life form group (LFG)¹. ¹ Species were assigned to life form group considering the Raunkiaer system. T, therophytes; H,

hemicyclopedia; Caesp, plant that begins to branch from below to form a dense clump or bush; Scap, plant with an upright habit with a well-defined main stem (scape); Rept, plant with creeping habit, adhering to the ground.

Botanical family	Life span	Scientific name	EG	LFG
Brassicaceae	Annual	<i>Brassica juncea</i> L. Czern. <i>Brassica napus</i> L.	Autumn-winter	T scap T scap H scap
		<i>Brassica nigra</i> (L.) W.D.J. Koch		T scap
		<i>Sinapis alba</i> L.		T scap
	Biennial	<i>Raphanus raphanistrum</i> L.	Indifferent	H scap T scap
		<i>Brassica rapa</i> L.	Autumn-winter	H scap T scap
	Perennial			
Fabaceae	Annual	<i>Cicer arietinum</i> L. <i>Lens culinaris</i> Medik. <i>Medicago hispida</i> Gaertner <i>Medicago rugosa</i> Desr. <i>Medicago scutellata</i> (L.) Mill. <i>Medicago truncatula</i> Gaertn. <i>Medicago litoralis</i> Rohde ex Loisel. <i>Pisum sativum</i> L. <i>Trifolium alexandrinum</i> L. <i>Trifolium incarnatum</i> L. <i>Trifolium subterraneum</i> L. <i>Vicia benghalensis</i> L. <i>Vicia faba</i> L. <i>Vicia sativa</i> L. <i>Vicia villosa</i> Roth	Autumn-winter	T scap T scap H bienn

Table 2 (continued)

Botanical family	Life span	Scientific name	EG	LFG
Hydrophyllaceae	Perennial	<i>Ornithopus sativus</i> Brot.	Spring-summer	T scap
		<i>Vigna unguiculata</i> (L.) Walpers		T scap
		<i>Lotus corniculatus</i> L.	Autumn-winter	H scap
		<i>Trifolium fragiferum</i> L.	Spring-summer	H rept
		<i>Trifolium pratense</i> L.	Indifferent	H scap
	Annual	<i>Trifolium repens</i> L.		H rept
		<i>Phacelia tanacetifolia</i> Benth.	Autumn-winter	T scap
		<i>Avena sativa</i> L.	Autumn-winter	T scap
		<i>Bromus hordeaceus</i> L.		T scap
		<i>Hordeum vulgare</i> L.		T scap
Poaceae	Perennial	<i>Lolium multiflorum</i> Lam.		T scap
		<i>Secale cereale</i> L.		T scap
		<i>Triticum aestivum</i> L.		T scap
		<i>Vulpia myuros</i> (L.) C.C. Gmel.		T caesp
		<i>Sorghum bicolor</i> L. Moench	Spring-summer	T scap
		<i>Festuca arundinacea</i> Schreb.	Autumn-winter	H caesp
		<i>Festuca ovina</i> L.		H caesp
		<i>Festuca rubra</i> L.		H caesp
		<i>Ceratochloa carinata</i> (Hook. & Arn.) Tutin	Spring-summer	H scap T scap
		<i>Dactylis glomerata</i> L.		H caesp
Polygonaceae	Annual	<i>H. brachyantherum</i>		H caesp
		<i>Melica californica</i> Scribn.		H caesp
		<i>Nassella cernua</i> (Stebbins & R.M. Love) Barkworth		H caesp
		<i>Lolium perenne</i> L.	Indifferent	H caesp
		<i>Fagopyrum esculentum</i> Moench	Spring-summer	T scap

1030 mm under conventional tillage improved maize yields by ~6% compared to no CC (Maughan et al. 2009). On the contrary, in a 6-years field experiment conducted by Nielsen and Vigil (2005) in a site with mean annual rainfall of 428 mm, legume green fallow CC under conventional tillage reduced soil water and wheat yields (about -33%) respect to no CC. Reduction of subsequent crop yields is commonly associated to both direct and pre-emptive competition of CCs, especially for soil water and N (Thorup-Kristensen et al. 2003). This issue, however, could be overcome by acting on planting date and termination stage, as reported for instance by Alonso-Ayuso et al. (2018), who adopted the WAVE (Water and Agrochemicals in the soil and Vadose Environment) model. Also, the rooting depth of the succeeding crop may affect pre-emptive competition, which is indicated to be lower when the CC is followed by a fibrous-rooted crop than by a dicotyledonous crop with tap root system (Thorup-Kristensen et al. 2003).

Furthermore, climate conditions not only affect emergence and termination stage of CCs, but can be used to assess

optimal emergence dates. Using a metamodel based on the soil-crop model STICS predictions with nitrate leaching in a large-scale assessment over 20 years, Constantin et al. (2015) extrapolated optimal emergence and termination stages for CCs in France. The authors found that mean optimal dates were closely correlated to climatic characteristics, with earlier optimal emergence dates in Northern France (cold and rainy) than in the south (warm and dry) and optimal destruction dates between October and December. Moreover, optimal emergence dates were earlier for vetch (late July) than for ryegrass (early August) and white mustard (late August). Tribouillois et al. (2018) indicated that water availability influences emergence the most, with the number of consecutive days without water input after sowing as the most significant variable in the STICS model. Concerning CC species, they recommended brassicaceae for late summer sowing due to their fast germination after rainfall, in contrast to legume CCs and phacelia (*Phacelia tanacetifolia* Benth.) that have longer emergence durations caused by their large seeds. In agreement with these results, in another space-replicated field experiment carried

out in France with varied soil and weather conditions, Dorsainvil et al. (2005) reported that emergence duration of white mustard lasted from 3 days to several weeks in relation to soil water content, temperature, and sowing depth, with reduced tillage that gave as good results as ploughing with lower costs, provided that rainfall occurred.

Soil conditions (especially texture, pH and active lime content) also play a strong influence on CC adaptation. For instance, crimson clover is reported to adapt better on poorly drained soils and on well-limed soils than hairy vetch, while the latter and subterranean clover were more tolerant of soil acidity (Reeves 1994). Further, Moncada and Sheaffer (2010) indicated that winter rye and ryegrass are more suitable for sandy or loamy soils, and that rapeseed and mustard prefer neutral soils. In general, Poaceae CCs are suitable in clayey-alkaline soils, where Fe-insolubilization phenomena are common, because of their ability in enhancing Fe availability.

The choice of CCs is closely related to the intended benefit provided. In fact, CCs with high biomass production and growth rate are commonly more indicated for weed control, protection of soil erosion, and increase of SOM, but they could compete with the cash crop for water, light, and nutrients, thus decreasing crop yields. In this matter, a useful guide for CC choice in relation to the pursued goal is provided by Blanco-Canqui et al. (2015). Reinbott et al. (2004) reported significant differences between CC species in a 3-year experiment under a no-till system, with Austrian winter pea better performing than hairy vetch, hairy vetch + oat, winter pea + oat, and fallow soil in increasing both maize and sorghum grain yield. The benefit level may also vary within the same species, such as in the case of clovers and grasses. Ramírez-García et al. (2015) applied a multicriteria decision analysis (ground cover, biomass production, N uptake, N-fixation, C/N ratio, dietary fiber content and residue quality) on 5 CC species and 20 varieties for targeted CC selection. They found that grasses were the most suitable as a cover crop, catch crop, and fodder, while the vetches were the best for green manuring, especially those varieties with aptitudes as cover and catch crop. Overall, the ideal characteristics of a CC include quick soil coverage and easy establishment, complementary biological characteristics with the main crop, the ability to thrive without input supply and to suppress weeds and pests, the resistance to diseases, the capacity to not act as hosts for pathogens, and the easy termination (Lemessa and Wakjira 2015; Reeves 1994). Mixtures of CCs are recommended when a multifunctional effect is desired, since each species can deliver a specific function. For example, in legume–brassica mixtures, brassicaceae CCs can reduce pest pressure or disease while legumes can fix atmospheric N. Legume–brassica mixtures were found to be more stable and productive than the same species alone (Wortman et al. 2012). Mixing legume and grasses CCs is another common practice in temperate

climates, because legumes can increase plant available N and grasses the soil organic carbon (Ball et al. 2020). However, CC mixture do not provide always a benefit in terms of yield increase, at least in the short-term period, as found by Andraski and Bundy (2005) for oat, triticale and rye CCs in maize under conventional tillage, in which significant yield increases were observed after two and, even more, three years. In addition, the economic return of this practice should be considered prior to its adaptation since challenges in planting (e.g., differences in densities or seed size between CC species) and increased seed costs are frequent.

