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Intercropping with service crops provides multiple services in temperate arable systems: a review

Antoine Gardarin¹, Florian Celette², Christophe Naudin³, Guillaume Piva³, Muriel Valantin-Morison¹, Sylvain Vrignon-Brenas⁴, Valentin Verret¹ and Safia Médiène¹

• Antoine Gardarin and Florian Celette: first coauthorship

Corresponding authors: Antoine Gardarin, UMR Agronomie, Avenue Lucien Brétignières, 78850 Thiverval-Grignon, France, antoine.gardarin@inrae.fr; Florian Celette, UP AGE, ISARA, 23 rue Baldassini, 69364 Lyon Cedex 07, France, fcelette@isara.fr

¹ Université Paris-Saclay, AgroParisTech, INRAE, UMR Agronomie, 78850, Thiverval-Grignon, France

² ISARA (University of Lyon), Agroecology & Environment Research Unit, 69364, Lyon, France

³ USC 1432 LEVA, Ecole Supérieure d'Agricatures (ESA), INRAE, SFR 4207 QUASAV, 55 rue Rabelais, F-49007 Angers, France

⁴ LEPSE, University of Montpellier, INRAE, Institut Agro, Montpellier, France

Abstract

Service crops are crops grown to provide services to other cash crops, rather than for production purposes, with the ultimate aim of improving the environmental and production performances of cropping systems. Service crops can be intercropped with cash crops to facilitate interactions between crops and to optimize the use of the cropping season. Many terms exist to describe these practices, which highlights their diversity. However, this diversity of terms may be a source of confusion. Here, we present an overview of the current uses of intercropped service plants in temperate cropping systems, with the main services they provide and their management. (1) First, we show that a limited range of service crop species, mostly from the Fabaceae family, have been studied to date. This finding suggests that the diversity of species and cultivar resources that can be used as service crops has been poorly explored in the literature. In contrast, the combinations of service and cash crops tested appear wider. We address this diversity by defining synchronous intercropping, living mulch and relay intercropping. (2) Then, we show that intercropped service crops can efficiently reduce weed biomass and pest attacks and improve nitrogen cycling, thereby increasing soil fertility and improving crop nutrition. The intensity of these services is positively associated with service crop biomass, but excessive service crop biomass increases the risk of competition with cash crops. (3) The balance between the services and disservices provided can primarily be interpreted in terms of biomass production of coexisting crops. The resulting effect of service crops on cash crop yield is variable and reflects the integration of the effects of the various individual services, together with possible disservices. (4) The diversity in management methods makes it possible to manage this trade-off and to adapt the system to different conditions with a few tested species.

Keywords: competition; intercropping management; living mulch; nitrogen supply; pest regulation; relay intercropping; typology; weed control

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1 Introduction

Ecological intensification of agriculture is often proposed as a means of enabling agriculture to deal with current global challenges, such as global warming, biodiversity collapse and population growth (Tilman et al. 2014). This concept involves redesigning cropping systems to mobilize biotic interactions within agroecosystems rather than using external inputs (Tilman et al. 2014; Duru et al. 2015a). Indeed, increases in the use of external inputs, such as synthetic fertilizers, have had deleterious effects on the environment through eutrophication and contributions to greenhouse gas emissions (Ahlgren et al. 2010). Many pest species have rapidly developed resistance to pesticides, leading to technical dead ends (Bommarco et al. 2011; Robert et al. 2016). Pesticides can cause health problems when misused or if they end up in drinking water or in the air (Viel et al. 2015), and these compounds are responsible for biodiversity loss (Geiger et al. 2010). The idea underlying ecological intensification is that it should be possible to replace, at least partially, the expected functions of these inputs by biological processes and beneficial multitrophic interactions to promote crop growth and health (Altieri 1999; Médiène et al. 2011).

The transition toward biodiversity-based farming systems (Thérond et al. 2017), supporting ecological intensification, implies the management of greater agrobiodiversity (planned and associated biodiversity, Parris 2001). Introducing crops not directly used for production is an interesting option for promoting ecological processes that are already used by farmers (Casagrande et al. 2017). Service crops are species grown not for the purpose of direct primary production (i.e., as a cash crop for food, feed, or fibers) but to provide supporting and regulating ecosystem services (Zhang et al. 2007; Garbach et al. 2017). Here, we choose to use the expression “service crops”, which has been used in previous studies (for example, in Garcia et al. 2018), but the term “subsidiary crop” has also been employed (Reimer et al. 2019). Service crops can provide multiple and diverse ecosystem services, ranging from the regulation of weeds and pests to improving soil quality. By enhancing beneficial ecological processes, these crops make it possible to decrease the dependence of farming systems on external inputs while maintaining crop yield (Ilnicki and Enache 1992; Miura and Watanabe 2002).

Several options are open to farmers for the introduction of service crops into agroecosystems. The most frequent practice is probably when the service crop is sown after the cash crop has been harvested. Service crops of this type are often called “cover crops”, as they are sown to prevent a period of bare soil between two successive cash crops. The ecosystem services provided by this practice have been widely reviewed (e.g., Blanco-Canqui et al. 2015). They include protecting the soil against erosion, runoff and nutrient leaching and modifying soil properties by increasing the soil organic matter content. These are also the main services targeted in perennial cash crops, such as grapevines, in which service crops are mostly grown outside of periods of crop vegetative growth (Garcia et al. 2018).

It may be difficult to sow service crops after the harvest of winter crops due to water deficits during the summer. Global warming may increase these difficulties in future decades. Establishing service crops after spring or summer crops may also be complicated because the growing season is then short, leaving a time gap during which few services are provided by the service crop. The difficulty of establishing service crops after the cash crop harvest is, therefore, a primary factor limiting their adoption in arable systems (Hamilton 2016; Noland et al. 2018).

To better use the services provided by the interactions between the cash and service crops, the service crop can be intercropped with the cash crop species for a substantial portion of the life cycle of the cash crop (Fig. 1). The functioning and management of intercropping with two cash crops (Bedoussac et al. 2015; Brooker et al. 2015) or of service crops sown after cash crop harvest (Osipitan et al. 2019) have been reviewed in detail, but the specific case of intercropped service crops has received much less attention.

The provision of services by service crops largely depends on the interactions between crop management and environmental conditions (i.e., current biodiversity, soil and climate), and their effects on the functioning of the agroecosystem in terms of the services targeted (Duru et al. 2015b). Intercropped service crops interact more strongly with cash crops than service crops sown after cash crop harvest,

and unlike traditional intercrops, they provide services different from those expected of the cash crop. This renders their management highly specific and complex. In particular, management decisions must arbitrate trade-offs between the provision of ecosystem services by the service crop and cash crop performance, which may be impaired by interspecific competition for resources (Cheriere et al. 2020).

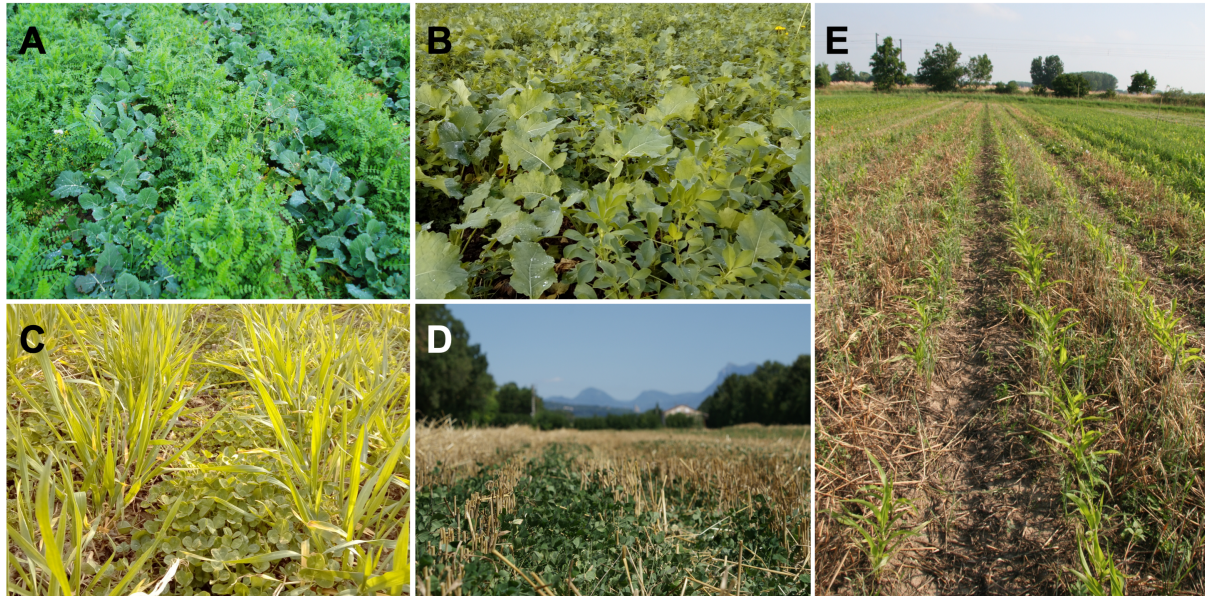


Figure 1. Examples of how service crops can be used in temperate cropping systems: (A) synchronous intercropping of *Vicia sativa* L. and oilseed rape (photo credit: LEVA, Group ESA), (B) winter oilseed rape sown in a living mulch of *Medicago sativa* L. (photo credit: A. Gardarin), (C) winter wheat sown in a living mulch of *Trifolium repens* L., here at tillering stage (photo credit: A. Gardarin), (D) living mulch of *Trifolium repens* L. after wheat harvest (photo credit: ISARA), and (E) relay intercropping of oats and maize (photo credit: LEVA, Groupe ESA).

