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PHENOTYPIC VARIABILITY OF GENETIC RESOURCES OF *LACTUCA* L., THEIR ECOBIOLOGY AND EXPLOITATION

PH.D. THESIS
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Abstract:

This Ph.D. thesis is focused on five various topics related to the *Lactuca* spp. germplasm, their phenotypic variation and ecobiology, as well as utilization in lettuce breeding. The first one is the development of *L. sativa* descriptor with 55 morphological characters created on the base of long-lasting observations of morphological and phenological variability of lettuce. The main topic is the study about morphological variability of achenes of *Lactuca serriola* L. (prickly lettuce) genetic resources in relation to different eco-geographical conditions. We evaluated achenes of *L. serriola* populations originating from six countries (Czech Republic, Germany, the Netherlands, United Kingdom, Slovenia, Sweden). Totally 8 quantitative morphological features relating to the achene body and pappus were searched. According to the achene morphology is possible to distinguish both *L. serriola* forms (f. *serriola* and f. *integrifolia*). Achenes of f. *serriola* are shorter, thinner, with shorter beak, lower length/width index and higher number of ribs in comparison to f. *integrifolia*. High significant differences between Slovene and Swedish populations were found in case of length and width of body, length of pappus bristles and pappus area. Significant positive and negative correlations were found between evaluated morphological features and studied eco-geographical factors. Based on morphology of *L. serriola* leaves, which is the third topic, only *L. serriola* f. *serriola* was recorded in Czech populations, whereas in United Kingdom forma *integrifolia* was clearly dominant. The next topic is related to study eco-geographical distribution of wild *Lactuca* spp. in North America - USA and Canada. More than 340 seed accesscions of 7 wild *Lactuca* spp., one hybrid and an undetermined *Lactuca* sp. were sampled during some collecting and exploration missions which were undertaken in the first decade of this century. These germplasm accessions were further used in morphological and molecular studies and in research about downy mildew resistance. The up to now knowledge from last 25 years of intensive study of the genus *Lactuca* L., other plans and directions in this field of research are summarized in the last topic.

Keywords: achene, biogeography, breeding, descriptor, distribution, ecology, genebanks, germplasm, *Lactuca sativa*, *Lactuca serriola*, lettuce, morphology, prickly lettuce, seed
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Abstrakt:

Předkládaná disertační práce je zaměřena na 5 různých témat týkající se genových zdrojů rodu *Lactuca* L., jejich fenotypové variability, ekobiologie a praktického využití ve šlechtění kultuního salátu (*L. sativa*). První část pojednává o souboru popisných morfologických znaků *L. sativa*. Soubor, který obsahuje 55 morfologických charakteristik, byl vyhotoven na základě dlouhodobého pozorování morfologické a fenologické rozmanitosti této významné listové zeleniny. V další části předkládané disertační práce jsou shrnuty dosavadní výsledky studia morfologické variability rozmnožovacích propagulí (nažek) genových zdrojů lociky kompasové (*L. serriola*) ve vztahu k různým ekogeografickým faktorům. Byly zde hodnoceny nažky populací *L. serriola* pocházející ze 6 zemí Evropy (z České republiky, Německa, Nizozemí, Velké Británie, Slovinska a Švédska). Studovali jsme 8 vybraných kvantitativních morfologických znaků těla nažek a jejich chmýru. Podle námi dosažených výsledků je možné i na základě morfologie nažek rozlišit obě listové formy *L. serriola* (*L. serriola* f. *serriola*, *L. serriola* f. *integrifolia*). Nažky formy *serriola* jsou kratší, užší, s kratším zobánkem, nižším indexem tvaru a větším počtem žeber než nažky formy *integrifolia*. Při studiu nažek *L. serriola* pocházejících ze Slovinska a Švédska byl prokázán statisticky signifikantní rozdíl v délce a šířce těla, v délce štětin chmýru a jeho ploše. Statisticky signifikantní pozitivní i negativní korelační závislosti byly prokázány mezi studovanými morfologickými znaky a vybranými ekogeografickými faktory. Ve třetí části jsou uvedeny dosažené poznatky hodnocení morfologické variability rosetových a stonkových listů populací *L. serriola* z České republiky a Velké Británie. Výsledky ukázaly, že v České republice byla dominantní *L. serriola* f. *serriola*, zatímco ve Velké Británii byl zaznamenán výskyt jen formy *integrifolia*. Další část je zaměřena na průzkum ekogeografického rozšíření planých druhů rodu *Lactuca* L. v Severní Americe, tj. v USA a Kanadě. Během výzkumně-sběrových expedic, které byly uskutečněny v těchto zemích v letech 2002-2008, bylo získáno více než 340 semenných vzorků 7 planých druhů rodu *Lactuca* L., jednoho křížence (*L. canadensis* x *L. ludoviciana*) a jednoho blíže neurčeného planého druhu lociky. Tyto genové zdroje byly rovněž využity v dalších morfologických a molekulárních studiích a také při studiu rezistence planých druhů locik vůči plísni salátové (*Bremia lactucae*). V poslední části jsou shrnuty dosavadní poznatky intenzivního výzkumu rodu *Lactuca* L. za posledních 25 let a rovněž jsou zde nastíněny směry budoucího výzkumu v této oblasti.

Keywords: biogeografie, deskriptor, ekologie, genové banky, genové zdroje, *Lactuca sativa*, *Lactuca serriola*, locika kompasová, morfologie, nažka, rozšíření, salát, semeno, šlechtění

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CONTENTS

1. INTRODUCTION

The genus *Lactuca* L. comprises about 100 wild *Lactuca* spp. (Lebeda et al., 2004; 2007b). Only about 22 wild *Lactuca* species are available in world genebank collections (Lebeda et al., 2002). According to the International *Lactuca* Database (ILDB) the substantial part (about 92%) is represented by accessions only of three species (*L. serriola*, *L. virosa* and *L. saligna*), mostly of European origin. The autochthonous species from Asia, America and Africa, which form ca. 83% of the *Lactuca* species, are represented very poorly in the world genebank collections (Lebeda et al. 2002; 2004). *L. sativa* (lettuce) is commercially produced as the most important leafy vegetable in many countries worldwide (Rubatzky and Yamaguchi, 1997). Lettuce is characterized by broad variability caused by its polyphyletic origin and a complicated process of domestication (Lebeda et al., 2007b). The crop comprises many cultivars which are maintained in germplasm collections all over the world.

Lactuca serriola L. (prickly lettuce, compass plant) is the most widely distributed species of the genus *Lactuca* L. (Lebeda et al. 2004; 2007b). It has been widely introduced to other regions except of Antarctica (Funk et al., 2005; Lebeda et al., 2004; 2007b). It was domesticated in the Mediterranean and the Near East regions (De Vries, 1997) and it is considered to be „r" strategist and a pioneer plant of open habitats (Feráková, 1977; Lebeda et al., 2004). It grows very often as a weed in the crop fields with reduced tillage, where it becomes an invasive and problematic weed (Weaver and Downs, 2003; Weaver et al., 2006).

In Europe, it has increased its geographical range towards the north during the last 250 years (D'Andrea et al. 2009). This invasive distribution is caused mainly by climate changes, especially by climate warming, extensive development in transportation and increasing number of man-made habitats (Carter and Prince, 1985; D'Andrea et al., 2009; Hooftman et al., 2006; Lebeda et al., 2001; 2004).

Into the North America, prickly lettuce was accidentally introduced in the late 1890s, possibly as a contaminant in seed (Brant and Holec, 2004). Later, it spread through southern Canada and over much of the USA except for areas in extreme northern Maine and southern Florida. In Canada, it is found in all provinces except Newfoundland (Weaver and Downs, 2003).

Spreading of *L. serrila* is provided with transport of reproductive propagules, the achenes. The riped achenes with attached pappus are primarily dispersed by wind, but are probably dispersed also by water (Weaver and Downs, 2003).

This Ph.D. thesis is focused on five various topics related to the *Lactuca* spp. germplasm, their phenotypic variation and ecobiology, as well as utilization in lettuce breeding. The first one is the development of *L. sativa* descriptor based on long-lasting observations of morphological and phenological variability of lettuce. Comprehensive descriptor of lettuce was not available the first decade of 21st century. The first chapter includes the descriptor list of morphological characters of lettuce (*L. sativa*) as the most important crop of leafy vegetables. This morphological descriptor comprises 55 morphological characters. It provides detailed characterization within the intraspecific variation of *L. sativa*. Practically it is useful for lettuce breeders and gene-bankers.

Next topic of this thesis is a detailed study of the morphological variability of achenes of *Lactuca serriola* (wild lettuce) genetic resources. *L. serriola* is considered to be the progenitor of cultivated lettuce (*L. sativa*) and it is very variable in terms of morphology, ecology and genetic (Lebeda et al., 2004; 2007b). Within the genus *Lactuca* L., the fruit (achene) has been recognized as the diagnostically most important organ by many authors. In most cases it is sufficient for specific or subspecific identification (Feráková, 1977). Morphological and anatomical study of fruit together with molecular and ecobiogeographical differences have also important role for delimination of sections in currenctly accepted classification of the genus *Lactuca* L. (Lebeda and Astley, 1999). However, the knowledge of morphological variability, including the achenes, is still very limited (Lebeda et al., 2007b). The main aim of the current research was to study the morphological variability of *L. serriola* achenes in relation to different ecogeographical conditions. For that purpose were used *L. serriola* germplasm accesions originated in many various locations of Europe (Czech Republic, Germany, the Netherlands, Slovenia, Sweden, United Kingdom), the USA and Canada. We investigated specific quantitative morphological characters of *L. serriola* achenes such as length and width of achene's body, number of ribs, length of beak, length of pappus bristles and pappus area, diameter of discus and index length/width (L/W).

According to the presence/absence lobes in the leaf blade Feráková (1977) recognized two varieties within *L. serriola*. Leaves of var. *serriola* were pinnate-lobed, whereas leaves of var. integrata were unlobed. Prince and Carter (1977) revised this taxonomic treatment according to the leaf-shape variation and they divided *L. serriola* for two leaf forms. The forma with runcinate-pinnatifid cauline leaves was named f. *serriola*. Unlobed cauline leaves are characteristic for f. *integrifolia*. This forma is more common in Britain, whereas the f. *serriola* is distributed mainly in continental Europe. Prickly lettuce is characterized by wide plasticity of leaf morphology in relation to the environmental conditions.

The third chapter is focused on the study of morphological variability of rosette and cauline leaves of *Lactuca serriola* plants. We investigated leaves of *L. serriola* plants of 16 populations from the Czech Republic and 10 populations from the United Kingdom. Totally two characters were evaluated on rosette and cauline leaves – depth of incisions and shape of apex. These descriptors were chosen from the list of morphological descriptors for wild *Lactuca* L. species (Doležalová et al., 2002).

The next chapter deals with study about distribution, ecogeography and ecobiology of germplasm accesions of wild *Lactuca* spp. from USA and Canada. Between the years 2002-2008 the collecting and observation missions were undertaken to the North American subcontinent. During these expeditions more than 300 seed accesions of 7 wild *Lactuca* spp. were collected in about 200 locations, mostly in California. The main aim of this vast research was to make a survey of ecogeographical distribution of wild *Lactuca* species in the subcontinent of North America. The seed samples collected during these missions were used to enrich the up to now knowledge of morphology, phenology, resistance to diseases and pests, biochemical and molecular diversity of genus *Lactuca* L.

The current status of wild *Lactuca* L. germplasm accessions in world genebank collections, the challenges in future research and exploitation in lettuce breeding are summarized in the fifth chapter. This part of Ph.D. thesis gives the summarizing information about the complete research on *Lactuca* germplasm during last 25 years. During this long period a lot of findings about taxonomy, morphology, ecobiology, molecular diversity, collecting and holding activities of germplasm accessions were achieved, This summary gives also future plans and prospects in this field of study.

The most important results of all these studies are summarized in chapter Conclusions. The results of Ph.D. thesis are summarized in five chapters, they are composed by eight papers which have been either published, are in press and/or have been submitted.

2. AIMS OF THE PH.D. THESIS

The main aims of the Ph.D. study could be summarized in the following points:

1. Process available literature relating to the topic;

2. Evaluation of phases of ontogenetic development of *Lactuca* spp. plants in long-day conditions in the glasshouse, on the basis of obtained data to participate in elaboration of *L. sativa* descriptor;

3. Measurement of quantitative and qualitative morphological characters of *L. serriola* achenes, including length and width of achene's body, number of ribs, length of beak, length of pappus bristles and pappus area, diameter of discus and index length/width (L/W);

4. Morphological variability of *L. serriola* leaves;

5. Taxonomic and morphological identification of *Lactuca* spp. genetic resources originating from the USA and Canada, their ecobiological characterization;

6. Genetic resources of wild *Lactuca* L. species and their exploitation in lettuce breeding – critical analysis.

3. LITERATURE OVERVIEW

3.1. Family Asteraceae (Compositae) and its characterization

The genus *Lactuca* belongs to the family Asteraceae (Compositae). It is the most diverse of all plant families with about 1600-1700 currently accepted genera and ca. 24 000-30 000 of described species occurring on all continents except Antarctica (Funk et al., 2005). According to the recent estimates, Asteraceae contains about 10% of species of flowering plants (Funk et al., 2005). Asteraceae is a monophyletic family with some characteristic features: a) the compound inflorescence, called a capitulum or a head made of clustered single flowers; b) the involucrum created by involucral bracts growing from the outer layer of disc arrangement; c) the single-seeded fruit type called achene and the development of the calyx into a pappus (Dempewolf et al., 2008; Funk et al., 2005). The members of Asteraceae are annual or perennial herbs, climbing plants, shrubs, trees, although few are true epiphytes (Funk et al., 2005). Some of them are strongly domesticated food crops – endive (*Cichorium endivia*), sunflower (*Helianthus annuus*), lettuce (*Lactuca sativa*). The others are medicinal plants and ornamentals (*Calendula officinalis*, *Echinacea* spp., *Tagetes* spp., *Zinnia* spp. (Dempewolf et al., 2008). Recently, the family Asteraceae is divided into 4 subfamilies (Asteroideae, Barnadesioideae, Carduoideae, Cichorioidae) and 16 tribes (Bremer et al., 1994; Bremer, 1996). The tribe Lactuceae Cass. (Cichorieae, according to Stebbins (1953)) contains 10 monophyletic subtribes (Gemeinholzer and Kilian, 2005). The subtribe Lactucinae comprises 17 genera including the genus *Lactuca* and approximately 270 species (Bremer et al., 1994).

3.2. General characterization of the genus *Lactuca* L.

The origin of the name of the genus *Lactuca* is in a Latin word „lac“. It means „milk“ in translation. The bitter milky juice latex is present in specific laticiferous cells in cambial regions throughout the stem, roots and leaf veins (Bushman et al., 2006; Lebeda et al., 1999). When the plant tissues are damaged, latex flows out and it gets stiff and brown (Feráková, 1977). Lactucarium (dry latex) was used as soporific medicine during the Middle Ages in Europe (De Vries, 1997).

The genus *Lactuca* and all closely related genera (*Cicerbita*, *Crepis*, *Ixeris*, *Lapsana*) are part of the Cichorium group and the subgroup Crepis (Jeffrey, 1966; 1995).

According to the recent literature, 98 wild *Lactuca* species have been described taxonomically. Totally 17 species are found in Europe, 51 in Asia, 43 in Africa, 12 in the Americas and 3 in Australia (Lebeda et al., 2004; 2007b).

3.2.1. Taxonomy of the genus *Lactuca* L.

The taxonomical position of the genus *Lactuca* is very unclear and the divergent opinions persist until the present time. Feráková (1977) desrcribed this situation by the words of Babcock, which he used for *Crepis*: „oscillation between splitting and lumping“. Uncertainties in the generic limits of the genus *Lactuca* are caused by the broad biodiversity within the genus and the occurrence of spontaneous hybridization, as well as the fact that the large *Lactuca* genus includes chorologically (spatially) strongly divergent groups of species (Lebeda et al., 2007b).