A proper and site-specific management (i.e., species or varieties choice, seeding rate, seeding period, termination stage, and termination methods) is crucial to overcome the adverse effects of CCs on the cash crop (i.e., competition, allelopathy, disease transfer) and optimize their benefits (Adetunji et al. 2020). Table 3 reports several effects of management options on CC efficiency. Choosing appropriate CC species or mixtures, as well as suitable termination stages and methods, can determine the success of cover cropping. About termination stage, its timing is a key factor affecting CC performance and varied based on pursued goal. For example, in water-limited or semiarid regions of temperate climates, CCs strongly compete with the cash crop for water and negatively influence subsequent crop yields (Nielsen and Vigil 2005), thus limiting often their adoption. However, these adverse effects on soil water availability can be reduced by anticipating the termination stage of CCs, as suggested by Krueger et al. (2011) for rye CC on maize. An early termination stage of CCs is also recommended in dry years of humid regions to increase the soil water content and subsequent crop yields (Blanco-Canqui et al. 2011). On the contrary, several authors suggested a delayed termination stage, especially with legume CCs, to attain a sufficient biomass build-up, decrease weed biomass (Mirsky et al. 2011), and increase soil organic C content (Hirpa 2013) and N use efficiency (Alonso-Ayuso et al. 2014). The topic of termination method is strictly associated to CC-based no tillage systems, where CCs are commonly annual species that reached an appropriate growth stage and are terminated without herbicides. In these situations, generally CCs are killed mechanically by using roller-crimpers, sickle bar mowers and flail choppers, or physically by flaming (Vincent-Caboud et al. 2019). According to Vincent-Caboud et al. (2019), the decision about the termination method should involve the persistence of the CC mulch on the soil surface, the labor, and fuel requirements as well as the level of soil disturbance.

Most of the time, the best choice is a compromise between potential benefits and drawbacks (Ingels and Klonsky 1998), but it should be borne in mind that the benefits are often achievable in the medium to long-term. Çerçioğlu et al. (2019), for example, indicated that the soil hydraulic properties (water content, water retention and hydraulic

Table 3 Effect of management options on cover cropping efficiency. * Values are referred to the last year of investigation, except for Francis et al. (1998).

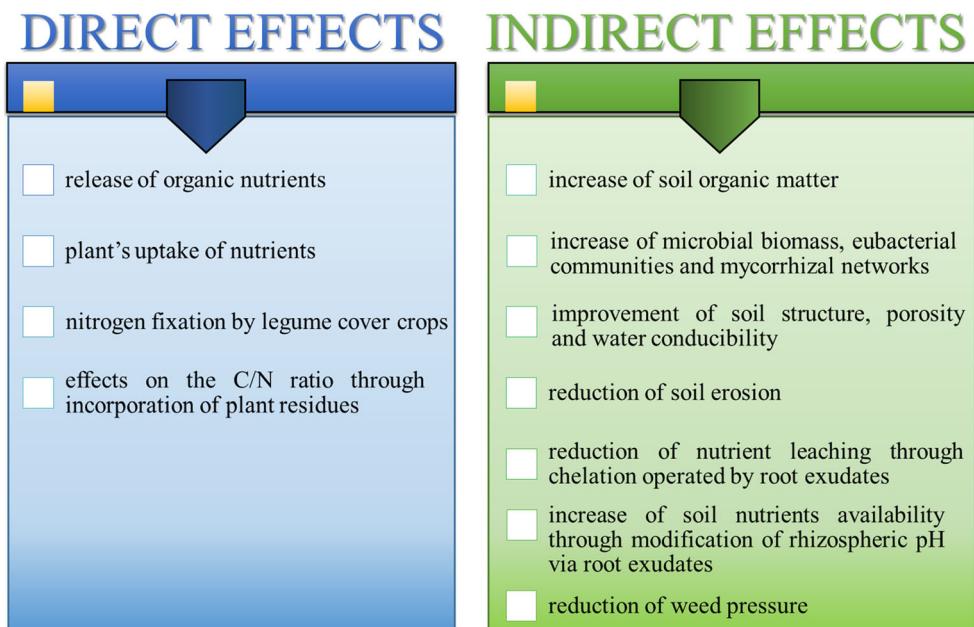
Cover crop management	Variables detected	Difference (%)*	Description	Reference	
Species and cultivars choice	Ground cover Crop biomass N uptake N-fixation C/N ratio Residue quality	+46 of barley <i>Albacete</i> +111 of triticale <i>Titania</i> +482 of mustard +40 of vetch <i>Aitana</i> +121 of triticale <i>Forricale</i> +131 of mustard		Applying a multicriteria decision analysis on 5 species and 20 varieties for different cover crop uses, grasses were the most suitable for the cover crop, catch crop and fodder uses, while the vetches were the best as green manures. Among the vetches, the best for green manuring were those varieties with aptitudes as cover and catch crop. Values are averaged over the other species and cultivars.	Ramírez-García et al. 2015
Number of species and mixture design	Soil N leaching	-80	Cover crop mixtures consistently reduced N leaching rates than individual species in an organically managed maize-soybean-wheat feed grain rotation. The reduction was more marked for the pea-red clover- rye mixture.	Kaye et al. 2019	
Cover typology and termination method	Soil weed seedbank Weed biomass Soil N-NH ₄ ⁺ Soil N-NO ₃ ⁻ <i>Nitrosomonas europea</i> <i>Azotobacter vinelandii</i> Soil organic matter Available P ₂ O ₅ Exchangeable K ₂ O Soil Fe, Mn, Zn and Cu	-57 -32 +194 +308 +109 +145 +15 +5 +14 +15, +28, +36, +24	Incorporating subterranean clover dead mulch into the soil showed higher performances than leaving residues on the soil surface and spontaneous flora cover cropping in reducing the soil weed seedbank and aboveground biomass, as well as in increasing of the levels of soil N-cycle bacteria, mineral N, organic matter, soil macro- and micro-elements. Values are compared to a fallow soil.	Restuccia et al. 2020; Scavo et al. 2021, 2021	
Termination method	Organic C Soil NO ₃ ⁻	linearly with C input +158 for vetch	Incorporating various winter cover crop residues in maize increased C input and the amount of soil organic C and NO ₃ ⁻ than removing.	Kuo and Jellum 2002	
Termination method	Soil total N Organic C <i>nirK</i> and <i>nirS</i> denitrifiers	above +9 above +5 above -2 for both bacteria	Regardless of cover crop mixtures, killing cover crop by frost increased the level of soil total N and organic C as compared to glyphosate termination. By contrast, glyphosate treatment resulted in lower denitrifier abundance than rolling.	Romdhane et al. 2019	
Seeding period	Aboveground biomass	+274 averaged over CCs	Cover crops sown early in the autumn produced more aboveground DM by the start of winter than crops sown in April or May.	Francis et al. 1998	
Termination stage	Soil organic C	+18	A delayed termination of legume cover crops from mid-vegetative to pod-setting stage determined a significant increase of soil organic C.	Hirpa 2013	
Termination stage	NDF, ADF, C/N Soil N mineralization	above +23, +29 and +28 +42	Postponing the termination stage of barley by a month increased the C/N ratio, the neutral detergent fiber (NDF) and the acid detergent fiber (ADF) of plant residues, mitigated nitrate losses and increased the N mineralization potential.	Alonso-Ayuso et al. 2014	
Termination stage	Soil water content	+16 of killed than harvested rye	Anticipating rye cover crop termination reduced water depletion and increased maize biomass.	Krueger et al. 2011	

conductivity) were slightly improved by cover cropping in claypan soils, but it took 5 years after CC establishment for the improvements to be significant. A better understanding of the impact associated to species selection, seeding rate, termination method, etc. should be at the center of future researches in order to guide the farmers in choosing the most suitable CC option to maximize the benefits.