Here, we aim to provide an overview of the current uses of intercropped service crops with arable cash crops, the main services they supply and the management options for optimizing these services. We focus our analysis on arable cropping systems in regions with a temperate climate in which the seasonality of vegetative growth has a strong impact on the rationale concerning the temporal overlap between cash and service crops. These cropping systems are mostly based on annual grain crops (Cox et al. 2010) and are largely mechanized, leading to small workforces operating in large fields. These conditions are not compatible with the careful management of each intercropped species or with different modes of row and inter-row management, as in vineyards (Garcia et al. 2018). Service crops sown for subsequent forage production are considered only during the cash crop cycle, generally the year of sowing, during which they are not harvested and therefore function exclusively as a service crop.

The diversity of the terms associated with the use of intercropped service crops reflects the large number of options for intercropping available and the many functions that can be expected of service crops. We therefore begin by proposing a definition of intercropped service crops and suggesting a typology for their classification based on the time periods for which they coexist with the cash crop in the field, strongly affecting the functioning of the plant cover and expected services. Then, we review the literature addressing the provision of ecosystem services by intercropped service crops. This review focuses on three main regulating services: weed regulation, pest regulation and the enhancement of soil nitrogen fertility. Previous studies have focused mostly on these three ecosystem services, probably because they can replace synthetic inputs like pesticides and fertilizers. We describe the general principles for managing intercropped service crops and then discuss how best to support or increase the services delivered by these systems, particularly through the management of competition between intercropped species.

2 Definition and typology of intercropped service crops

2.1 Methods

A literature review of peer-reviewed articles was performed with the Institute for Scientific Information Web of Science database (<http://apps.webofknowledge.com>) in February 2021 for the 1990-2021 period. The search equation (1) returned 2304 results.

(1) (undersow* OR “under-sow*” OR underseed* OR interseed* OR “companion plant*” OR “living mulch*” OR interplant* OR understory OR “subsidiary crop*”) NOT (vineyard OR pastures OR grassland OR orchard OR agroforestry OR “maize-cowpea” OR “pea-wheat” OR “pea-barley” OR “barley-pea” OR “tree” OR “forest”)

This initial corpus was enriched with the authors’ own bibliography. We then excluded studies focusing on vegetable cropping, intercropping of two cash crops, or including woody crops, and studies performed in the intertropical zone. We included 383 original articles assessing the utility of service crops in arable cropping systems in the final review (list available online: doi:10.5281/zenodo.4835638).

2.2 Definition

We considered service crops to be intercropped if the cash crop and the service crop were simultaneously present for a significant proportion of the life cycle of the cash crop. During the intercropping period, the primary role of the service crop is not production, although some service crops can be harvested after the cash crop is harvested or before the cash crop is sown, e.g., for forage provision. We included only systems in which the service crop and cash crop interact closely. Therefore, we included mixed intercropping, with no distinct row arrangement or species mixed within each row, and row intercropping with one species per row (Andrews and Kassam 1976), but we excluded strip intercropping and field margin planting (e.g., hedgerows and flowering strips), in which plant-plant interactions were low, and agroforestry systems, which raise specific questions in terms of niche partitioning and time scales (Casagrande et al. 2017). In service crop systems, the cash crop is generally sown at the optimum density for a sole crop to ensure that it is more competitive than the service crop and to maintain productivity levels (Blackshaw et al. 2010; Amossé et al. 2014; Lorin et al. 2015). The service crop is grown according to an additive design, with 100% cash crop and x % service crop, relative to the densities currently recommended for sole crops.

Intercropped service crops are sometimes difficult to identify in published studies because they can be concealed by diverse terminologies, some of which have different meanings for different authors, causing confusion. Some of the terms used relate to the period during which the service crop is grown relative to the cycle of the associated crop, whereas others focus more on the role of the service crop, e.g., catch crop, cover crop, manure crop, or nurse crop. In other instances, these two principles can be mixed, e.g., intersown cover crops. Furthermore, most terms are not specific to intercropped service crops (multiple-species systems, intercropping, interseeding, intersowing, interplanting, cocultivation, companion cropping, etc.) and can be used for systems based on the intercropping of two cash crops, e.g., a grain cereal intercropped with a grain legume. These terms refer more to the mode of inclusion of the additional species than to the objectives of its cultivation. Among the terms relating to the mode of inclusion, only “living mulch” is not used for the intercropping of two cash crops.

2.3 Typology of systems including intercropped service crops

The timing for which both the cash and service crops are present together in a field and the relative synchrony or asynchrony between their growth cycles are key features affecting service crop-cash crop interactions and the provision of services by the service crop. A service crop may be present during the full cash crop cycle. Alternatively, it may be present over several cash crop cycles if a perennial species is used, or it may be present temporarily if grown solely during part of the cash crop growth cycle. A service crop may disappear naturally by senescence if the species has a short life cycle or it may be killed by frost, if the species is cold-sensitive, or by chemical or mechanical means. Based on this diversity, we propose a typology of crop sequences including intercropped service crops according to their temporal organization. We built this typology relative to the cash crop cycle, considering the period

beginning at the previous crop harvest and finishing at the cash crop harvest. Thus, if the service crop is maintained over several cash crop cycles, it could be part of two different types, depending on the cash crop concerned. Here, we define three types according to i) the synchronicity/asynchronicity of the cash and service crop sowing times and ii) the duration of service and cash crop coexistence in the field (Fig. 2). We postulate that the timing of this coexistence greatly affects the functioning of plant cover, the expected services and the management rules, as detailed below.

- **Synchronous intercropping (SI)**, in which the cash and service crops have similar life cycles (Figs. 1 and 2), with synchronous sowing. The service crop is sown during the same time period as the cash crop. The cash and service crops may be sown in two different operations, separated by no more than a few days, or in a single operation. The cash crop and service crop are exposed to similar environmental conditions during their establishment and initial growth period, during which sowing conditions and species characteristics have a major influence on interspecific relationships and the performances of the intercropped system (Fayaud et al. 2014). The SI service crop may be destroyed or may complete its cycle before the cash crop is harvested. If it is an annual species, it may also be maintained after harvest until the new crop is sown. If the service crop is maintained over a second cash crop cycle, it becomes a living mulch.
- Asynchronous intercropping, in which the cash crop is directly sown into a **living mulch (LM)** formed by previously established service crops (Fig. 2). Hartwig and Ammon (2002) stated that “living mulches are service crops planted either before or with a main crop”. Here, we considered “living mulch” or pre-established service crops only because they provide soil cover, i.e., a mulch effect before the cash crop is sown (Costello 1994). Living mulch remains alive for part or all of the cropping season (Hartwig and Ammon 2002; Hooks and Johnson 2004). Depending on its sowing date, living mulch may open up possibilities for year-round soil cover (White et al. 1993). The main issue with this type of service crop is the management of early competition with the sown cash crop during its establishment. Perennial species can be used for more than one growing season, but annual species that reseed themselves (Kumwenda et al. 1993), such as subterranean clover (*Trifolium subterraneum*) and crimson clover (*Trifolium incarnatum*), can also be used.
- Asynchronous intercropping, in which the service crop is sown in an already established cash crop by **relay intercropping (RI)**. This term has been used in many different ways in previous studies. The first definition, by Andrews and Kassam (1976), included all systems with two plants in which the growth cycles of the two plants overlapped. Some authors have considered RI systems to be those in which the second plant is sown after the first crop has reached its reproductive stage but before it is harvested (Coolman and Hoyt 1993; Guldán et al. 1996). Finally, Roslon and Fogelfors (2003) and Amossé et al. (2013b) defined relay intercropping as the sowing of a (service) crop under an already established (indicating biomass or cover was already produced) cash crop canopy, regardless of its stage, having a competitive advantage over the service crop. We use this last definition of RI. In this case, the service crop emerges within the cash crop, growing slowly in the understory due to its limited access to sunlight (Figs. 1 and 2). After the harvest of the cash crop, the service crop has full access to radiation and continues to grow in the field. In specialized arable farming systems, this technique may be used for the establishment of a cover crop between two successive crops, whereas in mixed farming systems, it can be used for the establishment of a forage crop. Undersowing in spring is particularly useful in areas in which the climatic conditions after the cash crop harvest may limit the development of a late-sown service crop (Valkama et al. 2015).

