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Lettuce cropping with less pesticides. A review

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Abstract Agricultural intensification has increased crop productivity but decreased agroecosystem services. Agricultural intensification is occurring notably for horticultural crops such as lettuce. In conventional agriculture, lettuce protection is achieved mostly by preventive applications of pesticides with about eight treatments for a 60–90-day-long cycle in the Mediterranean region. However, new sustainable control strategies are needed due to pesticide impact on environment and human health, emerging pesticide resistance, and stricter policies on levels of pesticide residues in food. Here, we review knowledge and methods allowing to grow lettuce with less pesticides. Advances shown are based on pest ecology and pathogen control by the agroecosystem. The major points are as follows: (1) pest and pathogen community composition depends partly on climatic conditions. The identification of pests and pathogens that can threaten the crop is the first step to design innovative lettuce cropping systems less dependent on pesticides. (2) The numerous alternative techniques currently available should be combined to control lettuce pests and pathogens. The effects of alternative techniques on non-target organisms including non-target pests are poorly known so far. (3) Designing sustainable systems requires taking into

account ecological interactions and suitability of different management techniques of low impact.

Keywords *Lactuca sativa* · Pest and disease management · Agroecosystem services · Pesticides · Alternative techniques

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1 Introduction

Since the 1960s, agricultural intensification characterized both by the simplification and the artificiality of cultivated areas has led to a sharp increase in productivity (Stoate et al. 2009; Matson et al. 1997). In return, intensification has also brought many negative externalities (Stoate et al. 2001) including plant diversity losses at different scales, ranging from field-wide to region-wide effects (Mediene et al. 2011). It is now recognized that biodiversity, more precisely functional diversity, plays a key role in the provision of ecological services by agroecosystems, although this role is still poorly understood (Mace et al. 2012). Agricultural intensification has resulted in the loss of some ecosystem services that have been replaced by cultural practices and external inputs (Matson et al. 1997; Altieri 1999). These inputs have, in turn, impeded other services, as exemplified by Sanchez-Moreno and Ferris (2007), who showed that tillage, fertilizer, and herbicide inputs could hamper predation and soil-borne pest regulation services by disrupting high trophic levels of soil food webs. Consequently, intensively managed agrosystems have become heavily dependent on these compensatory practices.

Among agricultural practices that have supplanted ecosystem services, inputs of pesticides are probably the most criticized. Pesticides have gradually come to be used regularly as a performance insurance, rather than occasionally as a curative means to control pest and pathogen outbreaks (Lamine et al. 2010). This practice has greatly replaced and reduced natural pest regulation, which is promoted by

functional diversity within food webs (Altieri 1999; Moonen and Barberi 2008), thus decreasing the sustainability (Lewis et al. 1997). Agricultural intensification outcomes are particularly noticeable in horticultural crops such as lettuce in the Mediterranean region. Spain, Italy, and France are the three largest European producers, producing respectively 35 %, 21 %, and 13 % of the lettuce tonnage in Europe in 2010 (Eurostat 2012). In this region, the use of genetic breeding and external inputs has allowed lettuce cultivation in open fields or inside greenhouses almost all year long (Fig. 1). Different types of lettuce are grown for the fresh or processed markets. The main types are crisphead, butterhead, looseleaf (e.g., batavia, oak leaf lettuce), and romaine (Lebeda et al. 2007; Mou 2008). In France, the types the most produced are batavia (37 %) and oak leaf (31 %), while in Spain it is crisphead (Maisonneuve and Blancard 2011). In intensively managed cropping systems, lettuce is grown on specialized farms as a monoculture or sometimes within crop rotations which typically include Cucurbitaceae and Solanaceae. Nutrient recycling and soil aeration are replaced by fertilizer inputs and by plowing, respectively. Pest and disease control is achieved with pesticides, often in a systematic and preventative way. Similarly to other horticultural crops, the visual quality of fresh market lettuce is generally expected to be high, and this is often a justification for heavy pesticide use. In these conventional agroecosystems, sole reliance on chemical control for pest management has had numerous adverse consequences, such as the emergence of pesticide resistance among pest and pathogen populations (Brown et al. 2004; Davet and Martin 1993; Kift et al. 2004), the loss of biodiversity in agroecosystems and adjacent ecosystems (Stoate et al. 2001, 2009), the pollution of water and air, and adverse impacts on human health.

Currently, many governments, including those of the member states of the European Union, are implementing national plans aimed at reducing pesticide applications (Hillocks 2012). Efforts have been made in recent years, especially on cereal crops, to design and assess agricultural systems with reduced dependence on external inputs and compensatory practices (Debaeke et al. 2009). Studies have also been conducted to design and to assess vegetable cropping systems allowing improved management of soil-borne pests and pathogens (Tchamitchian et al. 2009; Navarrete et al. 2010). However, to our knowledge, no such studies have been undertaken with lettuce crops. The aim of this review is to examine the feasibility of reducing the reliance on pesticides without lowering the productivity of lettuce cropping systems. Although many advances on alternatives to chemical control have been achieved over several decades, these techniques usually have only partial effects on diseases and pests. These methods must be combined to provide efficient control, as proposed by Collange et al.

Fig. 1 Lettuce crops under shelter (near Montpellier—southeast of France) and in open field (near Tarascon—southeast of France)



(2011) for the root-knot nematode (*Meloidogyne* spp.), and are sometimes specific to a single pest species. It appears critical, however, to consider all the different species that are likely to threaten the crop because the elements of the agroecosystem interact. Moreover, strategies for disease and pest management must integrate techniques compatible with the biological functions of agroecosystems (Lewis et al. 1997). As a result, knowledge of the mechanisms involved is required to understand the effects of each technique on

ecosystem services and particularly on the biological control of pest populations. In addition, these practices and combinations of practices should also meet social and economic expectations to be accepted both by growers and consumers (Pannell 1999).

In this review, we first identify the main pests and pathogens that could threaten lettuce crops and the conditions that are conducive to their development. Secondly, we review the techniques, including the use of pesticides, that are available

for the management of these pests and pathogens. The theory supporting these techniques and their action spectra, efficacies, and effects on the agroecosystem properties are presented. Finally, we discuss the best ways to jointly implement these crop protection techniques within lettuce pest and pathogen management strategies, while promoting natural pest and pathogen regulation and other agroecosystem services. We focus on lettuce production under shelter and in open field in the Mediterranean region. However, much of the information can be extrapolated to other temperate climate areas.

2 Overview of the lettuce pests and pathogens

Lettuce is prone to many pests and pathogens. Extensive information is available (Blancard et al. 2003; Chamont et al. 2010). The aim of this section is not to provide an exhaustive list of diseases and pests but to present those that can cause significant and/or economic losses that lead to many pesticides applications.

2.1 Lettuce pathogens

2.1.1 Fungal diseases

One of the most important diseases of lettuce is downy mildew caused by *Bremia lactucae* (Regel). The pathogen may attack the plant throughout its crop cycle. The primary inoculum typically consists of airborne sporangia from diseased plants of the genus *Lactuca* located close to the crop or of mycelia present on plant debris in the soil. The sporangia of *B. lactucae* are typically released from the underside of leaves by sporangiophores, which form a white felt-like layer (Fig. 2) (Blancard et al. 2003). The optimal conditions for sporulation



Fig. 2 *Bremia lactucae* sporangiophores forming a white, felt-like layer on the underside of a lettuce leaf. (Photo E. Dorel—Green Produce & Variations)

are a high relative humidity and a temperature from 5 to 15 °C depending on the isolate (Nordskog et al. 2007). Propagules transported by wind ensure secondary contaminations within the crop (Blancard et al. 2003; Crute 1992a).

