

# Wild *Lactuca* species, their genetic diversity, resistance to diseases and pests, and exploitation in lettuce breeding

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**Abstract** Current knowledge of wild *Lactuca* L. species, their taxonomy, biogeography, gene-pools, germplasm collection quality and quantity, and accession availability is reviewed in this paper. Genetic diversity of *Lactuca* spp. is characterized at the level of phenotypic and phenological variation, variation in karyology and DNA content, biochemical traits, and protein and molecular polymorphism. The reported variation in reaction to pathogens and pests of wild *Lactuca* spp. is summarized, including the viral pathogens (Lettuce mosaic virus-*LMV*, Mirafiori lettuce virus/Lettuce big vein virus-*LBV*, Beet western yellows virus-*BWYV*, Tomato spotted wilt virus-*TSWV*, Cucumber mosaic virus-*CMV*, Lettuce necrotic stunt virus-*LNSV*), bacterial pathogens (corky root-*Rhizomonas suberifaciens*, bacterial leaf spot-*Xanthomonas campestris* pv. *vitians*), fungal pathogens (downy mildew-*Bremia lactucae*, powdery mildew-*Golovinomyces cichoracearum*, anthracnose-*Microdochium panattoniana*, stemphylium leaf spot-*Stemphylium* spp., sclerotinia drop-*Sclerotinia* spp., verticillium wilt-*Verticillium dahliae*, fusarium wilt-*Fusarium* spp., pythium wilt-*Pythium tracheiphylum*, *P. uncinatum*), nematodes (potato cyst nematode-

*Globodera rostochiensis*, root-knot nematode-*Meloidogyne* spp., *incognita*, *hapla*, *javanica*, *enterolobii*), insects and mites (the green lettuce aphid-*Nasonovia ribisnigri*, the green peach aphid-*Myzus persicae*, the potato aphid-*Macrosiphum euphorbiae*, leafminer-*Liriomyza* spp., *L. langei*). The approaches used to exploit wild *Lactuca* spp. in lettuce breeding (interspecific hybridization, cell and tissue culture, transformation) are discussed, and known examples of lettuce cultivars with traits derived from wild *Lactuca* spp. are described.

**Keywords** Taxonomy · Biodiversity · Gene-pools · Gene banks · Disease resistance · Molecular polymorphism · *L. serriola* · *L. saligna* · *L. virosa* · Pest resistance · Breeding strategies · Transfer of resistance · Wild lettuce · Germplasm

## Introduction

The potential of wild *Lactuca* species to be used in lettuce breeding is being demonstrated by means of classical biology and modern approaches and the study of their diversity has been a subject of theoretical research and practical application during the last 25 years (Ryder 1999; Lebeda et al. 2007c; Mou 2008). The currently available knowledge of wild *Lactuca* species as donors (sources) of traits important in lettuce breeding was thoroughly analyzed in our previous paper focused on wild *Lactuca* germplasm (Lebeda et al. 2009a, b). The main aim of this paper is to critically summarize the available information

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about interactions between wild *Lactuca* species and the most important lettuce pathogens and pests from the viewpoint of their resistance and their potential exploitation and utilization in lettuce breeding.

### Taxonomy of *Lactuca* spp.

The genus *Lactuca* L. (family Compositae/Asteraceae) is composed of one cultivated species-lettuce (*Lactuca sativa* L.), and about 100 wild *Lactuca* spp. of which nearly 95 % are autochthonous in Asia and Africa (Lebeda et al. 2007c). Species are arranged into seven sections and two geographic groups (Table 1). This broader generic concept summarized by Lebeda et al. (2007c) should be critically re-considered with regard to the molecular data on phylogenetic relationships among *Lactuca* species (Koopman et al. 1998, 2001).

### Eco-geographic characteristics

The genus *Lactuca* L. comprises annual, biennial or perennial herbs and rarely shrubs with various ecological requirements. The species *L. serriola*, *L. saligna* and *L. virosa* are weedy and occur on waste places and ruderal habitats, along roads, highways and ditches, *L. perennis*, *L. viminea*, *L. graeca*, *L. tenerrima* are calciphilous plants and colonise limestone and dolomite areas, mostly rocky slopes. Endemic lianallike species are found in rain forests of East Africa (Lebeda et al. 2001, 2004b, 2007c).

The greatest diversity of *Lactuca* species is confined to the Mediterranean basin and Southwest Asia (Doležalová et al. 2001; Beharav et al. 2008; Kitner et al. 2008; Lebeda et al. 2001, 2009a, b). The occurrence of valuable germplasm is expected in the Central and South Africa, Southwest and Central Asia, and North America regions (Lebeda et al. 2007c, 2011, 2012a).

### *Lactuca* germplasms and their availability

The concept of conservation and management of wild crop relatives, and conservation priorities were proposed by Maxted et al. (2008) and Ford-Lloyd et al. (2008). The linking of in-situ and ex-situ conservation with the use of wild crop relatives is the leading principle of their conservation and management (Maxted and Kell 2008). Access to wild genetic resources and the possibility to explore and exploit them depend upon the successful and reasonable protection of wild species *in-situ*, i.e. in their natural habitats (Iriando and De Hond 2008), upon the complex study of wild species in natural habitats and upon the possibility to exchange information and biological material (Azzu and Collette 2008). These research activities are regulated by national policies and the international conventions and protocols, e.g. the recent “Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization to the Convention on Biological Diversity” adopted by the Conference of the Parties to the Convention on Biological Diversity at its tenth meeting on

**Table 1** Taxonomy of the genus *Lactuca* L. (modified according Lebeda et al. 2007c)

Section	Subsection	Species	Biology
<i>Lactuca</i> L.	<i>Lactuca</i> L.	<i>L. aculeata</i> , <i>L. altaica</i> , <i>L. dregeana</i> , <i>L. livida</i> , <i>L. saligna</i> , <i>L. sativa</i> , <i>L. serriola</i> , <i>L. virosa</i>	annual, overwintering, annual, biennial
	<i>Cyanicae</i> DC.	<i>L. perennis</i> , <i>L. tenerrima</i>	perennial
<i>Phaenixopus</i> (Cass.) Benth		<i>L. viminea</i>	perennial
<i>Mulgedium</i> (Cass.) C.B. Clarke		<i>L. tatarica</i> , <i>L. sibirica</i> , <i>L. taraxacifolia</i>	perennial
<i>Lactucopsis</i> (Schultz Bip. ex Vis. et Pančić) Rouy		<i>L. quercina</i>	perennial
<i>Tuberosae</i> Boiss.		<i>L. indica</i>	perennial
<i>Micranthae</i> Boiss.		<i>L. undulata</i>	perennial
<i>Sororiae</i> Franchet		<i>L. sororia</i>	perennial
Groups (geographical view)			
North American		<i>L. biennis</i> , <i>L. canadensis</i> , <i>L. floridana</i> , <i>L. graminifolia</i>	biennial
African		<i>L. capensis</i> , <i>L. dregeana</i> , <i>L. homblei</i>	annual, perennial

29 October 2010 in Nagoya, Japan (<http://www.cbd.int/abs/about/> from 16 January 2013).

A recent inventory of The International Lactuca Database (ILDB) with passport data for 11,643 *Lactuca* accessions, and of the Dutch national *Lactuca* germplasm collection (van Treuren and van Hintum 2009; van Treuren et al. 2011) confirmed the conclusions regarding gaps in collection structures reported previously by Lebeda and Boukema (2001) and Lebeda et al. (2004a, 2009a, b). Wild *Lactuca* germplasms are not adequately conserved by official gene banks and the species spectrum and world geographic distribution of the genus are not adequately represented in their germplasm collections (Lebeda et al. 2004a, 2007b, c).

Basic errors in the taxonomic status of wild *Lactuca* accessions as declared by gene banks were found during recent studies (Doležalová et al. 2004, Lebeda et al. 2007b) and duplicates between and within germplasm collections were identified (van Hintum and Boukema 1999, Doležalová et al. 2007; Sretenović-Rajičić et al. 2008). In addition, we are missing basic information on wild *Lactuca* germplasm resistance to the most important diseases and pests of lettuce (Lebeda et al. 2009a, b).

### Gene pools of *Lactuca* spp.

The categorization of many *Lactuca* spp. into gene pools based on their crossing ability and fertility of F1 hybrids is still questionable and needs to be clarified. The primary gene pool of cultivated lettuce *L. sativa* comprises its cultivars and landraces, wild *L. serriola*, *L. aculeata*, *L. altaica*, *L. azerbaijanica*, *L. georgica*, *L. scarioloides*, and *L. dregeana* (Lebeda et al. 2007c). The categorization of *L. saligna* and *L. virosa* to secondary and tertiary gene pools is not resolved yet. Koopman et al. (1998) suggested that section *Lactuca* subsection *Lactuca* comprises the primary and secondary gene pool, while the sections *Phaenixopus*, *Mulgedium* and *Lactucopsis* include the tertiary gene pool (Table 1). Modern lettuce breeding has been mainly based on the utilization of wild *Lactuca* germplasm from the primary gene pool (*L. serriola*), however more recently it has shifted to the exploitation of secondary and tertiary *Lactuca* germplasm (Maisonneuve et al. 1995; Jeuken and Lindhout 2004). The main reason for this strategy is to broaden the genetic variation of cultivated lettuce by interspecific hybridization (Chupeau et al. 1994; Jeuken et al. 2001), including the introduction of a new and broader spectrum of

resistances to diseases and pests (Jeuken and Lindhout 2002; Lebeda et al. 2002, 2007c, 2009a, b)

### Genetic diversity of *Lactuca* spp.

#### Phenotypic variation

Descriptor lists as a tool for the correct taxonomic determination of wild *Lactuca* genetic resource accessions and for a definition of both interspecific and intraspecific variation have been produced at the national (Boukema et al. 1990; McGuire et al. 1993) and international levels (Doležalová et al. 2002, 2003a).

A large degree of variation in plant phenotypes has been described in greenhouse experiments among samples of two world-wide distributed species, *Lactuca serriola* (Doležalová et al. 2005; Lebeda et al. 2007a, 2011; Novotná et al. 2011), and *Lactuca saligna* (Křístková et al. 2007a; Beharav et al. 2008). This results from the evolutionary adaptation of plants under different climatical and ecological condition in their original habitats in different countries from Europe, Near East and North America. In contrast, a low level of phenotypic variation within *Lactuca aculeata* reflects the relatively limited distribution area of this species (Beharav et al. 2010a).

A high level of intraspecific variation is reported for many other species, e.g. for *L. virosa* (Feráková 1977) and has also been recently observed by the authors of this paper. However, this variation was not described in relation to the ecogeographic conditions and distribution of the accessions. The intraspecific classification of this and many other *Lactuca* species has not as yet been critically described. Recent broad application of wild *Lactuca* species in lettuce breeding and their influence on *L. sativa* phenotypic variation need a new treatment arising from the previous one (Lebeda et al. 2007c) based on application of various approaches (i.e. phenotyping, digital image analysis, numerical taxonomy, molecular polymorphism etc.).

#### Variation in phenology features

A high level of variation in phenological characteristics within the genus *Lactuca* was recorded among accessions grown in greenhouse experiments. Substantial differences in the time of flowering were recorded between samples of *L. serriola* originating from various

countries (Doležalová et al. 2005; Lebeda et al. 2007b, c, 2011, unpublished results). A similar phenomenon was recorded for *L. saligna* samples (Křístková et al. 2011). Differences in developmental rates of plants, which are influenced by the original eco-geographic conditions of samples (Lebeda et al. 2001), persist when plants are cultivated in uniform environmental conditions and have a genetic basis (Křístková et al. 2007b).

#### Karyology and DNA contents variation

Perennial wild *Lactuca* species of Europe and the Himalayas have haploid chromosome number  $n=8$ ; the haploid chromosome number  $n=9$  characterizes the majority of European and Mediterranean species, and species from the Middle East, Africa and India; species autochthonous from Canada to Florida possess the haploid chromosome number of  $n=17$  (Feráková 1977, Lebeda and Astley 1999). However, the chromosome numbers of numerous *Lactuca* species are not known (Lebeda and Astley 1999) and the actual chromosome numbers of many North American species may differ from the reported data (Doležalová et al. 2003b).

Chromosomal studies (Matoba et al. 2007) and approaches combining analysis of karyotype and variation in relative DNA content serve as tools for distinguishing some *Lactuca* species (Koopman 1999, 2000; Doležalová et al. 2003b), characterization of their evolutionary relationships (Koopman and De Jong 1996), and intraspecific variation (Koopman 2002). The relative DNA content was analysed for large sets of *L. serriola* and *L. saligna* samples originating from different eco-geographical conditions in Europe, Near East and North America (Lebeda et al. 2004c, 2007c, 2011). However, there was little variation and it seems that *Lactuca* species are highly conservative in DNA content at the intraspecific level.

#### Biochemical trait variation

Nearly 10 % of plant species, including *Lactuca* spp. produce latex which contains complex mixtures of terpenoids, phenolics, proteins, glycosides and alkaloids (Agrawal and Konno 2009). The most important subgroups of sesquiterpenoids within the tribe Cichorieae (Asteraceae) are costus lactone type quaianolides and lactucin derivatives, and they make up large numbers of the total of 360 different sesquiterpene lactones and precursors reported in the tribe (Zidorn 2008). Based

on sesquiterpene profiles the 31 genera of the tribe Cichorieae form seven main clusters, and within the second group with eleven genera the genus *Lactuca* is very close to the genera *Notoseris* and *Cichorium*. The integration of chemosystematic data to the botanical systematics is limited by the lack of standard specimens for verifying the identity of plant material (Zidorn 2008). When correctly identified plant material is available, the results of chemical analyses bring new light to evolutionary concepts and taxonomical relationships between different *Lactuca* spp. (Sessa et al. 2000; Kisiel and Michalska 2009; Michalska and Kisiel 2009, 2010; Lebeda et al. 2009a, b; Michalska et al. 2009; Beharav et al. 2010b).

The HPLC profile of sesquiterpene lactones from latex of several *L. sativa* cultivars differed to those of *L. serriola* and *L. virosa* genotypes resistant to important races of lettuce downy mildew (*Bremia lactucae*). Although this resistance was not correlated to the “SL” profile, heritability of this profile was demonstrated by analysis of progeny from a cross between *L. sativa* and *L. virosa* (Sessa et al. 2000).

Pharmacological exploitation of some chemical compounds in wild *Lactuca* species (e.g. sesquiterpene lactones, phenolics and glucosides, flavonoids) (Rees and Harborne 1984; Kisiel and Barszcz 1998; Kisiel and Zielinska 2000; Chen et al. 2007; Kim et al. 2007) or plant-produced antigens (Pniewski 2013) is another goal of studies aimed at their detection and characterization. This research is stimulated by the promising results of analgesic and sedative activities of lactucin from *Cichorium intybus*, a species chemotaxonomically closely related to lettuce (Wesolowska et al. 2006).

Most studies have focused on latex as a substance that reduces herbivory or the preference or performance of herbivores (Agrawal and Konno 2009). Latex from the resistant variety of lettuce ‘Valmain’ inhibited feeding of *Diabrotica balteata* when painted on leaves of lima bean, conversely the latex from the susceptible variety ‘Tall Guzmaine’ did not inhibit feeding (Huang et al. 2003). To our knowledge, there is no report of antiherbivore activities of latex from wild *Lactuca* species.