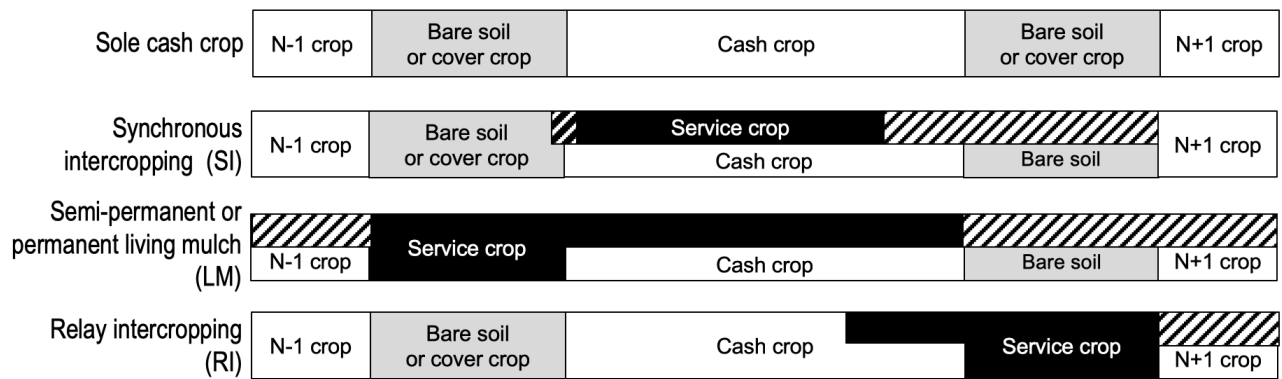


Figure 2. Three main ways in which service crops (black) can be incorporated into the cash crop sequence (white): living mulch (LM), synchronous intercropping (SI) and relay intercropping (RI). Other possible configurations are indicated in the dashed zones.

2.4 A literature largely focused on specific cash crop-service crop pairs

We analyzed the various service crop × cash crop species combinations that have been studied experimentally. For the various types of intercropping systems, we built a contingency table of these combinations and represented the service crop-cash crop pairs in networks drawn with the ‘qgraph’ package (version 1.3.2) in R 3.0.1 software (R Development Core Team 2015) (Fig. 3). We found a total of 942 experiments, where an experiment corresponds to a species combination in one article.

Globally, for all categories of the typology (i.e., LM, SI and RI), legumes (Fabaceae) were by far the most frequently used service crops (573 experiments) for intercropping (Fig. 2), followed by grasses (Poaceae) and brassicas (Brassicaceae). The other species identified belong to various plant families, including Hydrophyllaceae and Asteraceae. Most service crop mixtures were composed of a legume species and a grass or cereal species. Typical combinations of service crop mixtures included white (*Trifolium repens* L.) or red (*T. pratense* L.) clover with Italian ryegrass (*Lolium multiflorum* Lam.) or fescue (*Festuca* spp.), grown together with a cereal cash crop. Legumes are particularly useful, as they can fix nitrogen from the atmosphere, whereas grass species can be used to immobilize mineral nitrogen in the soil or to control weeds (see Section 3). Cereals are the most frequently associated cash crops, probably because they largely dominate arable cropping systems in temperate regions (Mudgal et al. 2010).

The largest number of species combinations was found in the SI system (371 experiments, Fig. 3). Winter and spring small-grain cereals, oilseeds and maize were identified as the most frequent cash crops grown (333 experiments) in SI systems and were mostly intercropped with medicks and clovers (165 experiments) as service crops. The type of inclusion used in this system leads to fewer technical constraints for sowing operations than those used in the LM and RI systems, which could partly explain why the SI system had the largest number of observed combinations. In living mulches, maize (*Zea mays* L.) and winter cereals are the two most frequently intercropped cash crop species (178 experiments over a total of 212). They are mostly grown in association with clovers (109 experiments) and, less frequently, with members of the Poaceae (60), such as Italian ryegrass, winter rye (*Secale cereale* L.) or fescue. Medicks (*Medicago* spp.) were also used in 17 experiments. Finally, relay intercropping (RI) was studied in 359 experiments, and it primarily involves winter cereals as cash crops (132 experiments), mostly intercropped with clovers (149) or medicks (33) as the service crop. These combinations may be popular because small-grained legume species can tolerate superficial broadcast sowing, providing a simple technique for preventing damage to the cash crop during sowing.

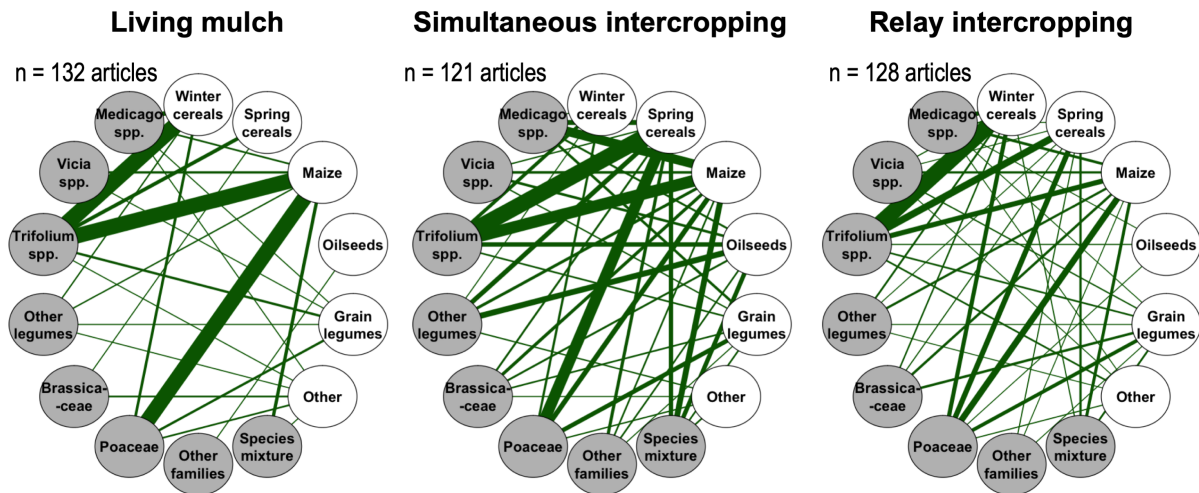


Figure 3. Pairs of cash crops (white) and intercropped service crops (gray) assessed in the corpus of the studies reviewed. These crop pairs are classified according to the way in which the service crop is introduced into the crop sequence (see typology in Fig. 1 and Section 2.3). The thickness of the lines is proportional to the number of articles for the pairs of crops that have been studied experimentally. Cereal-legume pairs are the most frequent type of cash crop-service crop combination studied.

Despite the wide diversity of species combinations reported in each intercropping system, most studies have focused on a small number of combinations between dominant cash crops, essentially cereals, and *Medicago* spp. and *Trifolium* spp. as service crops (Fig. 3). Only a few studies have experimented with species mixtures of service crops, such as Lorin et al. (2015), who studied annual legumes in synchronous intercropping or with forage and perennial species in relay intercropping.

3 Main regulating services provided by service crops

Intercropped service crops can provide a multitude of services. We focus here on the three most studied regulating services: weed regulation, insect pest regulation and soil nitrogen fertility. These services regulate the main limiting factors of temperate cropping systems, whether conventional or organic. For each service, we present (i) the mechanisms involved in service provision and (ii) the efficacy of service provision for the different types of service crop intercropping. We do not systematically refer to the service crop typology since (i) the processes are generic across types, and (ii) we refer to reviews or meta-analyses that do not distinguish between types. However, we highlight when service provision is strongly dependent on the type of intercropping.

3.1 Weed regulation

The ability of service crops to reduce weed growth depends on their ability to pre-empt weeds for resource use, especially water, nutrients and light (Liebman et al. 2001). After briefly describing the main mechanisms involved in weed regulation by service crops, we consider the impact of service crops on weed density and diversity.

3.1.1 Resource pre-emption as a way to mitigate weed infestation

Competition between service crops and weeds must occur from the seedling and early growth stages to be efficient (Liebman et al. 2001; Uchino et al. 2005). Intercropping systems, particularly those with additive designs, generally increase soil coverage, resulting in faster canopy closure and higher light interception than in fields with sole crops (Teasdale and Daughtry 1993). Thus, living mulch systems, are intrinsically the most efficient way to increase competition between service crops and weeds. In synchronous intercropping systems, this competition is dependent on species growth dynamics and the timing of weed emergence relative to the emergence of cash and service crops. Weed control continues

for as long as service crops are present, whether alive or dead. In relay intercropping, the late emergence of service crops may reduce their ability to mitigate weed infestation during the association, but they can greatly decrease weed density and biomass after cash crop harvest during the following fallow period because of the soil coverage they provide (Blaser et al. 2011; Amossé et al. 2013a; Vrignon-Brenas et al. 2016c).

To be competitive against weeds, a service crop must produce rapidly a large amount of biomass, resulting in broad soil coverage. Service crop (or cash crop plus service crop) biomass or soil coverage has frequently been shown to be inversely related to weed biomass or density (Uchino et al. 2009; Amossé et al. 2013a; Lorin et al. 2015). Several studies found that an amount of 2 t·ha⁻¹ of service crop dry matter biomass during fallow period in RI, or 4 t·ha⁻¹ of cash crop and service crop biomass in SI, to be required to achieve efficient weed control (Lorin et al. 2015; Vrignon-Brenas et al. 2016c; Carton et al. 2020). These studies suggested that the biomass production of service crops may lead to an important reduction in both weed density and biomass, even if the amount of biomass required for effective weed control depends on several conditions developed below.