Linnaeus in Genera Plantarum (1752) and Species Plantarum (1763) described totally 7 species of *Lactuca*: *L. quercina*, *L. sativa*, *L. canadensis*, *L. serriola*, *L. virosa*, *L. saligna* and *L. perennis*. Some species, which are recently accepted in the genus *Lactuca*, he included in the genera *Prenanthes* and *Sonchus* (Feráková, 1977).

Stebbins (1937), Tuisl (1968) and Feráková (1977) established three main generic concepts of *Lactuca*. Stebbins (1937) accepted the broad generic concept (s.l.) and he recognized in genus *Lactuca* five subgenera as following: *Mulgedium* Cass., *Lactucopsis* Schultz-Bip. ex Vis et Panč., *Mycelis* Cass., *Phaenixopus* Cass. and *Cicerbita* Wallr (with exception of *C. alpina* with very frail pappus and almost cylindrical and slightly flattened achenes). Tuisl (1968) supported the narrow generic concept and he divided *Lactuca* s.l. into six genera – *Scariola* F.W. Schmidt, *Steptorhampus* Bunge, *Cephalorrhynchus* Boiss, *Cicerbita* Wallr., *Mulgedium* Cass. and *Lactuca* L. He made this division on the basis of a morphological and anatomical study of fruit, flower, involucre and pappus (Feráková, 1977).

Feráková (1977) preferred the broad sense and she recognized within *Lactuca* four sections: *Phaenixopus* (Cass.) Benth., *Mulgedium* (Cass.) C.B. Clarke, *Lactucopsis* (Schultz-Bip. ex Vis. et Panč.) Rouy and *Lactuca*. This last section she divided for two subsections – *Lactuca* and *Cyanicae* DC.

According to Shih (1988a, b), the genus *Lactuca* involves only that species with 7-25 ligules, achenes with 1-10 ribs on each side and filiform beak in apex. This treatment limits the genus *Lactuca* only to the group of *serriola*-like species from the section

Lactuca subsection *Lactuca* (Feráková, 1977). The exception is only *L. virosa* and *L. livida* characterized by broadly elliptic achenes with narrow wings on the sides.

3.2.2. Recent classification of the genus *Lactuca* L.

The original taxonomic treatment of European species of the genus *Lactuca* (Feráková, 1977) was enriched by Lebeda (1998) and Lebeda and Astley (1999) for species from other continents. New taxonomic classification was established. The genus *Lactuca* is here divided into seven sections (Lactuca, Phaenixopus, Mulgedium, Lactucopsis, Tuberosae, Micranthae and Sororiae) and two geographical groups (African and North American ones). The first four sections as Lactuca, Phaenixopus, Mulgedium and Lactucopsis include the wild *Lactuca* species from Europe (Feráková, 1977) and other three sections (Tuberosae, Micranthae and Sororiae) comprise mostly Asian species (Lebeda, 1998; Lebeda and Astley, 1999).

3.2.2.1. Section Lactuca

The section Lactuca is divided into two subsections Lactuca and Cyanicae on the basis of life cycle of their representatives and the different chromosome numbers (Feráková, 1977). The members of the subsect. Lactuca (e.g. *L. serriola*, *L. sativa*, *L. saligna*, *L. virosa*) are annual, winter annual or biennial herbs with rich inflorescences. Capitulum has 10-30 (50) florets, ligules are yellow. Achenes have many ribs. The haploid chromosome number of these species is n=9.

The following species *L. perennis*, *L. tenerrima* and *L. graeca* belong to the subsect. Cyanicae. They are perennials. Their capitulum has less them 22 florets. The ligules are blue or lilac and achenes have normally 1-3 ribs. Their haploid chromosome number is n=8 (Doležalová et al., 2002; Feráková, 1977; Lebeda and Astley, 1999).

3.2.2.2. Section Phaenixopus

The species of this section occur mostly in the Mediterranean region, whereas some of them are endemic (e.g. *L. longidendata*, *L. viminea* subsp. *alpestris*). Some species are biennial (*L. longidentata*), the others are perennial (*L. acanthifolia*, *L. orientalis*). The members are characteristic by decurrent leaves, capitulum of 5-6 florets. The achenes are oblong-elliptical, with 5-11 ribs and a concolorous beak not longer than the body (Doležalová et al., 2002; Feráková, 1977; Lebeda and Astley, 1999).

3.2.2.3. Section Mulgedium

The representatives of this section are *L. tatarica* and *L. sibirica* occurring in northern Europe and Asia. The another member, *L. taraxacifolia*, comes from the mountains of Central Asia (Chalkuziev, 1974). These species are perennial, with few capitula of blue, lilac, rarely white colour. Achenes are oblong-elliptical, slightly compressed with many ribs and with a very short beak of same colour as body (Doležalová et al., 2002; Feráková, 1977; Lebeda and Astley, 1999).

3.2.2.4. Section Lactucopsis

The members of this section are biennial (*L. quercina*) or perennial (e.g. *L. aurea*) native in woodland and shrub of Europe and Asia. Capitulum has 6-15 florets. Achenes are oblong-elliptic with 2-5 ribs and with a concoloured beak 1/4 – 1/2 as long as the body (Doležalová et al., 2002; Feráková, 1977; Lebeda and Astley, 1999).

3.2.2.5. Section Tuberosae

This section comprises annual or biennial herbs with fusiform roots and morphologically variable leaves and inflorescences (Doležalová et al., 2002). Florets are yellow, however, they can be also blue or lilac in colour (*L. graciliflora*, *L. lessertiana*). Achenes are dinstinctly flattened and elliptic, black with short white beak, or brown with short thick beak (*L. graciliflora*). The most characterized member of this section is *L. indica* occurring in Japan, Korea, China, Indonesia and also in some parts of Africa (South Africa, Mozambique, Madagscar, Mauritius, Seychelles). Another member *L. indica* var. *laciniata* is common only in east Asia and Indonesia. *L. graciliflora* and *L. lessertiana* are described from India, China, Java and Sumatra. *L. raddeana* was also found in the Far East of Russia (Doležalová et al., 2002; Lebeda and Astley, 1999; Lebeda et al., 2007b).

3.2.2.6. Section Micranthae

The species belonging to this section are annual or bienniel plants. Corollas are violet or purple. Achenes are ± elliptic, mostly with one rib (max 3 ribs). The beak is mostly 2-4 times longer than seed. The notable members of this section are e.g. *L. auriculata* from the Central Asia, *L. glauciifolia* from Iran, Pakistan, Afganistan, India, China and Russia, *L. rosularis* from Iran and *L. undulata* from India (Doležalová et al., 2002; Lebeda and Astley, 1999; Lebeda et al., 2007b).

3.2.2.7. Section Sororiae

The representatives are perennial plants with purplish corollas. The achenes are barely flattened, narrowly oblong or narrowly fusiform. The section is probably closely related to the genus *Prenanthes*. The best described species of this section is *L. sororia* occurring commonly in Japan and *L. yunnanensis* from China (Doležalová et al., 2002; Lebeda and Astley, 1999; Lebeda et al., 2007b).

3.2.2.8. African group

This group is very large and heterogeneous (Lebeda and Astley, 1999). Most of species are considered as an autochtonous elements (e.g. liana-like species from tropical rain forests) (Jeffrey, 1966). Some of these species have limited area of distribution, e.g. *L. schulzeana* (Cameroun, Congo, Uganda), *L. dregeana* (South Africa). Some species belonging to the African group have worldwide distribution (*L. sativa*, *L. serriola*) (Doležalová et al., 2002; Lebeda and Astley, 1999).

3.2.2.9. North American group

Species of this group are distributed from Canada to Florida. They are characterized by the high haploid chromosome number n=17 (Babcock et al., 1937). They are considered of amphidiploid origin. They are annual or biennial plants with relatively high morphological variability, mainly in leaf shape (e.g. various forms of *L. canadensis*). Commonly they occur in thickets, clearings or at the edges of woods. The most common species is *L. canadensis* (Canada lettuce), which is distributed from northcentral USA up to some areas of Canada. Other relatively common species are *L. biennis* and *L. floridana* occurring in thickets, opening or open woods (Doležalová et al., 2002; Lebeda and Astley, 1999).

3.2.3. Morphological description of the genus *Lactuca* L.

The most important features of the genus *Lactuca* are: cylindrical involucre of several rows of upright and rigid or reflexed bracts, receptacle without scales, corolla tube glabrous, collecting hairs on style arms long, achenes homomorphic, distinctly but moderately compressed, with many ribs and a beak (rarely without beak). Pappus is always monomorphic, consisting of two equal rows of whitish or yellowish hairs, which are longer than the involucral bracts (Feráková, 1977; Grulich, 2004; Lebeda et al., 2004; 2007b).

3.2.4. Ecogeographical distribution of the genus *Lactuca* L.

The genus *Lactuca* L. is distributed mostly in temperate and warm regions of the northern hemisphere (Europe, Asia, North and Central America, Africa and Indonesia). Some species are naturalized in Australia (Feráková, 1977).

Most of the species are xerophytes, which tolerate dry climatic conditions. Indeed some species are scandent, liana-like endemic species occurring in central African mountains (Jeffrey, 1966).

The northern boundary of distribution of many Euroasiatic species is between 50-55°N. The northmost distribution (70°N in Europe) is known for *L. sibirica*. Relatively considerable changes are known in distribution of the most widely destributed wild *Lactuca* species, *L. serriola*. Feráková (1977) mentioned that this species reaches 65°N. Currently, D'Andrea et al. (2009) showed that the northern limit of the distribution are of *L. serriola* runs near the latitude 66°N through Sweden and then near 56°N through Scotland in Great Britain. On the basis of their hypothesis, *L. serriola* has been expanding due to global warming to the North.

The optimal elevation for most species is between 200 and 600 m. Rarely, the altitude gets over 600 m (Doležalová et al., 2001; Feráková, 1977; Lebeda et al., 2001; 2004; 2007b). Even though, some notes are recorded from the elevation about 2000-2500 m (Feráková, 1977; Lebeda et al., 2001).

From the ecological viewpoint, the genus *Lactuca* L. is very variable. The most common *L. serriola*, *L. saligna* and *L. virosa* are ruderal species. They prefer disturbed soil e.g. in waste places, embankments, field margins, along roads and ditches (Feráková, 1977; Lebeda et al., 2001; 2004; 2007b). Some species (*L. perennis*, *L. viminea*, *L. graeca*, *L. tenerrima*) are caciphilous occurring in limestone and on rocky slopes (Feráková, 1977). Other species as *L. canadensis* and *L. biennis* occur in woods, shrubs and clearings (Lebeda and Astley, 1999).

3.3. *Lactuca serriola* (prickly lettuce, wild lettuce, compass plant)

3.3.1. Taxonomy

According to the recent classification, *L. serriola* belongs to the section Lactuca, subsection Lactuca (Feráková, 1977; Lebeda and Astley, 1999). On the basis of the presence/absence of trichomes in the upper part of stem and in the infloresence and according to the morphology of leaves, Feráková (1977) recognized three varieties. *L. serriola* var. *coriacea* has upper part of stem and the inflorescence densely prickly, var. *serriola* has pinnate-lobed leaves and var. *integrata* has leaves without lobes.

Later, Prince and Carter (1977) simplified division of *L. serriola*. On the basis of the cauline leaves morphology and geographical destribution they distinguished two forms – *L. serriola* f. *serriola* and *L. serriola* f. *integrifolia*. The former is characterized by runcinate-pinnatifid leaves and the distribution mostly in Britain. On the second hand, f. *integrifolia* has unlobed leaves and it is more common in continental Europe.

L. serriola f. *integrifolia* is also known as *L. augustana* All. Fl. Ped., *L. scariola* ß *integrifolia* Bogenh., *L. dubia* Jord., *L. integrata* and *L. serriola* var. *integrata* Gren. et Godr.

The two leaf forms may occur intermixed but more often are found in separate populations (Oswald, 2000).

3.3.2. Morphology of *L. serriola*

L. serriola is annual or biennial therophyte reaching up to (30-)50- 200 cm with a taproot. Stiff and erect stem growing from the basal rosette is prickly on the base. Cotyledons are rounded, 4-8 mm long, with an indented or truncated apex. Rosette leaves are oval-rounded to elongated, widest near the apex. On the underside of the leaf is a row of spines along the midrib and the leaf margin is weakly spiny. Basal leaves oblong-ovate in outline, pinnate-lobed to pinnatisect with backwards orientated lateral lobes. They are 1-22 cm long and 0,4-10 cm broad. Cauline green waxy leaves are alternate, sessile and clasp the stem with small pointed lobes. They are entire or deeply lobed, with spiny-toothed margins, and with a prominent, white central vein bearing a row of spines on the underside. The cauline leaves are oriented vertically in full sun, in a north-south plane. Pyramidal panicle inflorescence is composed of many small flower heads (capitula), 8-12 mm in diameter. A head can contain usually (7)10-30 (50) pale yellow, ligulate ray flowers. When they get dry, they may appear bluish. Involucre is made of 3-4 rows of bracts, which are reflexed when achenes ripe. Achenes (cypselae) are oblong-ovate, olive green to greyish, 3-4 mm long, ±1 mm broad. Near the apex are short fine bristles, 5-7 longitudinal ribs on each side and the achene narrows to a white, filiform beak with an attached pappus. The beak is as long as or longer than the achene body and the pappus is 3-4,5 mm long, white and deciduous (Brant and Holec, 2004;

Doležalová et al., 2002; Dostál, 1989; Feráková, 1977; Grulich, 2004, Weaver and Downs, 2003).

3.3.3. Ecogeographical distribution of *L. serriola*

L. serriola is native to the Mediterranean Basin and to the Near East (De Vries, 1997). Currently it is the most common species in the genus with a synanthropic worldwide distribution (Lebeda et al., 2004; 2007b). Its occurrence was recorded from Australia, Tasmania and New Zealand (Lebeda et al., 2004). In Europe, North America, southern Africa and Argentina, *L. serriola* is considered as an invasive weed reducing the crop yield or quality (Lebeda et al., 2004; Weaver and Downs, 2003; Weaver et al., 2006).

According to Feráková (1977), the northern boundary of the distribution in Europe runs near the latitude 65°N in Finland and 55°N in Great Britain. In Norway and Sweden the northmost localities are at 60°N (Feráková, 1977) up to 65°N (Doležalová et al., 2001). The western limit of *L. serriola* distribution in Europe is 5°W (Lebeda et al, 2004; 2007b).

In Europe, it has increased its geographical range towards the north during the last 250 years (D'Andrea et al., 2009). This invasive distribution is caused mainly by climate changes, especially by climate warming, extensive development in transportation and increasing number of man-made habitats (Carter and Prince 1985; D'Andrea et al. 2009; Hooftman et al. 2006; Lebeda et al. 2001, 2004).

L. serriola is distributed from lowland to montane regions. Its occurrence is limited by warm summers (Lebeda et al., 2004, 2007b). In Europe it is mainly recorded at elevations of 200-600 m (Doležalová et al., 2001; Feráková, 1977; Lebeda et al., 2001). In Switzerland *L. serriola* extends up to the altitude 1560 m and in the northern Himalayas up to 3600 m (Lebeda et al., 2004; 2007b). In Great Britain it can occur only at altitude 96 m (Lebeda et al. 2007a).

Into the North America, prickly lettuce was accidentally introduced as a contaminant in seeds (Brant and Holec, 2004). The first record of *L. serriola* on the North American continent was in 1863, in the state of Massachusetts (Weaver and Downs, 2003). Later, it spread through southern Canada and over much of the USA except for areas in extreme northern Maine and southern Florida (http://www.oardc.ohio-state.edu/weedguide/singlerecord.asp?id=1010). *L. serriola* was first collected in Canada in 1891 near Windsdor and Niagara, Ontario. In Canada, it is found in all provinces except Newfoundland (Weaver and Downs, 2003).

In the Czech Republic, *L. serriola* is very common from lowlands up to highlands, but it is quite rare in montane region. It prefers the areas of elevation between 500-600 m (Lebeda et al., 2001). In higher altitude it grows only for transient time along the roads. Its the highest occurrence is in Kubova Huť in Šumava at altitude 1080 m (Grulich, 2004).