5 Cover crops and soil nutritional status

Cover crops may influence the soil nutritional status — understood as the set of physical, chemical, and biological properties closely related to nutrients availability — in many different ways, both directly and indirectly, positively or negatively (Fig. 3). All these aspects are closely

Fig. 3 Direct and indirect effects of cover crops on the soil nutritional status.



linked to each other, determining a multiple cascading effect. If CC species and the management options have been properly chosen, then the negative effects mainly deriving from competitive and allelopathic phenomena are minimized.

5.1 Influence on the physical and hydraulic soil properties

Water availability in the rhizosphere is an important issue in agriculture, especially in mid-latitude agricultural areas characterized by extreme rain events and drought. In Mediterranean agroecosystems, for example, where the evapotranspiration demand exceeds rainfall for long periods of the year, water is a yield limiting factor. Water availability does not depend solely on the soil water balance, but also on the hydraulic properties of the portion of the soil explored by roots. It is well-recognized that CCs have positive effects on the soil physical and hydraulic properties such as bulk density, total porosity and microporosity, water infiltration, water holding capacity, hydraulic conductivity, etc. (Gabriel et al. 2019; Haruna et al. 2020). In such context, CCs with significant biomass are reported to reduce soil erosion, raindrop impact, and nutrient losses caused by high rainfall intensity (Kaye and Quemada 2017). In water-limited regions, CCs can reduce the water available for the next cash crop and this is the main reason for their limited adoption in the semiarid zones of temperate climates. Concerning the impact on the soil water balance and groundwater recharge, CCs lose water through transpiration, thus reducing drainage, i.e., the transfer of water below the zone of the soil explored by crop roots. However, a proper CC management and favorable environmental

conditions can lessen, even considerably, the differences in the water balance between covered and bare soils. Meyer et al. (2019), performing a meta-analysis on the impact of CCs on drainage under temperate climates over 28 published papers, quantified a mean drainage reduction of 27 mm compared to bare soil. However, the reduction of drainage caused by CCs does not always imply a decreased soil water content (SWC), as demonstrated by Meyer et al. (2020) in a two-year trial in which CCs (sown in July-August) and bare soil were compared in temperate climate conditions (southwestern France, annual rainfall 655 mm). More in detail, three treatments with CCs were carried out as follows: (1) CC crushed in autumn and left as mulch on the soil surface until the following spring; (5) CC crushed in autumn and buried by plowing; (17) CC terminated in April. Under the trial conditions, CCs reduced drainage by 20 to 60 mm, compared to bare soil. The soil texture, field capacity, and wilting point values (120 cm deep) of the soils described in Meyer et al. (2020) were used in the equations collected by Saxton and Rawls (2006). These equations were employed to construct the water retention curves shown in Fig. 4. In the first year (Fig. 4a), no significant differences in SWC were observed between treatments (with and without CCs) thanks to the more abundant rainfall than in the second year (504 mm vs 343 mm of cumulative rainfall from sowing to termination). Furthermore, rainfall in the first year was better distributed than in the second year. The effect of the treatments, however, clearly emerged in the second year (Fig. 6b). Among CC treatments, the one in which the CC was crushed in November and subsequently buried by ploughing showed a SWC very close to that of the bare soil (26.4 vs 26.5 %). The lowest SWC resulted from the treatment in which the CC was crushed in April of the following year

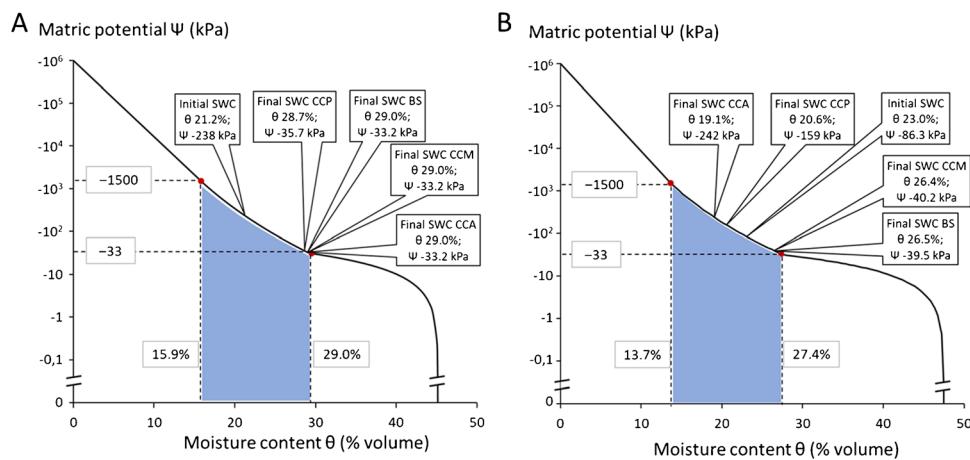


Fig. 4 Water retention curves of the two soils described in Meyer et al. (2020). Graph **a** refers to the soil of the plot in which the experimentation was carried out in the first year, while Graph **b** refers to the soil of the plot used in the second year. In both graphs, the blue colored areas represent the plant available water, between matric potential values of -33 kPa (field capacity) and -1500 kPa (wilting point). The values of the matric potential were expressed in the vertical axis in a base 10 logarithmic scale. To construct the curves, the equations collected in Saxton and Rawls (2006) were used. SWC, soil water content; BS, bare soil; CCM, CC

crushed in autumn and left as mulch on the soil surface; CCP, CC crushed in autumn and buried by plowing; CCA, CC destroyed in April. In the first year, thanks to abundant and well distributed rainfall, no significant differences were observed between treatments, unlike in the second year. This means, on the one hand, that the use of CCs does not necessarily result in a reduction of the water content in the soil and, on the other, that an appropriate management can limit water losses caused by CCs in years when rainfall is not abundant.

(Fig. 4b). In conclusion, in temperate climates, incorporating CCs into the soil in autumn seems to be a good compromise between their benefits and drawbacks (i.e., water consumption). In this regard, according to Kaye and Quemada (2017), a proper adaptive management could increase the drought resilience of CCs, for instance by choosing a suitable termination stage in order to reduce transpiration rates and improve soil water storage by mulching.

Many studies demonstrated that CCs improve the amount of soil carbon, enhance the aggregate stability, provide a balanced macropores/micropores ratio, and reduce the bulk density (Adetunji et al. 2020; Kaye and Quemada 2017). In this respect, there is a linear relationship between the amount of soil carbon and the amount of soil water contained at -10 kPa matric potential (Emerson 1995). Analyzing the continuous in-field soil water measurements from 2008 to 2014 in Central Iowa, USA, a site with average annual rainfall of 954 mm and that has included a winter rye cover crop in a maize-soybean rotation for thirteen years, Basche et al. (2016) found that rye CC not only increased SWC at field capacity by more than 10% as compared to bare soil, but also the plant available water by more than 21%, likely due to the increased amount of SOM (Hudson 1994; Huntington 2020). These improvements in soil physical properties generally reflect to an increase in water infiltration, faster downward movement of water and enhanced water storage capacity (Haruna et al. 2020). In a recent review by Blanco-Canqui and Ruis (2020), CCs were found to improve aggregate stability by 5% and cumulative infiltration by 43% on average, while negligible

effects were observed on SWC at field capacity and plant available water. They also concluded that the positive effects of CCs on the physical and hydraulic soil properties are more evident when combining cover cropping with no-tillage. Most of these effects are clearly observable only in the long-term (Keisling et al. 1994), while no significant differences between with and without CCs treatments are commonly observed up to 3-years of continuous cover cropping (Gabriel et al. 2019; Villamil et al. 2006).