3.1.2 Impact of intercropped service crops on weed density and diversity

The impact of service crops on weed density is highly variable and context-dependent, influenced by factors such as weed community composition, growing conditions and service crop biomass (Ross et al. 2001; Moyer et al. 2007; Amossé et al. 2013a). Depending on these factors, intercropping with service crops generally leads to a reduction of weed infestation, but it could also have no significant impact or even increase weed biomass or density (Teasdale et al. 1991; Liebman and Dyck 1993). In a meta-analysis, Verret et al. (2017) showed that service crop intercropping, regardless of its type, reduced weed biomass by a mean of 56% relative to an unweeded sole crop and by 42% relative to a weeded sole crop. Nevertheless, the success of weed control seemed to be dependent on the associated cash crop. Even with very competitive service crops, weed suppression is generally not as complete as herbicide application, since the competition for resources is partial and some weeds may survive due to their plasticity (Vijaya-Bhaskar et al. 2014).

Service crop intercropping also affects the composition of the weed community, but the results are less clear-cut. In some cases, higher weed diversity was observed in terms of richness and evenness (in winter wheat-lucerne intercropping, Barilli et al. 2017), which could lead to more complex assemblages in which dominant and harmful weeds were of less importance (Liebman et al. 2001). Service crops may also decrease weed species richness in the field (Kwiecińska-Poppe et al. 2009).

In summary, intercropped service crops can be very efficient to decrease weed density and biomass even if this effect is variable and highly dependent on intercropping biomass production.

3.2 Reduction in insect pest attacks

The abundance of insect pests and the damage they cause are generally lower in systems with high levels of plant diversity (see the meta-analysis of Iverson et al. 2014 including service crops). According to Malézieux et al. (2009), several mechanisms may improve pest regulation in cropping systems: (i) a bottom-up disruption of pest activity through crop habitat modification and (ii) enhanced biological control by predators and parasitoids (Trenbath 1993; Hooks and Johnson 2003). Since there are few examples where mechanisms of pest control in arable crops have been studied, we chose to use examples from vegetable production, which has been extensively investigated (Sarkar et al. 2018).

3.2.1 Bottom-up disruption of pest activity and damage through crop habitat modification

Service crops modify insect habitats through their biomass and architecture. The strongest effects of service crops on pest abundance and damage have been demonstrated for SI. In this type, the service crop produces sufficient biomass to dilute the cash crop resources available to specialist insects and imposes a barrier between the insects and the host plant (Malézieux et al. 2009). Service crops also

modify the architecture of the crop canopy by increasing its structural heterogeneity, and they make it more difficult for pests to find their hosts (Finch and Collier 2000; Brose 2003; Mansion-Vaquié et al. 2020). In cruciferous crops, these effects decrease pest oviposition rates (Åsman et al. 2001) and they decrease winter stem weevil damage on oilseed rape (Cadoux et al. 2015). The pest damage-decreasing effects of service crops increase with total service crop biomass. However, in some cases, heterogeneous vegetation cover makes it more likely that prey will evade their natural enemies in dense vegetation (Brose 2003).

Plant-insect interactions can also be modified in service crop-cash crop associations due to differences in attractiveness to insects (Badenes-Pérez 2018). Push-pull strategies often make use of this mechanism (Pickett et al. 2014). Service crops could act as trap crops, with a “pull” feature, if the species used are more attractive than the cash crop species to pests (Trdan et al. 2006). Service crops can also displace pests away from crops, with a “push” feature if they have repellent properties (Beizhou et al. 2012). These attractive and repellent properties have been little explored in service crops. Promising results were recently obtained for the root fly, *Delia radicum*, in horticultural cabbage crops (Lamy et al. 2018), but too little is currently known for the effective development of push-pull strategies for use in temperate arable crops (Cook et al. 2007).

When grown in living mulch, and even when they produce little biomass, service crops can change the physicochemical qualities of cash crops, making them less attractive to pests and thus contributing to a slight decrease in pest attacks and damage (Theunissen 1994). For example, intercropping cabbages with red clover decreased the cabbage concentration in glucosinolate (a molecule involved in anti-herbivory defenses), which may limit attacks by specialist insects that use these molecules as a marker to identify their hosts (Björkman et al. 2008).

Thus, several mechanisms by which service crops can contribute to the control of pests by modifying habitats have been identified in horticultural production but little evidence already exists regarding arable crop production.

3.2.2 Enhancement of biological control by natural enemies

Intercropped service crops can also improve top-down pest regulation by natural enemies by providing non-prey trophic resources, such as nectar and pollen, and shelter for insects at higher trophic levels, necessary to complete their life cycle. These resources can be provided by service crops, but this ability has been poorly investigated to date. Some examples exist in oilseed rape crops, where the extrafloral nectar produced by associated faba beans increases the general fitness of the hymenopteran parasitoid *Diaeretiella rapae* M’Intosh, the rate of parasitism and parasitoid survival (Jamont et al. 2014). In the case of lettuce and broccoli crops on organic farms (Brennan 2013, 2016), *Lobularia maritima* (L.) Desv is simultaneously intercropped as a service crop to attract and reward hoverflies with pollen and nectar, and these predators control aphid infestations very efficiently.

When service crops are used as living mulch, the vegetation at ground level provides shelter for natural enemies and alternative prey for predators and parasitoids (Griffiths et al. 2008). This effect was observed in soybean grown with a living mulch of lucerne, in which the living mulch increased the abundance of natural enemies by 45%, resulting in a later establishment of soybean aphids and in lower peak populations below the economically damaging threshold (Schmidt et al. 2007).

The implementation of service crops to enhance functional biodiversity increases natural enemy populations, but this does not always significantly decrease the size of crop herbivore populations (Jonsson et al. 2008).

3.3 Soil nitrogen fertility and nitrogen nutrition services

Intercropped service crops may at least partly replace the need for external fertilizers for cash crops. Service crops may provide cash crops with nitrogen nutrition services in the short term and enhance N (nitrogen) retention in the soil in the long term through various mechanisms. Studies on nitrogen in synchronous intercropping have often involved mixtures of two cash crops where each cash crop provides services to the other.

3.3.1 Nitrogen supply and uptake during the service plant growth cycle

The intercropping of a nitrogen-fixing species with a non-nitrogen-fixing species can improve the use of environmental resources through complementarities linked to N uptake. The intercropping of cereals and N-fixing species reduces competition for soil N sources, leaving a larger proportion of the soil N for the cereal crop. Rodriguez et al. (2020) showed that each plant in a synchronous intercropping cover accumulated 53–67% more soil N than a cereal plant grown alone. The contribution of fixation to N accumulation is greater when competition is high for soil mineral N than in pure legume crops, both for SI with cash crop mixtures and for service and cash crop mixtures (Ledgard and Steele 1992; Corre-Hellou et al. 2006; Naudin et al. 2010). In the case of relay intercropping, legume N nutrition is mostly based on the fixation of N₂ from the atmosphere (Amossé et al. 2014). Legumes grown as service crops therefore play a significant role as a natural source of N. The distribution of the roots of the two species in the soil can also partly be responsible for complementarity in soil mineral N use, particularly at the start of synchronous intercropping with service crops (Jamont et al. 2013b).

N may also be transferred between plants through rhizodeposition (Fustec et al. 2010), particularly in pluriannual intercropping systems. For instance, under perennial plant cover, legumes increase the soil N pool. Grasses can benefit from the nitrogen provided by the roots of neighboring legumes (Paynel et al. 2008; Pirhofer-Walzl et al. 2012). In older plants, roots turnover leads to N recycling, which benefits to the associated species over long-term (Hogh-Jensen and Schjoerring 2001). Several studies have also indicated that indirect transfers occur between plants (de Varennes and Goss 2007) following the inoculation of the soil with both arbuscular mycorrhizal fungi (AMF) and rhizobia and can promote the growth of crops and improve legume or non-legume yield and nutrient uptake (Duchene et al. 2017).

In summary, the effect on nitrogen availability for cash crops is larger and more immediate in situations of complementarity between plants grown in synchronous intercropping or when the service crop (SI or LM) is destroyed early in the cash crop cycle, thus making the N contained in its tissues rapidly available. This effect may be extended after the intercropping period.

3.3.2 Nitrogen supply and enhancement of soil fertility by service crop residues

Service crops can enhance nitrogen retention in the soil. Legume service crops can supply cash crops with N, either after their destruction or through the turnover of above- and belowground biomass, depending on the incorporation of legume service crops.

After their destruction, both legume and non-legume service crops, regardless of their type (SI, RI or LM), release scavenged or fixed N into the soil through residue mineralization. Thus, this N becomes available to cash crops in the same year, and the remaining N is available to the crops grown in subsequent years (Stern 1993). The N transferred from the destroyed service crop to the subsequent cash crop depends on the amount of accumulated biomass, the rate of mineralization, and the N needs of the cash crop when mineralization occurs (Hauggaard-Nielsen et al. 2003; Lorin et al. 2016). The chosen species and crop management, including intercropping type, systems can influence mineralization, its dynamics and the use of the N released by subsequent cash crops (Jones 1992; Breland 1996; Amossé et al. 2014).