Of both *L. serriola* forms, *L. serriola* f. *serriola* is much more frequent species then f. *integrifolia*. It is mostly described from the lowland areas of Europe (Feráková, 1977). However, *L. serriola* f. *integrifolia* is generally considered to be rare. It has more southern range than f. *serriola*. Its occurrence was recorded in Italy, southeastern part of France. Some records originate from the Netherlands and Germany (Lebeda et al., 2001). In the Czech Republic, its occurrence is very rare (Křístková and Lebeda, 1999). Nevertheless, *L. serriola* f. *integrifolia* is also a prevalent form in southeastern and central England (Prince and Carter, 1977; Lebeda et al., 2001).

L. serriola is considered to be „r“ strategist and a pioneer plant of open habitats (Brant and Holec, 2004; Feráková 1977; Lebeda et al. 2004). It occurs in fertile, carbonate-rich soils on roadsides, grassy ditches, dust-heaps, ruderal communities, and weed communities in agricultural crops. It can be found also on stony road surface, asphalt cracks, along the walls, roads, highways, railways and embankments. The spreading of *L. serriola* is related mainly with transport and human activities (Doležalová et al. 2001; Feráková, 1977; Lebeda et al., 2001; 2004, 2007b).

3.4. *L. serriola* and its relationship to cultivated lettuce (*L. sativa*)

The wild *Lactuca* species were categorized into three gene pools (Harlan and de Wet, 1971) based on their relationship to *L. sativa*. The primary gene pool comprises the cultivated crop species, their landraces and the wild species without the crossing barriers (*L. serriola, L. aculeata*, *L. altaica*, *L. dregeana*, *L. sativa*,) (Lebeda et al., 2004; 2007b; Zohary, 1991). In the secondary gene pool are wild species that exchange genes with the crop to a limited degree (e.g. *L. saligna*). The tertiary gene pools includes wild species (e.g. *L. virosa*) with very difficult crossing barriers with the primary gene pool species (Lebeda et al., 2004; 2007b; McGuire et al., 1993; Zohary, 1991).

On the bases of some biochemical and molecular studies (Koopman, 1999; Koopman et al., 2002), the primary geen pool comprises wild *Lactuca* species (*L. serriola*, *L. altaica*, *L. aculeata*, *L. dregeana*), which are closely related to *L. sativa*. The secondary geen pool includes *L. saligna* and *L. virosa*. And the tertiary geen pool consists of species as *L. quercina*, *L. sibirica*, *L. tatarica* and *L. viminea*.

Some authors consider on the bases of some molecular studies, *L. sativa* conspecific with *L. serriola* (Koopman et al., 1998; 2001; De Vries, 1996). Both species are considered as subspecies: *L. sativa* subsp. *serriola*, *L. sativa* subsp. *sativa* (De Vries, 1996). Koopman et al. (2001) proposed the name *L. sativa* for both *L. sativa* and *L. serriola*. Despite of close evolutionary relationship, both species are considered to be individua species by majority of taxonomists (Feráková, 1977; Grulich, 2004).

L. serriola is the closest wild *Lactuca* species to cultivated lettuce. In natural conditions they are fully cross-compatible and fully interfertile (Lebeda et al., 2004; 2007b). Predominantly both species are self-pollinated, but the hybridisation was observed. D'Andrea et al. (2006) found the pollen flow from cultivated lettuce to its wild relatives is high at close distance. At distance 0-1 m, the incidence of hybridisation was higher than 80%. Even at long distance (40 m), 4-5% of the wild plants produced hybrids. Against cross-pollination between *L. sativa* and its wild relatives a physical barier or a minimum of 2 m between different cultivars is recommended (George, 1999; Lebeda et al., 2007b).

3.5. Germplasm descriptors of genetic resources of *Lactuca* L. species

The lists of morphological characters of genetic resources of cultivated lettuce (*L. sativa*) or of wild *Lactuca* L. species are called germplasm descriptors. Doležalová et al. (2002) developed the set of morphological descriptors (English-Czech version) as a tool for determination of wild species within the genus *Lactuca* L. and for a characterization of *Lactuca* infraspecific morphological variability. It was created on the bases of study of wild *Lactuca* L. species genetic resources of the National Gene Bank Collection of the Czech Republic, description of the genus *Lactuca* L. in determination keys (Dethier, 1982; Feráková, 1976; Iwatsuki et al., 1995; Jeffrey, 1966; 1975; Stace, 1997) and „The Descriptor List of Western Regional Plant Introduction Station Pullman, Washington (USA)" (Anonym) (Doležalová et al., 2002).

The set includes totally 88 morphological descriptors and 13 of them describe the fruit (achene). The important morphological characters of achene are e.g. colour of achene body, shape in outline, number of ribs on both sides, length of achene including beak, colour of beak, length of beak, colour and length of pappus (Doležalová et al., 2002).

The list of descriptors for cultivated lettuce was created for the characterization and evaluation of genetic resources in the Czech collection of *L. sativa* (Křístková et al., 2008). The descriptor list contains 55 characterization and evaluation descriptors whereas 3 of them concern about fruit – colour of achene, shape in outline and „thousand seeds weight".

3.6. Fruit morphology

The fruit type of Asteraceae family is called achene. It has been recognized as the diagnostically most important organ by many authors. Mostly it is sufficient for subspecific or specific indentification (Feráková, 1977).

Stebbins (1937) used as the most important characters to deliminate the genus the shape of the achene, especially that of the beak, and the presence of outer pappus. Tuisl (1968) divided *Lactuca* s.l. into six genera on the basis of a morphological and anatomical study of fruit, flower and involucre as well as of pappus. In this study he did also a broader description of fruit anatomy. He focused on the surface of the achene and the anatomy of the ribs.

Feráková (1977) considered the shape, size and anatomy of achene, the length of beak and the pappus form as very important taxonomic features to deliminate the genus. She also mentioned that microscopic hairs on the ribs, especially in the apical part of achene are constant feature of *Lactuca*. The basic shape of the achene, especially the ratio of the beak to the body of the achene, she used as the main character to determine the section. Feráková (1977) mentioned that the ratio length of beak to the length of body is not always a constant value.

The longest beaks are found in the representatives of the sect. Phaenixopus. Their achenes are oblong-elliptical, with 5-11 ribs and a beak not longer than body. Pappus is white. The ratio of length of beak to the lenght of body is very important feature to deliminate subspecies within *L. viminea* (L.) J. et C. Presl (Feráková, 1977). *L. viminea* subsp. *chondrillaeflora* is characterized by the beak as long as 1/4-1/2 of the achene body. Subsp. *viminea* and subsp. *ramosissima* have beaks as long as the achene body or longer.

The achenes of sect. Mulgedium are oblong-elliptical, many-ribbed, slightly compressed with very short stout concolorous beak, which is in some cases hardly noticeable (Feráková, 1977). Pappus is white or yellowish in colour (Lebeda and Astley, 1999).

The members of sect. Lactucopsis have oblong-elliptical achenes, with 2-5 (10) ribs and a concolorous beak of 1/4-1/2 length of body (Feráková, 1977; Lebeda and Astley, 1999). According to the length of beak, Feráková (1977) distinguished two subspecies within *L. quercina* L. The beak of subsp. *quercina* is shorter than 1/2 of achene body, whereas subsp. *wilhelmsiana* has the beak at least as long as 1/2 of achene body.

Achenes of sections Tuberosae are flattened, elliptical, black in colour with short white beak or brown with short thick beak. Sect. Micranthae is characterized by more or less elliptic achenes, mostly with one rib (max 3 ribs) and with long beak (mostly 2-4 times longer than seed). Representatives of sect. Sororiae have barely flattened, narrowly oblong or narrowly fusiform achenes (Lebeda and Astley, 1999).

Achenes of sect. Lactuca are elliptical to obovate, narrowed in the upper part, with 1-3 (9) ribs and with distinct filiform pale beak at least as long as body. Achenes of subsect. Lactuca have on the surface many ribs, whereas achenes of subsect. Cyanicae have only 1-3 ribs (Feráková, 1977; Lebeda and Astley, 1999).

L. sativa achenes are flattened, obovate, narrowed and often finely hairy at the apex. Their length is 6-8 mm, whereas the length of achene body is approximately 3 mm and the width ± 1 mm. Achenes are greyish in colour, with 5-9 ribs on the surface and with white, filiform beak, as long as body. Pappus is white (Feráková, 1977; Grulich, 2004).

Taxonomicaly very closely related species to *L. sativa* are: *L. aculeata*, *L. altaica*, *L. azerbaijanica*, *L. dregeana*, *L. georgica*, *L. scarioloides*, *L. serriola* (Zohary, 1991). Achenes of *L. aculeata* are brown, mostly 7,5 mm long, with many ribs and whitish trichomes on the surface. Beak is pale, 4,5 mm long with whitish pappus of 3,5 mm in length (Jeffrey, 1975). Achenes of *L. altaica* are obovate-elliptical, brownish or greyish in colour, 6-10 mm long and ± 1 mm broad, setose at apex, with 5-10 ribs. Beak is white, filiform, as long as body and pappus is also white. (Feráková, 1977). Achenes of *L. azerbaijanica* are dark brown in colour, with many ribs and white pappus (Rechinger, 1977). Achenes of *L. dregeana* are grey-brown, ± 1 mm broad, with some ribs and thin beak of the same colour as body (Jeffrey, 1975). *L. georgica* have achenes of blakish colour, 7,5-8 mm in length, with many ribs and with beak of 2,5-3,5 in lenght. Their pappus is white, ± 5 mm long (Jeffrey, 1975). Achenes of *L. scarioloides* are 9,5 mm long, brownish, with 4-4,7 mm long beak of the same colour as body. Pappus is white, approximately 5,5-7 mm long (Jeffrey, 1975).

L. serriola achenes are slightly compressed, oblong-ovate, brown-greyish with irregular spots on the surface. They are 3-4 mm long, ± 1 mm broad with short fine bristles near the apex. There are 4-7 longitudinal ribs on each side of achene body. Beak is whitish, filiform, as long as or longer then the achene body. Pappus is white, deciduous, 3-5 mm long (Brant and Holec, 2004; Feráková, 1977; Grulich, 2004).

On average, 15-22 seeds per capitulum are produced (Prince and Carter, 1985). Solitaire *L. serriola* plants growing in 1999 in Prague-Suchdol produced 18 achenes per capitulum and in 2000 only 14 achenes (Brant and Holec, 2004). The average weight per seed is approximately 0,6 mg with the range 0,45-0,8 mg (Prince and Carter, 1985). The average number of capitula per plant at experimental fields of the University of Agriculture in Prague in 1999 and 2000 was 990-1262, giving approximately 17 668-17 820 seeds per plant (Brant et al., 2002). These authors also studied the influence of cuttings on the development and reproductive ability of *L. serriola*. They found that cuttings of *L. serriola* plants in early development stages significantly decrease the total production of achenes.

The riped achenes with attached pappus are primarily dispersed by wind, but are probably dispersed also by water. Some *L. serriola* plants were found along rivers and lakes in Canada (Weaver and Downs, 2003).

References:

Anonym. Codes for *Lactuca* evaluation descriptors.Western Regional Plant Introduction Station, Pullman, Washington (USA).

Anonym. Ohio Perennial & Biennial Weed Guide. [cit. 27th June 2011]. Available from www: <http://www.oardc.ohio-state.edu/weedguide/singlerecord.asp?id=1010>.

Babcock, E.B., Stebbins, G.L., Jenkins, J.A. (1937) Chromosomes and phylogeny in some genera of the Crepidinae. Cytologia. Tokyo, Fujii Jub., pp. 188-210.

Brant, V., Bělka, J., Svobodová, M. (2002) Einfluss des Schnittes auf Wachstum und Reproduktion des Kompass-Lattichs (*Lactuca serriola* L.). J. Plant Dis. Protect. 18: 287-291.

Brant, V. and Holec, J. (2004) Locika kompasová (*Lactuca serriola* L.). Rostlinolékař 15/5: 24-27.

Bremer, K. (1996) Major clades and grades of the Asteraceae. In: Hind D.J.N., Beentje H.J. (Eds.) Compositae: Systematics. Proceedings of the International Compositae Conference Kew (1994). Vol. 1, Kew: Royal Botanic Gardens, pp.1-7.

Bremer, K., Anderberg, A.A., Karis, P.O., Nordenstam, B., Lundberg, J., Ryding, O. (1994) Asteraceae: Cladistic and Classification. Portland: Timber Press.

Bushman, B.S., Scholte, A.A., Cornish, K., Scott, D.J., Brichta, J.L., Vederas, J.C., Ochoa, O., Michelmore, R.W., Shintani, D.K., Knapp, S.J. (2006) Identification and comparison of natural rubber from two *Lactuca* species. Phytochemistry 67: 2590-2596.

Carter, R.N. and Prince, S.D. (1985) The geographical distribution of prickly lettuce (*Lactuca serriola*). I. A general survey of its habitats and performance in Britain. J. Ecol. 73: 27-38.

Chalkuziev, P. (1974) Species novae flora Schachimardanicae. Bot. Mat. Gerb. Inst. Bot. Akad. Nauk Uzbek. SSR 19: 58-61.

D'Andrea, L., Broennimann, O., Kozlowski, G., Guisan, A., Morin, X., Keller-Senften, J. and Felber, F. (2009) Climate change, anthropogenic disturbance and the northward range expansion of *Lactuca serriola* (Asteraceae). J. Biogeogr. 36: 1-15.

D'Andrea, L., Felber, F., Guadagnuolo, R. (2006) Direct evidence of gene flow by pollen from cultivated lettuce (*Lactuca sativa* L.) to its wild relative prickly lettuce (*L. serriola* L.). Laboratoire de Botanique évolutive, Institut de Botanique, Université de Neuchâtel, Rue Emile-Argand 11. Switzerland. In: D'Andrea, L. Historical and molecular biogeography of prickly lettuce (*L. serriola* L.) and evaluation of hybridisation with the crop (*L. sativa* L.). Ph.D. Diss., Université de Neuchâtel, pp. 68-91.

Dempewolf, H., Rieseberg, L.H., Cronk, Q.C. (2008) Crop domestication in the Compositae: a family-wide trait assessment. Genet. Resour. Crop Evol. 55: 1141-1157.

Dethier, D. (1982) Le genre *Lactuca* L. (*Asteraceae*) en Afrique centrale. Bull. Jard. Bot. Nat. Belg. 52: 367-382.

De Vries, I. M. (1996) Characterization and identification of *L. sativa* cultivars and wild relatives with SDS-electrophoresis (*Lactuca* sect. Lactuca, Compositae). Genet. Resour. Crop Evol. 43: 193-202.

De Vries, I. M. (1997) Origin and domestication of *Lactuca sativa* L. Genet. Resour. Crop Evol. 44: 165-174.

Doležalová, I., Křístková, E., Lebeda, A., Vinter, V. (2002) Description of morphological characters of wild *Lactuca* L. spp. genetic resources (English-Czech version). Hort. Sci. 29: 56-83.

Doležalová, I., Lebeda, A., Křístková, E. (2001) Prickly lettuce (*L. serriola* L.) germplasm collecting and distribution study in Slovenia and Sweden. Plant Genet. Resour. Newsl. 128: 41-44.

Dostál, J. (1989) Nová květena ČSSR, 2. díl. Academia Praha, pp. 1112-1115.

Feráková, V. (1976) *Lactuca* L. In: Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M., Webb, D.A. (Eds.) Flora Europea. Vol. 4, Cambridge: Cambridge University Press, pp. 328-331.

Feráková, V. (1977) The Genus *Lactuca* L. in Europe. Komenský University Press, Bratislava (Czechoslovakia).

Funk, V.A., Bayer, R., Keeley, S., Chan, R., Watson, L., Gemeinholzer, B., Schilling, E., Panero, J. L. Baldwin, B. G., Garcia-Jacas, N., Susanna, A. and Jansen, R. K. (2005) Everywhere but Antarctica: using a supertree to understand the diversity and distribution of the Compositae. In: Friis, I., Balslev, H. (Eds.) Proceedings of a Symposium on Plant Diversity and Complexity Patterns – Local, Regional and Global Dimensions. Copenhagen.

Gemeinholzer, B. and Kilian, N. (2005) Phylogeny and subtribal delimination of the Cichorieae (Asteraceae). XVII International Botanical Congress, Vinna, Austria, 17-23 July 2005, Abstracts, p. 103 Abstract 6.11.4.