5.2 Influence on soil microbial and faunal communities

A large body of literature indicates the capacity of CCs in providing a favorable environment for soil microbial communities and earthworm populations (Clapperton et al. 2007; Vukicevich et al. 2016) (Fig. 5). Soil biological fertility, intended here as the capacity of soil biota to contribute to the nutritional requirements of plants and acting as a bridge between physical and chemical fertility, is widely influenced by a suitable habitat. Modifications on soil physical properties (i.e., structure, porosity, moisture, temperature) are the first level of such influence. Cover crops, thanks to root deepening, root exudates, above- and belowground residues, contribute to develop soil structure and a pore network, thus partitioning resource patches and trophic levels (Clapperton et al. 2007). The influence of CCs on soil physical properties depends on CC roots traits. Root architecture closely affects the size and density of soil aggregates and pores (Haruna et al. 2020); at

the same time, rhizodeposition (i.e., release of ions, mucilage and organic acids) promotes the formation and stability of aggregates through the adsorption with colloids (Scavo et al. 2019). Moreover, the physical presence of a cover on the soil surface regulates soil moisture and temperature (Haruna et al. 2020). By improving soil water infiltration and retention, CCs generally decrease soil temperature in summer and increase it in winter. In a field experiment conducted in the Canadian prairies, Kahimba et al. (2008) reported that the topsoil subjected to *Trifolium alexandrium* L. CC was 3 °C warmer in autumn and 4 °C cooler in spring. More in detail, CCs generally reduce the soil temperature fluctuations between day and night by decreasing the maximum soil temperature and increasing the minimum one (Thapa et al. 2021a, b). The magnitude of this effect depends on CC species, canopy cover, and residue input, as well as on tillage system and season (Blanco-Canqui et al. 2015). Plant residues, which act as a physical barrier intercepting solar radiation, regulate the soil temperature fluctuations more efficiently when they are left on the soil surface than when ploughed (Thapa et al. 2021a, b). In fact, in a meta-analysis conducted by Muhammad et al. (2021) on 81 studies, it was found that CC residues incorporated into the soil increased phospholipid-derived fatty acids (PLFA), total bacteria, actinomycete, arbuscular mycorrhizal fungi (AMF) root colonization, and spore density compared to surface-placed or removed residues, likely due to an increased residue contact with soil microbes that enhanced C and N substrate availability. Elfstrand et al. (2007) suggested that direct incorporation of fresh red clover was more effective than both biogas slurry from fermented red clover and composted red clover in enhancing soil microbial biomass and enzyme activity. Studying the soil ecosystem services provided by three different tomato cropping systems (namely, 1, 2, and 3) in a 3-year field experiment in Central Italy, Massaccesi et al. (2020) found that organic farming with CCs plus conventional tillage (1) and organic coupled with CC mulching and no-tillage (5) showed significantly higher invertebrate biodiversity (carabid beetles and Araneae), microbial biomass (bacterial phospholipid fatty acids and AMF) and total organic C than a conventional integrated system (17). Moreover, CC effects on soil temperature may vary with residue quality and specifically with C/N ratio, in the sense that CCs with low C/N ratios such as legumes decompose more rapidly than non-legume CCs and thus they have a lower efficiency in moderating soil temperature. It should be considered also that the decomposition rates of CC residues may change based on soil texture, since they are higher in coarse-textured soils than in fine-textured ones, which is the reason why clayey soils commonly show a greater microbial biomass (Brennan and Acosta-Martinez 2017).

Along with better habitat conditions for soil biota, CCs attract specific microbial and faunal rhizosphere communities both directly and indirectly (Fig. 5). Cover crop exudates

(rhizodeposits and C-compounds such as amino acids, proteins, organic acids, sugars, phenolics, secondary metabolites, etc.) provide a continuous energy supply for the organisms living in the rhizosphere. In this regard, Marschner (1995) estimated that 5 to 21% of all photosynthetically fixed carbon is exudated into the rhizosphere by higher plants. For this reason, the cultivation of CCs is often correlated to an increase of the biomass and diversity of N-fixing bacteria (Scavo et al. 2020), plant growth-promoting rhizobacteria (Shen and Lin 2021), AMF (Morimoto et al. 2018) and earthworms (Korucu et al. 2018). Cover crop root exudation may vary between plant species and within the same species based on plant age and season (Scavo et al. 2019). Given the high chemical heterogeneity of root exudates among CCs, Housman et al. (2021) indicated an enhanced enzymatic activity and microbial biomass of CC mixtures compared to single-species legume green manure. Shifts in microbial community structure are dependent on CC chemical traits. In general, the growth of fungi is more favored than bacteria by CCs, but fungi thrive better with grass CCs that increase C substrate availability while bacteria and actinomycetes are promoted in the N-rich environment of legume CCs (Brennan and Acosta-Martinez 2017; Muhammad et al. 2021). In addition, not only different fungal communities can be associated to different CC species (Benitez et al. 2016), but also CCs can regulate both quantity and chemical composition of their root exudates in order to modulate the rhizosphere microbial communities and establish specific associations (De-la-Peña et al. 2008).

Cover crops can also affect rhizosphere organisms indirectly by means of the plant litter left as surface- or incorporated-dead mulching. Depending on the quantity, chemical composition (C/N ratio, dry matter, lignin content, total nutrients, etc.), and biomass management (termination method and stage), CC amendments are another important source of nutrients that regulate the complex soil food webs and the ecological successions (Scow and Werner 1998). High-quality plant litters (characterized by low C/N ratio and rapid decomposition) commonly stimulate faster-growing copiotrophic microorganisms, whereas grass residues (with high C/N ratio and persistence on the soil surface) favor oligotrophic microorganisms (Bastian et al. 2009). Regarding the ecological successions, the first decomposers are earthworms that, thanks to the fuel provided by C-compounds exuded from living mulches, ingest CC residues, excrete nutrient-rich casts, and accelerate humus formation (Lee 1985). Furthermore, earthworms stimulate microbial activity on leaving the decomposition products of plant litter to bacteria, mites, moulds, and actinomycetes (Scow and Werner 1998). Each successional change consumes energy and is governed by food source. Hence, adequate quantities of litter need to be maintained to renew the decomposer community.

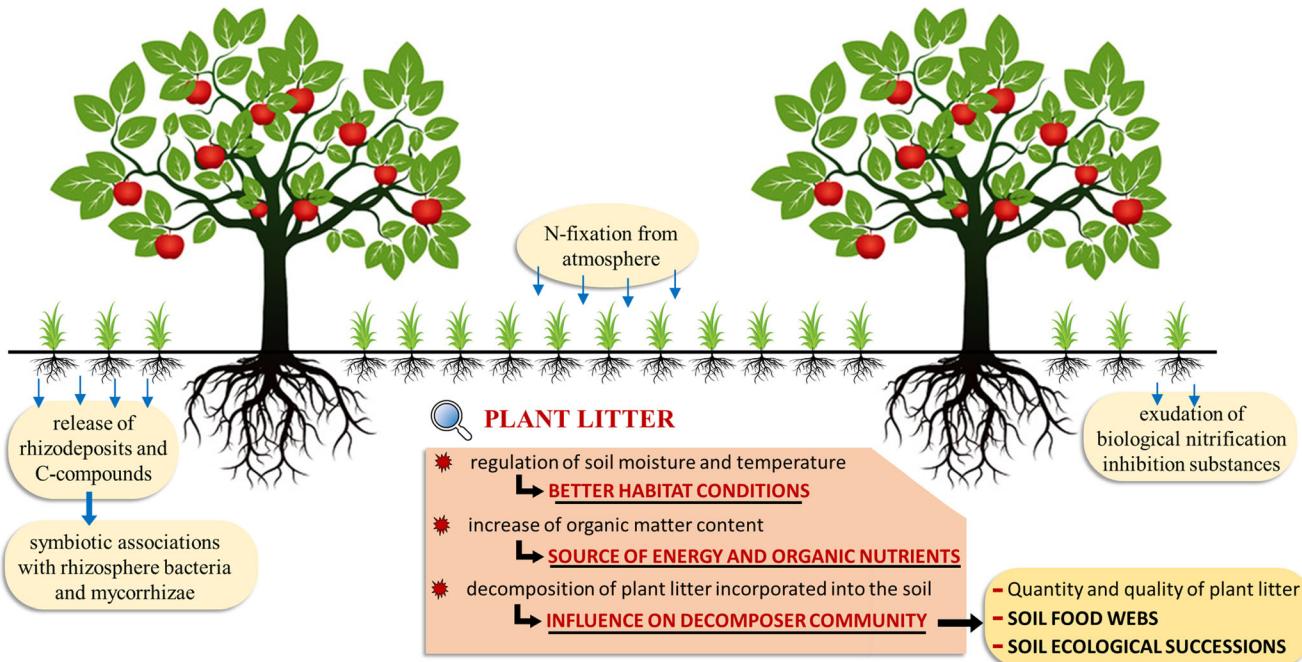


Fig. 5 Influence of cover crops either as living mulches or dead mulches on soil microbial and faunal communities.