Service crops may help to decrease nitrate leaching risk in the following fall (Thorup-Kristensen 1994). A meta-analysis on relay intercropping with non-legume service crops in Nordic countries demonstrated a decrease in nitrate leaching by approximately 50% on average, whereas legume service crops may increase the soil inorganic N content in the following fall (Valkama et al. 2015). In another example involving non-legume service crops, Tuulos et al. (2015) demonstrated that winter turnip rape, either undersown with barley or sown after barley, efficiently decreased soil mineral nitrogen, thereby

decreasing the risk of leaching. In contrast, Amossé et al. (2014) observed no significant change in leaching risk with relay-intercropped legumes. These results mainly demonstrate a benefit from service crops but with varying effects among studies.

Studies on legume residues decomposing under field conditions have shown that less than 20% of the N present in the legume crop is recovered by the subsequent crop, with much of the legume N being retained in the soil in organic forms that gradually become available over the course of a few years (Harris et al. 1994). The long-term use of no-till and living mulch systems promotes the recycling of N-rich leguminous living mulch residues, leading to a substantial decrease in the need for N fertilization (Carof et al. 2007). Benefits to subsequent crops have frequently been demonstrated in terms of improvements in N status and higher yields (Jones 1992).

In summary, in addition to the immediate effect of service crops on N uptake during the crop growth cycle, service crops also contribute to soil N availability and to soil fertility in general over the entire crop sequence, especially in the RI and LM systems.

We focused here on the three main services expected from intercropped service crops. As seen in this section, the efficiency of service crops for the provision of expected services is highly dependent on the synchronicity of the cash and service crop cycles and on biomass production (Abdin et al. 1997). We investigate below how service crop management can support or even increase the delivery of these services.

4 Managing intercropped service crops

The principal practices routinely used in crop management, such as variety choice, the manipulation of relative sowing densities, tillage, weeding operations, fertilizer application and irrigation, modify the environment and the amount and availability of resources, thereby affecting emergence conditions, root and shoot growth and competitive relationships between the intercropped species (Blaser et al. 2012). Each management practice can be modulated and should be considered in a systemic manner and adapted to the local context to achieve a balance between processes, as shown in Fig. 4. The timing of coexistence and the service crop biomass production greatly affect the functioning of plant cover and the expected services as seen in section 3. We therefore consider three main critical stages of intercropped service crop management for the delivery of their expected services: i) establishment, ii) management during the period of coexistence with the cash crop and iii) destruction.

4.1 Establishment of service crops: which roles of species choice and sowing arrangement?

4.1.1 Conditions and challenges for the establishment of service crops

Regardless of the type of intercropping system, stand density and early growth dynamics are crucial to ensure the success of service crop establishment and provision of services. Nutrient availability is rarely a limiting factor. Service crop requirements are generally low during early growth stages, and nitrogen needed in initial stages comes from seeds. In later stages, the important use of N-fixing species as service crops, particularly in cropping systems with little or no synthetic fertilizer use, may largely limit their requirements for nitrogen. Besides, water availability, which may be restricted by climate conditions and soil properties, is often the main factor limiting the establishment of a service crop (Gooding et al. 1998; Thiessen Martens and Entz 2001; Vijaya-Bhaskar et al. 2014; Vrignon-Brenas et al. 2016b). Under temperate conditions, this limitation is particularly frequent for service crops sown in late summer (e.g., simultaneous sowing of rapeseed and service crops) or in a dry spring (e.g., relay intercropping of a service crop into a winter cereal). Consequently, intercropping should be avoided in situations in which there is insufficient rainfall, water reserves are far from full, or irrigation is not possible during the sowing period (Eberlein et al. 1992; Thiessen Martens and Entz 2001; Blackshaw et al. 2010). Several

technical choices are available to farmers to overcome these challenges in each type of service crop. They include species and cultivar selection and sowing arrangement in terms of space, time and density.

4.1.2 Synchronous intercropping

In synchronous intercropping, the species or cultivar selection and the sowing schemes are the main levers to manage competition throughout the cash crop growth. Service crops should have life cycles and characteristics or traits complementary to those of the corresponding cash crop to prevent the two crop types from competing for the same resources at the same time.

Legumes are ideal service crops for preventing competition with cash crops for soil mineral nitrogen (Fig. 4). During early growth, before nodule initiation, legumes acquire mineral nitrogen from the soil, similar to non-legume species. Considerable interspecific variability has been observed for all traits affecting soil nitrogen uptake. Fenugreek, lentil and lucerne are considered weak competitors for soil mineral nitrogen due to their low biomass and low level of lateral root expansion (Dayoub et al. 2017). Conversely, pea (*Pisum sativum* L.) and soybean (*Glycine max* (L.) Merr.) have higher soil nitrogen uptake levels. Due to its greater nodule biomass, higher levels of N₂ fixation and lower seed reserve depletion rates, faba bean (*Vicia faba* L.) can fix and uptake high amounts of nitrogen during early growth (Dayoub et al. 2017).

Rapid germination, vigorous growth (relative growth rate), the development of a large leaf area, greater plant height and profuse branching enhance the speed of soil coverage and canopy closure by a service crop and, thus, increase competition with weeds (Pester et al. 1999; den Hollander et al. 2007a; Tardy et al. 2015). However, service crops with such traits may also be highly competitive with the intercropped cash crop. The trade-off between the competition with weeds and with the cash crop has to be managed. In SI systems, the option may consist in trying to find the best complementarity in space and time between the cash and service crops.

Temporal and spatial sowing schemes are among the most important factors affecting light competition and plant growth in a mixed-species canopy and can be used to reduce early interspecific competition (Liebman 1989; Kleinhenz et al. 1997). Adjustments can be made by modulating the precise sowing dates of each species in the case of SI service crops and by manipulations of service crop location (between the cash crop rows or sown over the entire area), the width of cash crop inter-rows and the sowing densities of the cash and service crops. In SI systems, slightly delaying the sowing of the service crop after the establishment of the cash crop gives the cash crop a head start, decreasing its sensitivity to competition, particularly when grown with a vigorous service crop (Ohlander et al. 1996; Uchino et al. 2009; Shili-Touzi et al. 2010; Vijaya-Bhaskar et al. 2014). This practice is an efficient way of preventing yield loss (Kandel et al. 1997; Jeranyama et al. 1998; Lawson et al. 2007) but it may not always be sufficient (Lotz et al. 1997).

Spatial complementarity may take different forms. Individuals of different species growing in close proximity may have root architectures very different from those that develop when grown in pure stands. For example, the roots of oilseed rape and faba bean have complementary architectures, resulting in physical niche complementarity and leading to better nitrogen acquisition by both species when grown in mixed stands than when grown in pure stand conditions (Jamont et al. 2013b). Ramirez-Garcia et al. (2015) showed that in barley-common vetch intercropping, vetch roots extend deeper in the soil, to a depth of 1 m, when high levels of nitrogen are present in the topsoil (150 kg N·ha⁻¹) than in control conditions without nitrogen supply. In maize-white clover SI systems, white clover sown in strips between maize rows competes less strongly with the cash crop than broadcast-sown service crops (Vrabel et al. 1981).

4.1.3 Relay intercropping

Relay intercropping strategy has been mainly developed to reduce the competition of the service crop with the cash crop. However, the main challenge is competition for light and water between the service crop seedlings and the previously established cash crop. Access to light has been highlighted as a critical factor limiting service crop establishment (Klebesadel and Smith, 1959, in Blaser et al. 2011; Amossé et al. 2013b). The transmission of light to the soil triggers seedling emergence and promotes early

growth following the establishment of photosynthetic capacity. The service crop must therefore establish itself in conditions with low incident radiation, with a risk of failure under crop canopies with a high leaf area index (Blaser et al. 2011). Additionally, the presence of an already established crop may complicate soil preparation for sowing the service crop. This complication could make the implementation of small-seed service crops (such as perennial legumes) difficult, as maximal soil-seed contact is important, to favor the rapid emergence and early development of the service crop.

Competition for water with the established cash crop is also likely to lead to a failure of the service crop to become established in water-limited conditions. Protection of the soil surface and seedlings from evaporation is a crucial point in this situation, as the service crop root system is located in the topsoil layer during the first stages. Thus, regular rainfall or irrigation during the establishment period may largely benefit the service crop and its survival.

The sowing density of the cash crop may be decreased to promote the establishment of the service crop in RI systems. Although this is rarely done as it may decrease the number of tillers and the final yield of the cash crop (Blaser et al. 2006). In highly shaded cereal canopies, a wide drill-spacing technique can also decrease light and soil water competition with relay-intercropped legumes (Queen et al. 2009).

4.1.4 Living mulch

In living mulch systems, the use of perennial species, which establish slowly, may prevent important competition with the cash crop during this period. However, nutrient availability may affect the relative competitive abilities of the species later in the cycle (Carton et al. 2018). In contrast to the other types of service crops, the service crop is easier to establish and may mobilize resources before the cash crop is sown. However, LMs deplete the soil water and nutrients and intercept light, with potential effects on cash crop establishment (Eberlein et al. 1992; Carof et al. 2007; Blackshaw et al. 2010).

The variability of service crop characteristics can also be optimized at the intraspecific level. Singer et al. (2006) compared the behavior of 15 red clover cultivars differing in ploidy level, in origin, and in selection history, and grown with winter wheat in a relay intercropping system. They found large differences in red clover biomass production before completion of the cash crop cycle, particularly when spring conditions were unfavorable. Bergkvist (2003b) found that less winter hardy white clover (*Trifolium repens* L.) cultivars were less competitive in spring than other cultivars in LM winter wheat, demonstrating the importance of cultivar choice for intercropped service crops.