Sclerotinia sclerotiorum (de Bary), *Sclerotinia minor* (Jagger), *Botrytis cinerea* (Pers.), *Rhizoctonia solani* (Kühn), and *Pythium tracheiphilum* (Matta) are important soil-borne fungal pathogens (Blancard et al. 2003). *S. minor* and *S. sclerotiorum* cause lettuce drop and are of major concern for the cultivation of lettuce because they may affect a wide range of plant species and their sclerotia may remain latent into the soil for more than 8 years (Melzer et al. 1997; Bolton et al. 2006). Furthermore, the five pathogens cited above are involved in the development of a shared symptom of basal rot (Fig. 3). The populations of these pathogens fluctuate depending on the growing season. The sclerotia and mycelia of *R. solani* are most frequently found in soil in the summer, whereas the sclerotia and mycelia of *B. cinerea* are most abundant in the winter, when *B. cinerea* injury to the lettuce leaves is enhanced by cool and moist conditions (Van Beneden et al. 2009). Additionally, *Fusarium oxysporum* f. sp. *lactucae* is a host-specific lettuce pathogen that has been emerging in Europe, notably in Italy, since 2002 (Garibaldi et al. 2002). This pathogen, a causal agent of Fusarium wilt, is promoted by high temperatures and can cause leaf chlorosis and eventually plant death. It can be transmitted by seeds (Garibaldi et al. 2004) or by resting forms, which can be propagated by tillage tools (Scott et al. 2012). Similarly, *Verticillium dahliae* (Kleb), the causal agent of verticillium wilt, can survive for 10 years in the soil as microsclerotia and be propagated. Although *F. oxysporum* f. sp. *lactucae* and *V. dahliae* are currently geographically localized, they could become widespread problems in the coming years. *Golovinomyces cichoracearum* (DC), causal

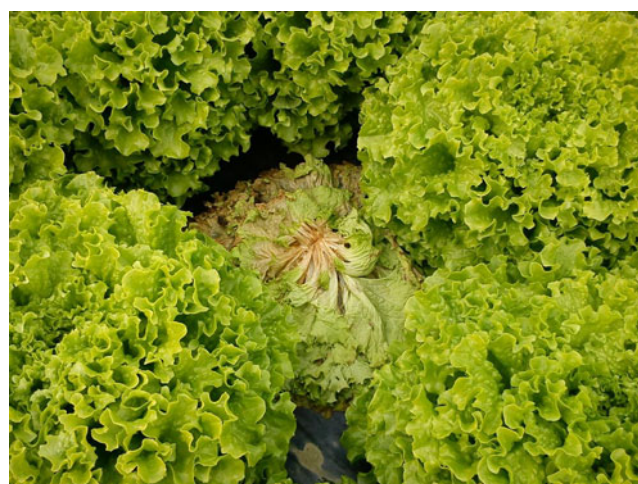


Fig. 3 Extended basal rot caused by *Rhizoctonia solani*, leading to the complete drop of lettuce

agent of powdery mildew, is perceived as a minor pathogen but may also cause damage on lettuce. The proper temperature range for its development is 18–25 °C, so it occurs mainly in the summer and early autumn (Lebeda and Mieslerova 2011).

Finally, the fungus *Olpidium brassicae* (Woronin) is not a direct threat to lettuce, but it is a vector for two lettuce viruses that can cause significant damage: Mirafiori lettuce virus, responsible for “big vein” disease; and lettuce big-vein associated virus, suspected to be the agent of ring necrosis (Lot et al. 2002; Verbeek et al. 2012). This fungus is able to remain dormant in the soil or on plant debris for several years in the form of chlamydospores (Blancard et al. 2003).

2.1.2 Bacterial diseases

Lettuce crops are also prone to bacterial diseases. *Pseudomonas cichorii* (Swingle) is the causal agent of varnish spot and *Xanthomonas campestris* pv. *vitiens* (Brown) is the causal agent of bacterial leaf spot of lettuce. Both develop under wet conditions and temperature ranging from 20 to 25 °C and from 26 to 28 °C, respectively, for *P. cichorii* and *X. campestris* pv. *vitiens*. Seeds, crop residues, or weeds can be sources of inoculum (Blancard et al. 2003; Toussaint et al. 2012; Barak et al. 2001).

2.2 Lettuce pests

Many pests, whether host-specific or not, can also be potential threats depending on the cropping period. These pests include several aphid species, such as *Nasonovia ribisnigri* (Mosley), specific to lettuce; *Myzus persicae* (Sulzer), the green peach aphid; *Aulacorthum solani* (Kaltenbach); *Macrosiphum euphorbiae* (Thomas); and *Hyperomyzus lactucae* (L.). Temperature is the factor that affects most the development of aphids. The highest growth rate of *N. ribisnigri* populations occurs between 20 and 24 °C (Diaz and Fereres 2005). In addition to feeding damage and the loss of product quality due to their presence when the lettuce is marketed, aphids are also vectors of viruses, such as the lettuce mosaic virus. Moreover, *Pemphigus bursarius* (L.) is an aphid that attacks lettuce roots. The presence of poplars, its main host, close to the crop fosters its occurrence on lettuce, especially at the end of spring. The larvae of several moths [*Autographa gamma* (L.), *Helicoverpa armigera* (Hübner), and *Mamestra brassicae* (L.)] and slugs (*Deroceras* sp. and *Arion* sp.) also cause feeding damage to lettuce. In a production area such as southeastern France, these pests are present mainly in the spring and fall, with a greater occurrence in open fields. In addition, the thrips *Frankliniella occidentalis* (Pergande), the leafminers *Liriomyza* spp., and the whiteflies *Trialeurodes vaporariorum* (Westwood) and *Bemisia tabaci* (Gennadius) can also occasionally cause significant damage (Palumbo et al. 1997; Mou and Liu 2004;

Costa et al. 1993). *F. occidentalis* is also a vector of tomato spotted wilt virus, which can cause significant yield losses, especially in the summer. Finally, plant parasitic nematodes (in particular in the genus *Meloidogyne* spp.) can attack lettuce crops (Koenning et al. 1999; Djian-Caporalino 2012). The development of the nematodes is enhanced by crop used in rotation in southeast of France; indeed, Solanaceae (tomato or eggplant or pepper) and Cucurbitaceae (melon or cucumber) are susceptible to the same root-knot nematodes.

The composition of lettuce pests and pathogens that could threaten the crop at some point changes throughout the year. Across the entire Mediterranean region, diseases such as downy mildew and grey mold tend to be more problematic in the winter, whereas pest pressure is more significant in the spring and fall. It appears necessary to clearly identify the climatic conditions suitable for pest and disease development to know which period is favorable for pests and pathogens (Table 1). However, in addition to climatic conditions, other factors such as crop history, landscape framework, and soil type also affect the composition of lettuce enemies. The identification of pest and pathogen is the first step to design innovative lettuce cropping systems less dependent on pesticides.

3 Techniques for the management of lettuce pests and diseases

3.1 Limiting the invasion of pests and pathogens

3.1.1 Installing physical barriers

Tillage and crop residue management The simplest and oldest method to reduce primary inoculum is to remove and destroy crop residue (i.e., unharvested leaves and pivot roots) after harvest. This sanitation method can significantly reduce the incidence of diseases; however, the method is seldom used because it is time consuming.

Some cultural practices that affect the structure of the environment can also impact the primary inoculum of lettuce pathogens. For example, tillage that buries crop residues may decrease the survival of stress-resisting forms of the pathogens (Adams 1987; Imolehin and Grogan 1980). However, deep and repeated plowing also induces an increased incidence of some diseases. Indeed, plowing may bring viable sclerotia to the surface and also disperse sclerotial aggregates, thus increasing the probability that the sclerotia come close enough to a host plant to infect it (Subbarao et al. 1996; Wu and Subbarao 2003). In addition, intensive tillage may also have a negative impact on beneficial soil organisms. Chan (2001) has reviewed the effects of tillage on earthworm populations and reported that repeated deep plowing can reduce their abundance and diversity, while Rodriguez

Table 1 Climatic conditions fostering pest and pathogen development and epidemic risks in Mediterranean lettuce crops depending on production type and season

Main pests and pathogens of lettuce	Climatic conditions fostering pest or pathogen development	Risk of occurrence in the Mediterranean area					
		Open field			Under shelter		
		Spring	Summer	Early autumn	Late autumn	Winter	Early spring
<i>Bremia lactucae</i>	Low temperature and high humidity . Optimal temperatures: 5–15 °C (Nordskog et al. 2007)			+++ ^c	++ ^b	+++	+ ^a
<i>Sclerotinia sclerotiorum</i> and <i>S. minor</i>	High soil moisture. For <i>S. sclerotiorum</i> : development temperature ranges from 10 to 25 °C. Optimal temperature: 15 °C (Bolton et al. 2006) For <i>S. minor</i> : development temperature ranges from 6 to 30 °C. Optimal temperature: 18 °C (Hao et al. 2003)			++	+	+	++
<i>Botrytis cinerea</i>	High relative humidity and low temperature. Optimal temperature: 10–20 °C (Elad and Shtienberg 1995)				+	+++	+
<i>Rhizoctonia solani</i>	Optimal temperature: 20–30 °C (Grosch et al. 2004)			+	++	+	++
<i>Pythium tracheiphilum</i>	High soil moisture. Development temperature ranges from 5 to 43 °C. Optimal temperature: 20–24 °C (Blancard et al. 2003)			+	++	+	+
<i>Fusarium oxysporum</i>	Optimal temperature: 20–30 °C (Scott et al. 2010)		+				
<i>Golovinomyces cichoracearum</i>	Optimal relative humidity: 95–98 %. Optimal temperature: 18–25 °C (Lebeda and Mieslerova 2011)			++			
Viruses transmitted by <i>Olpidium brassicae</i>	Low temperature and high humidity. Optimal temperature: 10–16 °C (Chamont et al. 2010)					+++	
Aphids— <i>Nasonovia ribisnigri</i> and <i>Myzus persicae</i>	For <i>N. ribisnigri</i> : development temperature ranges from 3 to 35 °C. Optimal temperature: 26 °C (Diaz et al. 2007) For <i>M. persicae</i> : development temperature ranges from 6 to 37 °C. Optimal temperature: 27 °C (Davis et al. 2006)	+++	+	++	+	+	+++
<i>Meloidogyne</i> spp.	Development temperature ranges from 5 to 38 °C. Optimal temperature: 18–27 °C (Blancard et al. 2003)	+	+	++	+		+
<i>Helicoverpa armigera</i>	For <i>H. armigera</i> : optimal temperature: 27,5 °C (Mironidis and Savopoulou-Soultani 2008)	++	+	+++			