George, R.A.T. (1999) Vegetable Seed Production, 2nd ed., Wallingford: CABI Publishing, 1999.

Grulich, V. (2004) *Lactuca* L. In: Slavík, B., Štěpánková, J. (Eds.) Květena České republiky 7. Academia, Praha, pp. 487-497.

Harlan, J.R., de Wet, J.M.J. (1971) Towards a rational classification of cultivated plants. Taxon 20: 509-517.

Hooftman, D.A.P, Oostermeijer, J.G.B., den Nijs, J.C.M. (2006) Invasive behaviour of *Lactuca serriola* (Asteraceae) in the Netherlands: Spatial distribution and ecological amplitude. Basic Appl. Ecol. 7: 507-519.

Iwatsuki, K., Yamazaki, T., Boufford, D.E., Ohba, H. (1995) Flora of Japan. Vol. IIIb. Kodansha, Tokyo.

Jeffrey, C. (1966) Notes on Compositae I. The Cichorieae in East tropical Africa. Kew Bull. 18: 427-486.

Jeffrey, C. (1975) *Lactuca* L. In: Davis, P.H. (Ed.) Flora of Turkey and the East Aegean Islands. Edinburgh University Press, Edinburgh, pp. 776-782.

Jeffrey, C. (1995) Compositae systematics 1975-1993. Developments and desiderata. In: Hind, D.J.N., Jeffrey, C., Pope, G.V. (Eds.) Advances in Compositae Systematics. Kew, The Royal Botanic Gardens, pp. 3-21.

Koopman, W.J.M. (1999) Plant systematics as a useful tool for plant breeders: Examples from lettuce. In: Lebeda, A., Křístková, E. (Eds.) Eucarpia Leafy Vegetables ’99. Palacký University Olomouc, Czech Republic, pp. 117-131.

Koopman, W.J.M., Guetta, E., Van de Wiel, C.C.M., Vosman, B., Van den Berg, R.G. (1998) Phylogenetic relationships among *Lactuca* (Asteraceae) species and related genera based on ITS-1 DNA sequences. Amer. J. Bot. 85: 1517-1530.

Koopman, W.J.M., Hadam, J., Doležel, J. (2002) Evolution of DNA content and base composition in *Lactuca* (Asteraceae) and related genera. In: Koopman, W.J.M., Zooming in on the lettuce geonome: Species relationships in *Lactuca* s.l. inferred from chromosomal and molecular characters. Ph.D. Diss., Wageningen University, pp. 97-124.

Koopman, W.J.M., Zevenbergen, M.J., Van den Berg, R.G. (2001) Species relationships in *Lactuca* S.L. (Lactuceae, Asteraceae) inferred from AFLP fingerprints. Amer. J. Bot. 88: 1881-1887.

Křístková, E., Doležalová, I., Lebeda, A., Vinter, V., Novotná, A. (2008) Description of morphological characters of lettuce (*Lactuca sativa* L.) genetic resources. Hort. Sci. (Prague) 35 (3): 113-129.

Křístková, E. and Lebeda, A. (1999) Collection of *Lactuca* spp. genetic resources in the Czech Republic. In: Lebeda, A., Křístková, E. (Eds.) Eucarpia Leafy Vegetables ’99. Univerzita Palackého, Olomouc (Česká republika), pp. 109-116.

Lebeda, A. (1998) Biodiversity of the interactions between germplasms of wild *Lactuca* spp. and related genera and lettuce downy mildew (*Bremia lactucae*). Report on research programme OECD Biological Resource Management for Sustainable Agricultural Systems. HRI Wellesbourne, UK.

Lebeda, A. and Astley, D. (1999) World genetic resources of *Lactuca* spp., their taxonomy and biodiversity. In: Lebeda, A., Křístková, E. (Eds.) Eucarpia Leafy Vegetables ’99. Univerzita Palackého, Olomouc (Česká republika), pp. 81-94.

Lebeda, A., Doležalová, I. and Astley, D. (2002) Representation of wild *Lactuca* spp. (Asteraceae, Lactuceae) in world genebank collections. Genet. Resour. Crop Evol. 00:1-8.

Lebeda, A., Doležalová I., Feráková V., Astley D. (2004) Geographical distribution of wild *Lactuca* species (Asteraceae, Lactuceae). Bot. Rev. 70: 328-356.

Lebeda, A., Doležalová, I., Křístková, E., Dehmer, K.J., Astley, D., Van de Wiel, C.C.M., Van Treuren, R. (2007a) Acquisition and ecological characterization of *Lactuca serriola* L. germplasm collected in the Czech Republic, Germany, the Netherlands and United Kingdom. Genet. Resour. Crop Evol. 54: 555-562.

Lebeda A., Doležalová I, Křístková E. and Mieslerová B. (2001) Biodiversity and ecogeography of wild *Lactuca* spp. in some European countries. Genet. Resour. Crop Evol. 48: 153-164.

Lebeda A., Doležalová I., Křístková E., Vinter V., Vránová O., Doležal K., Tarkowski P., Petrželová I., Trávníček B., Novotný R., Janeček J. (1999) Complex research of taxonomy and ecobiology of wild *Lactuca* spp. genetic resources. In: Lebeda, A., Křístková, E. (Eds.) Eucarpia Leafy Vegetables '99. Univerzita Palackého, Olomouc (Česká republika), pp. 117-131.

Lebeda, A., Ryder E. J., Grube R., Doležalová I., Křístková E. (2007b) Lettuce (Asteraceae; *Lactuca* spp.) In: Singh, R. J. (Ed.) Genetic Resources, Chromosome Engineering, and Crop Improvement Series, Vol. 3, Vegetable Crops. Boca Raton, CRC Press, Taylor and Francis Group, pp. 377-472.

McGuire, P.E., Ryder, E.J., Michelmore, R.W., Clark, R.L., Antle, R., Emery, E., Hannan, R.M., Kesseli, R.V., Kurtz, E.A., Ochoa, O., Rubatzky, V.E., Waycott, W. (1993) Genetic resources of lettuce and *Lactuca* species in California: An assessment of the USDA and UC collections and recommendations for long-term security. Report No. 12. University of California Genetic Resources Conservation Program, Davis.

Oswald, P.H. (2000) Historical records of *Lactuca serriola* L. and *L. virosa* L. in Britain, with special reference to Cambridgeshire (v.c. 29). Watsonia 23: 149-159.

Prince, D.S. and Carter, R.N. (1977) Prickly lettuce (*Lactuca serriola* L.) in Britain. Watsonia 11: 331-338.

Prince, D.S. and Carter, R.N. (1985) The geographical distribution of prickly lettuce (*Lactuca serriola*). III. Its performance in transplant sites beyond its distribution limit in Britain. J. Ecol. 73: 49-64.

Rechinger, K.H. (1977) Flora Iranica. Flora des Iranischen Hochlandes und der Umrahmenden Gebirge. Graz: Academische Druck-u. Verlagsanstalt.

Rubatzky, V.E., Yamaguchi, M. (1997) World Vegetables. Ed. 2. Chapman & Hall, New York.

Shih, C. (1988a) Revision of *Lactuca* L. and two new genera of the tribe Lactuceae (Compositae) on the mainland of Asia. Acta Phytotax. Sin. 26: 382-393.

Shih, C. (1988b) Revision of *Lactuca* L. and two new genera of the tribe Lactuceae (Compositae) on the mainland of Asia (cont.). Acta Phytotax. Sin. 26: 418-428.

Stace, C. (1997) New Flora of the British Isles. Ed. 2. Cambridge University, Cambridge.

Stebbins, G.L. (1937) Critical notes on *Lactuca* and related genera. J. Bot. (London) 75: 12-18.

Stebbins, G.L. (1953) A new classification of the tribe Cichorieae, family Compositae. –Madroño 12,3: 65-81.

Tuisl, G. (1968) Der Verwandtschaftskreis der Gattung *Lactuca* L. im iranischen Hochland und seinen Randgebieten. Selbstverlag Naturhistorisches Museum Wien, Vienna.

Weaver, S., Cluney, K., Downs, M., Page, E. (2006) Prickly lettuce (*Lactuca serriola*) interference and seed production in soybeans and winter wheat. Weed Sci. 54: 496-503.

Weaver, S.E., Downs, M.P. (2003) The biology of Canadian weeds. 122. *Lactuca serriola* L. Can. J. Plant Sci. 83: 619-628.

Zohary, D. (1991) The wild genetic resources of cultivated lettuce (*Lactuca sativa* L.). Euphytica 53: 31-35.

4. RESULTS

4.1. Development of *Lactuca sativa* descriptor

4.2. Morphological variability of *Lactuca serriola* achenes

4.3. Morphological variability of *Lactuca serriola* leaves

4.4. Distribution, ecogeography and ecobiology of germplasm accessions of wild *Lactuca* species from USA and Canada

4.5. Genetic resources of wild *Lactuca* L. spp., their exploitation in lettuce breeding

4.1. Development of *Lactuca sativa* descriptor

Description of morphological characters of lettuce (*Lactuca sativa* L.) genetic resources

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ABSTRACT: Lettuce (*Lactuca sativa*) is the most important crop in the group of leafy vegetables. It is characterized by considerable morphological and genetic variation. The crop comprises seven main groups of cultivars (including oilseed lettuce) differing phenotypically; they are usually described as morphotypes. Lettuce breeding is primarilly focused on various morphological features and resistance against diseases and pests. The accurate description of lettuce germplasm provides basic information useful for lettuce breeders. The construction of a lettuce descriptor list has been stimulated by the international genebank community. This list consists of 55 descriptors with 15 elucidated by figures. It provides a tool for detailed characterization of and discrimination within the intraspecific variation of *L. sativa*, verification of old varieties, and identification of putative duplicates and gaps in germplasm collections. These descriptors, along with descriptors of wild *Lactuca* species, provide an efficient analytical tool for studying the complex morphological variability of this genus and relationships among the species.

Keywords: biology; characterization; descriptors; gene bank collections; gene pool; germplasm conservation; morphotypes; origin; regeneration; resistance; taxonomy; variability

Lactuca sativa L. (Asteraceae) is considered as the most important vegetable in the group of leafy vegetables. It is almost exclusively used as a fresh vegetable in salads, but some forms are also cooked (Rubatzky, Yamaguchi 1997; Lebeda et al. 2007). Lettuce is produced commercially in many countries worldwide and is also widely grown as a vegetable in home gardens (Rubatzky, Yamaguchi 1997). It is especially important as a commercial crop in Asia, North and Central America, and Europe. China, U.S., Spain, Italy, India and Japan are among the world's largest producers (Lebeda et al. 2007; Mou 2008).

Diverse landraces and local varieties are cultivated in different regions, with a broad spectrum of landraces and old varieties held in the world's genebanks (Lebeda et al. 2007). Conventional and modern breeding methods are providing new cultivars well tailored for the specific needs of producers and consumers.

International cooperation among genebanks has been promoted by the International Plant Genetic Resources Institute (IPGRI), established in 1974. Since 1 December 2006, IPGRI and the International Network for the Improvement of Banana and Plantain (INIBAP) operate under the name *Bioversity International* (www.bioversityinternational.org). The need for broad international cooperation among European institutions holding collections of lettuce was expressed in the Eucarpia Conference on Leafy Vegetables Research and Breeding, held in 1999 in Olomouc, Czech Republic (Lebeda, Křístková 1999). In May 2000, in Vila Real, Portugal, the ECP/GR Vegetables Network Coordinating Group, acting with an IPGRI mandate, recommended to extend collaborative activities also to leafy vegetables (Lebeda, Boukema 2001). The *ad hoc* Group on Leafy Vegetables met for the first time during the ECP/GR Vegetables Network Meeting in Skierniewice, Poland, May 2003 (Lebeda, Boukema 2005). A proposal to establish a formal ECP/GR Working Group on Leafy Vegetables was prepared and endorsed by the ECP/GR Steering Committee in October 2003. The first meeting of the formal Working Group was

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held in Olomouc, Czech Republic, 13–14 October 2005 (Maggioni et al. 2008).

The International *Lactuca* Database (ILDB) was established in 2000 and is currently maintained at CGN, Wageningen, the Netherlands. The database concentrates primarily on passport data of all *Lactuca* species conserved in the world's genebanks (Stavělíková et al. 2002).

Descriptive data for each accession held by genebanks promote the efficient use of accessions in research and breeding. However, descriptor lists for lettuce accessions, as elaborated by each national genebank, are used only locally. The international project GENE-MINE, funded by the European Commission within the 5th Framework Programme, aimed at a broad study of wild *Lactuca* species, made considerable progress (Hodgkin 2004) and both Czech national and international descriptor lists for wild *Lactuca* species were developed (Doležalová et al. 2002a, 2003a; Křístková, Chytilová 2005).

A broad international descriptor list for cultivated lettuce, suitable and acceptable for the international genebank community has not yet been elaborated. A minimum set of the most important descriptors for *Lactuca sativa* genetic resources was composed in order to foster cooperation within the ECP/GR Working Group on Leafy Vegetable Genetic Resources (Lebeda, Boukema 2005). The next international project aimed at the group of leafy vegetables including cultivated lettuce, was adopted by the European Commission in 2006. In this paper, a draft descriptor list for accessions of cultivated lettuce is presented. After discussion within the genebank community, it can be used as a base for development of an international descriptor list. Together with descriptors for wild *Lactuca* species (Doležalová et al. 2002a, 2003a; Lebeda et al. 2004b), it will provide a tool to facilitate the characterization of lettuce genetic resources.

TAXONOMY, BOTANICAL CHARACTERIZATION, KARYOLOGICAL STATUS, BIOCHEMICAL AND MOLECULAR MARKERS OF *L. SATIVA*

Taxonomy of the genus *Lactuca*

The genus *Lactuca* L. belongs to the family Asteraceae (Compositae), the largest of the dicotyledonous families (Judd et al. 1999; Funk et al. 2005). The tribe Lactuceae of subfamily Cichorioideae, formerly known as the Cichorieae, is perhaps the best known and most easily recognized tribe of the family (Tomb 1977). In spite of that, precise delimitation of the genus *Lactuca* is problematic. Based on the available literature, the genus *Lactuca* comprises approximately 100 species; however the number of *Lactuca* taxa differs from author to author (Feráková 1977; Meusel, Jäger 1992; Bremer et al. 1994; Lebeda 1998; Lebeda, Astley 1999; Lebeda et al. 2004a, 2007).

Five major generic concepts of *Lactuca* were developed by Stebbins (1937), Tuisl (1968), Feráková (1977), Shih (1988), and Koopman et al. (1998). Stebbins (1937) defined the genus broadly (*sensu lato, s.l.*) and included the subgenera *Mulgedium* Cass., *Lactucopsis* Schultz-Bip. ex Vis. et Panč., *Phaenixopus* Cass., *Mycelis* Cass., and part of *Cicerbita* Wallr. (excluding *C. alpina*, with a coarse pappus and nearly columnar, slightly compressed achenes). Tuisl (1968) defined the genus in a narrow sense on the basis of morphological and anatomical studies of fruit, flower, involucre and pappus. He divided *Lactuca s.l.* into the following six genera: *Mulgedium* Cass., *Scariola* F.W. Schmidt (= *Phaenixopus* Cass.), *Cicerbita* Wallr., *Cephalorrhynchus* Boiss., *Steptorhamphus* Bunge and *Lactuca* L. The narrow generic concept of *Lactuca* has been supported among others, by Soják (1961, 1962), who accepted *Scariola* and treated *Lactuca* sect. *Mulgedium* (Cass.) C. B. Clarke on a generic level as *Lagedium* Soják (a genus of an intermediate position between *Lactuca* and *Mulgedium*), and also by Jeffrey (1975).

Feráková (1970, 1977), with regard to both above-mentioned classifications, created a new concept. The genera *Mulgedium*, *Lactucopsis* and *Phaenixopus* (*Scariola*) were re-classified into corresponding sections. She recognized four sections within the genus: *Mulgedium* (Cass.) C.B. Clarke, *Lactucopsis* (Schultz-Bip. ex Vis. et Panč.) Rouy, *Phaenixopus* (Cass.) Benth. and *Lactuca*, which was further divided into two subsections, *Lactuca* and *Cyanicae* DC, while *Mycelis* Cass., *Steptorhampus* Bunge and *Cephalorrhynchus* Boiss. were considered as separate genera.