#### Protein and molecular polymorphism

Genotyping with molecular markers for genetic diversity detection, assessment of population structure,

selection of desirable genotypes for lettuce breeding, mapping of genes, identification and variation of resistance genes has become common place in modern exploitation of wild lettuce progenitors. The studies related to use of protein and molecular markers in *Lactuca* spp. germplasm collections have been reviewed by Dziechciarková et al. (2004). In the present contribution we want to summarise recent progress on the comprehensive molecular based research on the genus *Lactuca* spp. The survey of studies including wild *Lactuca* species as well as studies using offspring from crosses between cultivated lettuce and wild progenitors and mapping populations derived from these crosses are presented in Table 2.

In general, in the first decade of 21<sup>st</sup> century there has been a dramatic shift in the number of papers based on isozyme studies (Lebeda et al. 2009a, b, 2012a, b) to more advanced studies utilising microsatellite and AFLP markers (e.g. Kitner et al. 2008; van de Wiel et al. 2010; Lebeda et al. 2009a, b), NBS profiling (e.g. van Treuren and van Hintum 2009) and high-resolution DNA melting analysis (Simko et al. 2009, 2010). However, during the last 2 years there has been an increase in the number of papers using new high throughput marker technologies based on single nucleotide polymorphism (SNP) or single position polymorphism (SPP) arrays on Affymetrix and Illumina genechips (e.g. Kwon et al. 2012; Stoffel et al. 2012; Uwimana et al. 2012b, c).

There are several studies by Koopman et al. (1998, 2001) and Koopman (2002) using molecular markers primarily describing relationships among *Lactuca* species and related genera, which are based on ITS1 sequencing and AFLP's. Several other studies have commented on the phylogenetic relationships between *Lactuca* species as well, but either this has not been a primary aim of the study, or has been restricted to a more narrow frame of *Lactuca* genetic pools (Matoba et al. 2007; Yang et al. 2007; Stoffel et al. 2012) (Table 2).

Several types of molecular markers have been applied in studies of genetic variation in natural populations and for germplasm maintenance and characterisation (Table 2). These studies were frequently carried out with microsatellites (Lu et al. 2007; Riar et al. 2011; Uwimana et al. 2012a) or AFLP markers (Kitner et al. 2008; Kuang et al. 2008; Lebeda et al. 2009a, b) or combination of both methods, sometimes extended

with additional markers (van Treuren and van Hintum 2009; van de Wiel et al. 2010; Hoofman et al. 2011). Several studies describing genetic diversity were primarily focussed on marker development, especially on EST- or genomic-microsatellite design (Simko 2009; Rauscher and Simko 2013). These SSR-based markers with publicly available primer sequences provide an important tool for researchers for future studies of wild lettuce populations. Some of these SSR markers are linked to herbicide resistance genes 2,4-D and ALS resistance (Riar et al. 2011). In fact, the number of population-based studies is limited and was mainly performed with AFLP's or non-publicly available SSR's, on lettuce germplasm pseudopopulations originating from a larger geographical scale and/or with a sampling period of several years (van de Wiel et al. 2010; Lebeda et al. 2009a, b, 2012b; Uwimana et al. 2012a) than e.g. comparisons of true populations of local character originating from several regions/countries and sampled within a short period of time. To conclude, we expect that current advances in lettuce genomics (Kwon et al. 2012; Stoffel et al. 2012) will stimulate researchers to use these commercially available genechips based on SNP or SPP features for fast and cost-efficient population-genetic studies in the near future.

Several genetic linkage maps have been published for lettuce. Truco et al. (2007) presented a consensus map of 2,744 markers integrating seven intra- and inter-specific mapping populations and included information from five previously published genetic maps (Kesseli et al. 1994; Witsenboer et al. 1997; Waycott et al. 1999; Johnson et al. 2000; Jeuken et al. 2001). These maps are continuously updated according to marker developments (Schwember and Bradford 2010; Argyris et al. 2011; Aruga et al. 2012; Rauscher and Simko 2013). Such studies are closely associated to QTL studies, design of molecular markers for marker-assisted selection (Simko et al. 2009, 2010, 2011), detection of interspecific hybrids, distribution of crop alleles in natural populations (Uwimana et al. 2012b, c), and finally studies analysing and describing the background of resistance gene clusters, their identification and variability screening (Kuang et al. 2008; McHale et al. 2009).

To conclude, the genome of lettuce has been sequenced using 'next-generation' DNA sequencing, the sequenced genome has been assembled and annotation is underway (Michelmore 2012).

**Table 2** Timeline of different types of molecular marker studies of wild *Lactuca* species

<i>Lactuca</i> spp.													References								
Method																					
cross	sat	ser	sal	vir	per	ind	other	AFLP	CHIP	HRM	NBS	RFLP	RAPD	SEQ	SNP	SSR	SSAP	TRAP	other		
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		Kesseli et al. (1991) <sup>D,T</sup>
*	*	*	*	*	*	*	a)	*	*	*	*	*	*	*	*	*	*	*	*		Vermeulen et al. (1994) <sup>T</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		Hill et al. (1996) <sup>T</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	SAMPL		Witsenboer et al. (1997) <sup>M,D</sup>
*	*	*	*	*	*	*	b)	*	*	*	*	*	*	*	*	*	*	*	SCAR		Koopman et al. (1998) <sup>T</sup>
*	*	*	*	*	*	*	c)	*	*	*	*	*	*	*	*	*	*	*			Sicard et al. (1999) <sup>R</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			van de Wiel et al. (1998) <sup>M,D</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			van de Wiel et al. (1999) <sup>M</sup>
*	*	*	*	*	*	*	d)	*	*	*	*	*	*	*	*	*	*	*			Koopman et al. (2001) <sup>T</sup>
X	*	*	*	*	*	*	e)	*	*	*	*	*	*	*	*	*	*	*			Jeuken et al. (2001) <sup>G,H</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			van Hintum (2003) <sup>D</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	EST		Jeuken and Lindhout (2004) <sup>G,H</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			Argyris et al. (2005) <sup>O,H</sup>
*	*	*	*	*	*	*	b)	*	*	*	*	*	*	*	*	*	*	*			Hu et al. (2005) <sup>D,T</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			Koopman (2002) <sup>T</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			Kuang et al. (2006) <sup>R</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			Syed et al. (2006) <sup>G,H</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			Lu et al. (2007) <sup>R</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	FISH		Matoba et al. (2007) <sup>C,T</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			Truco et al. (2007) <sup>G,H</sup>
X	*	*	*	*	*	*	f)	*	*	*	*	*	*	*	*	*	*	*			Yang et al. (2007) <sup>D,T</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			D'Andrea et al. (2008) <sup>H</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			Kitmer et al. (2008) <sup>D</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			Kuang et al. (2008) <sup>R,T</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			Simko and Hu (2008) <sup>D,G</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	ISO		Lebeda et al. (2009b) <sup>D</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	EST		Jeuken et al. (2009) <sup>R,H</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	SSCP		McHale et al. (2009) <sup>R,H</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			Simko (2009) <sup>M,D</sup>
*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	EST		Simko et al. (2009) <sup>G</sup>

**Table 2** (continued)

Lactuca spp.		Method													References							
		cross	sat	ser	sal	vir	per	ind	other	AFLP	CHIP	HRM	NBS	RFLP		RAPD	SEQ	SNP	SSR	SSAP	TRAP	other
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	SRAP	van Leeuwen et al. (2009) <sup>G,H</sup>
X	*	*	*	*	*	*	e)	*	*	*	*	*	*	*	*	*	*	*	*	*	*	van Treuren and van Hintum (2009) <sup>D</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Argyris et al. (2011) <sup>Q,H</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Schwember and Bradford (2010) <sup>Q,H</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Simko et al. (2010) <sup>M,R,H</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	van de Wiel et al. (2010) <sup>D</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Argyris et al. (2011) <sup>Q,H</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Hooftman et al. (2011) <sup>R,H,G</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Lebeda et al. (2011) <sup>D</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Riar et al. (2011) <sup>M,D</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Simko et al. (2011) <sup>G,M</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Michelmore (2012) <sup>G,H,M,R,Q</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Stoffel et al. (2012) <sup>M,D,T</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Uwimana et al. (2012a) <sup>D,H</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Uwimana et al. (2012b) <sup>Q,H</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Uwimana et al. (2012c) <sup>Q,H</sup>
X	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Rauscher and Simko (2013) <sup>M,G</sup>

Explanation to terms and acronyms used in the table: cross, interspecific hybridisation; sat, *L. sativa*; ser, *L. serriola*; sal, *L. saligna*; vir, *L. virosa*; per, *L. perennis*; ind, *L. indica*; AFLP, Amplified Fragment Length Polymorphism; CHIP, genechip; EST, markers based on Expressed Sequence Tags; FISH, Fluorescence *In Situ* Hybridization; HRM, High-Resolution DNA Melting analysis; ISO, isozymes; NGS, Next Generation Sequencing; NBS, Nucleotide Binding Site profiling; RAPD, Randomly Amplified Polymorphic DNA; RFLP, Restriction Fragment Length Polymorphism; SAMPL, Selectively Amplified Microsatellite Polymorphic Loci; SCAR, Sequence Characterized Amplified Regions; SEQ, sequencing; SNP, Single Nucleotide Polymorphism; SSAP, Sequence-Specific Amplification Polymorphism (retrotransposomes); SSCP, Single Strand Conformation Polymorphism; SSR, microsatellites; SRAP, Sequence-Related Amplified Polymorphism; TRAP, Target Region Amplification Polymorphism; a) *L. alpina*, *L. tatarica*; b) *L. aculeata*, *L. tatarica*, *L. dregeana*, *L. altaica*, *L. tennerrima*, *L. sibirica*, *L. quercina*, *L. viminea*, other species; c) *L. angustana*, other species; d) *L. altaica*, *L. tatarica*, *L. dregeana*, *L. tennerrima*, *L. sibirica*, *L. quercina*, *L. viminea*; e) *Lactuca* spp., other species; f) *L. georgica*, other species; g) *L. aculeata*. Aims of study: C, cytological; D, population/germplasm diversity; G, genetic mapping; H, interspecific hybridisation; M, marker development; Q, quantitative trait loci; R, variation/identification of resistance genes; T, taxonomical/phylogenetical study

## Variation of wild *Lactuca* spp. in reaction to pathogens and pests

### Viral pathogens

The viral pathogens are after fungi the most economically important pathogens of plants. The impact of virus infection is seen in a reduction of yield, decrease quality of size, shape, taste, structure, composition (sugar content) of plants, decrease of viability (sensitivity to dry, cold), predisposition to infection of other pathogens, short shelf life and decrease of fertility. All viruses are obligate parasites that depend on the cellular machinery of their hosts to reproduce (Gergerich and Dolja 2006). Most plant viruses are transmitted by passive transmission from plant to plant and active transmission from infected to healthy plants by a living organism termed a vector. Plant-feeding arthropods, nematodes and plant-parasitic fungi are the major types of vector organisms for plant viruses (Walkey 1991). All types of plant viruses are important disease causing agents and are responsible for losses in crop yields and quality in all parts of the world. Among the most serious lettuce viruses are: *Lettuce mosaic virus*, *Mirafiori* (big vein) *lettuce virus*, *Beet western yellows virus*, *Tomato spotted wilt virus*, *Cucumber mosaic virus* and *Lettuce necrotic stunt virus*. Lettuce is at risk of infection by these viruses and production of new resistant cultivars is a priority. In breeding programmes cross between cultivars and wild species such as *Lactuca serriola*, *L. saligna*, *L. virosa* and *L. perennis* offer a way of introgressing new resistances.

### *Lettuce mosaic virus* (LMV)

*Lettuce mosaic virus* has been a serious worldwide disease problem in lettuce and a few other leafy vegetable species, for a long time (Ryder 2002). It was first described in Florida (Jagger 1921) and now is distributed worldwide, probably because the virus is seed transmitted and lettuce seeds have been exchanged internationally over many years (Dinant and Lot 1992). The worldwide distribution of LMV includes Europe, North and South America (Mexico, USA, Argentina, Brazil, Uruguay), the West Indies (Bermuda), Africa, the Middle East (Egypt, Israel, Iraq, Iran, Jordan and Turkey), Asia (China and Japan) and Oceania (Australia, Tasmania, New Zealand) (German-Retana et al. 2008).

LMV belongs to the genus *Potyvirus* of the family *Potyviridae*, which is seed-borne in lettuce and disseminated by aphid vectors-*Myzus persicae*, *Macrosiphum euphorbiae*, *Aphis gossypii*. The characteristic symptoms on susceptible lettuce cultivars are dwarfism, mosaic, distortion and yellowing of the leaves with sometimes a much reduced heart (failure to form heads). The differences in virus strains, cultivars and the physiological stage of the host at the moment of the attack cause different symptom severity; from a very slight discoloration of the veins to severe necrosis leading to death of the plant (German-Retana et al. 2008). The genomic organization of LMV is typical of potyviruses, with a single positive-sense genomic RNA of 10,080 nucleotides encapsidated as flexuous rods (Krause-Sakate et al. 2002). The viral genomic RNA has a viral encoded protein covalently linked at the 5' end, a poly-A tail at the 3' end, and contains a single open reading frame (ORF) which encodes a large polyprotein with 3,255 amino acids (Revers et al. 1997a). This polyprotein undergoes self-cleavage as it is translated, generating 8–10 viral proteins (Shukla et al. 1994; Revers et al. 1997b).

Three phylogenetic groups of LMV isolates were discriminated, correlating with geographical origin of the isolates rather than with their pathogenicity. The largest group includes isolates from western Europe and California. A second group includes three isolates from Greece whereas the third group consists, so far, of a single isolate from the Yemen Arab Republic (Revers et al. 1997b). LMV isolates have been classified into four pathotypes, according to their virulence on lettuce varieties carrying the three resistance or tolerance genes *mo* (*mo*<sup>1</sup>, *mo*<sup>2</sup>) and *Mo*<sup>2</sup>, which were identified in *L. sativa* cultivars (Pink et al. 1992a; Bos et al. 1994) and LMV genes *Mo*<sup>3</sup> and *Mo*<sup>4</sup>, which are described in *L. virosa* sources but which are difficult to introgress and not well-characterized. These dominant genes have not currently been used in the field.

In Brazil, and in most European countries, LMV has been controlled through the use of resistant cultivars (Krause-Sakate et al. 2001). Two sources of resistance were identified in the late 1960's – the first recessive gene *mo*<sup>1</sup> (formerly named *g*) in Argentina, in a Latin-type cultivar Gallega de Invierno (Bannerot et al. 1969) and European lettuce breeders used the Gallega source of resistance to incorporate the *g* gene in numerous varieties of lettuce, including butterhead, Batavia, cos and crisphead types (Pink et al. 1992b). Later in the



USA the recessive gene *mol*<sup>2</sup> (previously *mo*) was identified in three Egyptian wild *Lactuca sativa* lines (Ryder 1970), this recessive gene *mo* has been used by North American breeders, who introduced it into crisphead and cos types of lettuce. Two of these genes *mol*<sup>1</sup> and *mol*<sup>2</sup>, are recessive and are believed to be either closely linked or allelic (Pink et al. 1992b) and which encode alleles of the cap-binding protein, eIF4E. EIF4E-this identification was based on three converging lines of evidence: (1) allelic sequence co-variation between the eIF4E gene and *mol*<sup>1</sup> and *mol*<sup>2</sup> resistance status of plants; (2) co-segregation of mutations in the eIF4E gene and the *mol*<sup>1</sup> and *mol*<sup>2</sup> resistance status and finally (3) functional complementation using a viral transient expression vector to vector to restore LMV susceptibility in *mol*<sup>1</sup>-or *mol*<sup>2</sup> carrying lettuce plants using the eIF4E allele from susceptible plants (Nicaise et al. 2003). The resistant alleles of the eIF4E gene in lettuce, *mol*<sup>1</sup> and *mol*<sup>2</sup>, are currently the only genetic determinants used to protect lettuce crops from LMV; the third resistance (dominant) gene Mo2, found in the cv. Ithaca (Pink et al. 1992a, b) is not effective in practice for LMV control, because it is overcome by most LMV isolates.