This table allows the identification of pests and pathogens that could threaten the lettuce crop at some point of the year and for a specific production framework. However, other factors, such as crop history, landscape characteristics, and soil type, also affect the composition of lettuce pests and pathogens

^a (+) Potential risk

^b (++) Significant risk

^c (+++) Major risk

et al. (2006) noted a deleterious effect of such plowing on the abundance of arthropods, especially on spiders and hymenopteran parasitoids, under the Mediterranean climate. Although the effects of intensive tillage are well documented, the short-term consequences of reduced tillage on lettuce pests and yield are rarely addressed in the literature. Further studies are needed to determine the most favorable tillage protocols for balancing the trade-offs among pest control, yield, and other ecosystem services, such as nutrient cycling and soil restructuring by arthropods and earthworms.

Insect-proof nets Insect-proof nets may provide an effective protection against pests both in protected crops and in open fields (Weintraub and Berlinger 2004). This technique aims to prevent infestation by establishing a physical barrier between the invading pest and the crop. This barrier also

protects the plants from contamination by pest-transmitted viruses, such as those carried by aphids. Nevertheless, nets present the drawback of modifying the microclimate in the canopy (increased temperature and relative humidity) by limiting air flow.

Colored mulch material The behavior of some pests, such as winged aphids, is partially conditioned by visual stimuli. According to Döring et al. (2004), two visual impediments may affect host-plant infestation by aphids. First, the lower the contrast between the target and its background, the more difficulty aphids have to land on their target. Second, a background with high reflectance of short wavelength light disturbs host recognition. For example, when a trap used to simulate a green host plant was surrounded by a white or silver background, significantly fewer *M. persicae* were

caught than when the background was black or red or consisted of bare soil. In addition, Fricke and Piepenbrock (2005) observed a fivefold reduction in populations of winged aphids (species not specified) on lettuce when a silver mulch is used instead of a green one. Furthermore, Döring et al. (2004) argued that the structure of the background may also act as a barrier to infestation because aphids that land on a smooth structure like a leaf tend to probe and, if unsuccessful, quickly depart, whereas aphids that land on a rough structure, such as soil, move around the area before probing. In addition to limiting the growth of weeds and reducing evaporation, mulch can play a significant role in the control of pest populations. For this purpose, mulch color, structure, and contrast with the crop must all be considered. Fricke and Piepenbrock (2005) reported a trend for increased caterpillar populations (including *M. brassicae* and *A. gamma*) in broccoli fields with ultraviolet-reflecting mulches. Studies should be conducted to determine which mulch material best prevents pest infestations and to evaluate how mulching affects the plants, the pests, and the natural enemies of those pests.

Ultraviolet protection cover Light, particularly in the ultraviolet range with wavelengths from 280 to 400 nm, can affect organisms, trophic interactions, and thus agroecosystem functions (Paul and Gwynn-Jones 2003; Lagier 2005). It may play an important role in establishing relationships between plants and pathogens or pests (Raviv and Antignus 2004). Changes in the spectral characteristics of incident light, obtained for example by filtering out ultraviolet wavelengths, can alter several behavioral traits of pest insects, such as orientation and host or food finding (Díaz and Fereres 2007). Antignus et al. (1996) have shown that the absence of ultraviolet light can disrupt the navigation of some insects, such as thrips and whiteflies. Díaz et al. (2006) have demonstrated that the use of ultraviolet-absorbing films in lettuce fields can reduce the abundance of aphids (*M. euphorbiae*), thrips (*F. occidentalis*), and *A. gamma* larvae. Similarly, the modification of electromagnetic radiation within greenhouses may impact pathogen populations, although their responses are not necessarily consistent (Raviv and Antignus 2004). Nevertheless, ultraviolet-B generally tends to decrease the survival of spores of pathogenic fungi, whereas ultraviolet-A appears to enhance pathogen reproduction (Paul and Gwynn-Jones 2003). Regarding lettuce pathogens, ultraviolet-B (280–320 nm) decreases the viability of *B. lactucae* sporangia (Wu et al. 2000) and *S. sclerotiorum* ascospores (Caesar and Pearson 1983), while ultraviolet-A may increase the production of spores by *B. cinerea* (Nicot et al. 1996; Paul and Gwynn-Jones 2003). Changing the light spectrum, particularly in the ultraviolet-B range, also changes the defense-related metabolism of plants (Paul and Gwynn-Jones 2003); for example, an increase in ultraviolet-B may increase the production of phenolic acids

and flavonoids known to be involved in defenses against herbivores and pathogens. In addition, plants grown under ultraviolet-opaque films may have a modified morphology or taste (Paul et al. 2005), which could discourage the adoption of this technology by lettuce growers. The establishment of a zero-ultraviolet environment under shelter is possible because spectral conditions can be easily modified using screens that filter ultraviolet radiation. In fact, most currently used plastic films partially absorb ultraviolet radiation (Tsormpatidis et al. 2010), although the effect of ultraviolet-blocking materials on the various lettuce pathogens, pests, and beneficial organisms still remains to be investigated (Díaz and Fereres 2007). These issues must be addressed before considering the integration of this technique into pest and disease management strategies.

3.1.2 Eliminating persistent forms of pests and pathogens before lettuce planting

Rotation Plant species diversity within agroecosystems plays a major role in the management of crop pests and diseases (Ratnadass et al. 2012; Letourneau et al. 2011). Increasing diversity through crop rotation is one of the ways to reduce the detrimental effects of pests and diseases. Koike et al. (1997) investigated the potential of barley, fodder radish, and fava beans as winter crops to control *S. minor* and found that the planting of these crops, which are not *S. minor* hosts, helps to maintain a low incidence of disease in the next lettuce crop. Similarly, in a study conducted in California, Hao and Subbarao (2006) have shown that growing broccoli before lettuce could reduce not only the number of *S. minor* sclerotia in the soil but also the incidence of disease on the following lettuce crop. All these crops may be appropriate candidates for the diversification of rotations; however, their susceptibility to other lettuce pests should be considered (Koike et al. 1997).

Solarization Solarization is a passive physical technique used to reduce soil-borne populations of pathogens (or pests) before a crop cycle. The principle is to increase soil temperature to lethal levels by trapping solar radiation with a polyethylene film (Fig. 4). The film is laid on wet soil in open fields or under shelters and left on the soil surface for several weeks when the solar irradiance is maximal. Solarization induces changes in the physical, chemical, and biological properties of the soil (Stapleton 2000). The viability of *S. sclerotiorum*, *S. minor*, *R. solani* sclerotia and *O. brassicae* (the fungal vector of lettuce big-vein associated virus), root-knot nematode, and many weeds is strongly affected by the high temperature, high soil moisture, and low oxygen levels produced by solarization (Candido et al. 2008; Patrício et al. 2006; Pares and Bressoud 2010).



Fig. 4 Solarization performed under shelter to reduce soil inoculum

Nevertheless, a drawback of solarization is that the abundance of some beneficial organisms (e.g., arthropods) may also be decreased (Seman-Varner 2006). However, solarization-induced changes in the soil biota also promote heat-resistant or tolerant species and fast recolonizers, such as certain bacteria (*Bacillus* spp.), fungi (*Trichoderma* spp.), and free-living nematodes, that can enhance pest control services (Stapleton 2000). Solarization is well suited to the Mediterranean climatic conditions (Candido et al. 2008). It also fosters nutrient cycling because prolonged high temperatures promote nitrogen mineralization in the soil, which in turn can benefit the succeeding crop and even increase its yield (Hasing et al. 2004; Patricio et al. 2006).