5.3 Influence on soil organic matter and soil nutrient availability

A wide literature documents the capacity of CCs in significantly improving the SOM and organic C levels across different temperate zones due to the above and belowground biomass produced (Blanco-Canqui et al. 2015; Ding et al. 2006; Hirpa 2013). The use of a mixture of species, rather than a single species, often results in higher biomass production and, consequently, in greater SOM accumulation and C sequestration (Cong et al. 2014). The increase in SOM caused by CCs also depends on soil texture, tillage, and time of establishment. Generally, CC benefits are favored under silt-loam than sandy soils (Haruna et al. 2020), in no-till systems (Blanco-Canqui et al. 2015) and over the long-term (Acuña and Villamil 2014). Cover crops can also indirectly improve SOM content and reduce nutrient losses by preventing land degradation caused by wind and water (Mohammed et al. 2021). In western Kansas, USA, a region with mean annual precipitation of 426 mm and silt-loam soil, winter triticale CC was found to reduce soil water erosion by 79% if compared to bare soil, and this reduction was more marked than that provided by spring triticale (-61%), winter lentil (-39%) and spring pea (-68%), likely due to its higher biomass production (Blanco-Canqui et al. 2013). The management of CCs can also influence the chemical and structural composition of SOM, which is an important characteristic affecting soil nutrient cycling and fertility. In this regard, Ding et al. (2006) found that different CCs may affect the structure and composition of humic substances in the soil. Using the ^{13}C NMR and the diffuse

reflectance infrared Fourier transform (DRIFT) spectroscopy to characterize SOM under different CC systems, they found that soils under rye showed more aromatic and less aliphatic humic acids than vetch/rye mixture. On the other hand, the latter showed higher O/R ratios of fulvic acids, which may indicate that SOM in the vetch/rye plots was more chemically and biologically active.

Soil organic matter, together with rhizodeposits released into the rhizosphere by CCs, provides energy for soil microbial activity. Soil microorganisms, in turn, release inorganic nutrients through SOM mineralization, stimulate the soil enzymatic complex, influence plant nutrient acquisition, and drive nutrient cycling (Wagg et al. 2014). Cover crops can establish different forms of associations (symbiosis, mutualism, commensalism) with root-associated microorganisms such as AMF, N-fixing bacteria and various endophytic fungi and bacteria (Van der Heijden et al. 2008). Arbuscular mycorrhizal fungi are known to be important drivers of P cycling due to the increase of the root area through the extraradical hyphal network, which allows a wider exploration of soil and therefore a better absorption of P (Morimoto et al. 2018). Recently, Arruda et al. (2021) found that CCs increase AMF abundance for the succeeding cash crop and alter P fractions by increasing the organic labile pool in the top-soil compared to fallow, with species-specific effects on P pools. Some CCs, including red clover (*T. pratense*) and cowpea [*Vigna unguiculata* (L.) Walp.], exude strigolactones, especially under P-deficiency, to stimulate the hyphal branching of AMF (Scavo et al. 2019; Yoneyama et al. 2008). At certain concentrations, however, strigolactones may inhibit AMF shoot branching

(Gomez-Roldan et al. 2008). Moreover, thanks to their extensive mycelium, AMF contribute to enhance C sequestration (Zhu and Michael Miller 2003). In addition to AMF, legume CCs can fix the atmospheric N into plant available ammonium by associations with N-fixing rhizobacteria. These specific symbioses are regulated through the exudation of isoflavonoids by the host plant and lipochitooligosaccharides by rhizobia (Scavo et al. 2019). Moller et al. (2008) reported nearly 60 to 80 kg ha⁻¹ N fixed by CCs. Many CC species such as *Pisum sativum* L., *Medicago sativa* L., *Trifolium* sp., *Phaseolus* sp., etc. also establish symbiotic relationships with AMF (Wang and Qiu 2006), highlighting how AMF can also indirectly contribute to N cycle (Van der Heijden et al. 2008).

In soils with severe nutrient deficiencies, CCs can also indirectly enhance the phytoavailability of soil nutrients via root exudation of secondary metabolites (phytosiderophores) or organic acid secretion into the rhizosphere (Bais et al. 2006). Phytosiderophores exudation is a well-known mechanism adopted by grasses under metallic micronutrient deficiency (especially Fe-deficiency). Phytosiderophores are chelating agents of metallic nutrients forming organic-phytosiderophore complexes, which can be transported across plasma membranes with YSL protein transporters (Curie et al. 2001). Cesco et al. (2006) found that *Poa pratensis* L. and *Festuca rubra* L., two perennial grasses normally grown as CCs in fruit orchards, were able to improve Fe-nutrition in citrus trees grown on calcareous soils by enhancing ⁵⁹Fe-up-take through 2'-deoxymugineic acid exudation. Dicotyledons and non-graminaceous monocotyledons follow a different strategy to improve metallic nutrient acquisition, called strategy I, which is an “acidification/reduction” mechanism consisting of the root exudation of protons and other reducing substances such as phenols (isoflavonoids, coumarins, phenolic acids) and organic and inorganic acids, to bring down the rhizosphere pH and enhance the ferric reduction activity at the root plasma membrane (Kumar et al. 2016). This strategy, adopted by legume CCs like alfalfa, cowpea, chickpea, vetches, clovers, etc., is mostly important under P-deficiency and for Al³⁺ detoxification (Dakora and Phillips 2002; Scavo et al. 2019; Valentiniuzzi et al. 2016).

Concerning the soil N cycle (Fig. 6), CCs residues and especially legume species with low C/N ratio can build up N concentrations, improve the available N for the subsequent crops, and reduce N fertilizer requirements (Adetunji et al. 2020). In a 4-year field experiment carried out in a Mediterranean apricot orchard, Scavo et al. (2021) found that subterranean clover cover cropping with the incorporation of dead mulches into the soil increased N-NH₄⁺ and N-NO₃⁻ by 194% and 308%, respectively, compared to a fallow soil, as the result of the improved levels of SOM (+ 15%) and the N-fixing bacteria *Nitrosomonas europaea* and *Azotobacter*

vinelandii. In another 4-year field experiment performed in Northern Europe, De Notaris et al. (2018) reported that N leaching was positively correlated to N surplus at the rotation scale, with CCs that increased N output (expressed as N yield in crops and N in green manure cuts) and reduced N leaching by 60%, irrespective of conventional and organic management system, without differences between legume and non-legume CCs. Moreover, the rotation with green manure was the system with the highest risk of N leaching, which was closely correlated to growing degree days and biomass of the main cereal crop. Generally, CC residues are characterized by lower losses of nitric N and lower emissions of N₂O than inorganic N fertilizers, thus showing a higher N efficiency (Delgado et al. 2010). Unfortunately, knowing the amount of plant-available N from decomposing CC residues is very difficult in the field, given that residue decomposition is affected by multiple factors including chemical traits (C:N ratio, N content), residue placement (surface vs incorporated), environmental conditions, and soil characteristics (Cabrera et al. 2005). In this regard, several computer simulation models have been proposed to estimate the N mineralization from CC residue decomposition both under controlled conditions (Thapa et al. 2021a, b) and in the field (Melkonian et al. 2017), but they still need large-scale studies over a broader range of soils and climate. Seo et al. (2000) estimated an amount of 50–155 kg ha⁻¹ of N fertilizer equivalent provided by hairy vetch in maize. According to Doran and Smith (1991), CCs with C/N ratios <20 have higher N fertilizer equivalents than CCs with C/N ratios >35 because legume CCs commonly show a higher decomposition and N mineralization rate than grass CCs. In general, legume CCs decrease N fertilizer requirements due to fixed N while non-legume CCs increase N fertilizer requirements due to N immobilization (Williams et al. 2018). Grass-legume CC mixtures, such as the barley–vetch mixture in Mediterranean conditions, are more effective than pure stands in reducing NO₃⁻ leaching risk, assuring a stable N accumulation and adjusting the N efficiency (Tosti et al. 2014). The ‘microbial N mining’ theory states that the N mineralization rate and the activity of N-degrading enzymes are positively correlated to root exudate rates due to the induced microbial growth in the rhizosphere provided by readily useable C (Kuzyakov and Blagodatskaya 2015). The microbial hot moment, i.e., the critical period for soil microbes to actively decompose residue and mineralize N, corresponding to the peaks of soil microbial abundance and N mineralization, can vary from few days up to 50 days after input (Kuzyakov and Blagodatskaya 2015). During the hot moments, soil fungi and bacteria cooperate in the processes of decomposition and N mineralization (Chinta et al. 2021). During hotspots of microbial activity within the rhizosphere and detritusphere, CCs induced the strongest priming effect to accelerate SOM decomposition and nutrient release, mainly mineralizing organic N (Kuzyakov 2010). This priming effect can be either positive