Furthermore, the various species and cultivars used as cash crops differ in their competitive ability. The rationale underlying species and cultivar choices for intercropping should also be based on traits relating to competitiveness, such as height, vigor, growth rate, intensity of tillering, and tolerance to shade and drought (Moynihan et al. 1996; Blaser et al. 2011; Schipanski and Drinkwater 2011; Ziyomo et al. 2013).

Increasing the sowing rate for the cash crop and decreasing that for the service crop shifts the competitive balance toward the cash crop (Ohlander et al. 1996; Bergkvist 2003b). However, the use of this technique alone is not always sufficient to manage the competitiveness of the service crop, particularly in LM systems, in which competition with the cash crop can be intense (Hiltbrunner et al. 2007c). Reducing the biomass of the service crop is also a lever to facilitate the establishment of the cash crop. Superficial soil tillage and strip tillage reduce competition with cash crops (Thorsted et al. 2006a). Destruction, by strip tillage, of 30% of the ground cover provided by LM facilitated the effective establishment of maize before reclosure of the service crop canopy (Flynn et al. 2013). Leary and DeFrank (2000) and Wiles et al. (1989) suggested that controlling the roots of LM species by shallow tillage before sowing the cash crop is the key to improving cash crop establishment (Liedgens et al. 2004; Thorsted et al. 2006b). However, soil disturbance may also promote weed germination and subsequent competition (Bergkvist 2003b).

4.2 Managing the services while both crops are present

4.2.1 Managing competition and complementarity between crops

Major interspecific interactions occur as soon as the cash crop and service crop are both established (Fig. 4). These interactions include competition for available resources, such as light, nitrogen, and water (Bergkvist 2003a; Harris et al. 2007). The capacity of each of the component species to acquire resources dictates the distribution of resources between the intercropped species (Fayaud et al. 2014). This competition may induce stress in the cash crop, reducing its production.

Competition for light depends on the relative heights and spatial positions of the different intercropped plants in the canopy (Duiker and Hartwig 2004; Uchino et al. 2012). The ability to compete for light is governed by three key plant traits: early development, rapid vertical growth and a large specific leaf area (Olesen et al. 2004; Carof et al. 2007). Service crops also compete for water and nutrients, potentially leading to an important reduction in cash crop yield. This phenomenon may be particularly detrimental in situations with low water or nutrient availability and turnover. For solar radiation partitioning, farmers seek to foster cash crop production by intercropping complementary species. For example, competition for soil mineral nitrogen is likely to be weaker for legume than for non-legume service crops because legume crops receive most of their nitrogen from biological nitrogen fixation (Thorsted et al. 2006a; Corre-Hellou et al. 2009). However, some service crops may compete strongly with the cash crop for soil mineral nitrogen (Smeltekop et al. 2002).

To influence relative competitiveness with the cash crop (Fig. 4), intercropping systems can be managed either by decreasing the competitiveness of the service crop, e.g., through physical or chemical control, or by increasing the competitiveness of the cash crop (Kandel et al. 1997; Hiltbrunner et al. 2007b). Nitrogen fertilization may be applied to promote cash crop growth at the expense of the service crop. Chemical and physical treatments that selectively damage service crops are the principal means of reducing service crop competitiveness and limiting competition for short periods.

4.2.2 Synchronous intercropping

In synchronous intercropping, competition between the cash and service crops is highly variable, depending on the specific traits of the species involved, such as growth vigor. Species grown in SI systems are sometimes controlled at an early phase of growth to reduce competition at later dates corresponding to critical stages of cash crop development.

For all types of intercrops, but especially is SI, nitrogen fertilizers can be used to distort competitive interactions by promoting cash crops at the expense of service crops. This distortion has been mostly found in systems where the service crop is a legume and the cash crop is a tall nitrophilic plant (White et al. 1993; Angus et al. 2000; Hiltbrunner et al. 2007a; Bergkvist et al. 2011). Queen et al. (2009) showed that the amount of light reaching red clover through a wheat canopy was greatly lower with the application of increasing amounts of nitrogen. Conversely, legume service crop biomass is generally greatest in the absence of nitrogen application (Pearson et al. 2014; Stenerud et al. 2015; Vrignon-Brenas et al. 2016a). Furthermore, the localized application of fertilizer to maize rows did not favor ryegrass grown as a service crop (Garibay et al. 1997).

4.2.3 Relay intercropping

In relay intercropping systems, the impact on cash crop yield is generally limited, as the overlap between crop cycles is restricted in time, and the emerging service crop produces a small biomass, with a small leaf area during the period of crop coexistence. The undersowing of established winter cereals with forage legumes in the spring typically has no negative impact on the yield of the winter cereal crop (Hesterman et al. 1992; Thiessen Martens and Entz 2001; Amossé et al. 2013b). However, yield losses have been reported for winter wheat (*Triticum aestivum* L.) grown with highly vigorous black medick (*Medicago lupulina* L.) and Persian clover (*Trifolium resupinatum* L.) in some resource-limited conditions (Hartl 1989; Amossé et al. 2013b). In such systems, the competition between service and cash crops may occur late in the cash crop cycle, offering few options to manage this competition.

4.2.4 Living mulch

The living mulch can cause significant competition to the service crop since the service crop has already formed an established cover when the cash crop is sown. The impact of this competition on cash crop grain yield may be substantial, and large cash crop yield losses have been observed (Eberlein et al. 1992; Liedgens et al. 2004; Reddy and Koger 2004; Ziyomo et al. 2013). Several studies have highlighted the potential of temporal complementarity to increase resource-use efficiency and reduce competition between crops in LM systems (Liedgens et al. 2004; Hiltbrunner et al. 2007b). However, service crops can make use of resources that would otherwise be lost in some situations, due to nitrate leaching or soil evaporation for example.

The complementarity between service crop and cash crop life cycles and traits has to be thought to prevent the two crops from competing for the same resources at the same time (Weiner et al. 2017). For example, an ideal service crop for perennial ground cover in maize fields would be a short, slow-growing crop with a spreading habit and is tolerant to shade (Pülschen 1992; Flynn et al. 2013). Some of these traits may correspond to clover species. Subterranean clover initiates growth in late summer or early fall, subsequently entering senescence in spring. This could be useful for intercropping living mulches with spring crops, such as maize (Ilnicki and Enache 1992).

To prevent early competition, service crops may also be controlled at a later stage if competition is potentially detrimental. For example, hairy vetch must be controlled before maize sowing, as it enters a period of rapid growth near the time at which maize is normally sown (Reddy and Koger 2004). Partial and temporary destruction may also be used to delay living mulch development and to ensure that lucerne pod formation does not coincide with cereal crop maturity (Harris et al. 2007).

The defoliation of service crops by mowing (Brandsæter et al. 1998), cutting back (Thorsted et al. 2006a), sheep grazing (Jones and Clements 1993; Gooding et al. 1998) or chemical weeding (Barilli et al. 2017) efficiently decreases aboveground and belowground competition. The success of defoliation depends on the developmental stage of the plants, the ability of the species to grow back, and the speed at which it does so. For example, the mowing of forage legumes, such as hairy vetch, at the early bud stage before the sowing of maize (cash crop) stimulated vigorous regrowth of the legume compared with mowing after flowering (Hoffman et al. 1993; Ghosheh et al. 2004; Romanekas et al. 2012), and it reduced early competition with maize.

During the period of coexistence, the early control of lucerne, at the start of wheat stem elongation, slightly decreased the impact of the service crop on wheat growth relative to later control or an absence of control (Barilli et al. 2017). Herbicide-resistant varieties can be used to avoid damage to the cash crop (Affeldt et al. 2004).

4.3 Service crop destruction practices

In synchronous intercropping and in living mulch, the service crop may be managed chemically or physically to prevent competition at late development stages of the cash crops. Herbicide application is considered to be the simplest way to control service crops in no-till cropping systems, whereas physical methods are frequently used in organic farming. Under cold conditions, frost can sometimes be used to kill service crops without the need for herbicides or machinery.

4.3.1 Synchronous and relay intercropping

Frost-sensitive service crops may be sown in spring as a relay intercrop in an existing winter crop or synchronously with a cash crop in fall. In the latter situation, the benefits of synchronously intercropping frost-sensitive legumes were recently evaluated for winter oilseed rape (Cadoux et al. 2015; Lorin et al. 2015). The disappearance of the service crop during the winter prevents competition with the cash crop in spring and has implications for the timing of N availability to the cash crop or following crops, with a greater risk of N leaching if destruction occurs just before winter.

Special care must be taken to check the frost sensitivity of the candidate service crop species, as destruction may be only partial in temperate climates (Storr et al. 2021). The efficiency of frost

destruction depends on species, cultivar choice, and sowing date, with plants most sensitive to frost when they are close to flowering. This destruction method is becoming much less reliable in the context of climate change, resulting in its replacement by herbicide use in some cases.

Mowing is also an option in crops sown with wide inter-rows. In maize synchronously intercropped with various service crops, double-mowing operations at the maize stages of six unfolded leaves and stem elongation eliminated oilseed rape, mustard and spring barley more efficiently than a single mowing and prevented competition and yield losses (Romaneckas et al. 2012). However, they also found that Italian ryegrass, black medick, Persian clover and red clover had substantial regrowth capacity, resulting in losses of maize grain yield.