Biofumigation Biofumigation is typically carried out by growing an intermediate crop, which is shredded and incorporated into the soil. Once in the soil, the plant residues degrade, releasing natural compounds which can kill plant pathogens or pests. For this purpose, the potential of crucifers (particularly species in the genus *Brassica*) has been extensively studied. They have proven useful against several of the main soil-borne pathogens of lettuce, such as *Sclerotinia* spp. and *R. solani* (Sarwar et al. 1998) and against root-knot nematodes (Zasada et al. 2010). Although certain

species of *Brassica* may be hosts of root-knot nematodes and *Sclerotinia* spp., the incorporation of their crop residues promotes the release of isothiocyanates, which have nematicidal and fungicidal effects, and can also show insecticidal, phytotoxic, and antibiotic properties. Several isothiocyanates can inhibit the growth of *S. sclerotiorum* mycelia and reduce sclerotial viability and germination. In field studies, seven isothiocyanates were shown to decrease the incidence of lettuce drop by 63 % to 83 % (Kurt et al. 2011). Biofumigation is effective only if the *Brassica* crop has high biomass and glucosinolate content. Optimal biofumigation also requires fast hydrolysis of the glucosinolates, which can be achieved with finely ground plant tissues, high temperature, and high soil moisture (Gimsing and Kirkegaard 2009). Thus, although farmers have begun to adopt the use of *Brassica* (especially *Brassica juncea*) residues as biofumigants, the effectiveness of this method is still variable.

Other plants in addition to *Brassica* species can be used as biofumigants, including those that contain cyanoglucosides that release hydrogen cyanide upon degradation, as cyanide has broad biocidal effects. Viaene and Abawi (1998) and Widmer and Abawi (2002) have shown that sudangrass (*Sorghum sudanense* cv. Trudan 8) used as a green manure before a lettuce crop slows the development of root-knot nematode eggs (*Meloidogyne hapla*) and reduces the number of galls on lettuce roots. However, these authors stressed that the decomposition of sudangrass could also have a phytotoxic effect on lettuce and thus eventually reduce yields.

Chemical fumigation Another method to eliminate soil-borne pathogens is chemical fumigation of the soil. Until its ban in 2010 in European Union, methyl bromide was the most-used chemical fumigant for the control of soil-borne fungi such as *R. solani* and *Sclerotinia* spp., plant parasitic nematodes, and *O. brassicae* (Duniway 2002). Currently, several chemical alternatives to methyl bromide are available; however, their efficacy may be lower and their spectrum of activity more limited. For example, 1,3-dichloropropene is highly effective against nematodes but exhibits variable efficacy against fungal pathogens (Qiao et al. 2010; Zasada et al. 2010). Furthermore, the protective effect of alternative fumigants may not carry over beyond the first crop. This was observed for example in a lettuce field experiment (Ceustermans et al. 2010). For these reasons, combinations of several soil disinfectants are commonly used.

3.2 Limitation of pest and pathogen development on plants

As mentioned earlier, to eliminate the sources of primary inoculum within and close to the crop, it is critical for the grower to purchase or produce healthy lettuce seedlings.

Currently, the protection of seedlings in nurseries is primarily achieved by pesticide applications. After securing the sanitary quality of seedlings, several techniques can be used during the culture to limit pest and pathogen developments.

3.2.1 Limitation mediated by the plant

Genetic resistance Genetic resistance through breeding programs is commonly exploited for pest and disease management because it is easy for growers to use and has little to no negative effect on the environment (Cuartero et al. 1999). For lettuce, resistance to pests and diseases is one of the major objectives of the breeding programs. Accordingly, breeding programs for resistance to downy mildew started in 1950 in England (Crute 1992b) and still continue worldwide. The first sources of resistance were found in old lettuce varieties (*L. sativa*), followed by *Lactuca serriola*, a related and compatible wild species, which has been extensively used (Crute 1992b). More recently, resistance genes from *Lactuca saligna* (Jeuken and Lindhout 2002) and *Lactuca virosa* (Maisonneuve 2003) have been studied, but their introgression in lettuce is more difficult (Maisonneuve 1987; Maisonneuve et al. 1995). The list of genetic resistance to disease in these species has been recently reviewed by Lebeda et al. (2009). Currently, breeding efforts focus primarily on resistance to downy mildew, with the identification and pyramiding of the major resistance genes involved in a specific gene-for-gene interaction. These programs are led by private companies. However, resistance breakdown caused by new virulent strains of *B. lactucae* is common and leads to a rapid turnover of lettuce varieties (Michelmore and Wong 2008). Resistance to the lettuce mosaic virus has also been introduced in European field cultivars from a Latin lettuce, Gallega de Invierno, and in American crisphead cultivars from the Egyptian wild lettuce *L. sativa* (Dinant and Lot 1992). Resistance to the leaf aphid, *N. ribisnigri*, due to the *Nr* gene identified in *L. virosa* (Eenink et al. 1982), has been introduced in many European varieties for summer field culture (Arend and Schijndel 1999). This resistance has recently been circumvented by a new biotype named *Nr: 1*, but searches to find *Nr: 1* resistance sources are progressing (Cid et al. 2012). Finally, in a few varieties, other resistance genes have been introduced to protect the plant against *P. bursarius* (Ellis et al. 1994) or against *Fusarium oxysporum* f. sp. *lactucae* (Scott et al. 2012) in exposed areas.

Many other examples of genetic resistance have been identified and studied in *Lactuca* spp. (Pink and Keane 1993) but have not yet been used in commercial varieties. This is the case for genetic resistance to *Sclerotinia* spp. Complete resistance has not been observed but some varieties of *L. sativa* exhibit different susceptibilities to the disease, suggesting the presence of partial resistance genes. The

lowest susceptibilities to the disease may be partially correlated with morphological features of the plant, such as early bolting or upright plant architecture, which confer an ability to avoid the pathogen. Nevertheless, the integration of these morphological characteristics into breeding programs is not desirable because these traits do not meet the needs of producers and consumers (Grube and Ryder 2004). Differences in susceptibility to *Sclerotinia* spp. have also been observed in lettuce varieties that display similar architectures (Grube and Aburomia 2004; Hayes et al. 2010). These observations support the involvement in plant defenses of partial resistance genes, which do not influence plant architecture and could be more easily integrated into breeding programs; however, to our knowledge, none of these genes have yet been identified. According to Whipps et al. (2002), a way to distinguish these two types of resistance expression is to perform screenings using two separate methods (by natural contamination vs. by inoculations). Natural contaminations can highlight partial resistance based on plant architecture, whereas inoculations can reveal partial resistance that arises from defenses within the plant tissues.

As mentioned above, pests and pathogens could overcome genetic resistance, especially those which involve one or a few genes. To enhance the sustainability of genetic resistance, several strategies were proposed: the identification and regular introduction of new resistance genes, the combination of a maximum number of resistance genes in one genotype, and the introduction of partial resistance (Dogimont et al. 2010; Pink 2002). These partial resistance genes could be more sustainable because they are less specific and exert less selection pressure on pest populations. In this regard, Hand et al. (2003) have detected several quantitative trait loci (QTL) of resistance to both *B. lactucae* and *M. persicae* in a population from a cross between two varieties of *L. sativa*. Then, by crossing *L. sativa* (susceptible) and *L. saligna* (non-host resistance), Zhang et al. (2009) were able to combine backcross inbred lines containing three QTL from *L. saligna* and demonstrate a complete resistance to the two strains of *B. lactucae* tested (Bl:14 and Bl:16). These authors have shown the potential of vertical resistance for the sustainable control of lettuce diseases and pests; however, the non-host nature of *L. saligna* resistance to *B. lactucae* has been challenged by Petrezlova et al. (2007).

Another way to sustain plant defenses is to combine several varieties with complementary resistances in the field to dilute pathogen pressures (Schaerer 2008; Maisonneuve et al. 2006). However, few studies have been conducted on lettuce crops, and the genetic resources of resistance are still poorly characterized, except for *B. lactucae*.

Resistance inducers The expression of plant resistance against diseases and pests may be constitutive or inducible.

Constitutive plant defenses are provided by both inherent physical barriers and antimicrobial metabolites. By contrast, induced resistance refers to a plant defense that must be initiated by a stimulus, which can be a direct interaction with a pest or the perception of a signal from chemical compounds or biological organisms. Induced resistance can be divided into two categories (Hammerschmidt 1999; Walters and Heil 2007): (1) systemic acquired resistance is generally effective against a broad spectrum of pathogens, requires a salicylic-acid signal, and involves the production of pathogenesis-related proteins, such as chitinases and glucanases; and (2) induced systemic resistance is initiated by interactions between plant roots and beneficial soil-born organisms, such as plant-growth-promoting rhizobacteria, and has a signal that is generally mediated by a jasmonate/ethylene pathway. Indeed, salicylic acid, jasmonic acid, and ethylene are the main phytohormones involved in the signaling pathways of the induced defenses, and crosstalk between these pathways is expected to allow plants to modify their defense responses (Pieterse et al. 2009).