More of studies were done on cultivars of *L. sativa* (the most frequently tested cultivars were: Trocadéro, Mantilia, Floribibb, Ithaca, Salinas 88, and Vanguard). Among the most frequently tested isolates of lettuce mosaic virus on these cultivars were isolates LMV- 0, LVM-1, LMV-9, LMV-E, LMV-13 and AF-199. Additional sources of resistance to lettuce mosaic virus are known in accessions of *Lactuca virosa* and *Lactuca serriola* (Table 3).

#### *Mirafiori lettuce virus (Lettuce big vein virus, LBV)*

Lettuce big vein disease (LBVD) was first described in California (Jagger and Chandler 1934), and it occurs widely in regions of the world with temperate or Mediterranean-type climates (Coutts et al. 2004). LBVD is associated with a complex of two viruses, *Lettuce big-vein associated virus* (LBVV and LBVaV, genus *Varicosavirus*) and *Mirafiori lettuce big vein virus* (MLBVV, *Ophiovirus*) (Rogerio et al. 2000). Its natural host range is limited to lettuce (*Lactuca sativa*), endive (*Cichorium endivia*) and sow thistle (*Sonchus oleraceus*). The vector for both viruses is the root-infecting fungus *Olpidium brassicae* (Coutts et al. 2004).

Both LBVaV and MLBVV have segmented ssRNA genomes, and their virions contain RNA molecules of

both polarities. The LBVaV genome contains two RNA segments-RNA1 is 6797 nucleotide length with a single large open reading frame (ORF), and RNA2 has a slightly smaller size than RNA1 (6081 nt) having coding capacities for five ORFs (Navarro et al. 2005). LBVV particles of virus are fragile, rather rigid rods 320 to 360 nm in length and 18 nm in diameter, with central canal and an obvious helix of pitch=5 nm, MiLV particles, like those of recognized ophioviruses, are highly kinked filaments =3 nm in diameter that form masses of two distinct sizes but of undetermined contour length; they probably form closed circles, because free DNAs are very seldom seen (van Regenmortel et al. 2000)

The mechanism of resistance in cultivated lettuce is not known, and more research is needed to determine the relative role of virus resistance and symptom expression in big vein resistance. Among wild relatives of lettuce, only accessions of *L. virosa* have demonstrated a complete lack of symptom expression in inoculation trials (Bos and Huijberts 1990) (Table 3). *L. virosa* accession IVT280 was identified as 100 % asymptomatic in the greenhouse inoculation trials. Analysis by RT-PCR demonstrated no viral amplification, indicating apparent immunity in this accession (Hayes et al. 2006) Currently, no genotype of *L. sativa* has been identified as immune to big vein (Ryder and Robinson 1995), cultivars Pacific, Thompson, Margarita and Pavana are considered resistant (Ryder and Robinson 1995; Hayes et al. 2006). Crossing between *L. virosa* and *L. sativa* cultivars was difficult to perform (Hayes et al. 2004), nevertheless introgression of big vein tolerance from *L. virosa* to cultivars of lettuce has been successful (Hayes et al. 2004; Hayes and Ryder 2007).

#### *Beet western yellows virus (BWYV), Turnip yellows virus (TuYV)*

*Beet western yellows virus* (BWYV) was originally identified in the USA during the late 1950s as an important virus causing stunting and chlorosis in a wide range of plant species resulting in yield losses in crops such as sugar beet, spinach, lettuce and turnip (Duffus 1961). Beet western yellows virus has been associated with lettuce production since at least the 1950s, when it and the complex of virus diseases affecting spring crops of lettuce were referred to as June Yellows (Davis et al. 1997). BWYV belongs to the genus *Polerovirus* in the family *Luteoviridae* and recently a BWYV isolate,

**Table 3** Resistance of wild *Lactuca* species to viruses

Name of pathogen	Source of resistance	No. of accession/sample	Type of resistance	Remark	References
	<i>Lactuca</i> spp.				
LMV 0	<i>L. virosa</i>	PIVT 1398 (CGN 9365)	Complete resistance	LMV resistance gene Mo3 effective against all known isolates	Maisonneuve et al. (1999) Maisonneuve (2003) Mazier et al. (2003)
		PIVT 280 (CGN 4683)	Complete resistance		Maisonneuve (2003)
LMV-1	<i>L. virosa</i>	PIVT 1398 (CGN 9365)	Resistance	LMV resistance gene Mo3 effective against all known isolates	Maisonneuve et al. (1999) Mazier et al. (2003)
		PIVT 1398 (CGN 9365)	Complete resistance	<i>in vitro</i> experiment, DAS ELISA test	Mazier et al. (2003)
LMV-9	<i>L. virosa</i>		Complete resistance		Maisonneuve (2003)
		PIVT 280 (CGN 4683)	Complete resistance		Maisonneuve (2003)
LMV-13	<i>L. virosa</i>	PIVT 1398 (CGN 9365)	Resistance	LMV resistance gene Mo3 effective against all known isolates	Maisonneuve et al. (1999)
		PIVT 280 (CGN 4683)	Complete resistance		Maisonneuve (2003)
LMV-E	<i>L. virosa</i>	PIVT 1398 (CGN 9365)	Complete resistance	LMV resistance gene Mo3 effective against all known isolates	Maisonneuve et al. (1999)
		PIVT 280 (CGN 4683)	Complete resistance		Maisonneuve (2003)
LMV_Ls-252	<i>L. perennis</i>	n.s.	Complete resistance		Maisonneuve (2003)
	<i>L. tatarica</i>	n.s.	Resistance	Plants symptomless, but positive in ELISA	Bos et al. (1994)
LMV (strain not specif.)	<i>L. serriola</i>	PI 251245	Resistance	Original source of resistance used in breeding program	Bos et al. (1994) Ryder (2002)
LBVV	<i>L. virosa</i>	IVT 280	No symptoms, resistance; high level of resistance		Bos and Huijberts (1990)
		IVT 280	Asymptomatic	14/14 plants remained asymptomatic by testing RT-PCR	Ryder et al. (2003) Hayes et al. (2006)
		n.s.	No symptoms, resistance; high level of resistance		Bos and Huijberts (1990)
		n.s.	n.s.	Greenhouse reaction-62 asymptomatic <i>L. virosa</i> ; 7 <i>L. virosa</i> with leaf crinkling and 1 <i>L. virosa</i> with typical vein banding symptoms	Ryder et al. (2003) Hayes et al. (2008)
LBVV (big-vein)	<i>L. virosa</i>	IVT 280, PI 271938, SAL 012	n.s.	Asymptomatic	Hayes et al. (2008)
		CGN 16272	n.s.	34 tested plants-9 % symptomatic	Hayes et al. (2008)
		CGN 16273	n.s.	35 tested plants-17 % symptomatic	Hayes et al. (2008)
		CGN 16274	n.s.	32 tested plants-13 % symptomatic	Hayes et al. (2008)

**Table 3** (continued)

Name of pathogen	Source of resistance	No. of accession/sample	Type of resistance	Remark	References
	<i>Lactuca</i> spp.				
MLBVV	<i>L. virosa</i>	CGN 16275	n.s.	34 tested plants-15 % symptomatic	Hayes et al. (2008)
		CGN 16276	n.s.	34 tested plants-6 % symptomatic	Hayes et al. (2008)
		CGN 16277	n.s.	35 tested plants-3 % symptomatic	Hayes et al. (2008)
		SAL 177	n.s.	34 tested plants-3 % symptomatic	Hayes et al. (2008)
		CGN 16272	n.s.	9 plants tested-89 % symptomatic	Hayes et al. (2008)
		CGN 16273	n.s.	12 plants tested-92 % symptomatic	Hayes et al. (2008)
		CGN 16274	n.s.	10 plants tested-100 % symptomatic	Hayes et al. (2008)
		SAL 177	positive MLBVV	12 plants tested-33 % symptomatic (by the help NASH test-92 % positive)	Hayes et al. (2008)
		SAL 012	n.s.	12 plants tested-0 % symptomatic (by the help NASH test-17 % positive)	Hayes et al. (2008)
		IVT 280	n.s.	12 plants tested-17 % symptomatic (by the help NASH test-75 % positive)	Hayes et al. (2008)
BWYV- FL1	<i>L. virosa</i>	IVT 280	Asymptomatic	14/14 plants remained asymptomatic-by testing RT-PCR	Hayes et al. (2006)
		IVT 280	Resistant	in the field conditions	Maisonneuve et al. (1991)
		IVT 280	Complete resistance	lab conditions; maintained by replication <i>Myzus persicae</i> on <i>Physalis floridana</i> ;	Maisonneuve (2003)
		IVT 280	Complete resistance	(no symptoms, and no virus detectable ELISA) Wageningen NL	Hayes et al. (2008)
LNVV	<i>L. serriola</i>	IVT 1145	Partly resistant		Maisonneuve et al. (1991)
		IVT 1398	Complete resistance	lab conditions; maintained by replication <i>Myzus persicae</i> on <i>Physalis floridana</i> ;	Maisonneuve (2003)
		273597	Field tolerance	(no symptoms, and no virus detectable ELISA) Wageningen NL + 21 samples <i>L. serriola</i> susceptible + 61 species <i>L. serriola</i> moderately tolerant	Ray et al. (1989)
		491118	Field tolerance	+ 21 samples <i>L. serriola</i> susceptible	Ray et al. (1989)
		491133	Field tolerance	+ 61 samples <i>L. serriola</i> moderately tolerant	Ray et al. (1989)
	<i>L. saligna</i>	PI 261653	Resistance		Haley and McCreight (1990)
		490999, 491001, 491206, 491208, WP233, WP238, WP239, WP242, WP246, WP246A, WP247, 261653	Field tolerance		Ray et al. (1989)

Table 3 (continued)

Name of pathogen	Source of resistance	No. of accession/sample	Type of resistance	Remark	References
TSWV	<i>L. scariola</i> = <i>L. serriola</i>	n.s.	n.s.	North Carolina, experiment	Groves et al. (2002)
CMV	<i>L. saligna</i> × <i>L. sativa</i>	PI 261653×Saladcrisp	Viral strain specific		Provvidenti et al. (1980)
	<i>L. saligna</i> × <i>L. sativa</i>	F7 generation of var. Montello× (Vanguard 75× <i>L. saligna</i> PI 261653)	Resistance		Tamaki et al. (1995)
	<i>L. serriola</i>	n.s.	Tolerance	Tolerant to three strains of CMV studied, but this tolerance has not been transferred to any current commercial variety	Zitter and Murphy (2009)
CMV-B	<i>L. saligna</i>	PI261653	Resistance		Edwards et al. (1983)
CMV-L2 (previously LsS)	<i>L. serriola</i>	ACC 500-4	Resistance	No symptoms	Edwards et al. (1983)
CMV-L3	<i>L. serriola</i>	n.s.	Necrosis		Edwards et al. (1983)
CMV-LsR	<i>L. saligna</i> × <i>L. sativa</i>	F1 plants from crosses of PI261653 with varieties of <i>L. sativa</i>	Not specified		Provvidenti et al. (1980)
LNSV	<i>L. serriola</i>	UC96US23, PI 491178, PI271940	Resistant		Grube et al. (2005a)
	<i>L. saligna</i>	PI490999, PI509525, PI 491204	Resistant		Grube et al. (2005a)
	<i>L. virosa</i>	PI 273597, IVT 280	Resistant		Grube et al. (2005a)

which does not infect sugar beet was renamed *Turnip yellows virus* (TuYV) (Stevens et al. 2005).

BWYV is transmitted by aphid vectors—especially *Myzus persicae* (Sulz.), *Macrosiphum euphorbiae* (Thos.) and induced symptoms are chlorotic (yellow) symptoms, which are first observable at the tips or margins of leaves and soon spread to cover whole leaves. Intervinal chlorosis first occurs in older leaves and progress acropetally, followed by necrosis (Maisonneuve et al. 1991; Hampton et al. 1998).

The genome of BWYV is composed of a single-stranded plus-sense RNA, approximately 5,6 kb in length. The genome contains six large open reading frames (ORFs, ORF0-ORF5), a short 5'- untranslated region (UTR), a 3'-UTR without tRNA-like or poly (A) structure, and an intergenic non-coding region (NVR) between ORF2 and ORF3 about 200nt (Stevens et al. 2005).

#### *Lettuce necrotic yellows virus (LNYV)*

LNYV was first found in 1954 in Australia (Stubbs and Grogan 1963). LNYV is the type species of the genus *Cytorhabdovirus*, members of which are characterised by accumulation of enveloped virions, which is transmitted by *Hyperomyzus lactucae* L.

Lettuce plants naturally infected with LNYV acquire a dull green appearance, the young leaves developing bronzing and necrosis, especially along the veins, and older leaves become chlorotic or mottled and plants often die (Fry et al. 1972). Among the tested wild species are *L. serriola* and *L. saligna* (Table 3) and some accessions show a resistant response.

The LNYV genome consists of a monopartite, negative-sense, single-stranded RNA of 12–15 kb, which encodes five functionally conserved proteins (Dietzgen et al. 2006). The physical map of the LNYV genome is 3' leader – N – P – 4b – M – G – L – 5'trailer, where N is the nucleocacid gene, P is phosphoprotein gene, 4b encodes a putative movement protein, M is the matrix protein gene, G is the glycoprotein gene and L is the polymerase gene (Wetzel et al. 1994).

#### *Lettuce chlorotic virus (LCV)*

*Lettuce chlorotic virus* (LCV) is a member of the rapidly emerging genus *Crinivirus*, family *Closteroviridae* (Duffus et al. 1996). It is transmitted by silverleaf whitefly *Bemisia tabaci* and *B. argentifolii* with about the

same efficiency. This is a major difference between LCV and *Lettuce infectious yellows virus* (LIYV) since LIYV is transmitted very inefficiently by *B. argentifolii* (Davis et al. 1997; Wintermantel 2004).

LCV has a large bipartite RNA genome encoding several open reading frames (at least 13 ORFs). RNA1 encodes functions involved in virus replication, while RNA2 encodes up to 7 ORFs involved in virion assembly, vector transmission and other functions, many of which remain to be determined (German-Retana et al. 1999). Virions are encapsidated into long flexuous rods averaging between 650 to 900 nm in length.

*Lettuce chlorotic virus* resistance has only been assessed in *L. sativa* accessions.

#### *Tomato spotted wilt virus (TSWV)*

*Tomato spotted wilt virus* (TSWV) belongs to the genus *Tospovirus*, family *Bunyaviridae*, it is a one of the most widely spread plant viruses and the causal agent of economically important yield losses in many crops. TSWV was first found in 1915 in Australia (Brittlebank 1919). Since then, its known host range has increased to over 900 dicotyledonous and monocotyledonous plant species worldwide (Peters and Goldbach 1998). Many horticultural crops and weeds are hosts. TSWV is transmitted by several thrips species, of which the western flower thrips (*Frankliniella occidentalis*) is the most efficient vector (Hobbs et al. 1993). Infection reservoirs from which TSWV spreads to susceptible crops include nearby plantings of TSWV-susceptible crops, volunteer crop plants and weeds (Cho et al. 1989; Groves et al. 2002). TSWV is readily transmitted mechanically from sap of naturally infected plants. For manual inoculation *Nicotiana tabacum*, *N. glutinosa* and *N. bethamiana*, which develop large necrotic local lesions followed by systemic mosaic and necrosis are used to provide inoculum (Parella et al. 2003).