A more recent revision of *Lactuca* is that of Shih (1988). He restricted the genus *Lactuca* to those species having 7–25 yellow ligular florets and 1–10 longitudinal ribs on each side of the achene, with an acute to filiform beak at its apex. Such a definition limits the genus to the *serriola*-like species from the sect. *Lactuca* subsect. *Lactuca* according to Feráková (1977), excepting *L. virosa* and *L. livida*, species with broadly elliptical, narrowly winged achenes.

A completely different concept of the lettuce gene pool was proposed by Koopman et al. (1998). Based on analysis of DNA ITS-1 sequences, supported with data from crossing experiments (Thompson et al. 1941; Chupeau et al. 1994; Maisonneuve et al. 1995; Mazier et al. 1999), he adjusted genus limitation to coincide with the lettuce gene pool. He stated that the species in subsection *Cyanicae* do not belong to the lettuce gene pool and therefore should be excluded from *Lactuca*. Section *Lactuca* subsection *Lactuca* would then comprise the primary and secondary gene pools, while the sections *Phaenixopus*, *Mulgedium* and *Lactucopsis* comprise the tertiary gene pool.

In the context of these past treatments, the taxonomy of *Lactuca* genetic resources, including seven sections (*Lactuca* [subsect. Lactuca and Cyanicae], *Phoenixopus, Mulgedium, Lactucopsis, Tuberosae, Micranthae and Sororiae*), and two geographical groups (the African and North American ones), has been elaborated by Lebeda and Astley (1999) and most recently been reviewed in detail by Lebeda et al. (2007).

Origins and genepools

Recent evidence indicates that the origin of cultivated lettuce is polyphyletic (DeVries 1997). It resulted from human selection within a large genepool of *L. serriola,* with simultaneous introgression of genes from other *Lactuca* species or, alternatively, as an independently selected species (Lindqvist 1960). The region of the Middle East (Egypt and Iran) is considered a centre of lettuce origin. Many wild *Lactuca* species occur between the Euphrates and Tigris Rivers (Zohary 1991).

The primary genepool of *L. sativa* is represented by its numerous cultivars, primitive landraces and by wild species with no crossing barriers – the cosmopolitan *L. serriola,* plus *L. aculeata, L. scarioloides, L. azerbaijanica, L. georgica, L. altaica* occurring in Asia and by *L. dregeana* from South Africa (Zohary 1991). *Lactuca saligna* belongs to the secondary gene pool. The tertiary gene pool includes *L. virosa* and some other wild species which can be crossed with *L. sativa* only with difficulty (DeVries 1990; van Soest, Boukema 1997; Lebeda et al. 2002, 2007).

Morphological description, karyological status, molecular and biochemical markers of *L. sativa*

Lactuca sativa is an annual glabrous herb with a thin tap root and an erect stem 30–100 cm tall, branched in the upper part. Leaves are spirally arranged, forming a dense rosette or a head before bolting. Their shape is oblong to transverse elliptic, orbicular to triangular, undivided to pinnatisect. The leaf margin is entire to setose dentate, often curly. Stem leaves are oblong elliptic, with a cordate base. The inflorescence (capitulum, head) is composed of 7–15 (35) yellow ligules (florets). The heads form a corymbose, densely bracted panicle. Anthocyanin can be distributed on the cotyledons and true leaves, stems and ligules. The involucre is 10–15 mm long, cylindrical; involucral bracts are broadly to narrow lanceolate, light green, with white margins, erect at the stage of fruit maturity. The fruit (achene) has 5 to 7 setose ribs on each side, a beak and a white pappus. Its length (including beak) is 6–8 mm, and its colour is white, cream, gray, brown or black. It is a diploid with a basic chromosome number of $n = 9$ (Dostál 1989; Rubatzky, Yamaguchi 1997; Doležalová et al. 2002b; Grulich 2004).

Electrophoretic detection of polymorphic proteins has been applied to the study of genetic variation among *L. sativa* cultivars and a wild *Lactuca* species (DeVries 1996; Lebeda et al. 1999; Doležalová et al. 2003b; Mizutani, Tanaka 2003). The application of molecular genotyping methods: RFLP (Restriction Fragment Length Polymorphism) (Kesseli et al. 1991), RAPD (Random Amplified Polymorphic DNA) (Yamamoto et al. 1994), AFLP (Amplified Fragment Length Polymorphism) (Hill et al. 1996; Johnson et al. 2000; Jeuken et al. 2001; Jeuken, Lindhout 2004; Kitner et al. 2008; Rajicic, Dehmer 2008), TRAP (Target Region Amplification Polymorphism) (Hu et al. 2005), minisatellites and microsatellite fingerprinting or SSR (Simple Sequence Repeat) (Witsenboer et al. 1997; Sicard et al. 1999; Van de Wiel et al. 1999) has contributed to the elucidation of various aspects of the taxonomy, variability and biodiversity of the genus. SSRs and AFLPs have also been used to characterize the entire lettuce collection of the Centre for Genetic Resources (CGN, Wageningen) (van Hintum et al. 2003; Jansen et al. 2006; Jansen, van Hintum 2007). An overview of these methods as applied to *L. sativa* germplasm screening and identification has been presented by Dziechciarková et al. (2004). The mapping of the *L. sativa* genome (Landry et al. 1987) and the study of biochemical and molecular markers provide tools for the determination of putative duplicates within collections of genetic resources, for the discrimination of differences among accessions (van Hintum 1999; Waycott et al. 1999; Van de Wiel et al. 1999; Sretenović-Rajičić et al. 2008), and for the identification of suitable markers linked to resistance to biotic and abiotic factors (Kesseli et al. 1994; Maňez et al. 1994; Toyomasu et al. 1995; Montesclaros et al. 1997).

Classification and morphological types of *L. sativa*

The species *L. sativa* is characterized by a high genetic diversity resulting from its polyphyletic origin and a complex domestication process (Kesseli et al. 1991). A survey of lettuce cultivars and classification of types was provided by Rodenburg (1960). The most recent comprehensive overviews of taxonomic and phenotypic analyses of lettuce cultivars were presented by DeVries and van Raamsdonk (1994), DeVries (1997) and Mou (2008). The crop comprises seven main groups of cultivars (including oilseed lettuce) differing phenotypically; they are usually described as morphotypes. The following treatment of *L. sativa* morphotypes is taken from Lebeda et al. (2007).

(1) **Butterhead lettuce** (var. *capitata* L. *nidus tenerrima* Helm) (Kopfsalat, Laitue pommé)
A heading type with soft and tender leaves, eaten raw. It is most popular in England, France, the Netherlands and other western and central European countries (Ryder 1986). In recent decades many cultivars have been bred and grown in the USA (Ryder 1999b; Mikel 2007).

(2) **Crisphead lettuce** (var. *capitata* L. *nidus jäggeri* Helm) (Iceberg type, Eissalat, Batavia)
A heading type with thick crisp leaves and flabellate leaf venation, eaten raw. It is mainly cultivated in the USA (Ryder 1999b; Mikel 2007). However, it is also grown now in western and central European countries, including the Netherlands, the United Kingdom, France, Spain, Belgium, Germany, Poland and the Czech Republic, as well as in Japan, China, and Australia (Lebeda et al. 2007).

(3) **Cos lettuce** (var. *longifolia* Lam., var. *romana* Hort. in Bailey) (Römischer Salat, Laitue romaine)
Plants with tall loose heads, which are sometimes tied up; oblong rigid leaves with a prominent midrib running almost to the apex, are eaten raw or cooked. The name of the morphotype is taken from the Greek island Cos (Kos), where the type has long been cultivated. Cos lettuce is most common in the Mediterranean countries of Europe, Western Asia and North Africa (Ryder 1986). According to Boukema et al. (1990), many landraces of this type maintained at the CGN genebank collection originated mainly from Egypt, Iran, Turkey and Syria.

(4) **Cutting lettuce** (var. *acephala* Alef., syn. var. *secalina* Alef., syn. var. *crispa* L.) (Gathering lettuce, Loose-leaf, Picking lettuce, Schnittsalat, Laitue à couper)
Non-heading type harvested as whole, open rosettes, occasionally as separate leaves, eaten raw. Cutting lettuces have been very popular in the U.S., Italy, France, the Czech Republic and Slovak Republic (DeVries 1997). This morphotype is extremely heterogeneous. Cultivars may have entire, curled or fringed leaves, from non-lobed to deeply incised margins. The leaves are elongated or broad, having various shades of green, and various patterns and intensities of anthocyanin pigmentation. The Greeks and Romans cultivated cutting lettuces. Boukema et al. (1990) stated that CGN genebank landraces of this type came from Turkey and Greece.

(5) **Stalk (Asparagus) lettuce** (var. *angustana* Irish ex Bremer, syn. var. *asparagina* Bailey, syn. *L. angustana* Hort. in Vilm.) (Stem lettuce, Stengelsalat, Laitue-tige)
Plants with swollen stalks, which are eaten raw or cooked like asparagus. Leaves can be eaten raw in a very young stage or cooked like spinach (Lebeda, Křístková 1995).
According to Lindqvist (1960) there are two types recognized within this group. The Chinese cultivars have light grey leaves resembling cos lettuce leaves; the second type has long lanceolate leaves with pointed apices. According to Helm (1954), stalk lettuce originated in Tibet, which would account for its extensive cultivation in China, in the Pamirs and India (Rodenburg 1960; DeVries 1997). However, the lettuce illustrated in Egyptian tombs is also stalk lettuce and dates back to about 2500 B.C. If lettuce originated in Mesopotamia, it is even older in the Middle East. Both asparagus types and cos-like types are found in Egypt. We think it is more likely that the original types migrated to the Far East overland, showing up there up to 1,500–2,000 years later. It is possible that Helm (1954) was referring to *L. indica*, which is common in the Far East and grown in China, Japan, and some Southeast Asian countries (Rubatzky, Yamaguchi 1997). Stalk lettuce material collected in Afghanistan appeared to be an intermediate between cos and stalk lettuces and is sometimes used as a food for livestock (Boukema et al. 1990).

(6) **Latin lettuce** (without scientific name)
Plants have loose heads with thick leathery leaves, dark green color and are eaten raw. It is mainly cultivated in the Mediterranean countries, including North Africa, and in South America (Rodenburg 1960).

(7) **Oilseed lettuce**

Because of the bitter taste of its leaves, this type is not eaten as a vegetable. Oilseed lettuce is characterized by a high percentage (35%) of oil in the seeds, which is used for cooking. The oil contains Vitamin E, an essential nutrient (Boukema et al. 1990). In Egypt, cultivation of oil-producing forms has continued to the present time (Ryder 1986). Boukema et al. (1990) mentioned that some of its forms may be either *L. serriola* or *L. sativa* or intermediate types between these two species.

Following the concept of DeVries and van Raamsdonk (1994), based on a detailed comparison from multivariate analysis of the vegetative characters of lettuce cultivars, two supergroups can be defined, one that includes the Butterhead group, the Crisphead (Iceberg or Cabbage) group, and Latin group; and the other comprising the Cos group, the Cutting group, and the Stalk (Asparagus) group.

Survey of *L. sativa* genetic resources maintained in gene bank collections

Considerable information is available about lettuce germplasm collections (Boukema et al. 1990; McGuire et al. 1993; Cross 1998; Lebeda 1998; van Hintum, Boukema 1999; Lebeda, Astley 1999; Ryder 1999a,b; Lebeda, Boukema 2001, 2005; Thomas et al. 2005; Lebeda et al. 2007; Mou 2008). These sources provide general information about the holdings, maintenance conditions, availability, evaluation, and documentation of the most important of the world's collections, emphasizing national genebanks and working collections. In addition, information about the holdings of the world's largest collections of leafy vegetable germplasm was summarized as part of the Food and Agriculture Organization's effort to present The State of the World's Plant Genetic Resources for Food and Agriculture (FAO 1998).

In the U.S., germplasm research regarding conservation, evaluation and utilization of lettuce resources is overseen by Leafy Vegetable Crop Germplasm Committees (CGC) under auspices of the US Department of Agriculture – Agricultural Research Service's National Plant Germplasm System.

STANDARDS FOR REGENERATION AND EVALUATION OF GENETIC RESOURCES ACCESSIONS

Regeneration of *L. sativa* accessions

Standards for regeneration of cultivated lettuce, used in gene banks of eleven European countries, were summarized within the framework of the ECP/GR Working Group on Leafy Vegetables (IPGRI) by Lebeda and Boukema (2005). In the Czech Republic, standards for regeneration for *L. sativa* accessions were adopted by the Council for Plant Genetic Resources of the Czech Republic (Chytilová et al. 2004).

The inflorescence of lettuce (capitulum), contains approximately 24 florets. They are highly developed for self-pollination and the crop is therefore largely self-fertilizing. However, some cross-pollination, up to 5%, can be observed between lettuce cultivars (George 1999). For commercial purposes, most authorities regard it as a self-pollinating crop and only require a physical barrier (e.g. adjacent sections of greenhouse) or a minimum of 2 m between different species for production of seed (George 1999). The regeneration of accessions kept by genebanks in insect-proof isolation cages is highly recommended to prevent potential cross-pollination and infection of LMV.

Under climatic conditions of the Czech Republic, accessions are regenerated in greenhouse isolation cages covered by glass or plastic net. Seeds are sown in the last third of March in Perlite; seedlings with well developed cotyledons are transplanted to beds in garden soil. By the end of April, plantlets with 10–12 well developed leaves are transplanted to soil under isolation cages. Each accession is represented by 15–20 plants spaced 50 × 50 cm.

Heading types and especially cultivars bred for cultivation in summer, are treated with aqueous solution of gibberellic acid (20–500 ppm GA_3) at least three times at 7–10 day intervals before heart formation. This treatment stimulates bolting and prevents the plants from rotting (George 1999).

Mature seeds are harvested periodically, by cutting the dry seed heads. Harvested seeds are dried at room temperature, cleaned, and further dried to 5–8% moisture content, placed in hermetically closed jars and stored at a temperature of about –5°C (George 1999). A new method of "ultra-dry seed" storage was successfully adopted for *L. sativa*. Seeds dried to 3% moisture content and stored in airtight jars at 20°C (Gómez-Campo 2006) kept good germination parameters equal to storage at –20°C (Astley 1985).

A SET OF DESCRIPTORS FOR ACCESSIONS OF *L. SATIVA*

Morphological and biological descriptors

A set of descriptors for cultivated lettuce has been developed for the characterization and evaluation genetic resources (Table 1, Figs.). In the Czech Republic, a set of minimum descriptors has been adopted by the Council for Plant Genetic Resources of the Czech Republic (Chytilová et al. 2004). An extensive list of descriptors also provides tools for determining interspecific hybrids of *L. sativa* with wild *Lactuca* species, and for the characterization of *L. sativa* intraspecific variability. This set was created from a broad study of the Czech collection of genetic resources (Superatová 2005), traditional and recent cultivars of lettuce (Křístková, Lebeda 1999), descriptions of *L. sativa* in Czechoslovak monographs (Feráková 1977), the Czech flora (Grulich 2004) and a broad description of important traditional cultivars (Rodenburg 1960).

"Codes for *Lactuca* evaluation descriptors" from the Centre for Genetic Resources (CGN), Wageningen, the Netherlands (Anonymous b) and the Western Regional Plant Introduction Station, Pullman, Washington, USA (Anonymous a), and "Guidelines for the conduct of tests for distinctness, homogeneity and stability, Lettuce (*Lactuca sativa* L.)" (UPOV 1981) were used as primary sources for the development of recent Czech descriptors. During the construction of this descriptor list, the authors also participated in the development of minimal descriptor lists for leafy vegetables, including *L. sativa*, within the framework of the ECP/GR Working Group on Leafy Vegetables (IPGRI) (Lebeda, Boukema 2005).

The descriptor list includes 55 characterization and evaluation descriptors, with 15 elucidated by figures in the Annex. Items comprising a minimal set of highly discriminating descriptors are marked with an asterisk (*).

Resistance to biotic and abiotic factors

Resistance to biotic and abiotic factors must be evaluated in separate trials by using precise, standardized methods (Lebeda 1986; Miranda, Lebeda 2008), such as pathogen tests in growth chambers after artificial inoculation.