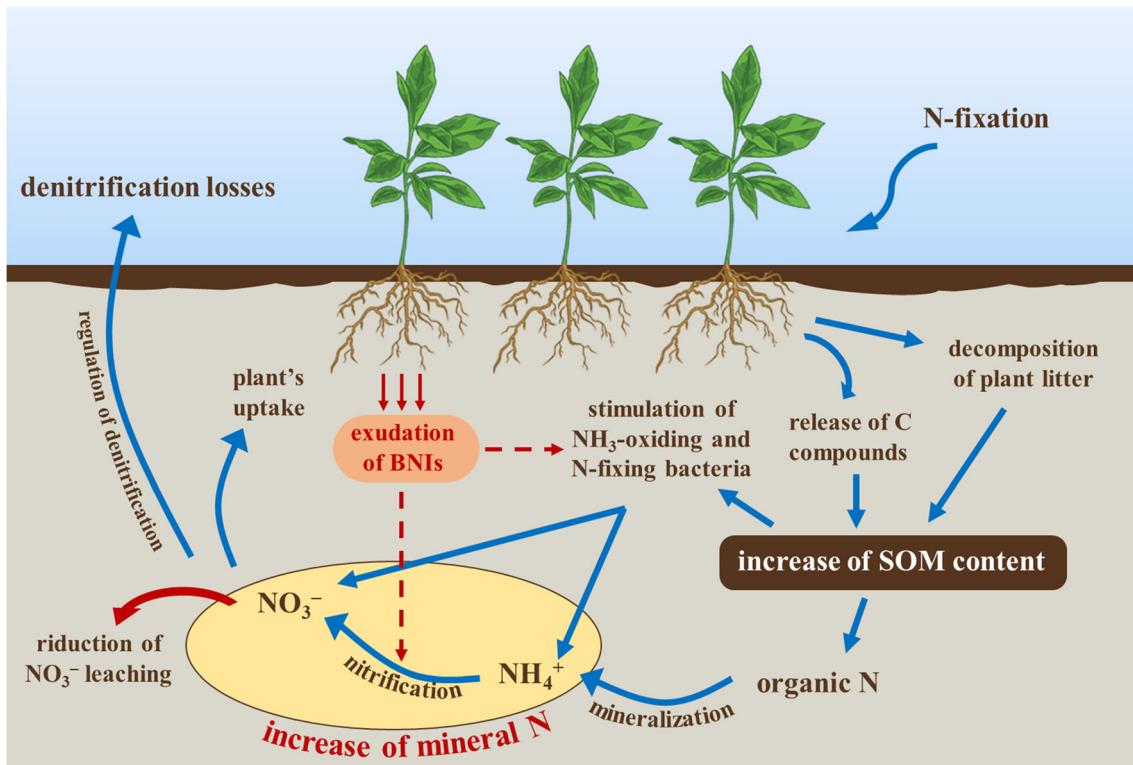


Fig. 6 Effects of CCs on soil N dynamics. Nitrogen can directly enter into the soil via biological N-fixation of legume CCs and decomposition of plant litter. Also, N can indirectly enter by increasing the soil organic matter (SOM) content caused by the release of C compounds. Carbon serves as a feed for the microorganisms involved in soil N cycle (ammonia-oxidizing and N-fixing bacteria) that, combined with the

enhanced SOM content, contribute to increase the N mineral forms. Part of mineral N is removed by plants. Moreover, on the one side CCs reduce NO_3^- leaching and, on the other side, regulate denitrification and nitrification dynamics by exuding biological nitrification inhibitors (BNIs) into the rhizosphere, thus increasing the N-use efficiency.

or negative (i.e., reduction in SOM decomposition and N immobilization), depending on the amount and quality of CC exudates.

Cover crops are also effective at scavenging nutrients and reducing their leaching losses (Justes et al. 2012), particularly those of post-harvest soil nitrate (NO_3^-) which is highly susceptible to losses during high drainage events of temperate zones. With reference to soil N, CCs can scavenge and convert NO_3^- into organic forms, thus retaining N in the root zone and releasing it gradually during residue decomposition, which in turn reduced NO_3^- leaching and increases N-use efficiency (Blanco-Canqui et al. 2015). Growing vetch, rye, and rye-vetch CCs in large packed soil cores, Rosecrance et al. (2000) found that vetch and rye-vetch cores showed net N mineralization combined with high denitrification and potential leaching, while net N immobilization was observed in rye cores. This study suggests that, although CCs reduce NO_3^- leaching compared to fallow soils (Kaspar and Singer 2011), the degree of such reduction is species-dependent since it is higher in legume than in non-legume CCs (Quemada et al. 2013). Other field trials supported that non-legume CCs such as wheat, oat, ryegrass, or mustard are more effective than legume CCs at reducing NO_3^- leaching losses (Kaspar and Singer 2011). In a 2-year study conducted in no-till upland

soils in Mississippi (USA) and cultivated with cotton, winter wheat CC reduced both N and P losses than winter fallow (Adeli et al. 2021). Indeed, increased inorganic P levels due to cover cropping under no-tillage conditions (Scavo et al. 2021; Varela et al. 2017). However, in some cases, CCs can uptake highly soil P_2O_5 and convert it into organic forms, thus reducing soil available P (Villamil et al. 2006). Increased levels of soil exchangeable K_2O and microelements (Fe, Mn, Zn, and Cu) have also been found in Mediterranean semiarid agroecosystems (Scavo et al. 2021).

Combining legume and non-legume CCs could be an efficient option to further enhance the benefits of cover cropping on soil N cycling due to the optimization of C/N balance. Latati et al. (2019), in a two-year field experiment with durum wheat and chickpea, cultivated both in intercropping and in a sole crop, observed that on the one hand intercropping significantly enhanced the use-efficiency of rhizobial symbiosis in chickpea and, on the other, increased N and P availability in durum wheat rhizosphere and grain yields as well as N nutrition in chickpea shoots compared to sole cropping. Improved N uptake were also observed in maize/faba bean (+20%) (Li et al. 2003), maize/soybean (+32%) (Zhang et al. 2021), and wheat/maize (+93%) (Liu et al. 2020) intercropping, among others, due to the plasticity and complementary of root

architecture among different crops. When the soil N is not abundant, the roots can avoid each other or enhance density and depth to increase the competitiveness. In legume/non-legume mixtures, the increased N uptake of the non-legume can be attributable to the higher root length densities in the mixtures compared with the legume and thus to the improved soil N competitive ability of the non-legume (Corre-Hellou et al. 2007). Generally, non-legumes are dominating in intercropping systems, especially with higher N levels. For instance, Ramirez-Garcia et al. (2015), studying the barley/vetch intercropping under greenhouse conditions, found that barley outcompeted the vetch for N uptake in the deepest soil layer, and that the intercropped barley plants produced more roots and twice the root length of the monocropped barley plants, thus inducing an increased N uptake of barley and decreased one of vetch, compared to monocrops. In intercropped systems, therefore, each species can maximize the ecosystem services compared to sole crop due to the principle of niche separation, which depends on the degree of complementary of the mixture (Tribouillois et al. 2016).