TSWV virions are 80–120 nm diameter, spherical, enveloped, and studded with surface projections composed of two glycoproteins G1 and G2. Virion composition is 5 % nuclei acid (RNA), 70 % protein, 5 % carbohydrate, and 20 % lipid. The genome consists of three negative or ambisense ssRNA species designated as S (2.9 kb), M (4.8 kb) and L (8.9 kb) (Parella et al. 2003).

Introgression of genes for resistance into to lettuce cultivars is a possible strategy for control of *Tomato spotted wilt virus*. However, screening of some wild *Lactuca* species (*L. serriola*, *L. virosa* and *L. floridana*)

have shown only susceptible reaction (Hobbs et al. 1993; Parella et al. 2003). Resistance was recorded only in one accession of *L. serriola* by Groves et al. (Groves et al. 2002; Table 3), but without any detailed specification.

#### *Cucumber mosaic virus (CMV)*

*Cucumber mosaic virus* (CMV) is the type species of the genus *Cucumovirus*, family *Bromoviridae*. CMV occurs worldwide and is a very important disease agent in temperate, tropic and subtropic regions of the world. It is a virus with a very wide host range including plants from approximately 365 genera and at least 85 families (Roossinck et al. 1999). CMV is an important pathogen of many vegetable crops and is the target of breeding programs for resistance. The *Cucumoviruses* are transmitted by aphids (especially *Myzus persicae*, *Aphis gossypii*), which ensures a multiplicity of inoculation sufficient to reliably establish infection. Symptoms of CMV infection in lettuce consist of leaf mottling, severe roughness of the leaf and occasional necrosis within the leaf tissue. Plants are usually stunted if infected at an early stage of development (Zitter and Murphy 2009).

CMV consists of three spherical particles, each approximately 28 nm in diameter (Zitter and Murphy 2009). The genome is divided into three plus-sense, single-stranded, RNA molecules, designated RNA 1, RNA 2 and RNA 3. Each RNA molecule is enclosed within a protective protein coat with each being a distinct single spherical-shaped particle. CMV contains five open reading frames (ORFs). These can be used for phylogeny estimation of the species of the *Cucumovirus* genus (indicating evolutionary histories for each RNA strongly supporting the occurrence of re-assortment in the evolutionary history of the genus (Roossinck 2002).

CMV resistance has been derived from *L. saligna* (Table 3), introgression of resistance in to lettuce was done by backcrossing with *L. sativa*. By the F7 generation of cultivar Montello×(Vanguard 75×*L. saligna* PI 261653) (Tamaki et al. 1995), and *Lactuca saligna*×*L. sativa* (Saladcrisp) (Provvidenti et al. 1980) the introgression was successful, and these lettuce lines are resistant to CMV.

#### *Lettuce necrotic stunt virus (LNSV)*

LNSV causes lettuce dieback, a disease resulting in stunting, necrosis, and lack of marketability in lettuce, it is likely that it has been present under the name brown

blight since the 1920s (Wintermantel and Anchieta 2012). LNSV can infect lettuce through the soil in the absence of fungal vectors. Fields with high disease incidence are usually poorly drained and variation in soil salinity influences LNSV infection of lettuce (Wintermantel et al. 2003). Lettuce necrotic stunt virus is caused by several members of the soilborne virus family Tombusviridae, including the type member, *Tomato bushy stunt virus* (TBSV), and *Lettuce necrotic stunt virus* (LNSV) (Obermeier et al. 2001). Tombusviridae is a relatively large and diverse family of soil-borne viruses that have single-stranded, positive-sense, RNA (ribonucleic acid) genomes and that share morphological, structural, molecular and genetic features. Resistance against LNSV is conferred by *Tvr1-a* single, dominant gene that provides durable resistance (Grube et al. 2005b; Simko et al. 2009). Table 3 shows the resistance to LNSV of accessions of the wild species *L. serriola* (UC96US23; PI 491178; PI 271940), *L. virosa* (PI 273597; IVT 280) and *L. saligna* (PI 271940; PI 490999).

#### Bacterial pathogens

##### *Corky root (Sphingomonas suberifaciens, formerly Rhizomonas suberifaciens)*

Corky root of lettuce has been observed in several major lettuce producing areas of the world, including North America, Western Europe, Australia and New Zealand. The symptoms of disease are dark discolouration and longitudinal cracks on the taproot, penetrating to the cortical region and the disease causes slow progressive deterioration of the root system of infected plants and lettuce seedlings and plants wilt under water stress. In severely infested fields of California and Florida, yield losses from reduced head size can reach 30 % to 70 % (Mou et al. 2007); the reduced development of heads is correlated with reduced root growth. The pathogen most commonly isolated from diseased roots is the bacterium *Sphingomonas suberifaciens* (Yabuuchi et al. 1999), formerly *Rhizomonas suberifaciens* (van Bruggen 1997).

The use of resistant cultivars is the most efficient strategy to avoid economic losses (Mou 2011a). The first resistant lettuce cultivars Marquette, Montello and Green Lake developed by Sequiera (1970, 1978) were released from crosses with a resistant line PI 171669. This line was identified by Dickson (1963) as a local lettuce landrace from Turkey.

The resistance to corky root is conferred by a recessive allele (*cor*) at a single locus (Brown and Michelmore 1988), which is present in many modern crisphead lettuce cultivars, e.g. Bronco, Cannery Row, Glacier, Premiere, Misty Day, Sharp Shooter, Sniper (Mou et al. 2007), however there are few leaf lettuce varieties with this resistance (Mou 2011a). Recently two breeding lines 06–831 and 06–833 of green leaf lettuce were released from the cross between green leaf cultivar Waldmann’s and the crisphead cultivar Glacier (Mou 2011a).

Brown and Michelmore (1988) identified resistant lines within the wild species *L. serriola*, *L. saligna*, *L. dentata*, *L. virosa* and *Lactuca* spp. (Table 4). Mou and Bull (2004) identified three *L. serriola* and one *L. virosa* accessions consistently resistant to corky root in growth chamber, greenhouse and field experiments (Table 4), and they demonstrated significant genotype by environment interactions for corky root severity. Moreover, none of these four resistant lines possessed the two molecular markers closely linked to the *cor* allele suggesting that they may be sources of a new resistance factor (Mou and Bull 2004).

*Bacterial leaf spot (Xanthomonas campestris pv. vitians)*

Bacterial leaf spot of lettuce caused by *Xanthomonas campestris* pv. *vitians* has been reported from different countries, since the beginning of the 20th century (Toussaint et al. 2012). On romaine cos type lettuce, symptoms typically appear at the leaf margin as water-soaked lesions which become black after a few days and may be surrounded by a chlorotic halo. Later on they enlarge and coalesce, and large necrotic areas on leaves may develop (Toussaint et al. 2012). Lesions may expand towards veins, resulting in V-shaped lesions. Small individual black spots on the leaf surface may also be observed (Sahin and Miller 1997). Seed collected from infected plants were found to be colonized by bacteria externally, but no bacteria were recorded from within the seed (Barak et al. 2002).

When the infection remains restricted to the older leaves, no economic losses occur, however, in severe epidemics, the inner leaves are infected and the lettuce is then unmarketable (Toussaint et al. 2012).

Populations of *X. campestris* pv. *vitians* can survive on lettuce plant debris and infect subsequent lettuce crops (Barak et al. 2001). The pathogen has also been

**Table 4** Wild *Lactuca* spp. with resistance to bacterial pathogen causing Corky root

Name of pathogen	Source of resistance	Type of resistance	Remark	References
<i>Sphingomonas suberifaciens</i> ( <i>Rhizomonas suberifaciens</i> )	<i>Lactuca</i> spp.	No. of accession/sample		
	<i>L. dentata</i>	PI 234204	n.k.	Brown and Michelmore (1988)
<i>L. saligna</i>	<i>L. saligna</i>	PI 261653, PI 490999, PI 491204, PI 491206, UC83UK2, UC83US1	n.k.	Brown and Michelmore (1988)
	<i>L. serriola</i>	PI 2556665, PI 289064–1, PI 289064–2 PI 491096, PI 491110, PI 491239	n.k.	Brown and Michelmore (1988) Mou and Bull (2004)
<i>L. virosa</i>	<i>L. virosa</i>	PI 491249, PI 491250, PI 491251 PI 273597c	n.k.	Brown and Michelmore (1988) Mou and Bull (2004)
	<i>Lactuca</i> spp.	UC83UK1 PI 274376	n.k.	Brown and Michelmore (1988) Brown and Michelmore (1988)

recovered from leaves of several symptomless weed species collected around infested commercial fields, but not from weeds collected around previously infested fields during fallow periods. Thus, weeds may not be an important long-term source of *X. campestris* pv. *vitians*, possibly due to the lack of stable epiphytic populations on weedy plants (Barak et al. 2001). *Xanthomonas campestris* pv. *vitians* can infect not only cultivated lettuce but also the wild *Lactuca* species, *L. serriola* and *L. biennis*, and these species may serve as a reservoir for this pathogen (Toussaint et al. 2012).

The possibilities of chemical control of bacterial diseases on lettuce are limited (Toussaint et al. 2012) and so host resistance is the most likely means of controlling the disease. Several commercial cultivars of lettuce have been screened for resistance to this bacterial pathogen (Sahin and Miller 1997, Carisse et al. 2000) and activities aimed at the development of lettuce breeding lines resistant to bacterial leaf spot have been briefly reported (Anonymous 2005). However, the genetics of resistance to *X. campestris* pv. *vitians* and the response of wild *Lactuca* species to this bacterial pathogen have not yet been published.

## Fungal pathogens

### *Downy mildew (Bremia lactucae)*

Lettuce downy mildew (*Bremia lactucae*) has a very high economic impact on lettuce production (Crute 1992), and the study of its biology and epidemiology, sources of resistance, mechanisms and genetic control of resistance in *Lactuca* species, including germplasm evaluations have been a high priority of researchers and breeders in many countries (Lebeda et al. 2002, 2009a, b). The interaction between cultivars of *L. sativa* and *B. lactucae* is clearly race-specific (Crute and Johnson 1976; Lebeda 1984; Farrara and Michelmore 1987).

Of the 100 wild *Lactuca* species described (Lebeda et al. 2004b) only 14 are definitely known as natural hosts of *B. lactucae* (Lebeda et al. 2002). *L. serriola*, is the most common wild *Lactuca* spp. occurring around the world (Lebeda et al. 2004b), and could be an important weedy host. However, except for the Czech Republic, there is no detailed information on the natural occurrence of lettuce downy mildew and its epidemiological impact on this species (Lebeda et al. 2002, 2008a). There is only limited knowledge of virulence variation of *B. lactucae* in wild pathosystems (Lebeda

et al. 2008a). Only isolates originating from natural populations of *L. serriola* have been investigated for specific virulence variation (Lebeda et al. 2002, 2008a; Lebeda and Petrželová 2004). Generally, *B. lactucae* isolates from wild pathosystem are characterized in terms of v-factors mostly matching *Dm* genes or R-factors located or derived from *L. serriola* (Lebeda and Petrželová 2004).

Currently, searching for new sources of resistance and genes suitable for practical lettuce breeding (Lebeda and Zinkernagel 2003a; Beharav et al. 2006; Petrželová and Lebeda 2011; Petrželová et al. 2011; van Treuren et al. 2013) is considered to be very important. Accessions of *L. serriola* (reported as PI 91532 but subsequently shown to be PI 104584 and PI 167150) originating from Russia and Turkey were used in the 1930s in the USA as sources of resistance against *B. lactucae* (Lebeda et al. 2002). These sources created the breeding pool for a new generation of lettuce cultivars (Imperial 410, Calmar, Valmaine) for outdoor cropping which were introduced in the 1940s and 1950s (Whitaker et al. 1958). All of these cultivars have race-specific resistance (Table 5).

In Europe, the utilization of wild *Lactuca* germplasm was based on two different strategies (the Netherlands and Great Britain). In the 1950s, genes originating from old German and French cultivars of *L. sativa* were used mostly (Crute 1992). At the end of the 1960s in the Netherlands an interspecific hybrid between *L. sativa* (cv. Hilde) and an accession of *L. serriola*, described as H×B, Hilde×*L. serriola* was released. Resistance derived from this material was assigned to the race-specific gene *Dm11* (Lebeda et al. 2002) (Table 5).

In the 1970s and 1980s other sources of resistance to *B. lactucae*, derived from *L. serriola* with resistance genes (factors) described as *Dm16* and *R18* (Table 5), were used in the Netherlands. All of these genes have been used frequently in breeding programs in Europe during the last 20 years. However, resistance based on these genes is no longer effective against many *B. lactucae* isolates (Lebeda and Zinkernagel 2003b). From the end of the 1980s there was increasing interest (esp. in the Netherlands and U.K.) for the utilization of resistance located in the hybrid line *L. serriola* (Swedish)×*L. sativa* (Brunhilde) and line CS-RL (Lebeda and Blok 1991) was derived from this material. This line was highly resistant for a long time. However recently a new race overcoming the resistance was described (Lebeda and Zinkernagel 2003a).



**Table 5** Examples of race-specific resistance genes (*Dm*) or factors (R) located or derived from *Lactuca serriola* (modified according to Lebeda et al. 2002, 2007c)

<i>Dm</i> gene (R-factor)	<i>L. serriola</i> accession (line)	Origin	Occurrence in <i>L. sativa</i> cultivars <sup>a</sup>	Linkagegroup
<i>Dm5</i>	PI 167150	Turkey	Valmaine	2
<i>Dm5/8+10</i>	PI 91532	USSR	Sucrine	2
	PI 167150	Turkey		
<i>Dm8</i>	PI 91532	USSR	Avoncrisp	2
			Calmar	
			Salinas	
<i>Dm6</i>	PI 91532	USSR	Sabine	1
<i>Dm7</i>	LSE/57/15	UK	Great Lakes	3
			Mesa 659	
<i>Dm11</i>	IVT	<sup>b</sup>	Capitan	3
	Wageningen			
<i>Dm15</i>	PIVT 1309	Netherlands	<sup>c</sup>	1
<i>Dm16</i>	LSE/18	Czechoslovakia	Saffier	1
			Titania	
<i>Dm7+10+13</i>	PI 114512	Sweden	Vanguard	
	PI 114535	UK		
PI 125819		Afghanistan		
(+ <i>L. virosa</i> PI 125130)		Sweden		
R17	LS 102	France <sup>b</sup>	<sup>c</sup>	2
R18	LS 17	France <sup>b</sup>	Mariska	1
R19 (R18+ <sup>b</sup> )	CS-RL	Sweden	Libusa	1
	LJ88356		Miura	
<i>Dm7+R23</i>	CGN 5153	USSR (Krym) <sup>c</sup>		3,5 <sup>b</sup>
R24+R25	CGN14255	Hungary	<sup>c</sup>	3,5
R24+R26	CGN14256	Hungary	<sup>c</sup>	3,4
R24+R27	CGN14270	Hungary	<sup>c</sup>	3,4 <sup>b</sup>
R24+R28	CGN14280	Hungary	<sup>c</sup>	3, <sup>b</sup>
R24+R29	PI 491178	Turkey	<sup>c</sup>	3, <sup>b</sup>
R30	PI 491229	Greece	<sup>c</sup>	1
R <sup>b</sup> (+modifiers, probably RNS)	PI 281876	Iraq	<sup>c</sup>	<sup>b</sup>

<sup>a</sup> only selected examples;<sup>b</sup> not known or unclear;<sup>c</sup> *Dm* gene or R-factor not yet located in *L. sativa* cultivar(s).