The application on crops of compounds or organisms (named resistance inducers below) able to activate the inducible signaling pathways could strengthen plant defenses (Vallad and Goodman 2004; Walters et al. 2005, 2013). In the case of lettuce, several compounds, such as β -amino butyric acid or potassium phosphonate (K_2HPO_3), were identified as resistance inducers against *B. lactucae*. Both compounds cause a dose-dependent systemic resistance, which is completely efficacious in laboratory experiments up to 15 days following inoculation (Pajot et al. 2001). Under field conditions, β -amino butyric acid was also shown to effectively reduce *B. lactucae* infections on lettuce in a dose-dependent manner (Cohen et al. 2007). Beta-amino butyric acid, as a resistance inducer against *B. lactucae*, appears to act through a systemic acquired resistance pathway because the defense reaction is both local and systemic, not strain specific, and involves pathogenesis-related proteins. This defense inducer leads to a massive accumulation of callose between the mesophilic cells if mycelium is detected (Cohen et al. 2010, 2011). While the modes of action and resistance mechanisms of β -amino butyric acid have been clearly identified, those of potassium phosphonate are still unsolved. The phosphonate seems to act both through a direct fungitoxic effect by the release of phosphonate ions (HPO_3^-) known for their antimicrobial activities (inhibition of germination) and through the induction of systemic acquired resistance (Reuveni and Reuveni 1998). Other phosphate salts were found to be inducers of systemic acquired resistance in cucumbers, causing hypersensitivity reactions on the treated foliage and increased levels of free salicylic acid in the leaf tissues (Gottstein and Kuc 1989; Orober et al. 2002). Many other studies reviewed by Deliopoulos et al. (2010) have shown

the effect of phosphate salts on other plant defenses pathways against several fungal pathogens.

Fungi or bacteria can also induce resistance. An extensive description of the mechanisms underlying induced systemic resistance is beyond the scope of this review, and readers are invited to refer to an excellent recent review (Shoresh et al. 2010 and references therein). *Bacillus subtilis* and other *Bacillus* spp. are stimulators of induced systemic resistance, which enhances resistance against various pests. The production by *B. subtilis* of lipopeptides, including surfactin and fengycin, is at least partially responsible for inducing plant resistance against *B. cinerea* (Ongena et al. 2007). Similarly, *T. harzianum* T39 triggered an induced systemic resistance against *B. cinerea* in lettuce, pepper, tobacco, beans, and tomatoes by delaying or completely stopping the development of lesions (De Meyer et al. 1998). Furthermore, Yoge et al. (2010) demonstrated the induction of plant resistance—against *Fusarium oxysporum* and *Botrytis cinerea* in melon—by some composts. The mechanisms of resistance induction by composts remain unclear.

Induced resistance is expected to be difficult to overcome by pest and pathogen populations. Walters and Heil (2007) suggested that the selection pressures exerted on pest populations are minor because involved defense mechanisms are controlled by several genes and so appear difficult to overcome. In addition, the heterogeneity of responses to the induction of defenses allows the preservation of "refuges" (non-induced plants), limiting induced resistance breakdown. Recent laboratory experiments have also shown that different lettuce varieties vary in the intensity of their response to the same defense inducer (Maisonneuve et al. 2013). Finally, although induced resistance appears to have lower fitness costs than constitutively expressed resistance, several authors have demonstrated that induced systemic resistance and systemic acquired resistance also have costs for plants. Such costs may be linked to the production and transport of defense compounds or are ecological costs incurred when the induction of defenses disturbs the interaction between plants and their beneficial organisms (Heil and Baldwin 2002; Walters and Heil 2007). To avoid increasing fitness costs that could result in yield losses, the induction of defenses in the field by chemical compounds or biological organisms should be utilized according to incurred epidemic risks.

Fertilization Fertilization affects plant–pathogen as well as plant–pest interactions, but the mechanisms underlying the effects of fertilization on the susceptibility of plants to diseases and pests are still poorly understood. Fertilization is a determinant of the plant defense capabilities, which affect plant growth, resistance mechanisms, and pest population dynamics (Dordas 2008; Altieri and Nicholls 2003; Walters and Bingham 2007). For pests, Pakarinen et al. (1990) have

shown that the lettuce leaves most palatable for slugs (*Deroceras* sp.) were those that had the highest contents of nitrogen and phosphorus. There are currently no results on aphid behavior on lettuce; however, different levels of soluble nitrogen in the leaves of apple and peach have affected the reproduction rates of aphids (Rutz et al. 1990; Sauge et al. 2010). Sauge et al. (2010) have shown that the optimal nitrogen fertilization for *Myzus persicae* populations on peach had an intermediate value (6 mM of nitrate in the fertigation solution) and that low or high values diminished aphid population density. Regarding the effect of nitrogen fertilization on fungi and oomycetes, available studies report apparently inconsistent results which vary depending on the crop species, pathogen species and strain aggressiveness (Lecompte et al. 2010), the plant stages (Dordas 2008), and the input forms (Huber and Watson 1974). On lettuce specifically, Lecompte et al. (2013) have shown that damage on leaves inoculated with *B. cinerea* or *S. sclerotiorum* increased with the level of nitrogen fertilization applied. They suggested that, at least for *S. sclerotiorum*, the host susceptibility was linked to its sugar content, which varied depending on the nitrogen fertilization.

Actually, the balance among the different allocations of nitrogen in the plant could be responsible for the variable responses found among the above studies. Indeed, Walters and Bingham (2007) suggested that high plant nitrogen content promotes the development of pathogens by providing them more nutritional resources and that it can also affect the production rates of compounds involved in plant defenses. Despite some inconsistent reports, numerous authors agree that cultural practices related to plant nutrition (e.g., fertilization and irrigation) may significantly affect crop susceptibility and could be used to manage diseases and pests (Walters and Bingham 2007; Sauge et al. 2010). However, currently available data for lettuce are not sufficient and the opportunities of optimizing field fertilization to reduce pest damage remain to be investigated.

3.2.2 Limitation mediated by the abiotic environment

The germination of infectious forms (spores or sclerotia) of numerous pathogenic fungi depends on climatic factors such as humidity and temperature. Indeed, one of the most important factors for the germination of *B. lactucae* sporangia is the duration of leaf wetness (Scherin and Bruggen 1994). Three hours of leaf wetness are necessary for the sporangia to germinate and penetrate the host plant (Wu et al. 2002). When the air flow under a shelter is restricted, the duration of leaf wetness tends to increase and to promote the incidence of the disease (Boulard et al. 2004). The duration of leaf wetness is also an important factor for *B. cinerea* spore germination (Elad and Shtienberg 1995). Therefore, the

ventilation of greenhouses is a significant tool for the management of these diseases. Tools to forecast the epidemic risks of *B. lactucae* infection have been developed and are based mainly on climatic conditions (e.g., temperature, relative humidity, leaf wetness duration, and solar radiation) (Kushalappa 2001; Wu et al. 2002). These models predict the optimal timing of phytosanitary treatments and could reduce their numbers compared with a calendar-based treatment strategy (Hovius et al. 2007); however, the models are not now commonly used.

Irrigation is a cultural practice that also affects the microclimate (Scherin and Bruggen 1995). Irrigation applied directly at the soil level (furrow or drip irrigations) instead of above the canopy (sprinkler irrigation) reduces leaf wetness and thereby moderates the incidence of downy mildew caused by *B. lactucae*. In addition, Scherin and Bruggen (1995) revealed that climatic conditions created by a drip irrigation system are less favorable to the development of *B. lactucae* than are those established following furrow irrigation. Accordingly, studies conducted by Wu and Subbarao (2003, 2006) showed that drip irrigation (subsurface and surface drip) can reduce by 50 % the incidence of lettuce drop caused by *Sclerotinia* spp. compared with conventional irrigation (sprinkler or furrow). The reduced moisture at the soil surface and the increased soil temperature under subsurface drip irrigation could reduce the germination of sclerotia (Wu and Subbarao 2003).

As already demonstrated for *S. minor* on peanut crops (Dow et al. 1988; Maas et al. 2006), plant spacing and particular architectural features of the crop (e.g., upright lettuce vs. plants with flat bases) could influence the impact of soil-borne diseases by modifying the microclimate under the canopy. Eventually, the management of the macroclimate (under shelter) or the microclimate (under the canopy) may become an important method to prevent disease development.

3.2.3 Removal of pests and pathogens

Biological control Biological control is based on biotic interactions between pests or pathogens and their antagonists. Biological control agents may be predators, parasites, or competitors (Table 2). Several biological control techniques could be used to manage populations of lettuce pests and pathogens. The endemic populations of biological control agents could be promoted by habitat manipulation. The biological control agents could also be introduced preventively or curatively.