Cover crops can also improve N-recovery and the agronomic N-use efficiency by mitigating the nitrification and denitrification dynamics driven by soil microorganisms (Fig. 6). In a 4-year field trial performed in a dry sub-humid zone with average annual rainfall of 1000 mm, Gitari et al. (2018) reported that potato/dolichos (*Lablab purpureus* L.) intercropping increased the N-use efficiency and the P-use efficiency by 30 and 21%, respectively than stand of potato. In contexts where the loss of N following nitrification is significant, some CCs release biological nitrification inhibitors (BNIs) into the rhizosphere to counter the ammonia monooxygenase and hydroxylamine oxidoreductase pathways of ammonium- and nitric-oxidizing bacteria (Coskun et al. 2017). The BNI capacity is closely related to plant species and varieties, and it was found to be a widespread phenomenon in tropical pasture grasses such as *Brachiaria humidicola* (Rendle) Schweick and *B. decumbens* (Subbarao et al. 2007). Rocha et al. (2020) indicated that the abundance of microorganisms related to ammonification, nitrification and nitrogen fixing, and ammonia-oxidizing Archaea is affected by CC species and development stage. Biological nitrification-inhibiting substances are allelochemicals of a broad spectrum of chemical classes including phenols, terpenoids, alkaloids, carbohydrates, etc. Soil incubation experiments demonstrated that the incorporation of *Plantago lanceolata* L. leaf materials suppressed soil N mineralization and nitrification due to their leached allelochemicals, the polyphenol verbascoside and the iridoid glycosides aucubin, aucubigenin and catalpol (Dietz et al. 2013). In soils amended with Brassicaceae (*Isatis tinctoria* L., *Brassica napus* L., *B. juncea*, and *Sinapis alba* L.) residues, Brown and Morra (2009) detected a positive correlation between NH_4^+ and NO_2^- accumulation and glucosinolate concentration, thus

demonstrating the BNI capacity of glucosinolates. A comprehensive review on the role of BNIs in the soil system and their physiological effects on plants is provided by Coskun et al. (2017). Regulating denitrification (N losses as $\text{N}_2 + \text{N}_2\text{O}$) is another strategy adopted by CCs to improve the N-use efficiency. Legume CCs are generally indicated to stimulate soil denitrification rates, especially during soil saturation (Shelton et al. 2000). The enhanced denitrification associated to CCs is attributable to the supply with available C from CC root exudation and dead mulches for denitrifiers (Aulakh et al. 1991).

Cover crops can also indirectly enhance the soil nutrient availability for the cash crop or the subsequent crops through weed management, which entails a lesser competition for soil nutrients. Weed control operated by CCs is a well-documented aspect of cover cropping (Lemessa and Wakjira 2015; Osipitan et al. 2019; Scavo and Mauromicale 2021), both as a single technique or within an integrated management strategy (Bhaskar et al. 2021; Scavo and Mauromicale 2020), especially in the long-medium term (Restuccia et al. 2020). However, the role of CCs for weed management in agroecosystems is beyond the scope of this review.

6 Cover crops and plant nutritional status

Plant nutritional status is commonly detected through the analysis of nutrients (minerals, carbohydrates, secondary metabolites, etc.) in foliar tissues or fruits and by comparing the results to well-established standard values (Bianco et al. 2015). However, other rapid and non-destructive analytical methodologies have been proposed for the prediction of the plant nutritional status, such as the visible-near infrared spectrophotometric analysis (Menesatti et al. 2010), the diagnosis and recommendation integrated system (DRIS) (Römhild 2012), portable spectrometers, and the SPAD chlorophyll meter.

Results on the influence of CCs on the crop nutritional status contradict each other, since both positive and negative effects are reported in the literature (Table 4). The positive effects of CCs on the physical, chemical, and biological soil properties as indicators of soil quality are often associated to benefits (e.g., nutrient transfer) for the cash crops. Hence, especially in fruit orchards, cover cropping may provide additional indirect benefits to the crops, such as the enhancement of root development, tree vigor, yield, and fruit quality (Tahir et al. 2015). The incorporation of subterranean clover (*T. subterraneum*) dead mulches into the soil, compared to a spontaneous flora cover cropping, a conventional management and the optimal ranges reported in the literature, was found to increase the content of minerals (K, N, Ca, Fe, Mn) in apricot leaves and fruits and to balance the nutritional status of the trees (ΣDOP index) (Lombardo et al. 2021). In organic kale (*B. oleracea* var. *acephala*), CCs provided a considerable

Table 4 Effect of cover cropping on the crop nutritional status.

Cover crop	Cash crop	Difference (%)	Description	Reference
<i>Trifolium subterraneum</i> L.	<i>Prunus armeniaca</i> L.	Leaves: Mg (+100), K (+22), Ca (+18), N (+13), Fe (+25), Zn (+31) Fruits: K (+26), Mg (+22), Ca (+16), Fe (+34), Mn (+28), Zn (+22), Cu (+17)	Subterranean clover cover cropping with the incorporation of dead mulches into the soil, compared to spontaneous flora cover cropping and a conventional management, increased the content of macro- and micro-nutrients in apricot leaves and fruits with respect to the optimal ranges reported in the literature.	Lombardo et al. 2021
<i>Medicago scutellata</i> L. (<i>Kelson</i>), <i>Avena sativa</i> L., <i>Lolium perenne</i> L.	<i>Citrus x sinensis</i> (L.) Osbeck	Chlorophyll (+20), Ca (+41), Na (+30), Mg (+29)	The <i>Medicago-Avena-Lolium</i> cover crop sequence enhanced the total chlorophyll content and stimulated the concentrations of Ca, Mg and N and in the leaves.	Mauro et al. 2015
<i>Vicia faba</i> L. var. <i>minor</i> Beck.	<i>Triticum durum</i> Desf.	Grain N (+38), grain protein content (+13)	The durum wheat–faba bean temporary row-intercropping significantly improved the cereal N status and the grain protein content.	Tosti and Guiducci 2010
<i>Raphanus sativus</i> L., <i>Pisum sativum</i> L.	<i>Solanum tuberosum</i> L.	Ca (+99), K (+68), P (+36), N (+32), Mg (+9), B (+67), Zn (+36), Mn (+21), Fe (+15)	Forage radish and winter pea cover crops increased potato yield by 10–25% than no cover crop, reduced N fertilizers supply and enhanced tuber mineral concentrations. Values are referred to forage radish.	Jahanzad et al. 2017
<i>V. faba</i> , <i>V. villosa</i> , <i>P. sativum</i> , <i>L. perenne</i> and <i>T. incarnatum</i>	<i>Brassica oleracea</i> L. var. <i>acephala</i>	Stachyose + raffinose (+32), glucose (+17), fructose (+6), lignin (+51), Ca (+22), Fe (+70), Cu (+88)	Cover crops significantly increased the amount of proteins, minerals and prebiotic carbohydrates in organic kale, with results highly dependent on the cover crop species × kale cultivars interaction. Values are referred to crimson clover.	Thavarajah et al. 2019
<i>Allium sativum</i> L.	<i>Cucumis sativus</i> L.	Shoots: P (+23), K (+6), Fe (-14) Roots: N (+6), K (+3), Ca (+5), Fe (+7)	Intercropping cucumber with green garlic improved the nutritional status of the soil (organic matter, available N, P and K) and, consequently, of cucumber plants (biomass production, N, P, K, Ca and Mn levels).	Xiao et al. 2013
<i>L. perenne</i> , <i>Poa pratensis</i> L. and <i>T. repens</i>	<i>Malus domestica</i> Borkh.	Leaves: N (-43), K (+11), Ca (+25)	Two consecutive years of sandwich system (living mulch of mixed grasses combined with tillage) in an organic apple orchard, compared to a mechanical cultivation, showed an important weed control and significantly increased the nutritional status of trees, yield, fruit weight and fruit quality compared to other soil management systems.	Tahir et al. 2015
<i>V. faba</i> , <i>M. sativa</i>	<i>S. lycopersicum</i>	Leaves: N (+21), P (+4), K (+8) Fruits: N (+11), P (-6), K (-7)	The application of mobile green manure with faba bean fresh biomass in organic greenhouse tomatoes, significantly increased the plant available soil N, improved N nutrition and enhanced yield, fruit number per plant and mean fruit weight.	Gatsios et al. 2021
<i>Zea mays</i> L.	<i>Arachis hypogaea</i> L.	Fe in shoots (+134), roots (+27), seeds (+43) HCl-extractable Fe in young leaves (+96)	The peanut–maize intercropping, thanks to the rhizosphere interactions between plants, improved the Fe nutrition of peanut by improving the chlorophyll and HCl-extractable Fe concentrations in young leaves, while at the same time reducing the Fe-deficiency chlorosis symptoms.	Zuo et al. 2000
<i>Lupinus albus</i> L., <i>V. villosa</i> and other self-reseeding annual legumes	<i>Olea europaea</i> L.	N in leaves (+5), N in pulp (+23), N in pit (+12)	Mulching pure legume cover crops in two olive orchards did not provide a significant increase in N available in the soil after the legumes had been mulched. Nevertheless, the N status of the trees was only slightly improved, suggesting that most of N present in the legume species biomass was probably lost without having entered the soil. Values referred to the location Carrascal.	Rodrigues et al. 2013