RNS race-nonspecific

*L. saligna* and *L. virosa* may possess novel and very interesting resistance to *B. lactucae* (Lebeda et al. 2002). As a result of studies in the 1990s a new lettuce cultivar Titan (Sluis & Groot) with the race-specific gene *Dm6* plus resistance derived from *L. saligna* (pers. comm., K. Reinink, Rijk Zwaan, the Netherlands) was released in the Netherlands (Lebeda et al. 2002). However, this resistance is no longer effective

(Lebeda and Zinkernagel 2003a, b). Recently, a very intensive program of lettuce breeding based on introduction of newly located sources and genes of resistance from *L. serriola*, *L. saligna* and *L. virosa* was developed in the USA (Michelmore et al. 2005). Also new sources of resistance were located in wild *Lactuca* spp. originating mostly from the Middle East (Beharav et al. 2006; Petrželová et al. 2011).

The effectiveness of the expression of some *Dm* genes located in *L. serriola* can be dependent on environmental factors. Judelson and Michelmore (1992) showed that resistance (assessed as the absence of sporulation) based on *Dm6*, *Dm7*, *Dm11*, *Dm15*, and *Dm16* became less effective or ineffective at temperatures below 10 °C. The ecological and epidemiological consequences of this effect are not known (Lebeda et al. 2002).

The occurrence of race-specificity in other wild *Lactuca* species and related genera has not been analysed in detail. However, recent analyses (Lebeda et al. 2002) have shown that the occurrence of race-specific resistance in wild *Lactuca* species is a common phenomenon. In the section *Lactuca*, all of the species studied express race-specificity after inoculation with isolates of *B. lactucae* from *L. sativa* and *L. serriola*. The presence of race-specific resistance in *L. saligna* was described as questionable because most of the screened accessions exhibited complete or incomplete resistance at both the seedling and adult stage (Lebeda et al. 2002; Beharav et al. 2006), and recent results (Petrželová et al. 2011) showed that *L. saligna* may possess non-host resistance. A race-specific response was also confirmed in some species from other sections of the genus *Lactuca* (*L. viminea*, *L. tatarica*, *L. quercina*, *L. indica*, *L. biennis*) (Lebeda et al. 2002) and there is clear evidence of the occurrence of a race-specific response in some species of related genera (e.g. *Cicerbita*, *Mycelis*) (Lebeda et al. 2002).

Other types of resistance (race-nonspecific, field, non-host; for detailed description see Lebeda et al. (2002)) of *Lactuca* species against *B. lactucae* are not as well understood. There is only limited information available about race-nonspecific resistance in wild *Lactuca* spp. germplasm. The presence of race-nonspecific resistance has only been reported in *L. serriola* (Lebeda et al. 2002). Currently only two *L. serriola* accessions can be considered as potential sources of this type of resistance. It was recognised that accessions PI 281876 and PI 281877 at the seedling stage were infected by some *B. lactucae* isolates. However, the intensity of sporulation was mostly very low and in some interactions was followed by expression of a necrotic response (Lebeda 1986). Current thoughts are that this resistance is based on some major gene(s) and modifiers (Lebeda et al. 2002). *L. serriola* (PI 281876) has been used frequently in practical breeding programs (Lebeda and Pink 1998).

The most comprehensive experiments focused on field resistance of wild *Lactuca* spp. were carried out by Lebeda (1990). In total, thirty-one accessions of four *Lactuca* species (*L. serriola*, *L. saligna*, *L. aculeata*, *L. indica*/syn. *L. squarrosa*) and one *L. serriola*×*L. sativa* hybrid (line CS-RL) were studied in 3 years of field experiments. The disease incidence was significantly different across species and accessions. *L. saligna*, *L. aculeata* accessions and the *L. serriola*×*L. sativa* hybrid were free of infection during the observation period. This reaction implies the presence of effective unknown R-factors (Lebeda et al. 2002) in these genotypes. In the *L. serriola* accessions, significant differences in the level of field resistance were observed (Lebeda 1990). Some accessions were highly susceptible (e.g. PI 204753, PI 253468, PI 273596, PI 273617, PI 274359), in contrast, accessions PI 281876 and PI 253467 were free of disease symptoms (again implying the presence of effective unknown R-factors). However, the possible race-nonspecific resistance in PI 281876 is also likely to be expressed as field resistance (Lebeda 1990).

Nonhost resistance should be very effective, durable and not influenced by changes of environmental conditions (Lebeda et al. 2002). It was hypothesized that some *L. saligna* accessions may possibly possess nonhost resistance (Lebeda 1986). Recent experimental results with new highly virulent isolates of *B. lactucae* originating from *L. sativa* have not confirmed the presence of race-specific resistance in *L. saligna* (Lebeda and Zinkernagel 2003a). However, recent findings indicate that, at least some *L. saligna* accessions possess race-specific resistance factors (Jeuken and Lindhout 2002), in addition to possible non-host resistance to *B. lactucae* (Beharav et al. 2006; Petrželová et al. 2011).

There is only limited information available on the histological, cytological, biochemical and molecular background of resistance to lettuce downy mildew in *L. sativa* and wild *Lactuca* species. Some basic ideas and conclusions related to this subject were summarized by Lebeda et al. (2002, 2006, 2008b), Jeuken and Lindhout (2002, 2004). Data obtained in histological studies of resistance in wild *Lactuca* spp. suggest there are a wide range of resistance mechanisms in *Lactuca* spp. against *B. lactucae* (Lebeda et al. 2008b).

#### *Powdery mildew (Golovinomyces cichoracearum)*

Lettuce powdery mildew is considered as a disease of increasing importance (Lebeda and Mieslerová 2011).

The ascomycete *Golovinomyces cichoracearum* V.P. Gelyuta (previously *Erysiphe cichoracearum* DC. s.str. (Lebeda and Mieslerová 2011)) is the predominating powdery mildew species, however, another powdery mildew species, *Podosphaera fusca* was collected and described on *Lactuca sativa* in Korea (Shin et al. 2006). Great progress in the research of the taxonomy, distribution and biology of lettuce powdery mildew (*Golovinomyces cichoracearum sensu stricto*) has been achieved during the last 15 years (Lebeda and Mieslerová 2011).

Natural hosts of powdery mildew include *L. muralis*, *L. perennis*, *L. quercina*, *L. serriola*, *L. saligna*, *L. sibirica*, *L. viminea*, *L. virosa* (Lebeda 1985a, b; Lebeda and Mieslerová 2011), and *L. aculeata* (Lebeda unpubl.). One of the most common species in Europe is *L. serriola* (prickly lettuce) which also could be considered as a common host of *G. cichoracearum*. Substantial variation in expression of the degree of infection between different sites and/or populations was recognized. It was concluded that *L. serriola* could act as a reservoir of inoculum for lettuce infection (Lebeda et al. 2012c, 2013).

Lebeda (1985c) demonstrated in a set of 25 lettuce (*L. sativa*) cultivars substantial differences in disease severity. Only two cultivars (Amanda Plus, Bremex) were free of natural infection.

The screening of more than one hundred accessions of wild representatives of the genus *Lactuca* (*L. aculeata*, *L. dentata*, *L. perennis*, *L. saligna*, *L. serriola*, *L. tatarica*, *L. tenerrima*, *L. viminea*, *L. virosa*) under conditions of natural infection by *G. cichoracearum* revealed high variability in resistance (Lebeda 1985b, 1994). The accessions of *L. serriola* were attacked most severely and *L. saligna* showed highly variable levels of resistance, while the lowest levels of infection were found in accessions of *L. virosa*, *L. viminea*, *L. tenerrima* and *L. tatarica*. In some species (e.g. *L. saligna*, *L. serriola*) the interaction with the pathogen is probably based on race-specific resistance (Lebeda and Mieslerová 2011; Lebeda et al. 2012c, 2013) (Table 6).

Some *L. saligna* accessions are potentially useful sources of resistance, especially where they carry resistance to *Bremia lactucae* as well (Lebeda 1985b). *L. virosa* could be also considered as a suitable donor of resistance; however its resistance seems to depend on a certain stage of the ontogenetic development (Lebeda 1985a).

#### *Anthracnose (Microdochium panattoniana)*

Anthracnose (shothole disease, ringspot) caused by *Microdochium panattoniana* (Berl.) Sutton, Galea & Price is manifested as small circular brown spots primarily on the lower leaf blades. The centers of these spots dry and fall out. Lesions on the midrib become necrotic, sunken, and elongated. The initial infection may be soilborne or seedborne, the anthracnose conidia are spread in lettuce crops by splashes of rain or irrigation water (Galea et al. 1986). Lettuce ringspot causes serious damage of lettuce crops in the southern states of Australia, in California and throughout Europe especially under cool wet conditions when application of fungicides is difficult (Galea and Price 1988). Sources of resistance have been identified in wild *Lactuca* species *L. angustana*, *L. livida*, *L. perennis*, *L. serriola*, *L. saligna*, and *L. virosa* (Ochoa et al. 1987; Galea and Price 1988) (Table 7).

#### *Stemphylium leaf spot (Stemphylium spp.)*

Symptoms of *Stemphylium botryosum* f. *lactucum* Wallr. on lettuce leaves are small, round, and brown spots, which may appear sunken because the tissue becomes necrotic (Netzer et al. 1985). This fungal disease has been reported in many parts of the world (Raid 1997), but it has relatively small economic impact. The only known source of resistance to the disease is an unspecified line of *L. saligna* collected in Israel (Table 7). Resistance is controlled by two genes, with one allele dominant *Sm<sub>1</sub>* for resistance and the other recessive *sm<sub>1</sub>* (Netzer et al. 1985).

#### *Sclerotinia drop-lettuce drop (Sclerotinia spp.)*

Two fungal species, *Sclerotinia minor* and *Sclerotinia sclerotiorum* cause sclerotinia drop of lettuce, one of the most widespread and destructive disease worldwide in lettuce production (Purdy 1979; Subbarao 1998). Both *S. minor* and *S. sclerotiorum* survive mainly as sclerotia in soil. *S. minor* primarily infects lettuce by direct eruptive germination of soilborne sclerotia. This mode of infection is less frequent in *S. sclerotiorum*. The primary inoculum source of *S. sclerotiorum* is airborne ascospores from carpogenic germination of sclerotia (Abawi and Grogan 1979). *Sclerotinia* is difficult to control with cultural methods (Lebeda et al. 2007c), and it is difficult to elaborate

**Table 6** Sources of resistance in wild *Lactuca* species to lettuce powdery mildew

Name of pathogen	Source of resistance		Type of resistance	References
	<i>Lactuca</i> spp.	No. of accession/sample		
<i>Golovinomyces cichoracearum</i>	<i>L. aculeata</i>	LAC/92/2	n.k.	Lebeda (1985a)
	<i>L. dentata</i>	PI 234204	n.k.	Lebeda (1985a)
	<i>L. perennis</i>	09318, 09319, 09323	n.k.	Lebeda (1994)
	<i>L. saligna</i>	LSA/92/1, LSA/92/2	n.k.	Lebeda (1985a)
	<i>L. saligna</i>	05282, 05304, 05306, 05308, 05309, 05311, 05313, 05314, 05315, 05318, 05319, 05320, 05322, 05323, 05326, 05330, 05895, 09311, 09313	n.k.	Lebeda (1994)
	<i>L. saligna</i>	09-H58-1013	race-specific	Lebeda et al. (2013)
	<i>L. serriola</i>	PI 255665	n.k.	Lebeda (1985a)
	<i>L. serriola</i>	PI 273617	race-specific	Lebeda et al. (2013)
	<i>L. tatarica</i>	09389, 09390	n.k.	Lebeda (1994)
	<i>L. tenerrima</i>	09386, 09387, 09388	n.k.	Lebeda (1994)
	<i>L. viminea</i>	09326	n.k.	Lebeda (1994)
	<i>L. virosa</i>	LVIR/26, LVIR/57/1	n.k.	Lebeda (1985a)
	<i>L. virosa</i>	04678, 04679, 04680, 04681, 04682, 04683, 04954, 04955, 04956, 04963, 04964, 04970, 04972, 05020, 05077, 05145, 05148, 05266, 05268, 05270, 05283, 05331, 05332, 05333, 05793, 05794, 05816, 05869, 05941, 05978, 09315, 09316, 09364, 09365, PI 271938	n.k.	Lebeda (1994)
	<i>L. virosa</i>	LVIR/50	race-specific	Lebeda et al. (2012c)

protocols of resistance screening (Grube and Ryder 2004).

Extensive evaluation of lettuce germplasm has been carried out either for resistance to *S. sclerotiorum* (Chupp and Sherf 1960; Elia and Pigionica 1964; Whipps et al. 2002) or *S. minor* (Abawi et al. 1980; Subbarao 1998; Grube and Ryder 2004) but no complete resistance has been identified, and it is unknown whether resistance to the two species is correlated (Lebeda et al. 2007c). Wild *Lactuca* species were included in these tests but the numbers of accession was relatively low (Abawi et al. 1980; Whipps et al. 2002).

An accession of primitive oilseed lettuce *L. sativa* (PI 251246) may have partial resistance to *Sclerotinia* sp. infection (Whipps et al. 2002; Hayes et al. 2010), but this is very likely associated with its primitive growth habit (Grube 2004). *L. dentata* (PI 234204, later named as *Sonchus oleraceus* (Doležalová et al. 2004; Lebeda et al. 2007c)), *Lactuca* sp. (PI 274376) and *L. serriola* (PI 271938) were shown to be highly resistant to *S. minor* (Abawi et al. 1980), and the latter accession was also resistant to *S. sclerotiorum* (Whipps et al. 2002) (Table 7). In the *S. sclerotiorum*-infested field experiments, three *L. virosa* accessions (SAL 012,

IVT 280 and IVT 1398) demonstrated high levels of resistance (Table 7), although further analysis is needed to determine the role of the slow bolting/biennial nature of *L. virosa* in resistance (Hayes et al. 2010).

#### *Verticillium wilt (Verticillium dahliae)*

Verticillium wilt, is a relatively newly recognised lettuce disease caused by the soilborne fungus *Verticillium dahliae* Kleb. It was reported for the first time in a lettuce crop in the Pajaro Valley (California) in 1995 (Subbarao et al. 1997; Bhat and Subbarao 1999), in 1999 it was first observed on lettuce in the Salinas Valley (Atallah et al. 2011), in 2006 in northern Italy (Garibaldi et al. 2007). In 2009, this disease appeared in commercial fields in Japan (Usami et al. 2012). Losses of up to 100 % may occur in head lettuce: smaller losses occur in other lettuce types (Lebeda et al. 2007c).

*V. dahliae* was first isolated from *L. serriola* during a field survey carried out in Crete in 1992–2000 (Ligoxigakis et al. 2002). Disease symptoms and recovery of *V. dahliae* are known in wild *L. serriola* and other *L. serriola*-like species, *L. saligna*, and *L. virosa* (Hayes et al. 2009).