The most important lettuce diseases include *Lettuce mosaic virus* (LMV), lettuce downy mildew (*Bremia lactucae*), *Sclerotinia* spp., *Microdochium panattonianum*, *Rhizoctonia solani*, *Pythium* spp., *Botrytis cinerea*, lettuce powdery mildew (*Golovinomyces cichoracearum*) and *Septoria* spp. (George 1999). The most important lettuce pests include the aphids, *Myzus persicae, Nasonovia ribisnigri* and *Pemphigus bursarius* (Reinink 1999; Lebeda et al. 2007).

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Table 1. Morphological descriptors for *Lactuca sativa* L.

No.	Descriptor name	Descriptor state	Explanation/ Figure in Annex	Note
1. Morphological descriptors				
1.1. Seedling				
1.1.1.	Cotyledons – colour	3 light green 5 green 7 dark green 99 other		at a stage of fully developed seedling
1.1.2.*	Cotyledons – anthocyanin presence	0 absent 1 on hypocotyl 2 on cotyledons 3 on hypocotyl and cotyledons		at a stage of fully developed seedling
1.1.3.	Cotyledons – shape	1 elliptic 2 ovate 3 obovate 4 orbicular 5 spatulate 99 other	Fig. 1.1.3.	at a stage of fully developed seedling

No.	Descriptor name	Descriptor state	Explanation/ Figure in Annex	Note
1.1.4.	Cotyledons – trichomes	0 absent 1 present		at a stage of fully developed seedling
1.2. Young leaf				
1.2.1.*	Young leaf – position	 1 prostrate 5 semi-erect 9 erect	angle of 5^{th}–6^{th} true leaf with horizontal platform 1°–10° 41°–50° 81°–90°	at a stage of 10–12 true leaves
1.2.2. *	Young leaf – colour	1 yellow green 2 light green 3 green 4 dark green 5 gray green 6 blue green 99 other		at a stage of 10–12 fully developed true leaves
1.2.3.1.*	Young leaf – anthocyanin – distribution	0 absent 1 on the veins 2 on the blade margin 3 diffused on the entire lamina 4 in spots on the entire lamina 99 other		at a stage of 10–12 fully developed true leaves
1.2.3.2.	Young leaf – anthocyanin – intensity of coloration	3 slight 5 moderate 7 intense		at a stage of 10–12 fully developed true leaves
1.2.4.1.	Young leaf – blade	1 entire 2 divided		at a stage of 10–12 fully developed true leaves
1.2.4.2.*	Young leaf – blade – shape in outline	1 oblong elliptic 2 elliptic 3 broad elliptic 4 orbicular 5 transverse elliptic 6 transverse broad elliptic 7 obovate 8 spathulate 9 triangular 99 other	Fig. 1.2.4.2.	at a stage of 10–12 fully developed true leaves
1.2.4.3.*	Young leaf – blade – shape of apex	1 truncate 2 rounded 3 obtuse 4 subacute 5 mucronate	Fig. 1.2.4.3.	at a stage of 10–12 fully developed true leaves
1.2.4.4.	Young leaf – blade – shape of base	1 short attenuate 2 medium attenuate 3 long attenuate	Fig. 1.2.4.4.	at a stage of 10–12 fully developed true leaves

No.	Descriptor name	Descriptor state	Explanation/ Figure in Annex	Note
1.2.4.5.*	Young leaf – blade – margin	1 entire 2 crenate 3 dentate 4 double dentate 5 setose dentate 6 serrate 7 double serrate 8 irregularly dentate 9 nibbled 99 other	Fig. 1.2.4.5.	at a stage of 10–12 fully developed true leaves
1.2.4.6.	Young leaf – blade – vertical margin undulation	0 none 3 slight 5 moderate 7 intense		at a stage of 10–12 fully developed true leaves
1.2.5.	Young leaf – trichomes	0 absent 1 present		at a stage of 10–12 fully developed true leaves
1.2.6.*	Young leaf – venation	1 pinnate 2 flabellate	Fig. 1.2.6.	at a stage of 10–12 fully developed true leaves
1.3. Adult outer leaf (and leaf of non-heading types of lettuce)				
1.3.1.*	Outer adult leaf – colour	1 yellow green 2 green 3 gray green 4 blue green 5 red and green 99 other		at a harvest maturity
1.3.2.	Outer adult leaf – intensity of colour	3 slight 5 moderate 7 intense		at a harvest maturity
1.3.3.1.*	Outer adult leaf – anthocyanin – distribution	0 absent 1 on the veins 2 on the blade margin 3 diffused on the entire lamina 4 in spots on the entire lamina 99 other		at a harvest maturity
1.3.3.2.	Outer adult leaf – anthocyanin – intensity of coloration	0 none 3 slight 5 moderate 7 intense		at a harvest maturity
1.3.4.*	Outer adult leaf – glossiness on the upper side	0 none 3 slight 5 moderate 7 intense		at a harvest maturity
1.3.5.	Outer adult leaf – surface profile	1 concave 2 flat 3 convex	Fig. 1.3.5.	at a harvest maturity
1.3.6.*	Outer adult leaf – blade	1 entire 2 divided		at a harvest maturity

No.	Descriptor name	Descriptor state	Explanation/ Figure in Annex	Note
1.3.7.*	Outer adult leaf – entire – shape of blade in outline	1 oblong elliptic	Fig. 1.3.7.1	at a harvest maturity
		2 elliptic		
		3 broad elliptic		
		4 orbicular		
		5 transverse elliptic		
		6 transverse broad elliptic		
		7 obovate		
		8 spathulate		
		9 triangular		
		99 other		
1.3.7.2.*	Outer adult leaf – entire – margin of blade	1 entire	Fig. 1.3.7.2.	at a harvest maturity
		2 crenate		
		3 dentate		
		4 double dentate		
		5 setose dentate		
		6 serrate		
		7 double serrate		
		8 irregularly dentate		
		9 nibbled		
1.3.8.*	Outer adult leaf – divided – depth of incisions		Fig. 1.3.8. depth of incisions from blade margin to the main vein	at a harvest maturity
		3 pinnatilobed	up to 1/3	
		5 pinnatifid	up to 1/2	
		7 pinnatipart	up to 2/3	
		9 pinnatisect	more than 2/3	
1.3.9.*	Outer adult leaf – shape of apex	1 truncate	Fig. 1.3.9.	at a harvest maturity
		2 rounded		
		3 obtuse		
		4 subacute		
		5 mucronate		
		99 other		
1.3.10.	Outer adult leaf – shape of blade base	1 short attenuate	Fig. 1.3.10.	at a harvest maturity
		2 medium attenuate		
		3 long attenuate		
1.3.11.*	Outer adult leaf – blistering	0 none		at a harvest maturity
		3 slight		
		5 moderate		
		7 intense		
1.4. Head, leaf rosette				
1.4.1.*	Head – formation	0 absent		at a harvest maturity
		1 present		
1.4.2.	Harvested part – size of head and/or a rosette		horizontal diameter	at a harvest maturity
		3 small	< 25 (cm)	
		5 medium	25–40 (cm)	
		7 large	> 40 (cm)	

No.	Descriptor name	Descriptor state	Explanation/ Figure in Annex	Note
1.4.4.1.*	Head – shape in vertical section	1 oblong elliptic	Fig. 1.4.4.1.	at a harvest maturity
		2 elliptic		
		3 broad elliptic		
		4 orbicular		
		5 transverse elliptic		
		99 other		
1.4.4.2.	Head – overlapping of leaves	0 none	Fig. 1.4.4.2.	at a harvest maturity
		3 partly		
		5 half		
		7 complete		
1.4.4.3.	Head – firmness	3 low	established by palpation	at a harvest maturity
		5 medium		
		7 high		
1.4.4.4.	Head – weight	3 low	< 300 (G)	at a harvest maturity
		5 medium	300–600 (G)	
		7 high	> 600 (G)	
1.4.5.	Leaf rosettte – position of leaves		angle of leaves from middle part of rosette with horizontal platform	for non-heading types at a market maturity
		1 very upright	61°–90°	
		3 upright	46°–60°	
		5 medium	31°–45°	
		7 flat	16°–30°	
		9 very flat	0°–15°	
Note: For description of leaves of non-heading types use descriptors for adult outer leaf (part 1.3.)				
1.5. Stem				
1.5.1.	Stem – length		length including inflorescence	at a stage of a full flowering
		3 short	< 50 (cm)	
		5 medium	50–80 (cm)	
		7 high	> 80 (cm)	
1.5.2.	Stem – fasciations	0 absent		at a stage of a full flowering
		1 present		
1.5.3.*	Stem – anthocyanin	0 absent		at a stage of a full flowering
		1 present		
1.6. Flower, Inflorescence resp. (Fig. 1.6.)				
1.6.1.	Flower – colour of ligules	3 pale yellow		
		5 yellow		
		7 dark yellow		
		99 other		
1.6.2.1.	Flower – anthocyanin – distribution pattern on lower part of ligules	0 absent		
		1 in spots		
		2 on margin		
		3 diffused on surface		
		99 other		
1.6.2.2.	Flower – anthocyanin – intensity of coloration	3 slight		
		5 moderate		
		7 intense		

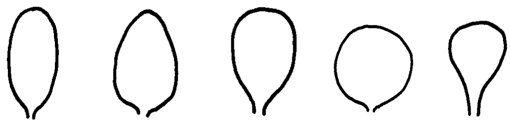
No.	Descriptor name	Descriptor state	Explanation/ Figure in Annex	Note
1.6.3.	Flower – margin of ligules		division of upper part of ligule	
		3 shallow	< 1 (mm)	
		5 medium	1–2 (mm)	
		7 deep	> 2 (mm)	
1.6.4.	Flower – anthocyanin in anther tube	1 absent		
		2 present		
1.6.5.	Flower – number of ligules in head	3 low	< 12	
		5 medium	12–20	
		7 high	> 20	
1.6.6.	Head – bracts – anthocyanin distribution pattern	0 absent		at a stage of a full flowering
		1 in spots		
		2 on margin		
		3 diffused on surface		
		99 other		
1.6.7.	Head – involucrum –trichomes	0 absent		
		1 present		
1.6.8.	Head – position of involucrum bracts	1 erect		at a stage of seed maturity
		2 reflected		
		99 other		
1.6.9.	Inflorescence – intensity of axillary sprouting (number of branches)	3 low	< 12	at a stage of a full flowering
		5 medium	12–20	
		7 high	> 20	
1.7. Fruit				
1.7.1.*	Achene – colour	1 white		after drying to a 15% R.H.
		2 grey white		
		3 cream		
		4 maroon		
		5 brown		
		6 grey		
		7 black		
		99 other		
1.7.2.	Achene – shape in outline	1 ovate		
		2 obovate		
		3 elliptic		
		99 other		
1.7.3.*	Fruit – "thousand seeds weight"	3 low	< 0.9 (G)	after drying to a 15% R.H.
		5 moderate	0.9–1.2 (G)	
		7 high	> 1.2 (G)	
2. Biological features				
2.1. Developmental stages				
2.1.1.*	Bolting	3 early	< 50	number of days after sowing to the visual symptoms of bolting in the field under a long day, without chemical treatment
		5 medium	50–70	
		7 late	> 70	
2.1.2.*	Flowering	3 early	< 60	number of days after sowing to the first fully developed flower in the field under a long day, without chemical treatment
		5 medium	60–80	
		7 late	> 80	

No.	Descriptor name	Descriptor state	Explanation/ Figure in Annex	Note
2.2. Resistance to biotic and abiotic factors				
	Factor	0 nonhost		
		1 very high		
		3 medium		
		5 low		
		7 very low		
		9 none		
2.2.1.	Reaction race specific	list of resistance factors		

An additional descriptor state = 99 is added to qualitative characters and should be used for accessions represented by heterogeneous populations (mixtures of individuals with different expression of characters). Its specification should list all states observed

* Highly discriminating descriptors

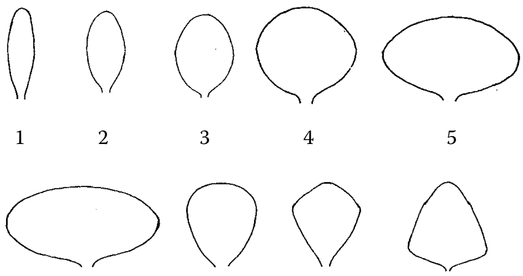
Annex: Figures to descriptors



1 2 3 4 5

Fig. 1.1.3. Cotyledons – shape

1 elliptic; 2 ovate; 3 obovate; 4 orbicular; 5 spatulate



1 2 3 4 5 6 7 8 9

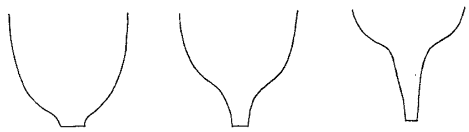
Fig. 1.2.4.2. Young leaf – blade – shape in outline and
Fig. 1.3.7.1. Outer adult leaf – entire – shape of blade in outline

1 oblong elliptic; 2 elliptic; 3 broad elliptic; 4 orbicular; 5 transverse elliptic; 6 transverse broad elliptic; 7 obovate; 8 spathulate; 9 triangular

1 2 3 4 5

Fig. 1.2.4.3. Young leaf – blade – shape of apex, and
Fig. 1.3.9. Outer adult leaf – shape of apex

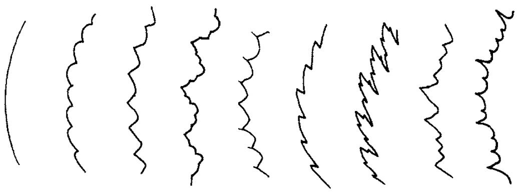
1 truncate; 2 rounded; 3 obtuse; 4 subacute; 5 mucronate



1 2 3

Fig. 1.2.4.4. Young leaf – blade – shape of base and
Fig. 1.3.10. Outer adult leaf – shape of blade base

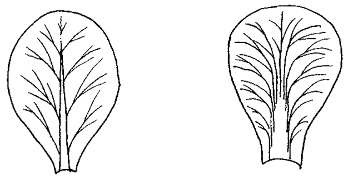
1 short attenuate; 2 medium attenuate; 3 long attenuate



1 2 3 4 5 6 7 8 9

Fig. 1.2.4.5. Young leaf – blade – margin and
Fig. 1.3.7.2. Outer adult leaf – entire – margin of blade

1 entire; 2 crenate; 3 dentate; 4 double dentate; 5 setose dentate; 6 serrate; 7 double serrate; 8 irregularly dentate; 9 nibbled



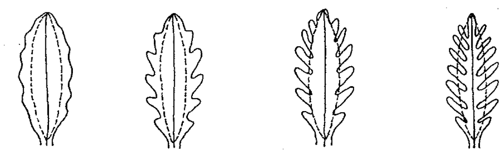
1 2

Fig. 1.2.6. Young leaf – venation

1 pinnate; 2 flabellate

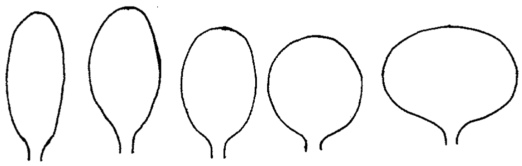
1 2 3

Fig. 1.3.5. Outer adult leaf – surface profile
1 concave; 2 flat; 3 convex



3 5 7 9

Fig. 1.3.8. Outer adult leaf – divided – depth of incisions
3 pinnatilobed; 5 pinnatifid; 7 pinnatipart; 9 pinnatisect



1 2 3 4 5

Fig. 1.4.4.1. Head – shape in vertical section
1 oblong elliptic; 2 elliptic; 3 broad elliptic; 4 orbicular; 5 transverse elliptic

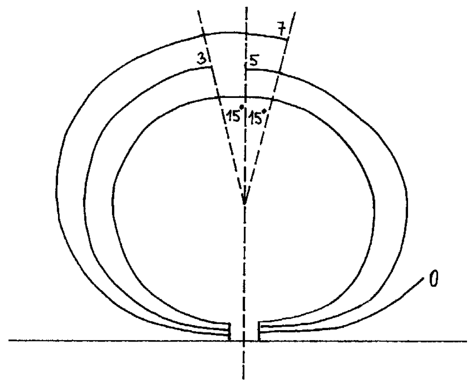


Fig. 1.4.4.2. Head – overlapping of leaves
0 none; 3 partly; 5 half; 7 complete

1 2

Fig. 1.6. Flower and Inflorescence
1 Flower (individual flower with ligule, anther tube, stigma, style and ovary with immature achene on the base), 2 Inflorescence = head

References

ANONYMOUS a. Codes for *Lactuca* evaluation descriptors. Western Regional Plant Introduction Station, Pullman, Washington.