Table 4 (continued)

Cover crop	Cash crop	Difference (%)	Description	Reference
<i>Hordeum vulgare</i> L.	<i>Vitis vinifera</i> L.	N in shoots (about -22) N in leaves (about -12) Total N (about -14) Anthocyanins (-23)	Barley cover crop decreased the availability of soil NO_3^- throughout the vegetative cycle of grapevine, causing a reduction in both N nutritional status and grapevine vigor, although an increase in the anthocyanin content of must was observed.	Pérez-Álvarez et al. 2013
<i>Ricinus communis</i> L., <i>P. vulgaris</i>		Common bean: N (-6), P (-26), K (+12), B (-23), Cu (-18), Fe (-11), Mn (-29)	The common bean–castor bean intercropping, compared to both crops in monoculture, decreased the amount of leaf minerals in common bean. No significant effects were observed on leaf minerals of castor bean.	de Araujo et al. 2020

increase of proteins, minerals, and prebiotic carbohydrates, especially when using faba bean (*V. faba*), with results highly dependent on the CC species × kale cultivars interaction (Thavarajah et al. 2019). Mauro et al. (2015) reported an increased content of minerals (Ca, Mg, and N) and chlorophylls in orange [*Citrus x sinensis* (L.) Osbeck] leaves when subjected to a *Medicago-Avena-Lolium* CC sequence. In accordance with these results, Jahanzad et al. (2017), studying the effect of forage radish (*Raphanus sativus* L.) and winter pea (*P. sativum*) CCs on potato (*Solanum tuberosum* L.), documented that CCs significantly increased potato yield, reduced N fertilizers supply, and enhanced tuber mineral concentrations compared to no CC. After observing in the field more severe Fe-deficiency chlorosis symptoms in peanut grown in sole cropping compared to that intercropped with maize, Zuo et al. (2000) carried out rhizobox experiments and pointed out that, thanks to the rhizosphere interactions between peanut and maize, the peanut–maize intercropping improved the peanut Fe nutrition, as demonstrated by the increase in the chlorophyll and HCl-extractable Fe concentrations in young leaves.

Concerning the negative effects of CCs, several studies indicate a decreased root and shoot growth, reduced fruit quality, and delayed fruit maturity in response to CCs (Atucha et al. 2013; Marsh et al. 1996). This is more common for CCs characterized by rapid initial growth, high biomass production and vigor, exerting a strong competitive effect on the cash crop for light, water and nutrients, in the case of direct competition; also, pre-emptive competition phenomena for N between CCs and cash crop play a key role in this process (Thorup-Kristensen et al. 2003). For instance, Pérez-Álvarez et al. (2013) found that barley CC decreased the availability of nitric soil N on one side, while on the other reduced the grapevine N nutritional status and vigor. Rodrigues et al. (2013) reported that the soil incorporation of legume CC dead mulches did not increase the levels of inorganic mineral N into the soil, most likely because most of N present in the legume biomass was lost without having entered the soil.

The influence of CCs on the crop nutritional status is closely correlated to the management options, with species selection, termination stage, and termination method being the most relevant factors. In the study conducted by Lombardo et al. (2021), for example, subterranean clover showed a better performance than spontaneous flora CC, but the best results were obtained by incorporating subterranean clover dead mulches into the soil, probably due to their more rapid decomposition which on one hand allowed a higher release of nutrients and, on the other, created a favorable environment for nutrients absorption. In another study, faba bean was found to be the most suitable CC for improving the nutrient composition of organic kale, whereas ryegrass CC determined a higher kale biomass production, thus highlighting the importance of species selection (Thavarajah et al. 2019). Gatsios et al. (2021), comparing the effects of two different mobile green manures in organic greenhouse tomatoes, indicated that faba bean green manure is more effective than alfalfa pellets in increasing the plant available soil N and tomato leaf N concentration. Faba bean green manure also proved to be economically advantageous, since it enhanced yield, fruit number per plant and mean fruit weight more than alfalfa pellets. Evaluating the effect of soil management system in an organic apple (*Malus domestica* Borkh.) orchard, Tahir et al. (2015) reported that the combination between tillage and a living mulch of mixed grasses (i.e., sandwich system for the whole year) provided a higher weed control, tree vigor, yield, fruit weight, and fruit quality compared to other soil management systems including living mulch alone. Studying the influence of intercropping and its relationships with N fertilization, de Araujo et al. (2020) found that common bean (*Phaseolus vulgaris* L.) – castor bean (*Ricinus communis* L.) intercropping caused lower levels of leaf macro- and micro-elements in both crops due to competitive effects between plants. However, according to the authors, this issue could be overcome by adopting the most suitable cultivars selection (Pérola and Energia, respectively) and N fertilization (a coverage split of 30:70 kg N ha^{-1} applied at 25 and 35 days after emergence). Cereal–legumes intercropping is a common

agronomic practice for regulating the N use efficiency but, in addition to technical difficulties related to grain separation, it is often difficult to optimize the interspecific competition. A field experiment carried out in an organic farming by Tosti and Guiducci (2010) indicated that durum wheat–faba bean temporary row-intercropping is a valid method for improving the cereal N status and the grain protein content regardless of wheat variety. This was due to the competitive effect of faba bean that was limited to the initial wheat phenological stages and, after incorporating faba bean into the soil, the wheat was able to recover solar radiation even if the legume was the dominant component of the intercrop, contrariwise to what generally happens in permanent intercropping systems. It is therefore clear how the impact of a CC on crop yields and product quality may be regulated by choosing appropriate managing options (i.e., species or cultivars selection, seeding rate to avoid competitive effects, termination stage and methods, fertilization supply, etc.).

7 Conclusive remarks

The inclusion of CCs into various agricultural systems has been proven to be a consolidated agronomic practice for enhancing the physical, chemical, and biological soil properties, thus increasing nutrient availability and reducing mineral fertilizers supply. In turn, these benefits are commonly reflected in the crop with an enhanced nutritional status. Knowing the reciprocal relationships between CCs, soil and plant nutritional status will allow improving soil fertility and crop productivity both qualitatively and quantitatively while at the same time limiting the adoption of auxiliary inputs. However, an effective cover cropping is closely related to suitable and context-specific management options (choice of species, seeding period, termination stage and termination method). Unfortunately, some of these aspects are still unknown, as well as several ecophysiological effects of CCs on soil and plant nutrition. It is therefore vital that the both scientific community and government policies increase their efforts in the next future to fill such gap. In particular, the set-up of large-scale and long-term studies conducted under a multidisciplinary approach would appear imperative for future researches.

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