**Table 7** Resistance of wild *Lactuca* species to fungal pathogens

Name of pathogen	Source of resistance	No. of accession, sample	Type of resistance	Remark	References
<i>Anthraco</i>					
<i>Anthraco</i> ( <i>Microdochium panattoniana</i> )					
	<i>L. angustana</i>	PI 190906			Ochoa et al. (1987)
	<i>L. livida</i>	PI 273585		re-determined as <i>Lactuca</i> sp. (Doležalová et al., 2004; Lebeda et al. 2007c)	Ochoa et al. (1987)
	<i>L. perennis</i>	PI 273594 PI 274415 PI 274378			Ochoa et al. (1987) Ochoa et al. (1987) Ochoa et al. (1987)
	<i>L. saligna</i>	LAG1	immune	coll. in Hillston, NSW	Galea and Price (1988)
		UC83US1 PI 273482 UC83UK2 PI 490999	resistant to races A, B, C, D, E		Ochoa et al. (1987) Ochoa et al. (1987) Ochoa et al. (1987) Ochoa et al. (1987)
	<i>L. serriola</i>	LAG2 PI 274372 PI 274457 PI 289064 PI 271939 PI 273579 PI 274375	highly resistant	coll. from Zoology Reserve, La Trobe University	Ochoa et al. (1987) Galea and Price (1988) Ochoa et al. (1987) Ochoa et al. (1987) Ochoa et al. (1987) Ochoa et al. (1987) Ochoa et al. (1987)
<i>Stemphylium botryosum</i> f. <i>lactucum</i>					
	<i>L. saligna</i>	not specified material	two genes, dominant Sm <sub>1</sub> and recessive sm <sub>1</sub>	collected in Israel	Netzer et al. (1985)
<i>Sclerotinia sclerotiorum</i>					
	<i>L. serriola</i>	PI 271938			Whipps et al. (2002)
	<i>L. virosa</i>	SAL 012 IVT 280 IVT 1398		this accession is probably <i>L. virosa</i>	Hayes et al. (2010) Hayes et al. (2010) Hayes et al. (2010)
<i>S. minor</i>					
	<i>L. dentata</i>	PI 234204		re-determined as <i>Sonchus oleraceus</i> (Doležalová et al., 2004; Lebeda et al. 2007c)	Abawi et al. (1980)
	<i>L. serriola</i>	PI 271938		this accession is probably <i>L. virosa</i>	Abawi et al. (1980)
	<i>Lactuca</i> sp.	PI 274376		USDA ARS GRIN, re-determined as <i>Sonchus oleraceus</i>	Abawi et al. (1980)
<i>Verticillium dahliae</i>					
	<i>L. virosa</i>	IVT 280			Grube et al. (2005a)

Two pathogenic races of *V. dahliae* were described, and currently race 2 predominates as a result of world-wide cultivation of lettuce cultivars resistant to race 1 (Hayes et al. 2006, 2007a, b, 2011b; Atallah et al. 2011). Despite widespread screening, complete resistance to race 2 has yet to be identified (Grube et al. 2005a; Atallah et al. 2011). Partial resistance to race 2, in the form of reduced disease incidence or delayed expression of symptoms, has been found in four PI accessions *L. sativa* (Hayes et al. 2011a).

The *L. virosa* accession IVT 280 (Table 7) and some other accessions have shown high levels of resistance in field tests (Grube et al. 2005a).

#### *Fusarium wilt (Fusarium spp.)*

*Fusarium wilt* was first reported on lettuce in Japan in 1955 (Matuo and Matahashi 1967), but it was not until many years later that its widespread occurrence and potential for economic damage was fully recognized (Fujinaga et al. 2003; Hubbard and Gerik 1993; Garibaldi et al. 2004). The disease is caused by *Fusarium oxysporum* f. sp. *lactucae* n.f. (same as f. sp. *lactucum* (Hubbard and Gerik 1993; Fujinaga et al. 2003). Three races of the fungus have been identified (Fujinaga et al. 2003). It is a disease of the root vascular system. As one of several wilting diseases exhibiting yellowing and wilting of leaves and stunting and plant death, the principal diagnostic symptom is a reddish brown discoloration of the cortex and upper crown (Matheron and Koike 2003). Higher temperatures tend to increase the severity of fusarium wilt in lettuce (Scott et al. 2010).

Resistance sources have been identified for races 1 and/or 2, but not for race 3 (Garibaldi et al. 2004; Tsuchiya et al. 2004). All sources are cultivars of the various lettuce types.

#### *Pythium wilt (Pythium spp.)*

Soilborne pathogens *Pythium tracheiphylum* and *P. uncinatum* were reported as causing vascular wilt and stem rot of lettuce in Italy in 1965 (Matta 1965) and subsequently in other parts of Europe (Blok and van der Plaats-Niterink 1978), North America (Tortolero and Sequeira 1978), Australia (Kumar et al. 2007) and Japan (Matsuura et al. 2010). Yield reductions up to 30 % have been recorded (Davis et al. 1995). In spite of the economic importance of these pathogens, the screening of wild *Lactuca* species for resistance is not reported.

## Nematodes

### *Root-knot nematode (Meloidogyne spp., incognita, hapla, javanica, enterolobii)*

Nematodes occurring on lettuce can be classified into 23 genera: *Aphelenchoides* (da Silveira 1990), *Meloidogyne* (e.g. Viaene and Abawi 1996, Blancard 2011), *Pratylenchus* (Moretti et al. 1981; Mani et al. 1997), *Rotylenchulus*, *Tetylenchus*, *Tylenchorhynchus* (e.g. Radewald 1969a; Philis 1995; Koenning et al. 1999; Kohl 2011; Pedroche et al. 2012), *Helicotylenchus* (Anwar and McKenry 2012), *Criconeoides*, *Heterodera*, *Hoplolaimus*, *Paratylenchus* (Machado and Inomoto 2001; Bao and Neher 2011), *Paratrichodorus* (Boydston et al. 2004), *Hemicycliophora* (Chitambar 1993; Blancard 2011), *Rotylenchoides*, *Tylenchus*, (Addoh 1971), *Longidorus* (Radewald 1969b, c; MacGowan 1982; Huang and Ploeg 2001), *Mesocriconea* (DAFF 2012), *Nacobbus*, *Paralongidorus*, *Xiphinema* (Sikora and Fernández 2005), *Aglenchus* (Ökten 1988), *Belonolaimus* (Chitambar 2007), *Radopholus* (Ferris 2013), *Merlinius* (Bridge 1976).

However the most important nematodes with documented impact on lettuce growth and yield include the needle nematode (*Longidorus africanus*), root-knot nematode (*Meloidogyne* spp.), root lesion nematode (*Pratylenchus penetrans*), and the spiral nematode (*Rotylenchus robustus*) (Davis et al. 1997). There are several other nematodes associated with lettuce in the field-stubby root nematode *Paratrichodorus minor*, the reniform nematode *Nacobbus aberrans*, and stunt nematodes *Tylenchorhynchus clarus* and *Merlineus* spp. (Davis et al. 1997).

The number of papers reporting occurrence of nematode infection/diseases on lettuce wild relatives is limited. The majority of reports are based on field observation of nematode infection on *L. serriola* (Table 8). There are just two reports related to identification of resistant accessions to root-knot nematode (*M. hapla*) in a larger germplasm collections. Abawi and Robinson (1991) evaluated 85 genotypes (including accessions of *L. serriola*, *L. virosa* and *L. saligna*) in two greenhouse tests, and in a recent study Kaur and Mitkowski (2010) analysed 494 lettuce accessions, including 36 *L. serriola*, 7 *L. virosa* and 8 *L. saligna* genotypes. Genotypes with moderate to highly resistant reaction to *M. hapla* inoculation were observed in these studies (Table 8). The occurrence of root-knot nematodes on

**Table 8** Resistance of wild *Lactuca* species to nematodes

Name of nematode	Source of resistance				
	<i>Lactuca</i> spp.	No. of accession/sample	Type of resistance	Remark	References
<i>Meloidogyne hapla</i>	<i>L. serriola</i>	3738 (M-HR)	n.k.	GRS	Abawi and Robinson (1991) Kaur and Mitkowski (2010)
	<i>L. saligna</i>	PI 281876, PI 491000, 261653, PI 273582 (M-HR)	n.k.	GRS	Abawi and Robinson (1991) Kaur and Mitkowski (2010)
	<i>L. virosa</i>	PI 273579, PI 271938, PI 273597 (M-HR)	n.k.	GRS	Abawi and Robinson (1991) Kaur and Mitkowski (2010)
<i>M. incognita</i>	<i>L. serriola</i>	n.s.	n.k.	FO, highly susceptible species WGT, highly susceptible to race 1	Gaskin (1958) Gharabadiyan et al. (2012)
	<i>L. saligna</i>	n.s.	n.k.		Rich et al. (2010)
	<i>L. saligna</i> var. <i>runcinata</i>	n.s.	n.k.	WGT, host species	Gowda et al. (1995)
<i>M. javanica</i>	<i>L. serriola</i>	n.s.	n.k.	WGT, highly susceptible	Gharabadiyan et al. (2012)
<i>Paratrichodorus allius</i>	<i>L. serriola</i>	n.s.	n.k.	host species for <i>P. allius</i> (vector for tobacco rattle virus)	Boydston et al. (2004) Mojtahedi et al. (2003)
<i>Pratylenchus neglectus</i>	<i>L. serriola</i>	n.s.	n.k.	WGT	Vanstone and Russ (2001)
<i>P. thornei</i>	<i>L. serriola</i>	n.s.	n.k.	WGT	Vanstone and Russ (2001)

Explanation of terms used in the table: *FO* field observation; *GRS* germplasm resistance screening in greenhouse; *M-HR* moderate-highly resistant genotype; *n.k.* not known; *n.s.* not specified; *WGT* weed greenhouse testing

weed hosts was investigated by Gowda et al. (1995), who reported light root gall intensity and small size of galls indicating resistance to *Meloidogyne incognita*. Davis and Venette (2004) considered *Meloidogyne falax* as potential risk (potential hosts) for several threatened and/or endangered wild *Lactuca* species (*L. floridana*, *L. hirsuta*, *L. tatarica* var. *pulchella*).

The information on the genetic basis of nematode resistance in wild *Lactuca* species is missing. In cultivated lettuce the resistance genes for *Meloidogyne* appears to be under control of a single gene locus, with predominantly additive gene action (for *M. incognita* races 1, 2, 3 and 4, and *M. kabanica*) (Gomes et al. 2000; Maluf et al. 2002; Cavalhi Filho et al. 2008). On the other hand de Carvalho et al. (2011)

proved that two different genes are involved in control of resistance to *M. incognita* race 1 in lettuce cultivars Grand Rapids and Salinas-88. Further, they reported that lines with higher levels of nematode resistance than either Grand Rapids or Salinas-88 could be selected in the F4 generation of the cross between these resistant parental lines indicating that the two parental cultivars possess different genetic factors for resistance.

There are also reports on transgenic lettuce lines bearing tomato root-knot resistance gene *Mi-1* (Zhang et al. 2010) and the linkage of tomato resistance genes to root-knot nematode (*Meloidogyne* spp) to leaf mold (*Cladosporium fulvum*) (Dickinson et al. 1993; Jones et al. 1993).

## Insects and mites

There are a number of aphid species, occurring both on cultivated lettuce and its wild relatives, these belong to the following genera—*Acyrtosiphon*, *Aulacorthum*, *Aphis*, *Dysaphis*, *Hyperomyzus*, *Macrosiphum*, *Myzus*, *Nasonovia*, *Neomyzus*, *Pemphigus*, *Protrama*, *Sitobion*, *Trama*, *Uroleucon* (Blackman and Eastop 2000), *Eucarazzia* (Stoetzel 1985) and *Rhopalosiphum* (Sangün and Satar 2012). However, we present here a review of papers using wild lettuce species as parents for resistance breeding to three aphid species—the green lettuce aphid (*Nasonovia ribisnigri*), the potato aphid (*Macrosiphum euphorbiae*) and lettuce root aphid (*Pemphigus bursarius*) and the leafminer (*Liriomyza langei*). There are other important aphid species (e.g. *Myzus persicae*, the green peach aphid, possibly the most important leaf-feeding pest on lettuce because of its ability to transmit several important viruses - see above), however no information related to resistance screening studies (or breeding) using wild lettuce species has been published so far. For a detailed survey of occurrence of various aphid species on other *Lactuca* spp. (see Blackman and Eastop 2000).

*Nasonovia ribisnigri* Mosley [the „green lettuce aphid“(GLA) or „currant-lettuce aphid“(CLA)] is commercially the most important lettuce pest (Martin et al. 1996) with a worldwide distribution (Blackman and Eastop 2000). It colonizes the interior of the lettuce head, making its control difficult both with contact insecticides (Liu 2004) and biological control (Mackenzie and Vernon 1988). The use of resistant cultivars is therefore the best option to protect lettuce from this pest. Resistance to biotype 0 (Nr:0) was first reported in *Lactuca virosa* accession IVT 280 (Eenink et al. 1982a,b) and characterized as complete (i.e. virtually no aphids survived), and genetically dominant to the partial resistance found in *L. virosa* accession IVT 273. Complete and partial resistances to Nr:0 were conditioned by two alleles, *Nr* (complete resistance) and *nr* (partial resistance). McCreight and Liu (2012) proposed the following system of allelic designation: *Nr:0<sup>C</sup>* for complete resistance and *Nr:0<sup>P</sup>* for partial resistance, with their relationships: *Nr:0<sup>C</sup>* (in IVT 280, ‘Barcelona’) > *Nr:0<sup>P</sup>* (in PI 491093) > *nr* (in susceptible genotypes) (McCreight and Liu 2012).

Subsequently, resistance in IVT 280 was successfully transferred to lettuce by a bridging cross to *L. serriola* (e.g. Eenink et al. 1982a, b; van der Arend et al. 1999). There

are a large number of modern lettuce cultivars with GLA resistance e.g. cvs. Barcelona, Campionas, Dynamite, Elenas, Fortunas, Irina, Krinas, Veronas, 83-67RZ (van der Arend et al. 1999; Liu and McCreight 2006) and in 2010 there were 88 commercially available lettuce varieties in Australia (McDougall and Troidahl 2010), produced by several breeding companies including: RijkZwaan, Nunhems, South Pacific Seeds, Lefroy Valley, Seminis Vegetable Seeds, Terranova Seeds. However, this widespread deployment of a single dominant gene for resistance has exerted a high selection pressure for the emergence of a resistance breaking phenotype and several *N. ribisnigri* populations feeding on resistant cultivars were detected in 2007. These were subsequently characterized as a resistance-breaking biotype of *N. ribisnigri* designated Nr:1 (Sauer 2008). This biotype has spread throughout the European continent (Cid et al. 2012).

Wild progenitors of cultivated lettuce appear to be a valuable source of resistance to GLA, as evident from the results of recent large germplasm screenings. McCreight (2008) identified two new potential sources for resistance to Nr:0 in *L. serriola* acc. PI 491093 (partial resistance) and *L. virosa* PI 274378 (complete resistance). This was a result of a large greenhouse screening of 1203 lettuce accessions (included 7*L. perennis*, 18*L. saligna*, 125*L. serriola*, and 6*L. virosa* accessions). Sixty-four *L. serriola* and *L. virosa* accessions (see Table 9) resistant to Nr:1 were reported in CGN germplasm collection (the Center for Genetic Resources, the Netherlands) (Anonymous 2008). For some of these (CGN13361, CGN16266, CGN16272), all five replicate plants were resistant while in other accessions (CGN04757, CGN04930, CGN04973) resistance segregated in the tested plants. Several accessions were resistant to both Nr:0 and Nr:1 (Anonymous 2008). Dominant resistance to Nr:0 and Nr:1 was also reported to have been found in the *L. serriola* accession 10G.913571 by Thabuis et al. (2011).