ANONYMOUS b. Codes for *Lactuca* evaluation descriptors. Centre for Genetic Resources, Centre for Plant Breeding Research, Wageningen.

ASTLEY D., 1985. Conserving genetic resources in vegetables. Span, *28:* 75.

BOUKEMA I.W., HAZEKAMP TH., HINTUM TH.J.L VAN, 1990. The CGN Collection Reviews: The CGN Lettuce Collection. Wageningen, Centre for Genetic Resources: 2–5.

BREMER K., ANDERBERG A.A., KARIS P.O., NORDENSTAM B., LUNDBERG J., RYDING O., 1994. Asteraceae: Cladistics and Classification. Portland, Oregon, Timber Press.

CHUPEAU M.C., MAISONNEUVE B., BELLEC Y., CHUPEAU Y., 1994. A *Lactuca* universal hybridizer, and its use in creation of fertile interspecific somatic hybrids. Molecular and General Genetics, *245*: 139–145.

CHYTILOVÁ V., KŘÍSTKOVÁ E., LOSÍK J., PETŘÍKOVÁ K., STAVĚLÍKOVÁ H., 2004. 7.9. Metodika řešení kolekce zelenin, aromatických a kořeninových rostlin, 7.9.1. Speciální část: Zelenina. Díl III. – Speciální plodinové metodiky (7.9. Methods of treating the collection of vegetable, aromatic and spice plants, 7.9.1. Special part: Vegetables. Volume III. – Special crop methods): 70–85. In: DOTLAČIL L., STEHNO Z., FÁBEROVÁ I., HOLUBEC V. (eds), Rámcová metodika Národního programu konzervace a využívání genetických zdrojů rostlin a agro-biodiverzity (Frame methods of the National programme of the conservation and utilization of plants and agro-biodiversity). Praha, Rada genetických zdrojů, Výzkumný ústav rostlinné výroby (Council for Genetic Resources, Research Institute of Crop Production), Genetické zdroje č. 90. (In Czech)

CROSS R.J., 1998. Review paper: global genetic resources of vegetables. Plant Varieties & Seeds, *11*: 39–60.

DOLEŽALOVÁ I., KŘÍSTKOVÁ E., LEBEDA A., VINTER V., 2002a. Description of morphological characters of wild *Lactuca* L. spp. genetic resources (English-Czech version). Horticultural Science (Prague), *29*: 56–83.

DOLEŽALOVÁ I., LEBEDA A., JANEČEK J., ČÍHALÍKOVÁ J., KŘÍSTKOVÁ E., VRÁNOVÁ O., 2002b. Variation in chromosomes numbers and nuclear DNA contents in genetic resources of *Lactuca* L. species (Asteraceae). Genetic Resources and Crop Evolution, *49*: 383–395.

DOLEŽALOVÁ I., KŘÍSTKOVÁ E., LEBEDA A., VINTER V., ASTLEY D., BOUKEMA I.W., 2003a. Basic morphological descriptors for genetic resources of wild *Lactuca* spp. Plant Genetic Resources Newsletter, *134*: 1–9.

DOLEŽALOVÁ I., LEBEDA A., DZIECHCIARKOVÁ M., KŘÍSTKOVÁ E., ASTLEY D., VAN DE WIEL. C.C.M, 2003b. Relationships among morphological characters, isozymes polymorphism and DNA variability – the impact on *Lactuca* germplasm taxonomy. Czech Journal of Genetics and Plant Breeding, *39*: 59–67.

DOSTÁL J. (ed.), 1989. Nová květena ČSSR, 2. díl. Praha, Academia: 1114.

DZIECHCIARKOVÁ M., LEBEDA A., DOLEŽALOVÁ I., ASTLEY D., 2004. Characterization of *Lactuca* spp. germplasm by protein and molecular markers – a review. Plant, Soil and Environment, *50*: 47–58.

FAO, 1998. The State of the World's Plant Genetic Resources for Food and Agriculture. Rome, Food and Agriculture Organization of the United Nations.

FERÁKOVÁ V., 1970. A biosystematic study of critical species of *Lactuca* sect. *Lactucopsis*. Folia Geobotanica et Phytotaxonomica, *5*: 401–427.

FERÁKOVÁ V., 1977. The genus *Lactuca* L. in Europe. Bratislava, Univerzita Komenského: 122.

FUNK V.A., BAYER R.J., KEELEY S., CHAN R., WATSON L., GEMEINHOLZER B., SCHILLING E., PANERO J.L., BALDWIN B.G., GARCIA-JACAS N., SUSANNA A., JANSEN R.K., 2005. Everywhere but Antarctica: Using a supertree to understand the diversity and distribution of the Compositae. Biologiske Skrifter, *55:* 343–374.

GEORGE R.A.T., 1999. Compositae. In: GEORGE R.A.T., Vegetable Seed Production. Wallingford, CAB International: 122–135.

GÓMEZ-CAMPO C., 2006. Long term seed preservation: updated standards are urgent. Monographs ETSIA, Universita Politécnica de Madrid, *168:* 1–4.

GRULICH V., 2004. *Lactuca* L. In: SLAVÍK B., ŠTĚPÁNKOVÁ J. (eds), Květena České republiky 7. Praha, Academia: 487–497.

HELM J., 1954. *Lactuca sativa* in morphologisch-systematischer Sicht. Kulturpflanze, *2*: 72–129.

HILL M., WITSENBOER H., ZABEAU M., VOS P., KESSELI P., MICHELMORE R., 1996. PCR-based fingerprinting using AFLPs as a tool for studying genetic relationships in *Lactuca* spp. Theoretical and Applied Genetics, *93*: 1202–1210.

HINTUM TH.J.L. VAN, 1999. Improving the management of genebanks: A solution from biotechnology. In: LEBEDA A., KŘÍSTKOVÁ E. (eds), Eucarpia Leafy Vegetables '99. Olomouc, Palacký University: 107–108.

HINTUM TH.J.L. VAN, BOUKEMA I.W., 1999. Genetic resources of leafy vegetables. In: LEBEDA A., KŘÍSTKOVÁ E. (eds), Eucarpia Leafy Vegetables '99. Olomouc, Palacký University: 59–80.

HINTUM TH.J.L. VAN, LEBEDA A., PINK D.A., SCHUT J.W. (eds), 2003. Eucarpia Leafy Vegetables 2003, Proceedings of the Eucarpia Meeting on Leafy Vegetables Genetics and Breeding, Noordwijkerhout, the Netherlands, 19–21 March 2003. Wageninen, Centre for Genetic Resources, the Netherlands (CGN).

HODGKIN T., 2004. GENE-MINE: Improving the use of germplasm collections with the aid of novel methods for genetic data sets. IPGRI Newsletter, *29*: 13.

HU J., OCHOA O.E., TRUCO M.J., VICK B.A., 2005. Application of the TRAP technique to lettuce (*Lactuca sativa* L.) genotyping. Euphytica, *144:* 225–235.

JANSEN J., HINTUM TH.J.L. VAN, 2007. Genetic distance sampling: a novel sampling method for obtaining core collections using genetic distances with an application to cultivated lettuce. Theoretical and Applied Genetics, *114:* 421–428.

JANSEN J., VERBAKEL H., PELEMAN J., HINTUM TH.J.L. VAN, 2006. A note on the measurement of genetic diversity within genebank accessions of lettuce (*Lactuca sativa* L.) using AFLP markers. Theoretical and Applied Genetics, *112:* 554–561.

JEFFREY C., 1975. *Lactuca* L. In: DAVIS P.H. (ed.), Flora of Turkey and the East Aegean Islands. Edinburgh, Edinburgh University Press: 776–782.

JEUKEN M.J.W., LINDHOUT P., 2004. The development of lettuce backcross inbred lines (BILs) for exploitation of the *Lactuca saligna* (wild lettuce) germplasm. Theoretical and Applied Genetics, *109*: 394–401.

JEUKEN M., VAN WIJK R., PELEMAN J., LINDHOUT P., 2001. An integrated interspecific AFLP map of lettuce (*Lactuca*) based on two *L. sativa* × *L. saligna* F-2 populations. Theoretical and Applied Genetics, *103*: 638–647.

JOHNSON W.C., JACKSON L.E., OCHOA O., VAN WIJK R., PELEMAN J., ST CLAIR D.A., MICHELMORE R.W., 2000. Lettuce, a shallow-rooted crop, and *Lactuca serriola*, its wild progenitor, differ at QTL determining root architecture and deep soil water exploitation. Theoretical and Applied Genetics, *101*: 1066–1073.

JUDD W.S., CAMPBELL C.S., KELLOGG E.A., STEVENS P.F., 1999. Plant Systematics: A Phylogenetic Approach. Sinauer Associates, Sunderland, MA.

KESSELI R., OCHOA O., MICHELMORE R., 1991. Variation at RFLP loci in *Lactuca* spp. and origin of cultivated lettuce (*L. sativa*). Genome, *34*: 430–436.

KESSELI R.V., PARAN I., MICHELMORE R.W., 1994. Analysis of a detailed genetic linkage map of *Lactuca sativa* (lettuce) constructed from RFLP and RAPD markers. Genetics, *136*: 1435–1446.

KITNER M., LEBEDA A., DOLEŽALOVÁ I., MARAS M., KŘÍSTKOVÁ E., NEVO E., PAVLÍČEK T., MEGLIC V., BEHARAV A., 2008. AFLP analysis of *Lactuca saligna* germplasm collections from four European and three Middle Eastern countries. Israel Journal of Plant Science (in press).

KOOPMAN W.J.M., GUETTA E., WIEL C.C.M. VAN DE, VOSMAN B., BERG R.G. VAN DEN, 1998. Phylogenetic relationships among *Lactuca* (Asteraceae) species and related genera based on ITS-1 DNA sequences. American Journal of Botany, *85*: 1517–1530.

KŘÍSTKOVÁ E., LEBEDA A., 1999. Collection of *Lactuca* spp. genetic resources in the Czech Republic. In: LEBEDA A., KŘÍSTKOVÁ E. (eds), Eucarpia Leafy Vegetables '99. Olomouc, Palacký University: 109–116.

KŘÍSTKOVÁ E., CHYTILOVÁ V., 2005. Genetic resources of leafy vegetables in the Czech Republic. In: THOMAS G., ASTLEY D., BOUKEMA I.W., DAUNAY M.C., DEL GRECO A., DIEZ M.J., VAN DOOIJWEERT W., KELLER J., KOTLIŃSKA T., LEBEDA A., LIPMAN E., MAGGIONI L., ROSA E. (comps), Report of a Vegetable Network. Joint Meeting with an *ad hoc* Group of Leafy Vegetables, 22–24 May 2003, Skierniewice, Poland. Rome, International Plant Genetic Resources Institute: 96–102.

LANDRY B.S., KESSELI R.V., TARTARA B., MICHELMORE R.W., 1987. A genetic map of lettuce (*Lactuca sativa* L.) with restriction fragment length polymorphism, isozyme, disease resistance and morphological markers. Genetics, *116*: 331–337.

LEBEDA A., 1986. Salát (*Lactuca sativa* L.). In: LEBEDA A. (ed.), Metody testování rezistence zelenin vůči rostlinným patogenům (Methods of Testing Vegetable Crops for Resistance to Plant Pathogens). VHJ SEMPRA, Výzkumný a šlechtitelský ústav zelinářský Olomouc (Research Institute of Vegetable Growing and Breeding Olomouc), Československá vědeckotechnická společnost (Czechoslovak Scientific-Technical Society), Olomouc: 101–113.

LEBEDA A., 1998. Biodiversity of the interactions between germplasm of wild *Lactuca* spp. and related genera and lettuce downy mildew (*Bremia lactucae*). Report on Research Programme OECD Biological Resource Management for Sustainable Agricultural Systems. HRI, Wellesbourne.

LEBEDA A., KŘÍSTKOVÁ E., 1995. Genetic resources of vegetable crops from the genus *Lactuca*. Horticultural Science (Prague), *22*: 117–121.

LEBEDA A., ASTLEY D., 1999. World genetic resources of *Lactuca* spp., their taxonomy and biodiversity. In: LEBEDA A., KŘÍSTKOVÁ E. (eds), Eucarpia Leafy Vegetables '99. Olomouc, Palacký University: 81–94.

LEBEDA A., KŘÍSTKOVÁ E. (eds), 1999. Eucarpia Leafy Vegetables '99. Olomouc, Palacký University.

LEBEDA A., BOUKEMA I.W., 2001. Leafy vegetables genetic resources. In: MAGGIONI L., SPELLMAN O. (comps), Report of a Network Coordinating Group on Vegetables; *ad hoc* Meeting, 26–27 May 2000, Vila Real, Portugal. Rome, International Plant Genetic Resources Institute: 48–57.

LEBEDA A., BOUKEMA I.W., 2005. *Ad hoc* meeting on leafy vegetables. In: THOMAS G., ASTLEY D., BOUKEMA I.W., DAUNAY M.C., DEL GRECO A., DIEZ M.J., VAN DOOIJWEERT W., KELLER J., KOTLIŃSKA T., LEBEDA A., LIPMAN E., MAGGIONI L., ROSA E. (comps), Report of a Vegetable Network. Joint Meeting with an *ad hoc* Group of Leafy Vegetables, 22–24 May 2003, Skierniewice, Poland. Rome, International Plant Genetic Resources Institute: 82–94.

LEBEDA A., PINK D.A.C., ASTLEY D., 2002. Aspects of the interactions between wild *Lactuca* spp. and related genera and lettuce downy mildew (*Bremia lactucae*). In: SPENCER-PHILLIPS P.T.N., GISI U., LEBEDA A. (eds), Advances in Downy Mildew Research. Dordrecht, Kluwer Academic Publisher: 85–118.

LEBEDA A., DOLEŽALOVÁ I., FERÁKOVÁ V., ASTLEY D., 2004a. Geographical distribution of wild *Lactuca* species (Asteraceae, Lactuceae). The Botanical Review, *70:* 328–356.

LEBEDA A., DOLEŽALOVÁ I., KŘÍSTKOVÁ E., NOVOTNÁ A., 2004b. Morphological and developmental characteristics of *Lactuca serriola* germplasm originating from Europe. In: Summaries and Program of 17th International Lettuce and Leafy Vegetable Conference, 28–31 August 2004, Montreal-Longueuil. Agriculture and Agri-Food Canada: 28–29 (Abstract).

LEBEDA A., RYDER E.J., GRUBE R., DOLEŽALOVÁ I., KŘÍSTKOVÁ E., 2007. Lettuce (Asteraceae; *Lactuca* spp.). In: SINGH R.J. (ed.), Genetic Resources, Chromosome Engineering, and Crop Improvement, Vol. 3, Vegetable Crops. Boca Raton, CRC Press, Tailor and Francis Group: 377–472.

LEBEDA A., DOLEŽALOVÁ I., KŘÍSTKOVÁ E., VINTER V., VRÁNOVÁ O., DOLEŽAL K., TARKOWSKI P., PETRŽELOVÁ I., TRÁVNÍČEK B., NOVOTNÝ R., JANEČEK J., 1999. Complex research of taxonomy and ecobiology of wild *Lactuca* spp. genetic resources. In: LEBEDA A., KŘÍSTKOVÁ E. (eds), Eucarpia Leafy Vegetables '99. Olomouc, Palacký University: 117–131.

LINDQVIST K., 1960. On the origin of cultivated lettuce. Hereditas, *46*: 319–350.

MAGGIONI L., LEBEDA A., BOUKEMA I.W. (eds), 2008. Report of a Working Group on Leafy Vegetables. First Meeting, 13–14 October 2005, Olomouc. Rome, International Plant Genetic Resources Institute.