4.3.2 Living mulch

In non-organic cropping systems, the living mulch is often managed and destroyed by the application of herbicides. The degree of management of the living mulch, from partial control to destruction, can be fine-tuned by dose adjustment and the use of selective products (Jones and Clements 1993; Zemenchik et al. 2000; Affeldt et al. 2004; Harris et al. 2007). As an alternative to treating an entire area, band-spraying techniques can be used to suppress living mulch in strips, into which the cash crop is then sown (Eberlein et al. 1992; Affeldt et al. 2004). For instance, an absence of maize yield loss was reported in conditions in which at least 60% of the total area of crimson clover (as LM) was killed chemically (Kumwenda et al. 1993).

In no-till cropping systems, roller-crimper has emerged as a promising tool for LM control and reducing herbicide use. It crushes the stems of the plants, and the resulting damage prevents the regrowth of the LM species. The maintenance of residues on the soil surface ensures the prolonged persistence of mulch cover, thereby promoting greater weed control than that achieved with other mechanical strategies (Vincent-Caboud et al. 2019). Finally, a combination of chemical and physical techniques has been shown to improve the success of intercropping in terms of the achievement of a number of objectives. For example, a combination of strip tillage and post-emergence herbicide application as a means of decreasing kura clover (*Trifolium medium* L.) competition was shown to be a promising option for the production of grain maize in a kura clover LM cropping system (Pearson et al. 2014). Research into a combination of physical methods with the selection of easy-to-manage service crop cultivars is urgently required to reduce herbicide dependence, particularly in conservation agriculture.

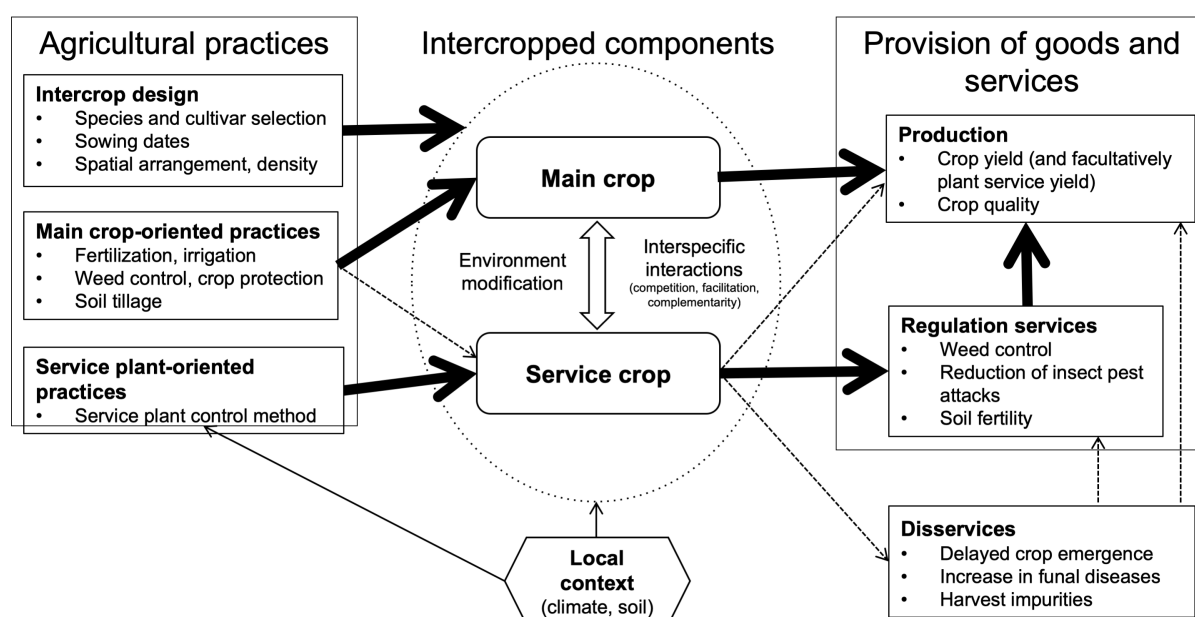


Figure 4. The interactions between the service crop and cash crop determine the degree of service provision by the intercropped species (provisioning and regulating services). Agricultural practices, such as intercropping design and management, can modify these interactions to optimize the growth and functioning of intercropped components. These practices should also limit negative or unexpected effects (dotted arrows).

To conclude this section on service crop management, the temporal arrangement of the species grown, the choice of service crop species or cultivar and the method used to control the service crop are the three main factors to be considered to manage the proportion of cash crop and service crop biomass, their interactions and to ensure the delivery of services.

5 Discussion

The review of 383 articles experimenting with intercropped service crops showed that they were markedly focused on very few combinations, mainly Poaceae and Fabaceae, likely because nitrogen is the main abiotic factor limiting crop growth (Oerke 2006) in cropping systems dominated by cereals. Even if experiments focused on a few genera, especially *Trifolium* spp., *Medicago* spp. and *Vicia* spp., there is within each one a diversity of species and varieties with short or high stature, with various growth dynamics, with a low, intermediate or high perenniality, adapted to diverse temperature, moisture and soil pH conditions (Leoni et al. 2020; AgroDiversity Toolbox contributors 2021). The low diversity of the service crops studied is also counterbalanced by several possibilities for the timing of the inclusion of the service crop relative to the cash crop cycle (i.e., as a living mulch or in synchronous or relay intercropping), the spatial organization of the intercropping system and a wide range of management methods. Then, service crops may provide several services simultaneously (e.g., competition with weeds, the provision of nitrogen and pest control) in different pedoclimatic contexts and with different intercropped cash crops, with only a few species.

5.1 Effectiveness and limits of the proposed service crop typology

To address the diversity of uses of intercropped service crops and the diversity of terms used to name them, we proposed a typology based on the coexistence periods between the service crop and cash crop. We distinguished (i) **synchronous intercropping**, where the coexistence period extends over the entire cash crop cycle (ii) **living mulch**, where the cash crop is sown in a previously established service crop, (iii) and **relay intercropping**, where the service crop is sown within an already established cash crop. This typology simplifies the multiple denominations and helps to understand the functioning of intercropped systems, including service crops. A strong connection exists between the type of intercropping and the management strategies of the service and cash crops, including the choice of the species and cultivars with simultaneous or delayed life cycles. We thus highlighted the key role of the establishment period in LM and RI. During this period, competition between service and cash crops must be managed to ensure the establishment of the sown crop in the pre-existing crop. Since a given service crop species can provide several services, depending on how it is managed, this typology also enables us to distinguish the periods at which the service crop has an important biomass and thus when and to what extent it is susceptible to delivering the expected services to the cropping system in terms of weed and pest regulation and nitrogen release.

These categories are obviously not strict, and farmers show great flexibility in the management of these service crops, which can lead to intermediate situations (Verret et al. 2020). For instance, in relay intercropping, a service crop with slow development, due to variety choice or limiting soil moisture, may be sown when the cash crop has a low biomass to facilitate its establishment when competition is limited. In contrast, a service crop with an expected important development (high stature, favorable climate and soil conditions) may be sown shortly before the cash crop harvest to prevent competition with the cash crop. Farmers also display opportunistic strategies for the termination of the service crop. The coexistence period may be shortened in case of risks of competition with the cash crop. In contrast, it may be extended over several cash crop cycles when competition between both crops and weeds is well managed. A perennial service crop sown in SI or RI can therefore become a LM. In such situations, the typology we proposed shows its limits, as the types are defined for each cash crop cycle and do not encompass the diversity of strategies to include service crops within a pluriannual cash crop sequence (Basche and DeLonge 2017).

5.2 What can be expected from intercropped service crops?

Focusing on intercropped service crops, the typology was relevant to analyze the provision of services that depend on a close interaction between the service crop and cash crop, such as competition or complementarity for the use of resources and the disruption of pest activity by habitat modification.

As shown in this review, the benefits of service crops are more important in unweeded crops. Nevertheless, service crops remain less effective than chemical control, particularly in situations where weed density is high. Weed biomass may be reduced, but the total biomass produced by both the service crop and weeds in the intercropped system is often higher than the biomass of weeds alone in a sole crop. This difference may result in cash crop yield losses (Chase and Mbuya 2008). A trade-off might be found between weed suppression and yield loss, as these performances may be antagonistic (den Hollander et al. 2007b). The literature has suggested that the best way to proceed is to favor rapid soil coverage and canopy closure to prevent weed emergence and early growth as much as possible (Tardy et al. 2015; Petit et al. 2018). Then, the service crop has to be selected and managed to prevent competition with cash crops for light and soil resources. Complementary weeding operations (i.e., chemical and/or mechanical weed management) are generally required to achieve satisfactory weed control (Swanton et al. 1996; Teasdale 1996; Carof et al. 2007). Service crops should, therefore, be used within an integrated and agroecological approach, together with other cropping practices at the cropping-system level, to enhance the natural regulation of weeds and insect pests and valorize the services provided by the planned and associated biodiversity (Casagrande et al. 2017a).