More recently, Cid et al. (2012) performed two tests: a greenhouse screening of 264 lettuce accessions including 40 accessions closely related to *L. sativa* (3*L. perennis*, 6*L. virosa*, 13*L. serriola* and 18*L. sativa* × *L. serriola*) and laboratory screening of 40 *L. virosa* accessions against both *N. ribisnigri* biotypes (Nr:0, Nr:1) and against a clone of *M. euphorbiae*. Three *L. virosa* accessions showed (Table 9) resistance against *N. ribisnigri*, two (CGN16272 and CGN13361) partial resistance to the Nr:1 biotype of *N. ribisnigri* and to *M. euphorbiae*. While near complete resistance to *M.*



**Table 9** Resistance of wild *Lactuca* species to aphids

Name of aphid	Source of resistance		Type of resistance	Remark	References
	<i>Lactuca</i> spp.	No. of accession/sample			
<i>Liriomyza langei</i>	<i>L. serriola</i>	PI 491178, PI 491181, PI 274901	R		Mou and Liu (2003, 2004)
	<i>L. saligna</i>	PI 490999, PI 261653-1, PI 509525	R		Mou and Liu (2003, 2004)
	<i>L. virosa</i>	PI 273597, PI 274375, PI 274901	R		Mou and Liu (2003, 2004)
<i>Macrosiphum euphorbiae</i>	<i>L. serriola</i>	n.s.	n.k.		Blackman and Eastop (2000) Barbosa (1998)
	<i>L. virosa</i>	CGN13355 CGN16272, CGN13361	HR PR		Cid et al. (2012) Cid et al. (2012)
<i>Nasonovia ribisnigri</i>	<i>L. serriola</i>	PIVT 252	S		Eenink and Dieleman (1983)
		PI 491093	R, psr		McCreight (2008) McCreight and Liu (2012)
		CGN04757, W6 21998	PR		Cid et al. (2012)
	<i>L. virosa</i>	PI 274378	R, psr		McCreight (2008)
		PIVT 273	PR		McCreight and Liu (2012)
		PIVT 275, PIVT 278, PIVT 280, PIVT 714, PIVT 731, PIVT 72723	CR		Eenink and Dieleman (1983) McCreight and Liu (2012)
		CGN13361	PR		Cid et al. (2012)
	<i>L. virosa</i> × <i>L. serriola</i>	CGN16272	PR	R to Nr:1	Cid et al. (2012)
		CGN13355, CGN16266, W6 23867	CR		Cid et al. (2012)
		CGN05148, CGN21399	CR	R to Nr:1	Cid et al. (2012)
CGN13361, CGN16266, CGN16272		R	R to Nr:0, Nr:1	Anonymous (2008)	
F1 (F1 (73723×255)×F1 (255×Suzan)) ×F1 (F1(254×280)×1037)		CR		Eenink et al. (1982b) Reinink and Dieleman (1989)	
CGN10885, PI 274378		CR, PR		Cid et al. (2012)	
<i>Pemphigus bursarius</i>	<i>L. serriola</i>	001562, HRIGRU1606, HRIGRU1573, HRIGRU7145	R		Cole et al. (1991)
	<i>L. saligna</i>	006186, 001627, HRIGRU1630	R		Cole et al. (1991)
	<i>L. virosa</i>	n.s.	HR		Cole et al. (1991); Ellis et al. (2002)
	<i>L. perennis</i>	n.s.	HR		Ellis et al. (2002)

Explanation of terms used in the table: *CR* completely resistant; *HR* highly resistant; *PR* partially resistant; *R* resistant; *S* susceptible; *n.k.* not known; *n.s.* not specified; *psr* potential source of resistance

*euphorbiae* was found in CGN13355 but this was susceptible to *N. ribisnigri* (Cid et al. 2012).

The „lettuce root aphid“ (LRA), *Pemphigus bursarius* (L.) is one of several aphid species that feed on cultivated lettuce (Blackman and Eastop 2000) and can cause severe damage to crops (Dunn, 1959). It is considered as an occasional pest of lettuce crops but can also cause severe losses in lettuce seed production. Additionally, it is able to colonise a variety of non-crop species, largely within the Compositae (Dunn 1959; Alleyne and

Morrison 1977). This aphid is regarded as holocyclic, alternating annually between sexual reproduction on a primary woody host, poplar (*Populus nigra*, L.) and parthenogenesis on its secondary hosts such as lettuce (see Dunn 1959; Miller et al. 2003, 2008). Lettuce root aphid is one of the first examples of successful insect resistance breeding in vegetable crop (Reinink 1999). As the most effective control of root aphids, highly resistant cultivars eliminating the aphid colonisation on lettuce roots. This resistance is controlled by one or two

genes as described by Ellis et al. (1994, 2002). At least one of these genes is not allelic to the existing *Lra* gene, which can be linked to downy mildew resistance gene DM6 (e.g. linked in cv. Avonscrisp but not in cv. Lakeland). There is only a single paper focussed on LRA resistance screening in germplasm collections by Ellis et al. (2002). This describes the testing of 55 *Lactuca* spp. accessions for resistance to *P. bursarius* and the identification of extremely high levels of resistance in accessions of the wild species *L. saligna*, *L. perennis*, *L. virosa*, and in the variety Grand Rapids. Cole et al. (1991) described the use of allozyme analysis to detect bands related to LRA resistance in a screening of four *Lactuca* species (*L. serriola*, *L. virosa*, *L. saligna* and primitive *L. sativa*, eight accessions per species). Out of the forty samples tested, only ten accessions were resistant to colonisation by the pest (*L. serriola*—001562, HRIGRU1606, HRIGRU1573, HRIGRU7145; *L. saligna*—006186, 001627, HRIGRU1630 and *L. sativa* 006779, 001886, 006612).

Leafminer (*Liriomyza langei* Frick) is a major insect pest of many important agricultural crops including lettuce (Mou and Liu 2003, 2004; Lebeda et al. 2007c). Successful breeding for resistance to leafminer in lettuce was reported by Mou and Ryder (2010). However, studies exploring genetic variation of leafminer resistance in lettuce germplasm, including wild progenitors, are limited (Mou and Liu 2003, 2004). Also the mechanism of leafminer resistance in lettuce is unknown (Mou and Liu 2004). Mou and Liu (2003) performed screening of 46 *Lactuca* accessions, including 2 accessions of *L. serriola*, 1 acc. of *L. saligna*, and 1 acc. of *L. virosa*. High levels of resistance were discovered in these wild genotypes. In a subsequent study by Mou and Liu (2004) fifty-four lettuce genotypes and 232 F<sub>2</sub> plants of crosses were evaluated for leafminer resistance, again a significantly lower occurrence of leafminers were found on the accessions of the wild species (*L. serriola*, *L. saligna*, and *L. virosa*) compared to the cultivars.

### Approaches to exploitation of wild *Lactuca* spp. in lettuce resistance breeding

#### Interspecific hybridization

Autogamy is the predominating breeding system within the genus *Lactuca*, especially in the marginal parts of its distribution area (Feráková 1977). Stebbins (1957)

estimated a higher occurrence of allogamy in the centre of distribution. Lindqvist (1960) proved experimentally that all species belonging to the “*serriola*” group were self-fertile. Spontaneous cross-pollination occurs through activity of various insect from the Hymenoptera and Diptera groups (Feráková 1977). In the commercial seed production of *L. sativa*, up to 5 % of cross-pollination has been observed (George 1999). Hybridization can occur not only within one species, but also between species. *Lactuca altaica* hybridizes spontaneously with *L. saligna* and *L. serriola*; *L. aculeata* hybridizes with *L. sativa* and with *L. serriola*; *L. serriola* hybridizes with *L. dregeana* (Zohary Zohary 1991). The close relationship of *serriola*-like species *L. serriola*, *L. dregeana*, *L. altaica*, and *L. aculeata* to *L. sativa* is supported not only by the same chromosome number but also by molecular (AFLP) markers (Koopman et al. 1998, 2001), and by DNA content (Koopman 2002).

Hybridization data on the species belonging to the different sections or groups of the genus *Lactuca* are limited to *L. viminea* and *L. tatarica*. Groenwold (1983) reported partly fertile hybrids between *L. viminea* (section *Phoenixopus*) and *L. virosa* (section *Lactuca*).

#### Natural hybridization

D’Andrea et al. (2008) proved in a field experiment conducted in Switzerland that natural hybridization between lettuce and *L. serriola* occurred up to the maximal distance tested (40 m), and hybridization rates varied between 0 to 26 %, decreasing with distance. More than 80 % of the wild plants produced at least one hybrid at within 1 m and 4 to 5 % at 40 m. In sympatric crop-wild populations, cross-pollination between cultivated lettuce and its wild relative has to be seen as the rule rather than the exception for short separation distances. However, in the northern parts of Europe, where expansion of prickly lettuce (*L. serriola*) took place, only a few putative hybrids with *L. sativa* were found. So, very probably mechanisms other than crop/wild gene flow, such as those connected to the human activities around building and transport are more likely explanations for this phenomenon (Hooftman et al. 2009; Uwimana et al. 2012a).

The phenotype of putative natural interspecific hybrids was recorded for primarily self-pollinated *Lactuca* species acquired during collecting missions in natural habitats: *Lactuca serriola* ( $\times$  *L. sativa*) acquired from natural populations *L. serriola* f. *serriola* in northern

Moravia in the year 1995 (Křístková et al. 2012). The hybrid character of plants *L. aculeata* ( $\times$  *L. serriola*) from a natural population *L. aculeata* collected in Israel in 2005 was confirmed by allozyme markers (Lebeda et al. 2012b). Hybrid characteristics of *L. saligna* ( $\times$  *L. serriola*) were observed on plants raised from *L. saligna* achenes collected in Jordan in 2007. Putative hybrid plants showed a low level of self-fertility (Křístková et al. 2012). The molecular profile of plants of *L. serriola* collected in Israel in 2009 suggests natural hybridization of *L. serriola* ( $\times$  *L. saligna*) (Křístková et al. 2012).

The phenotype of interspecific hybrids was recorded also on several *Lactuca* spp. accessions obtained from world germplasm collections. Species *L. sativa*, *L. serriola*, *L. saligna*, *L. dregeana* and *L. virosa* probably participated in the hybridization (Doležalová et al. 2007).

### Managed hybridization

Hybridization experiments have been used to: reveal evolutionary relations among *Lactuca* species (de Vries 1990) and aspects of domestication process of lettuce; serve as a base for plant genetic resources management (van de Wiel et al. 2010) and the practical application in breeding programmes; and recently for the assessment of ecological risk of transgenes (Giannino et al. 2008; Hooftman et al. 2011).

Three approaches are employed in order to prevent self-pollination and to perform sexual hybridization: manual removal of anthers, spraying with water of the self-pollen from the stigma prior the cross-pollination, and the exploitation of male-sterile lines as pollen recipients (Davey and Anthony 2011). Examples of interspecific hybridization with potential economic impact are given in this paper below in following chapters.

Hybridization experiments of lettuce with *L. serriola* and QTL analysis identified genomic regions with major QTL effects important for breeding programmes and plant transformation (Hartman et al. 2012, 2013a). Hartman et al. (2013b) show that there is a high likelihood in lettuce for novel crop-wild hybrids to arise with a higher fitness than the wild parent through combination of heterosis, linkage and transgressive segregation.

The genomic analysis of plants derived from the hybridization of *L. sativa* $\times$ *L. serriola* and their backcrosses proved that the domesticated parent contributed QTLs with either a positive or a negative effect on plant vigour, and there are genomic locations where transgenes could

be preferably located to mitigate (reduce) their persistence in natural populations in occasional crop-wild hybridization (Uwimana et al. 2012b, c).

Interspecific hybrids between the species with a low sexual compatibility have been obtained by using a bridging species (e.g. *L. serriola*) i.e. crossing one parent to the bridging species and then crossing the resultant F1 with the other parent (Thompson and Ryder 1961; Eenink et al. 1982b; Lebeda et al. 2007c).

### Cell and tissue culture

Tissue culture based procedures for the regeneration of fertile plants from tissue explants, cells and isolated protoplasts technologies are the basis for their exploitation in lettuce improvement. Techniques and approaches used for in vitro culture of lettuce have been reviewed thoroughly (e.g. Michelmore and Eash 1986; Alconero 1988; Pink and Keane 1993; Davey et al. 2007a, b; Lebeda et al. 2007c), however there is no recent reports of tissue culture technologies exploring wild *Lactuca* species in lettuce improvement.

In vitro rescue of immature embryos was used successfully for sexual hybridization between *L. sativa* and *L. virosa* (Maisonneuve et al. 1995; Maisonneuve 2003).

Protoplast fusion permitted the regeneration of somatic hybrids between *L. sativa* and either *L. tatarica* or *L. perennis* (Chupeau et al. 1994; Maisonneuve et al. 1995). Somatic hybrids between cultivated lettuce and *L. virosa* were produced by protoplast electrofusion (Matsumoto 1991). Hybrids had normal flower morphology, but all were sterile. *L. indica* (section *Tuberosae*) can be somatically hybridized with *L. sativa* to produce a viable callus (Mizutani et al. 1989).

So far, fertile interspecific hybrids have only been produced between species *L. sativa* (section *Lactuca*) and *L. tatarica* (section *Mulgedium*) by using somatic hybridization (Chupeau et al. 1994; Maisonneuve et al. 1995).

### Transformation

During the last 10 years, there are numerous reports on the gene introduction into lettuce by transformation (Davey et al. 2002, 2007a, b; Klocke et al. 2010). *Agrobacterium* inoculation of leaf explants is a universal approach for inducing genes into lettuce, and although this approach has been focused, to date, on *L. sativa*, wild *Lactuca* species could be exploited in a similar way (Davey and Anthony 2011).

Transformation of the plastid genome has several advantages over conventional nuclear transformation, mainly by the high level of transgene expression in chloroplasts, this is opening new possibilities for metabolic engineering, resistance management, and production of biopharmaceuticals (Davey and Anthony 2011). Plastid transformation was applied on the lettuce cv. ‘Cisco’ (Kanamoto et al. 2006) and cv. ‘Grand Rapid’ (Pileggi et al. 2001).

There are two ways that transgenic approaches could allow better access to the tertiary gene pool (*L. virosa*, *L. saligna* and others). One way would be through directly transforming *L. sativa* with characterized genes from wild species. The second method is less direct, and would be used in conjunction with somatic hybridization techniques. Transformation would be used to create a universal hybridizer by combining dominant antibiotic resistance and recessive albinism markers in the same genotype (Chupeau et al. 1994). Another potentially valuable use of this technology is to increase or decrease the expression of endogenous genes, or genes already present within cultivated lettuce.

Construction of transgenic plants follows various aims, e.g. production of vaccines, ascorbic acid, tocopherols, increase of iron uptake, decrease of nitrate accumulation, as reviewed by Davey and Anthony (2011) and Davey et al. (2002), Lebeda et al. (2007c), to induce the herbicide resistance (McCabe et al. 1999; Mohapatra et al. 1999; Torres et al. 1999; Dubois et al. 2005) or to delay leaf senescence (McCabe et al. 2001).

Transgenic male-sterile plants are valuable as recipient of donor pollen during hybridization (Curtis et al. 1996; Takada et al. 2007).

Viral genes to confer LMV resistance have been introduced into lettuce (Dinant et al. 1993; Dinant 1997; Gilberton, 1996). Kawazu et al. (2009, 2010) generated lettuce plants resistant to LBVaV, MLBVV by introducing coat protein in anti-sense orientation.