Conservation biological control The principle is to provide suitable resources and habitats for the timely establishment and development of endemic biological control agent populations (Landis et al. 2000). Plant diversity can play a major role in attaining these goals (Ratnadass et al. 2012). Habitat

Table 2 Main biological control agents of lettuce pests

Application type	Biological control agents	Target	Action	Requirements	References
Soil application	<i>Coniothyrium minitans</i>	<i>Sclerotinia sclerotiorum</i> , <i>Sclerotinia minor</i> , <i>Rhizoctonia solani</i> , <i>Botrytis cinerea</i> propagules	Sclerotia parasitism, reduction of disease incidence at the following lettuce crop	Optimum temperature for parasitism 15–25 °C. Latent period of 8 weeks between inoculation and lettuce planting. Need for direct contact with the sclerotia	(Van Beneden et al. 2010; Jones and Whipps 2002; Chitrampalam et al. 2008, 2010; Yang et al. 2010)
	<i>Trichoderma harzianum</i> T22	<i>Pythium</i> spp., <i>S. sclerotiorum</i> , <i>S. minor</i> , <i>R. solani</i> , <i>B. cinerea</i> propagules	Mycoparasitism, induced systemic resistance, competition	Optimum temperature 25–30 °C. The lowest temperature for <i>Trichoderma</i> sp. activity is 8 °C	(Ozbay and Newman 2004; Paulitz and Belanger 2001; Klein and Eveleigh 1998)
Foliar application	<i>Trichoderma harzianum</i> T39	<i>B. cinerea</i>	Competition, lytic enzyme production, induced systemic resistance	Optimum temperature 25–30 °C. The lowest temperature for <i>Trichoderma</i> sp. activity is 8 °C	(De Meyer et al. 1998; Paulitz and Belanger 2001; Klein and Eveleigh 1998)
	<i>Bacillus subtilis</i>	<i>B. cinerea</i> , <i>S. sclerotiorum</i> , <i>R. solani</i>	Production of antifungal metabolites, antagonism, induced systemic resistance	No irrigation on foliage because the bacterium is washable	(Fiddaman et al. 2000; Zhang and Xue 2010)
	<i>Bacillus thuringiensis</i>	<i>Helicoverpa armigera</i>	Bioinsecticide (insecticidal crystal protein)	No irrigation on foliage because the bacterium is washable. Toxins must remain on the plant to be ingested by phytophagous organisms	(Lacey et al. 2001)
	Steinernematidae/ Heterothabditidae	<i>H. armigera</i>	Entomopathogenic nematode associated with symbiotic bacteria	Conditions that promote the survival and mobility of nematodes (high humidity, low radiation, low air flow). Applications are more appropriate under tunnel than in open field	(Arthurs et al. 2004)
Introduction on banker plants or mass release	<i>Aphidius ervi</i>	<i>Myzus persicae</i> , <i>Macrosiphum euphorbiae</i> , <i>Aulacorthum solani</i>	Parasitoid	The lower temperature threshold for development is 6.6 °C (mummy to adult development). Complete development in 73 days	(Nebreda et al. 2005; Kavallieratos et al. 2004; Sigsgaard 2000)
	<i>Aphidius matricariae</i>	<i>M. persicae</i>	Parasitoid	The lower development threshold is 3.51 °C. The rate of parasitism increases with the temperature up to 25 °C	(Nebreda et al. 2005; Kavallieratos et al. 2004; Zamani et al. 2007)
	<i>Praon volucre</i>	<i>M. persicae</i> , <i>M. euphorbiae</i>	Parasitoid	The lower temperature threshold for development is 5.5 °C (mummy adult development). Complete development in 70 days	(Nebreda et al. 2005; Kavallieratos et al. 2004; Sigsgaard 2000)
	<i>Aphidius colemani</i>	<i>M. persicae</i> , <i>Nasonovia ribisnigri</i>	Parasitoid	The lower development threshold is 2.65 °C. The rate of parasitism increases with the temperature up to 25 °C	(Nebreda et al. 2005; Kavallieratos et al. 2004; Zamani et al. 2007)
	<i>Aphidius hieractorum</i>	<i>N. ribisnigri</i>	Parasitoid	Not specified	(Nebreda et al. 2005; Kavallieratos et al. 2004)
Mass release	<i>Chrysoperla carnea</i>	<i>M. persicae</i> , <i>H. armigera</i>	Polyphagous predator (larva)	The lower development threshold is 10 °C	(Honek and Kocourek 1988; Liu and Chen 2001; King and Coleman 1989; Reddy and Manjunatha 2000)
	<i>Episyrphus balteatus</i>	<i>N. ribisnigri</i>	Polyphagous predator	The lower development threshold is 7.1 °C	(Hart et al. 1997; Honek and Kocourek 1988; Hopper et al. 2011)

The lower development threshold may vary among aphid hosts, but is most likely close to the value estimated for *M. persicae*

manipulation tactics have to consider the foraging behavior of the natural enemies. Laboratory and field studies have shown that sugar and pollen improve the fecundity of aphid parasitoids and that aphid parasitism decreases when the distance to resources increases (Tylianakis et al. 2004). Thus, pollen- or nectar-rich flowering plants are often used. The morphology of flowers is also a criterion for the selection of plants because the natural enemies of pests require easy resource access (Landis et al. 2000). In addition to resource provision for the enemies of pests, the introduction of different plant species in the vicinity of a field can also serve as refuges for those natural enemies to take shelter during adverse conditions (e.g., high or low temperature or pesticide applications). However, this plant diversity can sometimes be detrimental by supporting pest populations (Landis et al. 2000); it should accommodate the needs of the natural enemies of the key pests and avoid attracting other crop pests.

Concerning lettuce crops, the introduction of plants which provide resource subsidies to pest predators and parasitoids are the most studied strategies for habitat manipulation (Sengonca et al. 2002; Pascual-Villalobos et al. 2006; Masetti et al. 2010). Pascual-Villalobos et al. (2006) found that planting strips of *Corandium sativum* and *Chrysanthemum coronarium* within a lettuce crop tended to promote syrphid populations, but the results were not statistically significant. However, they also observed that predators appeared only after the establishment of aphids. Similarly, Sengonca et al. (2002) showed an increase in populations of adults and predatory larva of four polyphagous predators, including *Chrysoperla carnea*, when weeds (*Artemisia vulgaris*, *Tanacetum vulgare*, or *Urtica dioica*) were planted within and near the lettuce crops. In the same way, Géneau et al. (2012) demonstrated that two parasitoid wasps of *Mamestra brassicae*, *Microplitis mediator* and *Diadegma fenestratale*, can be enhanced by the presence of nectar-producing species such as *Fagopyrum esculentum*, *Centaurea cyanus*, and *Vicia sativa*. The authors also showed that these plants do not improve the fitness of *M. brassicae*.

Further studies are needed to determine which plant species can be introduced safely to support endemic biological control agents.

Preventive introduction of natural enemies The introduction of banker plants into a crop is a preventive and long-term means of pest biological control. This technique has been studied for aphid control. Banker plants belong to a species which is different from the crop and they are infested with aphid species that do not use the crop as their host but are parasitized by natural enemies that also target those aphids that harm the crop. Thus, parasitoids that develop on the banker plant are present in the field when the crop pests arrive (Frank 2010). As an example, the complex formed

by the aphid *Rhopalosiphum padi* (L.), a specific pest of Poaceae, and the host parasitoids *Aphidius colemani* and *Aphidius ervi* can be used against aphid populations that thrive in lettuce crops because *A. colemani* and *A. ervi* are also parasitoids of the main lettuce aphids (*N. ribisnigri*, *M. persicae*, *M. euphorbiae*, and *A. solani*). In this case, the banker plant should be a Poaceae adapted to the climatic conditions of the season; barley, wheat, and oats are the most commonly used (Frank 2010). The effectiveness of this technique depends on the rate at which the parasitoids are released onto the crop, which depends on the density of the banker plants and on the climatic conditions that influence the development of the parasitoid (Frank 2010).

Biological control agents can also be introduced into the soil to manage soil-borne pathogens. *Coniothyrium minitans* is currently used in lettuce cropping systems to reduce *Sclerotinia* spp., *B. cinerea*, and *R. solani* propagules (Chitrampalam et al. 2008). This fungus preferentially parasitizes overwintering structures by synthesizing chitinases, glucanases, and antifungal metabolites (Zeng et al. 2012). *Trichoderma harzianum* is also known to disturb populations of *B. cinerea*, *Pythium* spp., *R. solani*, and *Sclerotinia* spp. in soil, acting either as a competitor or as a parasite (Ozbay and Newman 2004). However, the effects of biological control agents on non-target organisms need to be further explored; for example, it has been suggested that *T. harzianum* can parasitize species of the arbuscular mycorrhizal fungus (*Glomus* spp.) (Brimmer and Boland 2003).

Another way to introduce antagonistic organisms is to amend the soil with compost. The suppressive effect of soil-borne diseases by some composts is attributed to several mechanisms involving microbial communities, including competition, parasitism, and antibiosis (Hadar and Papadopoulou 2012). Although many studies have reported a suppressive effect of these composts on several diseases caused by soil pathogens such as *R. solani*, *Sclerotinia* spp., *Verticillium dahliae*, *Pythium* spp., and *Fusarium* spp., composts are currently poorly used (Pane et al. 2013; Bonanomi et al. 2007). This may be due to the varying efficacies of composts which are linked to their biotic and abiotic components.