Regarding pest control, a considerable diversity of cash crop host-insect pest pairs has been investigated in the literature. Any service crop approach needs to be very specifically tailored to the pest and beneficial species actually present to ensure that a sufficiently large effect is achieved. The effects of these interactions, e.g., chemical ecology, are far less generic than those of competition with weeds, which complicates the selection of appropriate plants and the development of such effects. In addition, the potential of service crops to regulate pest attacks has mostly been assessed for species not initially chosen for this purpose, explaining the limited operational results available. From the perspective of efficient pest biological control, this does not preclude these intercropped service crops from being combined with spatial arrangements of other service crops, such as trap crops in a push-pull system (Pickett et al. 2014), which are relevant to managing services depending on mobile organisms.

This literature review highlights the potential of intercropping service crops to reduce input use, especially fertilizer application. This practice has a positive effect on the environment, as demonstrated by a comparison of legume intercrops with sole crops (Naudin et al. 2014). These very interesting results can be explained by better nitrogen resource use in intercrops than in sole crops (Hauggaard-Nielsen et al. 2003; Jensen et al. 2012; Naudin et al. 2014).

We focused on the three principal regulating services studied to date in this review, but future investigations are likely to consider services that have been largely neglected to date, such as facilitation interactions increasing the accessibility of soil nutrients to plants and the enhancement of soil structure or biofumigation. Considering additional services should not decrease vigilance concerning the constraints and potential disservices due to intercropped service crops. A dense living mulch may slow soil warming in spring, thereby delaying the emergence and development of cash crops (Martin et al. 1999; Hooks et al. 2013) and nitrogen mineralization. The higher density of the plant canopy may also promote fungal diseases and crop lodging (Moynihan et al. 1996; Hiltbrunner et al. 2007b). Thus, appropriate management of intercropped systems is necessary to limit or overcome these problems.

5.3 Managing several services and limiting the disservices

The management of diversified plant cover with several objectives is more complex than the management of a sole crop. Despite the diversity of service crops and their modes of inclusion in the crop cycle, most trade-offs between services and disservices can be explained by biomass production.

The amount of nitrogen fixed or retained and possibly released thereafter, the ability to suppress weeds and the ability to control insect pests are strongly and positively associated with service crop biomass

(Naudin et al. 2010; Lorin et al. 2015; Carton et al. 2020). Moreover, excessive service crop biomass increases the risk of competition with cash crops and decreases the quality of the biomass, such as mineralization due to the C/N ratio. The destruction of the service crop may reduce nitrogen availability for the cash crop due to nitrogen immobilization. Furthermore, the dynamics of soil nitrogen mineralization may not be synchronized with the nitrogen needs of a cash crop (Feil et al. 1997; Thorsted et al. 2006a), depending on the crop cycle, stage, and local pedoclimatic conditions. Most management options therefore aim to minimize competition with the cash crop, through niche complementarity, without impairing direct competition with weeds through niche overlap by taking advantage of the spatial (Cheriere et al. 2020) and temporal (Amossé et al. 2013a) organization of the plants. These interactions at the plant community level are highly dependent on the architecture of the service crop and its growth dynamics, which can be managed physically or chemically. Nevertheless, competition between intercropped services and cash crops is unavoidable. The degree of competition increases with the duration of the period of coexistence between the service and cash crops in the field. Appropriate temporal and spatial complementarity relationships must be found between the intercropped components to make the best possible use of the available resources and to minimize deleterious effects (Vandermeer 1989; Zhang and Li 2003; Duchene et al. 2017).

The different intercropping systems provide a means of achieving temporal complementarity between service and cash crops, in some cases reducing or even preventing the detrimental impacts of resource competition on cash crop production (Thorsted et al. 2006a; Singer et al. 2007). Hence, the level of competition increases along a gradient running from relay intercropping to a living mulch service crop. Relay intercropping appears to be an efficient way to minimize potential competition with the cash crop. Nevertheless, decreasing the relative competitiveness of the service crop too much may lead to seedling failure in the service crop. The spatial arrangement and densities of intercropped species may be highly determinant for the intensity and dynamics of interspecific competition and thus for the services provided.

Due to the crucial importance of service crop biomass, most services and disservices provided by intercropped service crops are bundled, regardless of the service crop species, as already reported for service crops sown and grown between two cash crops (Finney and Kaye 2017). However, some services, such as pest control, are independent of service crop biomass. For example, the provision of trophic resources and habitats for predators and parasitoids (Jamont et al. 2013a), the emission of volatile compounds attracting or repelling specific insects, and the emission of allelopathic substances active against weeds or soil-borne pathogens are highly dependent on the species and variety of the service crop. These processes have been explored much less fully in temperate than in tropical cropping systems (Ratnadass et al. 2012).

Finally, targeting diverse services appears to be a relevant strategy because a decrease in crop yield due to competition with service crops may be compensated by other services, such as an increase in product quality (Germeier 2000) or a reduced cost of inputs (e.g., pesticides, fertilizers, and fuel) and workload.

5.4 Improving the choice of service crops by making use of trait variability

In addition to the species and management of the service crop, the trade-off between services and disservices also depends on the cultivar of the service crop grown. It is therefore necessary to better characterize the diversity of traits of species and cultivars (Dayoub et al. 2017; Carton et al. 2018) and their plasticity in interspecific mixtures, to identify ideotypes of service crops and to define new selection criteria, such as the ability to cover the soil rapidly, allelopathic and biofumigation capacities, or the exudation of amino acids and extracellular enzymes for stimulating soil fertility processes. These criteria should be evaluated not only at the individual plant level but also at the level of the entire plant community (Weiner et al. 2017); for example, to promote facilitative processes modifying interspecific competition.

Future progress in service crop selection may be based on the concept of plant functional traits (Wood et al. 2015). This approach is generic, as it embraces both between- and within-species variability. Between-species variability has already been explored, but plant traits are also highly variable within species (Kattge et al. 2011), with this intraspecific variability representing 25 to 32% of total plant trait

variation (Siefert et al. 2015), with important consequences for the associated functions. Intraspecific variability is notoriously high for morphological and architectural traits, due in part to plasticity (Colbach et al. 2019), but it is even higher for physiological (Martin et al. 2017) and chemical traits (Siefert et al. 2015). It should be possible to select service crops that satisfy new criteria from the existing plant variability. For example, service crops capable of adapting their morphology and growth to the available resources without competing with the cash crop, for instance by entering into dormancy, could be selected (Volaire and Lelièvre 2010). Efforts might be focused on the search for service crops occupying niches different from those occupied by cash crops in terms of phenology, architecture and soil mineral and water use but also in terms of biotic interactions.

The diversity of plant traits involved in resource acquisition promotes functional complementarity between the cash and service crops, leading to higher levels of biomass production in the intercropping system. This finding has been demonstrated on numerous occasions, particularly for mixtures of legumes and non-legumes (Wendling et al. 2017), but it is not always the case (Montazeaud et al. 2018), highlighting the need to improve our understanding of the functioning of highly diversified, multispecies plant covers. There are also trade-offs between plant traits in natural ecosystems (Wright et al. 2004), between the traits associated with resource acquisition, such as specific leaf area, positively associated with relative growth rate, and traits associated with resource conservation, such as leaf dry matter content, negatively associated with the biomass mineralization rate. However, the artificial selection of crop plants and the high levels of nutrient resources in crops have relaxed such trade-offs (Tribouillois et al. 2015), providing additional degrees of freedom in the selection of service crops.

The number of species should be increased for the development of multifunctional plant cover and to resolve trade-offs between services (Barot et al. 2017). Coupled with a dependency on local soil and climate conditions, it is further complicated to understand and manage highly diverse cash and service crop communities and to decipher all interactions with their environments and agricultural techniques. This high diversity of service crop combinations questions and renews the way to experiment and the way to produce knowledge. Farmer practices and knowledge cover a much larger number of combinations than those studied. This expertise can be investigated by innovation tracking (Verret et al. 2020) and by expert elicitation (Chen et al. 2019).

6 Conclusion

This review shows how intercropped service crops can provide cropping systems with multiple services of interest and can help to reduce input use, with some potentially negative effects on crop production. The typology we propose is relevant to catch the diversity of intercropped systems, including service crops, to understand their functioning and analyze the provision of services. Intercropped service crops can efficiently reduce weed biomass in temperate arable systems, in particular, by increasing light interception within and between crop cycles. Intercropped service crops also retain or fix nitrogen and release it to the soil to the benefit of current or subsequent cash crops. Service crops render the plant cover architecture more complex. They also provide predators and parasitoids with trophic resources and habitats, thereby reducing pest attacks. The resulting effect of service crops on cash crop yield is variable and reflects the integration of the effects of the various individual services, together with possible disservices, according to whether the effects are additive, synergistic or antagonistic. The diversity of these effects is highly dependent on cash and service crop management, especially species or variety choice, plant density and their temporal arrangement. Overall, this review highlights the central role of biomass in managing these interactions, particularly through the management of competition between intercropped species.

We provide an assessment of knowledge and a framework (Figs. 3 and 4) and avenues for the design of cropping systems, including service crops. This review was limited to defined crop sequences including intercropped service crops, but consideration of the inclusion of these crops over the entire crop rotation will be required for a full assessment of their benefits. Most research cited in the review was based on scientific experiments. However, recognizing and adding value to farmer knowledge and practices are

essential because farmers design crop mixtures that meet their own and diverse objectives and that are adapted to their context.

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