The cloning of genes (*Dm3*) for resistance to the lettuce downy mildew (*Bremia lactucae*) performed by Okubara et al. (1997) have led to clarification of the molecular basis of resistance to this pathogen,

Despite the potential value of some of these traits, no transgenic lettuce has yet been commercialized. In some cases the transgenes did not have the expected desirable effects on the plant phenotype possibly due to gene silencing mechanisms such as methylation (Dinant et al. 1993; McCabe et al. 1999). However, the main reasons for the lack of commercial application

of GM technology in lettuce is due to the currently high costs associated with the regulatory procedures for release of a transgenic cultivar and a worldwide lack of public acceptance of the technology in a fresh vegetable crop. Biotechnology-derived vegetables, including lettuce, will only succeed if clear advantages and safety are demonstrated to both growers and more importantly to consumers (Dias and Ortiz 2012a, b).

## Mutations

Induced mutation has led to the creation of lettuce lines with interesting traits, like dwarfing, early flowering, male sterility or herbicide tolerance (Mou 2011b). Lettuce mutants are useful in genomic studies of resistance to *Bremia lactucae*, and for gene cloning; combined with genomic advances and new technologies like TILLING (targeted induced local lesions in genome), mutagenesis is becoming more useful tool for lettuce breeders (Mou 2011b).

## Known examples of lettuce cultivars issued from exploitation of wild *Lactuca* spp.

Lettuce breeders have increased genetic diversity and achieved disease resistance through crossing cultivated lettuce with non-cultivated or wild lettuce types (Mikel 2007). Breeding aims, strategies and issues have been reviewed by Ryder (2001). Reviews of wild *Lactuca* species used in the lettuce breeding and description of breeding approaches and methods were given by Lebeda et al. (2007c), Mou (2008), and Davey and Anthony (2011).

Lebeda and Blok (1991) reported downy mildew resistance in the hybrid of *L. sativa* × *L. serriola*. More details about this and the historical consequences about the influence of *L. serriola* on lettuce resistance breeding to *B. lactucae* were summarized by Lebeda et al. (2002).

*Lactuca saligna* is known to produce hybrids with *L. sativa* and *L. serriola* when used as the female parent (Pink and Keane 1993). *L. saligna* was crossed to a cultivated iceberg type by R.W. Robinson (Provvidenti et al. 1980) who developed the cultivar ‘Salad Crisp’ from that cross. Jeuken and Lindhout (2004) developed backcross inbred lines in which chromosome segments from *L. saligna* were introgressed into cultivated lettuce and used for genetic analysis of resistance to *Bremia lactucae*.

Crosses between *L. sativa* as one parent and *L. virosa* as the other parent are made with a great difficulty, resulting in low seed set, unviable seeds, stunted plants and/or sterile hybrids (Lindqvist 1960). Viable hybrid plants were obtained only when *L. serriola* was used as a bridging species (Thompson and Ryder 1961; Eenink et al. 1982b). In 1958, the cultivar Vanguard was developed from a cross between a *L. sativa* × *L. serriola* which was then crossed to *L. virosa*. However, with some manipulations, crosses have been made and have led to development of cultivars (Ryder 1999).

During at least the last two decades there has been an increasing private sector breeding effort in lettuce cultivar development with a concomitant decrease in public sector breeding in many countries. In the USA the legal protection of cultivars is accomplished by their registration supplemented by their pedigree which are made publically available (Mikel 2007), in contrast to lettuce cultivars bred in Europe where such pedigrees are not released in to the public domain.

The pedigree analysis of 328 proprietary and publicly developed lettuce cultivars registered in the USA from 1970 through to 2004 showed that 1 % of these cultivars were developed from interspecific crosses (Mikel 2007). Three wild *Lactuca* species, *L. serriola*, *L. saligna* and *L. virosa* were involved in this process (Mikel 2007). A further analysis of pedigree history of 146 lettuce cultivars registered in the U.S. by Plant Variety Protection and/or utility patent of the era from 2000 through 2010 have led to the determination of a coefficient of parentage among these cultivars (Mikel 2013). Among three crisphead lettuce ancestors, cultivars ‘Vanguard’ and ‘Salinas’ descend from the interspecific cross of *L. sativa* with *L. virosa* and *L. serriola*. Among these three cultivars, ‘Vanguard’ is the major ancestor contributing 23.8 % of the genes to crisphead lettuce. Cultivars ‘Vanguard’ and ‘Salinas’ followed by the cultivar ‘Calmar’ (which has no *L. virosa* in its ancestry) were determined as elite programme cultivars, frequently used in lettuce breeding (Mikel 2007). Of the 37 progenitor cultivars, breeders at public institutions and private companies in the USA developed 31 new cultivars in the period of 1970–2004, and ten of these progenitors of today’s lettuce germplasm were developed before 1960 (Mikel 2007). The cultivar ‘Salinas’ was frequently crossed with romaine lettuce types and the romaine parental cultivar ‘Paris Island Cos’ was crossed with leaf types contributing to romaine and leaf lettuce genetic diversity (Mikel 2013).

Pedigree analysis of 146 lettuce cultivars registered in the USA in the period 2000–2010 demonstrated that leaf lettuce cultivars were more genetically diverse than romaine and crisphead cultivars (Mikel 2013). The lower diversity among romaine and crisphead cultivars is due to recurrent recycling of related cultivars in breeding programmes (Mikel 2013). This however, means that the percentage of cultivars possessing genes from wild species given above are likely to be underestimates as many modern day cultivars will have gained such genes through this recycling of parental cultivars most of which will have Vanguard and/or Salinas in their pedigrees both of which possess *L. virosa* genes.

### Conclusions and future prospects

Lettuce (*Lactuca sativa*) is one of the oldest domesticated plants and vegetable crops (Hancock 2012). However, our knowledge about the origin, process of domestication, diversification and spread of lettuce around the globe is still quite fragmentary (Lebeda et al. 2007c). The genus *Lactuca* L. comprises approximately 100 wild species, however, detailed information about the biogeography and ecobiology of most of these species is not available (Lebeda et al. 2004b, 2007c, 2009a, 2012a). The taxonomy of wild *Lactuca* species and related genera is currently unclear (Lebeda et al. 2007c; Funk et al. 2009), and needs more detailed elaboration at the level of the genus, involving all known described species (Lebeda et al. 2007c, 2009a). Also the collection, conservation and evaluation of wild *Lactuca* germplasm is incomplete. Most (ca 90 %) of the currently available wild *Lactuca* genetic resources in world genebank collections is represented by accession of only three species (*L. serriola*, *L. saligna*, *L. virosa*) originating mostly from Europe and from the primary center of origin (Lebeda et al. 2004a, 2007c, 2009a, b). Although some collections have been made for example in the territory of North America (Lebeda et al. 2011, 2012a) in general, field studies and collecting activities have been reduced and neglected in the last few decades (Lebeda et al. 2009a). In some areas of the world (Africa, Asia) local landraces are still grown but the breeding and widespread marketing of modern cultivars often on a regional basis by multinational companies is leading to a loss of genetic diversity and local adaptation in the crop (Lebeda et al. 2007c). For many traits (e.g. *Bremia* resistance) extensive screening for new

resistance genes/factors in gene bank accessions of the cultivated crop has led to a diminishing return in terms of new resistances. This is leading to an increase in the use of wild *Lactuca* species germplasm as sources of new beneficial alleles for a range of valuable characters for future breeding progress (Lebeda and Boukema 2005).

Lettuce is one of the main horticultural crops where a strategy of wild related germplasm exploitation and utilization in breeding programmes is most commonly used with very high practical impact. During the last 70 years, the genus *Lactuca* has been intensively studied with respect to exploitation of wild relatives in commercial lettuce breeding (Pink and Keane 1993; Lebeda et al. 2007c; Mou 2008). In the last three decades, significant progress has been made in germplasm enhancement and the introduction of novel traits into cultivated lettuce, mostly from the primary lettuce gene-pool, however more recently the secondary and tertiary gene-pools have been accessed, particularly for disease and insect resistances (Lebeda et al. 2007c, 2009a). Unfortunately, the process of resistance breeding is complicated because the variation in host plant resistance is mirrored by the diversity (emergence of new different strains, pathotypes and races) within pathogen/pest populations (Lebeda et al. 2007c). Nevertheless, as is evident from this review, wild *Lactuca* germplasm are being increasingly studied and used in lettuce breeding. Valuable sources of resistance have been located in many accessions of different *Lactuca* species and successfully introduced to recent commercial lettuce cultivars. However, despite the progress that has been made, there are still many questions and problems which must be solved by close cooperation between plant scientists, ecologists, plant pathologists, geneticists and lettuce pre-breeders and breeders.

Current areas of weakness are the lack of detailed floristic, bio-geographic and ecologic delimitation of the distribution of known *Lactuca* spp., and few recent collecting and exploration missions, especially to the areas of high species richness and diversity (e.g. South Africa and Asia) (Lebeda et al. 2009a). Such activities need to be linked with detailed observations and recording of the occurrence of diseases and pests on weedy growing *Lactuca* species (e.g. Lebeda et al. 2008a, 2011, 2012a, 2013) to provide a better understanding of host-pathogen/pest interactions in natural habitats and aid the exploitation of wild *Lactuca* germplasm in lettuce resistance breeding.

Another relatively under researched area is the agro-ecological interface (Burdon and Thrall 2008), i.e. interactions between wild (weedy growing *Lactuca* spp.) and crop (lettuce, *Lactuca sativa*) pathosystems. For *Lactuca* spp. and lettuce this has only really been considered for interactions with *Bremia lactucae* (Lebeda and Petřelová 2004; Lebeda et al. 2002, 2008a) and *Golovinomyces cichoracearum* (Lebeda and Mieslerová 2011; Lebeda et al. 2012c, 2013). This type of knowledge may yield a better understanding about the maintenance of a dynamic balance (homeostasis) between hosts and pathogens in wild pathosystems which could inform deployment strategies for resistance genes in the cultivated crop as well as identify the potential risks of pathogen transfer from wild to crop pathosystems from the viewpoint of potential breakdown of resistance introduced to lettuce from wild *Lactuca* progenitors as demonstrated by the example of *Lactuca serriola*/L. *sativa*-*Bremia lactucae* interactions studied by Lebeda et al. (2008a). In addition the potential transfer of genes from lettuce to weedy growing *Lactuca* species (Hartman et al. 2012; Uwimana et al. 2012a, b) should be investigated from the viewpoint of stability of both the wild and cultivated systems.

From this review, and previous reports (Lebeda et al. 2007c, 2009a), it is clearly evident that wild *Lactuca* germplasm are highly valuable sources of genetic variation and resistance to different biotic stresses. However, it is also evident that current knowledge about these interactions is fragmentary covering only a limited part of the potential variation in the host-pathogen/pest interaction. This can be addressed by screening large collections of well defined wild *Lactuca* germplasm for resistance to the most important lettuce pathogens and pests, followed by detailed genetical studies of the inheritance of resistance. Where knowledge of pathogen effectors is available these can be substituted for the pathogen isolates, with the aim of finding recognition factors which recognise effectors which are highly conserved within the pathogen population. However, again knowledge of the variation in effectors in wild *Lactuca* spp./pathogen interactions is necessary to inform this strategy.

One of the main goals of current lettuce breeding is multiple disease and pest resistance. A detailed characterisation of wild *Lactuca* germplasm resistances can contribute to this goal. At least some *Lactuca* accessions have been shown to possess multiple resistances which can be introduced to cultivated lettuce and

combined with agronomically important traits. The use of wild *Lactuca* spp. as sources of resistance has been hampered in the past by loss of quality characteristics, this has been particularly problematic when ‘poor’ quality loci have been linked to resistance loci e.g. stunting linked to *Nasonovia* resistance. However, many lettuce breeding companies have now addressed this by instigating ‘pre-breeding’ programmes which aim to produce resistant lines of sufficient quality to be included in a commercial lettuce breeding programme. The use of markers to select for recombinants where undesirable linkages have been broken has been a great step forward in this respect.

New technologies and knowledge offer new ways to screen germplasm collections for novel alleles. Currently 52 phenotypic loci that confer resistance in lettuce to 8 diseases (*Bremia lactucae*, *Sphingomonas suberifaciens*, *Microdochium panattonianum*, *Fusarium oxysporum* and *Verticillium dahliae*, lettuce root aphid, lettuce mosaic virus, and lettuce big vein) have been reported as being mapped in lettuce. For some of these diseases candidate genes have been identified and causality demonstrated for a subset of them using RNAi (Truco et al. 2013). This opens up a new more efficient strategy for assessing the value of *Lactuca* germplasm through resequencing to identify allelic variation to provide a library of alleles which can then be tested against the variation present in the pathogen either in the form of diverse isolates or where available, effectors. Those alleles which determine resistance against a broad spectrum of the variation in individual pathogens can then be combined using MAS to produce advanced breeding lines with multiple resistance (Michelmore 2013, pers. commun.).

In addition to the combination and pyramiding of race-specific resistance genes/factors (Lebeda et al. 2002; Pink 2002), exploitation of non-host resistance in lettuce breeding remains a challenge (Lebeda et al. 2002). In relation to lettuce non-host resistance was hypothesised for first time in the response of *Lactuca saligna* to infection by *Bremia lactucae* (Lebeda 1986). *L. saligna* is sexually compatible with *L. sativa* (Lebeda et al. 2007c). The concept of non-host resistance in *L. saligna* was later studied in detail from a mechanistic and population viewpoint (see e.g. Lebeda et al. 2002, 2008b; Petrželová et al. 2011), as well as a genetical viewpoint (Jeuken et al. 2008, 2009; Zhang et al. 2009). This resistance is hypothesised to be durable (Lebeda et al. 2002). However, the use of this

type of resistance in lettuce breeding is still at the early stages and requires further research to develop the tools and knowledge for its exploitation (Jeuken 2012).

Future developments in methodology of interspecific hybridization, as well as transfer of resistance genes are playing important role in accessing the genetic variation present in wild *Lactuca* germplasm collections (Lebeda et al. 2007c; Davey and Anthony 2011). Both conventional breeding and genetic manipulation approaches will be very likely applied for the improvement of the crop. Conventional breeding augmented by marker assisted selection will continue to play a key role in the introgression of genetic material from wild *Lactuca* species into cultivated lettuce, particularly where quantitative resistance under the control of several loci is involved or where the aim is to pyramid several resistance genes. Somatic hybridization will enable novel nuclear-cytoplasmic combinations, and the introgression of beneficial alleles from wild *Lactuca* species which are sexually incompatible with lettuce (Davey and Anthony 2011). Improvements in transformation technologies are opening up the possibilities of deploying resistance genes in multilines to provide a more durable resistance crop phenotype as described by Pink and Puddephat (1999) and Pink (2002).

It is also evident that our knowledge of the mechanisms of resistance in various *Lactuca*-pathogen/pest interactions is limited. Only in a few plant-pathogen interactions (e.g. *Lactuca*-*Bremia lactucae*) is more detailed information about the type and mechanism of resistance, including features of inheritance available (Lebeda et al. 2002, 2008b). For many lettuce/disease interactions the basic information about the type of resistance (non-host versus host, race-specific vs. race-nonspecific, field or durable resistance etc.) is not available. Again this knowledge will improve our efficiency in exploiting the *Lactuca* gene pool for lettuce crop improvement and allow the combination of different resistance mechanisms in a single cultivar in order to provide a potentially more durable resistance phenotype.

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