Curative biological control Lettuce pests can also be controlled with the mass release of beneficial organisms in the field, as a curative technique. Many species are known predators or parasitoids of lettuce aphids (Table 2). The larva of the generalist predator *Chrysoperla carnea* can ingest up to 270 *Myzus persicae* aphids per day (Liu and Chen 2001). Aphidophagous syrphids are other generalist predators that could participate in the management of the lettuce aphid. However, because only the larval stages are predators of aphids, additional food sources appropriate for the other life

stages are necessary to support population development. The presence of preys at the time of the mass release is critical.

Pesticide applications Insecticides and fungicides are the main pesticides commonly used on lettuce crops, weeds being managed mostly mechanically (e.g., through mulches). The active substances belong to different chemical families and can have contact or systemic actions. Their use can lead to the presence of pesticide residues on lettuce leaves (Gonzalez-Rodriguez et al. 2008); therefore, the shortest interval allowed between application and harvest is defined for each active ingredient. The main fungicides commonly applied to lettuce crops to manage the oomycetes *B. lactucae* or *Pythium* spp. belong to the dithiocarbamate and strobilurin families. The dithiocarbamates (e.g., mancozeb and methiram) have three complementary modes of action: inhibition of glucose oxidation, nucleic acid synthesis, and fatty acid degradation. The strobilurins (e.g., azoxystrobin) affect fungi through the inhibition of mitochondrial respiration. One strobilurin (pyraclostrobin) and chemicals of the dicarboximide, phenylpyrrole, and anilinopyrimidine families are used to manage *Sclerotinia* spp. and *B. cinerea*. The dicarboximides (e.g., iprodione) affect the osmotic regulation of fungal tissues. The anilinopyrimidines (e.g., cyprodinil and pyrimethanil) inhibit the synthesis of amino acids. Fungicide resistance is a widespread phenomenon in lettuce fields. Resistance to organophosphates and phenylamides has also been identified in *B. lactucae* strains in California, in Italy, and in France (Brown et al. 2004; Cobelli et al. 1998; Leroux et al. 1988). The resistance of *B. cinerea* is the most widely studied, and many *B. cinerea* strains are resistant to dicarboximides (Leroux et al. 2002; Wang et al. 1986). Similarly, the anilinopyrimidines have proven ineffective for the control of three *B. cinerea* phenotypes sampled in French vineyards: Ani R1, Ani R2, and Ani R3 (Leroux et al. 2002). Isolates of *S. minor* resistant to iprodione (dicarboximide family) have also been reported in Roussillon in southern France (Davet and Martin 1993).

Insecticides, such as the carbamates, pyrethroids, and neonicotinoids, act on different targets in the nervous systems of pests. Several manifestations of resistance to these insecticides have been identified within aphid and moth populations. Four strains of *Helicoverpa armigera* among 111 sampled in Spain were highly resistant to pyrethroids (deltamethrin and lambda cyhalothrin), and 21 other strains proved to be moderately resistant (Torres-Vila et al. 2002). Many studies on the lettuce-specific aphid *N. ribisnigri* have reported its resistance to carbamates (Kift et al. 2004; Rufingier et al. 1999; Workman et al. 2004), organophosphates (Workman et al. 2004), and pyrethroids (Kift et al. 2004). However, these results are dependent on sampling location because Cuthbertson et al. (2007) found no *N.*

ribisnigri resistance to pirimicarb (a carbamate) in New Zealand. The neonicotinoids are one of the newest marketed families of insecticides acting on the acetylcholine receptors of pests. Currently, the incidence of pesticide resistance is limited and localized (Jeschke and Nauen 2008; Nauen and Denholm 2005).

Whether in the case of the fungal pathogens or the insect pests of lettuce, the development of pesticide resistance has resulted from a selection of strains suited to pesticide-intensive management. This resistance can be related to various pest adaptations, such as behavioral or physiological adaptations that reduce exposure to the pesticide or limit its penetration, an increased capacity to detoxify pesticides or a conformational modification of the pesticide receptor site (Blümel et al. 2002; Leroux et al. 2002). Cultural practices can accelerate or delay the appearance of pesticide resistance. This resistance can be managed by (1) moderating the number of applications and doses of pesticides, (2) applying a mixture of substances with diverse actions, or (3) alternating pesticide applications among chemical families (Savary et al. 2006).

4 Toward innovative pest and disease management strategies that address environmental issues as well as economic and social expectations

4.1 One example of typical lettuce cropping systems: the production in the Mediterranean region

In the Mediterranean region, lettuces are cultivated all year round under shelter from September to April and in open fields from March to November. Water is supplied mainly by sprinklers, but in some cases by drip irrigation. Fertilization is brought before planting, with a mixture of NPK fertilizers, to achieve a soil N content before plantation of about 100–150 kg ha⁻¹. Lettuces are planted mostly on plastic mulches, especially under shelter, which limits weed development. Crop density is usually between 12 and 16 plants per square meter, depending on lettuce type and commercial destination. Cultivar choices are focused on agronomic criteria, but a few growers also choose cultivars with complete resistance to *B. lactucae* (Bl:1 to Bl:28). Resistance to *N. ribisnigri* (Nr:0) may also be a selection criterion in the case of open field crops. A few alternative techniques have been adopted recently by farmers. Solarization is generalizing, whereas bio-control and biofumigation techniques are sometimes used. A recent survey in French lettuce fields showed that, on average, eight pesticides are applied preventively during the 60–90-day-long crop cycle. In winter, these are mainly fungicides, whereas in summer, insecticides are predominant. Beyond the case of lettuce production in the Mediterranean basin, in conventional lettuce cropping systems worldwide,

pest and pathogen management is mainly achieved by preventive applications of pesticides. This crop-protection strategy provides acceptable economic performance but is not sustainable because it selects for pesticide resistance and endangers both the environment and human health.

4.2 No “silver bullet” but a combination of techniques

Scientists now agree that agronomic practices should be more strongly founded on biological processes occurring naturally within agroecosystems (Altieri 1989; Dore et al. 2011) to enhance ecosystem services, including pest and pathogen regulation. Considering the complexity of agroecosystems, there is no “silver bullet”, that is, a single and sustainable method for managing pests and diseases. As mentioned above, a significant number of alternative techniques are currently available for the management of lettuce pests and diseases; however, no single technique can provide an effective and sustainable management solution. Instead, these techniques operate at different stages of the pest cycle (invasion, development, and multiplication) and can be used in a complementary way. While many of these techniques are well defined, others require more investigation (Table 3). The design of crop-protection strategies less dependent on pesticides should therefore be based on the joint implementation of a consistent set of alternative techniques, each with partial effects on diseases and pests. These new protections for cropping systems could take the form of a set of decision rules that would allow customization of the practices to fit the local environment and constraints of each farm (Debaeke et al. 2009).

For some lettuce pathogens and pests such as moths, there are few current alternatives to pesticides, providing little leeway to reduce pesticide use; for other pathogens and pests, many alternative techniques are available. For example, the management of *Sclerotinia* spp. as well as many other soil-borne diseases in lettuce crops is currently based on preventive chemical control (two to three fungicide applications during the growing season) and sometimes on solarization techniques, but biological control agents, crop rotations, stimulation of plant defenses by induction or fertilization, biofumigation, and climatic management achieved by irrigation type and varietal choices could also be

implemented. In addition, these techniques have complementary modes of action; that is, solarization and crop rotation affect the survival of persistent pathogen forms, whereas the plant architecture and irrigation type affect pathogen development. Under these conditions, it appears feasible to significantly reduce fungicide applications against *Sclerotinia* spp. or to at least switch from a preventive to a curative use of the chemicals. The major efforts to reduce pesticide use in innovative cropping systems may initially focus on those pests and pathogens for which several alternative and complementary techniques are available.

4.3 Considering the ecological interaction within the agroecosystem

A required first step in the design of coherent combinations of techniques to manage diseases and pests is to consider all pests and pathogens that can threaten the crop and their corresponding life cycles. Many positive or negative direct interactions within this community, such as competition, facilitation, synergism, or antagonism, can affect its functioning and effects (Finney 1983). The most conspicuous illustration of these interactions is most likely the dependence of viruses on their vectors (e.g., aphids and thrips) to infect a plant. Such interactions are important because they can affect the success and ancillary effects of a pathogen or pest management technique. A secondary pest competing with a main one can replace it after the latter is eliminated by efficient control measures. Moreover, trophic interactions, which can be quite complicated and include intraguild predation (Polis et al. 1989) or apparent competition (Holt 1977), should be considered because of their key role in pest regulation (Matson et al. 1997; Van der Putten et al. 2001).

4.4 Prioritization of control methods

4.4.1 Based on compatibility and complementarity among techniques

Compatibility among techniques is decisive for the success of disease and pest management strategies. Currently, the most studied example is the compatibility between chemical

Table 3 Techniques for the implementation of pest and disease management programs in lettuce cropping systems by available techniques and those requiring further investigation before implementation

Type of control actions	Techniques available for implementation	Techniques requiring further investigation
Restricting the invasion of pests and pathogens	Solarization, introduction of biological control agents, insect proof nets, diversification of rotation, chemical fumigation	Biofumigation, ultraviolet protection cover, mulch, conservation biological control
Limiting pest and pathogen development and multiplication on plants	Release of natural enemies (preventives and therapeutics), abiotic condition improvement, genetic resistances (gene for gene), pesticide applications	Partial genetic resistances, resistance inducers, optimization of fertilization

and biological control. To introduce or promote auxiliary populations for pest management, it is necessary to assess non-target effects of pesticides on those populations (Blümel et al. 2002). Badawy and El-Arnaouty (1999) revealed that some organophosphorus and carbamate insecticides had, respectively, a high and moderate effect on the survival of eggs and larvae of *Chrysoperla carnea*. Insecticides may have not only direct toxic effects on the natural enemies of pests but also indirect non-target effects due to consumption of poisoned prey by predators (Walker et al. 2007; Badawy and El-Arnaouty 1999). Although the selectivity of active substances is increasingly considered for pesticide registration (Palumbo and Castle 2009), reports of non-target effects are common. To be relevant, the evaluation of side effects should be performed in conditions close to those of the field. The effects on *Coniothyrium minitans* of all the pesticides applied in lettuce crops in the UK have been investigated in this manner (Budge and Whipps 2001). Iprodione strongly affected the germination and mycelial growth of *C. minitans* in an agar plate test but not when the experiment was performed in a soil tray. Additionally, the joint application of a reduced rate of iprodione and a biological control agent (*C. minitans*) in a field study resulted in efficient control of *S. sclerotiorum*. Henderson et al. (2009) have shown that chemical compounds released by biofumigation with mustard can also affect the efficacy of biological control of plant parasitic nematodes by entomopathogenic nematodes such as *Steinernema felsiae*.

There is sometimes a conflict among biological control agents. Hindayana et al. (2001) highlighted the intraguild predation among aphidophagous predators, including *C. carnea* and *Episyrphus balteatus*. *C. carnea* could be a predator for *E. balteatus* and vice versa depending on their developmental stages. This interaction was exacerbated by the lack of more appropriate prey (aphids). Such results have to be considered for the implementation of efficient biological control.

Beyond compatibility, the design of innovative cropping systems aims to combine techniques that have complementary effects on diseases and pest. Such complementarity results in increased control of pests and diseases through the additional effects of the partial efficacies of each technique, and it is based both on the compatibility among techniques and complementarities of their modes of action. The techniques can be used separately at different times in the life cycle of the target pest and pathogen or simultaneously. Spadaro and Gullino (2005) have reviewed possible complementary techniques to be used in combination with biological control agents against soil-borne pathogens. These techniques include, for example, the use of other biological control agents, reduced applications of pesticides, or soil disinfection methods. According to Melo et al. (2011), an approach for improving the efficiency of *C. minitans* is the

development of mutants with greater capacities for parasitism, growth, and resistance to fungicides. In this case, biological control is associated with genetic modifications. In another approach, Van Beneden et al. (2010) have demonstrated the possibility of increasing *C. minitans* parasitism of sclerotia (*S. sclerotiorum*) by the incorporation into the soil of Kraft pine lignin, which is believed to promote the development of decomposers of the sclerotial walls. Currently, solarization is most likely the technique most commonly combined with others for the management of soil pests. To improve its effects on soil-borne pests and pathogens, solarization may be associated with the application of bio-control agents, chemical pesticides, or organic amendments with disinfectant properties (Gil et al. 2009; Stapleton and Devay 1983).

The complementarity of pest management techniques has also been investigated for the control of lettuce aphids. Fagan et al. (2010) assessed the combined effect of chemical control, which consisted in drenching seedlings with a systemic insecticide (imidacloprid), and biological control with natural predators of aphids (*N. ribisnigri*). They observed complete control of aphid populations in the mid-summer period. Similarly, Parker et al. (2002) have investigated the efficacy of integrated pest management programs against lettuce aphids and showed that varietal resistance, the introduction of entomopathogenic fungi, and seedling drenches with insecticide help reduce the number of foliar applications of fungicides during the crop cycle.

4.4.2 Based on their impact on agroecosystem services

In addition to the ecosystem service of pest and pathogen regulation, the productivity and sustainability of agroecosystems are based on their ability to provide other ecological services such as nutrient cycling or pollination. Consequently, external inputs and other compensatory practices that disturb the ecosystem should be overcome. Ecosystem services rely on beneficial organisms in the agroecosystem; therefore, the alternative techniques used to control pests and diseases should promote ecosystem biodiversity to enhance associated services. For example, to increase soil fertility in agroecosystems, the alternative techniques for managing pests and diseases should favor organisms that support nutrient cycling (e.g., organic matter decomposers and nitrogen-fixing bacteria). The techniques that could negatively affect these beneficial organisms and thereby reduce ecosystem services should be used only when less disruptive alternatives are unavailable (Lewis et al. 1997).

The consideration of ecological interactions within the agroecosystem, the compatibility among management techniques, and the selection of techniques with low impact on agroecosystem services appear to be key factors for achieving efficiency and sustainability of cropping systems. The

performances of such innovative cropping systems need to be assessed.

4.5 Performance assessments

Cropping system assessment is critical to ascertain whether environmental, economic, and social expectations are attained. Performance assessments of innovative cropping systems are conditioned by the definition of goals. For each goal, one or more performance indicators can be employed. Thus, indicators such as the amount of active ingredient applied per hectare, the treatment frequency index, or the environmental impact quotient (Kovach et al. 1992) may be used to assess the ability of the system to reduce pesticide applications. Agri-environmental indicators (e.g., biodiversity, soil properties, and water quality) can be used to estimate the effect of the joint implementation of agricultural practices on the biotic and abiotic components of the agroecosystem and consequently on the ecosystem services (Dale and Polasky 2007; Bockstaller et al. 1997). Others such as gross margin and yield are indicators of economic performance and can help determine whether a reduced reliance on phytosanitary products affects farm profitability. Finally, working time, the total number of operations, and the operation costs are indicators of social performance (Lancon et al. 2007).

The agroecosystem performances can be assessed one by one or with a multiobjective approach of agricultural sustainability, which can be translated into environmental, economic, and social goals (Hansen 1996; Lichtfouse et al. 2009). These objectives can sometimes be antagonistic. Therefore, multicriteria evaluations are helpful to design and assess innovative cropping systems (Ould-Sidi and Lescourret 2011). Multicriteria assessment tools have been designed for various crops to estimate qualitatively and ex ante (i.e., before system implementation) the sustainability of cropping system prototypes (Pelzer et al. 2012; Sadok et al. 2009). However, these tools have not yet been adapted for the assessment of lettuce cropping systems.

5 Conclusion

For decades, major advances have been made in the development of alternatives to pesticide application for the protection of lettuce crops. They include the manipulation of the biotic (e.g., diversification of rotations and the introduction of plant diversity) and abiotic environment (e.g., insect-proof nets and ultraviolet protection covers), methods to increase plant defenses (e.g., genetic resistance, inducers, and defenses), and biocide effects on pathogens and pests (e.g., solarization and the introduction of biological control agents). However, as for other crops, there is no "silver bullet" to manage sustainably the populations of lettuce pests and

pathogens, and consequently, the use of multiple alternative techniques with partial and complementary effects seems to be the best option to reduce phytosanitary inputs. In the current state of knowledge, the design of innovative cropping systems, adapted to the epidemic risks, appears feasible and should help to reduce the use of phytosanitary products. In the Mediterranean region, the main sources of epidemic risk for lettuce crops in winter are fungal diseases (see Table 1). In this case, solarization or introduction of biological control agents may be considered to reduce the soil primary inoculum. Then, the use of genetic resistance, the implementation of a drip irrigation, and the reduction of nitrogen input can create an unfavorable environment for pathogen development. The risk of infestation by aphids could be managed through the preventive introduction of biological control agents. In contrast, the implementation of insect-proof nets is not recommended since it may increase the humidity inside the greenhouse, which is generally favorable to pathogens.

This review provides a reflective tool for the design of such disease and pest management strategies. The approach proposed for managing pests and pathogens of lettuce goes beyond the integrated pest management approach because it advocates a prioritization of practices based on their effects on ecosystem services. As previously suggested by Lewis et al. (1997), techniques with biocide effects that disrupt the agroecosystem should be used as a last resort to promote the natural regulation of pest and pathogen populations, mediated by multitrophic interactions.

Furthermore, the absence of performance data for the joint use of alternative techniques is a severe hindrance to the adoption by growers of novel control strategies associating complementary techniques. So, studies should next focus on the implementation and assessment of cropping system prototypes that are based on available knowledge and designed according to the approach proposed above. Future research should also address the knowledge gaps identified in this review.

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