MAISONNEUVE B., CHUPEAU M.C., BELLEC Y., CHUPEAU Y., 1995. Sexual and somatic hybridization in the genus *Lactuca*. Euphytica, *85*: 281–285.

MAŇEZ S., RECIO M.C., GINER R.M., SANZ M.J., TERENCIO M.C., PERIS J.B., STUBING G., RIOS J.L., 1994. A chemotaxonomic review of the subtribe Crepidinae based on its phenolic constituents. Biochemical Systematics and Ecology, *22*: 297–305.

MAZIER, M., MAISONNEUVE B., BELLEC Y., CHUPEAU M.C., SPUCNE S., CHUPEAU Y., 1999. Interest for protoplasts in lettuce breeding. In: LEBEDA A., KŘÍSTKOVÁ E. (eds), Eucarpia Leafy Vegetables '99. Proceedings of the Eucarpia Meeting on Leafy Vegetables Genetics and Breeding. Olomouc, Palacký University: 239–244.

McGUIRE P.E., RYDER E.J., MICHELMORE R.W., CLARK R.L., ANTLE R., EMERY G., HANNAN R.M., KESSELI R.V., KURTZ E.A., OCHOA O., RUBATZKY V.E., WAYCOTT W., 1993. Genetic resources of lettuce and *Lactuca* species in California. An assessment of the USDA and UC collections and recommendations for long-term security. Report No. 12. Davis, University of California, Genetic Resources Conservation Program.

MEUSEL H., JÄGER E.J., 1992. Vergleichende Chorologie der Zentraleuropäischen Flora. Jena, Stuttgart, New York, Gustav Fischer Verlag.

MIKEL M.A., 2007. Genealogy of contemporary North American lettuce. HortScience, *42:* 489–493.

MIRANDA M., LEBEDA A. (eds), 2008. Disease Resistance. Mass Screening Techniques for Banana and Other Crops. Dordrecht, Springer (prepared for press).

MIZUTANI T., TANAKA T., 2003. Genetic analyses of isozyme in lettuce, *Lactuca sativa,* and its relatives. Journal of the Japanese Society for Horticultural Science, *72*: 122–127.

MONTESCLAROS L., NICOL N., UBALIJORO E., LECLERC-POTVIN C., GANIVET L., LALIBERTÉ J.-F., 1997. Response to potyvirus infection and genetic mapping of resistance loci to potyvirus infection in *Lactuca*. Theoretical and Applied Genetics, *94*: 941–946.

MOU B., 2008. Lettuce. In: PROHENS J., NUEZ F. (eds), Handbook of Plant Breeding. Vegetables I. Asteraceae, Brassicaceae, Chenopodiaceae, and Cucurbitaceae. New York, Springer Science: 75–116.

RAJICIC T.S., DEHMER K.J., 2008. Analysis of wild *Lactuca* gene bank accessions and implications for wild species conservation. In: MAXTED N., FORD-LLOYD B.V., KELL S.P., IRIONDO J.M., DULLOO M.E., TUROK J. (eds), Crop Wild Relative Conservation and Use. Wallingford, CABI: 429–436.

REININK K., 1999. Lettuce resistance breeding. In: LEBEDA A., KŘÍSTKOVÁ E. (eds), Eucarpia Leafy Vegetables '99. Olomouc, Palacký University: 139–147.

RODENBURG C.M., 1960. Varieties of Lettuce. An International Monograph. Zwolle, W.E.J. Tjeenk Willink.

RUBATZKY V.E., YAMAGUCHI M., 1997. World Vegetables. New York, Chapman & Hall.

RYDER E.J., 1986. Lettuce breeding. In: BASSETT M. (ed.), Breeding Vegetable Crops. Westport, AVI Publishing Co.: 433–474.

RYDER E.J., 1999a. Genetics in lettuce breeding: past, present and future. In: LEBEDA A., KŘÍSTKOVÁ E. (eds), Eucarpia Leafy Vegetables '99. Olomouc, Palacký University: 225–231.

RYDER E.J., 1999b. Lettuce, Endive and Chicory. Wallingford, CABI Publishing.

SHIH C., 1988. Revision of *Lactuca* L. and two new genera of the tribe Lactuceae (Compositae) on the mainland of Asia (cont.). Acta Phytotaxonomica Sinica, *26*: 418–428.

SICARD D., WOO S.S., ARROYO-GARCIA R., OCHOA O., NGUYEN D., KOROL A., NEVO E., MICHELMORE R., 1999. Molecular diversity at the major cluster of disease resistance genes in cultivated and wild *Lactuca* spp. Theoretical and Applied Genetics, *99*: 405–418.

SOEST L.J.M. VAN, BOUKEMA I.W., 1997. Genetic resources conservation of wild relatives with a user's perspectives. Bocconea, *7*: 305–316.

SOJÁK J., 1961. Bemerkungen zu einigen *Compositen,* I. Novitates Botanicae Horti Botanici Universitatis Carolinae Pragensis: 33–37. (In German))

SOJÁK J., 1962. Bemerkungen zu einigen *Compositen,* II. Novitates Botanicae Horti Botanici Universitatis Carolinae Pragensis: 41–50. (In German)

SRETENOVIĆ-RAJIČIĆ T., HINTUM TH.J.L. VAN, LE-BEDA A., DEHMER K.J., 2008. Analysis of wild *Lactuca* accessions: Charakterization and utilization, conservation and identification of redundancy. Plant Genetic Resources, *6*: 153–163.

STAVĚLÍKOVÁ H., BOUKEMA I.W., HINTUM TH.J.L. VAN, 2002. The International *Lactuca* database. Plant Genetic Resources Newsletter, *130*: 16–19.

STEBBINS G.L., 1937. Critical notes on *Lactuca* and related genera. Journal of Botany (London), *75*: 12–18.

SUPERATOVÁ L., 2005. Morfologická variabilita genových zdrojů hlávkového salátu odrůdy Atrakce (Morphologic variation of genetic resources of butterhead lettuce cv. Atrakce). [Absolventská práce.] Kostelec nad Orlicí, Vyšší odborná škola a Střední zemědělská škola. [Bachelor Thesis.] 72. (In Czech)

THOMAS G., ASTLEY D., BOUKEMA I., DAUNAY M.C., DEL GRECO A., DIEZ M.J., VAN DOOIJEWEERT W., KELLER J., KOTLINSKA T., LEBEDA A., LIPMAN E., MAGGIONI L., ROSA E. (eds), 2005. Report of a Vegetables Network. Joint Meeting with and *ad hoc* Group on Leafy Vegetables, 22–24 May 2003, Skierniewice, Poland. Rome, International Plant Genetic Resources Institute: 154.

THOMPSON R.C., WHITAKER T.W., KOSAR W.F., 1941. Interspecific genetic relationships in *Lactuca*. Journal of Agricultural Research (Washington D.C.), *63*: 91–107.

TOMB A.S., 1977. *Lactuceae* – systematic review. In: HEYWOOD V.H., HARBORNE J.B., TURNER B.L. (eds), The biology and chemistry of the *Compositae*, II. London, New York, Academic Press: 1067–1079.

TOYOMASU T., YAMAGUCHI T., YAMANE H., MUROFUSHI N., INOUE Y., 1995. C DNA cloning and characterization of gibberelin-responsive genes in photoblastic lettuce seeds. Bioscience, Biotechnology, and Biochemistry, *59*: 1846–1849.

TUISL G., 1968. Der Verwandtschaftskreis der Gattung *Lactuca* L. im iranischen Hochland und seinen Randgebieten. Wien, Selbstverlag Naturhistorisches Museum Wien.

UPOV, 1981. Guidelines for the conduct of tests for distinctness, homogeneity and stability, lettuce (*Lactuca sativa* L.). 26. 10. 1981.

VRIES I.M. DE, 1990. Crossing experiments of lettuce cultivars and species (*Lactuca* sect. *Lactuca, Compositae*). Plant Systematics and Evolution, *171*: 233–248.

VRIES I.M. DE, 1996. Characterization and identification of *L. sativa* cultivars and wild relatives with SDS-electrophoresis (*Lactuca* sect. *Lactuca*, *Compositae*). Genetic Resources and Crop Evolution, *43*: 193–202.

VRIES I.M. DE, 1997. Origin and domestication of *Lactuca sativa* L. Genetic Resources and Crop Evolution, *44*: 165–174.

VRIES I.M. DE, RAAMSDONK W.D. VAN, 1994. Numerical morphological analysis of lettuce cultivars and species (*Lactuca* sect. *Lactuca, Asteraceae*). Plant Systematics and Evolution, *193*: 125–141.

WAYCOTT W., FORT S.B., RYDER E.J., MICHELMORE R.W., 1999. Mapping morphological genes relative to molecular markers in lettuce (*Lactuca sativa* L.). Heredity, *82*: 245–251.

WIEL C. VAN DE, ARENS P., VOSMAN B., 1999. Microsatellite retrieval in lettuce (*Lactuca sativa* L.). Genome, *42*: 139–149.

WITSENBOER H., VOGEL J., MICHELMORE R.W., 1997. Identification, genetic localization, and allelic diversity of selectively amplified microsatellite polymorphic loci in lettuce and wild relatives (*Lactuca* spp.). Genome, *40*: 923–936.

YAMAMOTO T., NISHIKAWA A., OEDA K., 1994. DNA polymorphisms in *Oryza sativa* L. and *Lactuca sativa* L. amplified by arbitrary primed PCR. Euphytica, *78*: 143–148.

ZOHARY D., 1991. The wild genetic resources of cultivated lettuce (*Lactuca sativa* L.). Euphytica, *53*: 31–35.

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Popis morfologických znaků genových zdrojů salátu (*Lactuca sativa* L.)

ABSTRAKT: Salát (locika setá, *Lactuca sativa*) je nejvýznamnější plodinou ze skupiny listových zelenin. Je charakteristický rozsáhlou morfologickou a genetickou variabilitou. Celkem zahrnuje sedm hlavních fenotypicky odlišných skupin odrůd (včetně salátu olejného), které jsou obvykle popisovány jako morfotypy. Šlechtění salátu je primárně zaměřeno na morfologické znaky, dále pak na odolnost proti chorobám a škůdcům. Přesný popis genových zdrojů salátu poskytuje základní informaci užitečnou pro šlechtitele. Vypracování souboru popisných znaků salátu bylo iniciováno a podporováno mezinárodním společenstvím genových bank. Předložený soubor sestává z 55 popisných znaků, přičemž 15 z nich je provázeno obrázky. Tento soubor znaků je důležitým nástrojem nejen pro detailní charakterizaci a určení vnitrodruhové variability *L. sativa*, ale i verifikaci pravosti starých odrůd, identifikaci možných duplicit a chybějících položek v kolekcích genových zdrojů. Tyto deskriptory, společně s deskriptory pro plané druhy rodu *Lactuca*, představují efektivní analytický nástroj pro komplexní studium morfologické variability tohoto rodu, ale i vztahů mezi jednotlivými druhy.

Klíčová slova: biologie; charakterizace; deskriptory; genofondové kolekce; genový pool; uchovávání genových zdrojů; morfotypy; původ; regenerace; odolnost; taxonomie; variabilita

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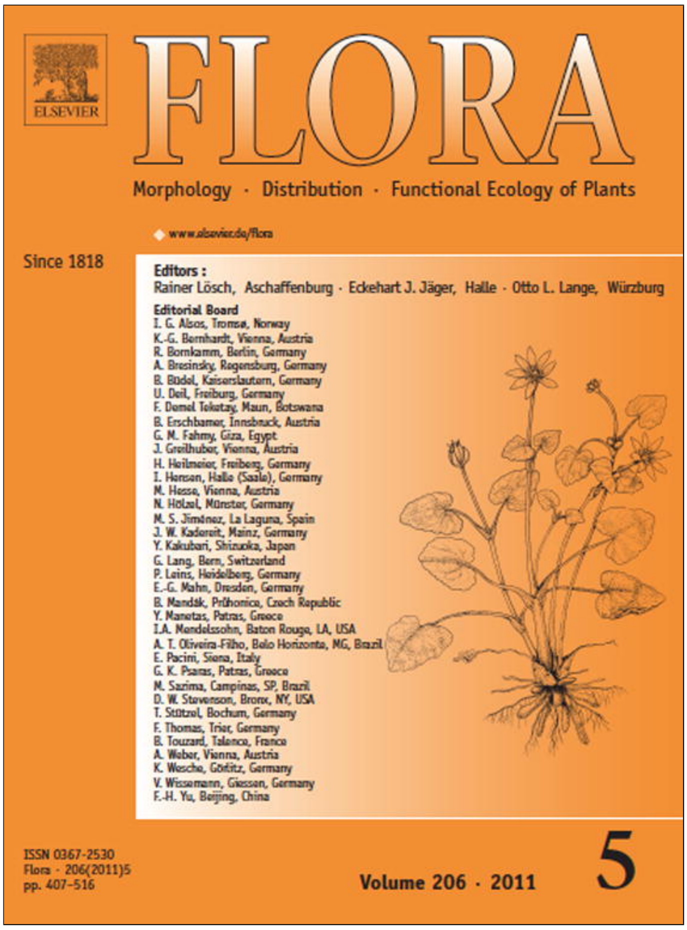
4.2. Morphological variability of *Lactuca serriola* achenes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Morphological variability of achenes of some European populations of *Lactuca serriola* L.

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ABSTRACT

This study focuses on the morphological variability of *Lactuca serriola* achenes in relation to eco-geographic features. Fifty *L. serriola* populations from four European countries, Czech Republic, Germany, the Netherlands and United Kingdom, were studied. Five morphological characters of the achenes – length and width of achene, length/width index, length of beak, and number of ribs – were evaluated. Significant differences exist in achene morphology of two leaf forms of *L. serriola*, forma *serriola* and forma *integrifolia*. Achenes of f. *serriola* are shorter, thinner, shorter beaked, lower length/width index, and higher number of ribs compared to f. *integrifolia*. There was significant variation in the measured characters. Statistical analysis indicated that achene length and width increased along an east–west transect from 2.95 to 3.35 mm and 0.93 to 1.00 mm, respectively. Mean beak length had a similar trend with the exception of German achenes. They had shorter beaks than achenes originating from the Czech Republic with 4.38 and Germany with 4.33 mm. The same trend was evident for L/W index from Czech with a ratio of 3.21 and Germany with 3.14. The number of ribs increased from east to the west in continental Europe, whereas the lowest number of ribs was recorded in achenes collected in Czech with 10.89 and the UK with 10.59. Achene morphology was significantly correlated with three eco-geographic features; longitude, latitude, soil texture of the habitats. The other eco-geographic factors, altitude and population size, did not significantly correlate with the studied characters of *L. serriola* achenes.

Introduction

Lactuca serriola L. (prickly lettuce, compass lettuce) is a meridional-temperate, western Euroasian species native to the Mediterranean (D'Andrea et al., 2009; Lebeda et al., 2004a,b) and the Near East (De Vries, 1997; Lebeda et al., 2004b). *L. serriola* is the most common species of the globally distributed genus *Lactuca* L. (Brant and Holec, 2004; Doležalová et al., 2001; Feráková, 1977; Lebeda et al., 2001, 2004b, 2007a). In Europe, it has expanded northwards during the last 250 years (D'Andrea et al., 2009), with the first European herbarium records of *L. serriola* originating in the early 18th century (http://linnaeus.nrm.se/botany/fbo/welcome.html.en, D'Andrea et al., 2009; Hooftman et al., 2006).

Recently, *L. serriola* has been rapidly expanding in Central, Western, and Northwestern Europe (Doležalová et al., 2001; Hooftman et al., 2006; Lebeda et al., 2001, 2007a,b). For example, in the Netherlands, a detailed survey of the distribution of prickly lettuce over the last half of the 20th century was made by Hooftman et al. (2006). They found that during the last 60 years, the occurrence of prickly lettuce increased rapidly and the plant now occupies a broader range of vegetation types. Prickly lettuce was found also in a more late-successional plant community with a lower pH and higher humidity, unlike the typical habitats of this species in open thermophilous vegetation with a continental character. The invasion of new habitats seems to be closely related to human activities (Lebeda et al., 2001, 2004b; Prince and Carter, 1977), such as transport and other activities that create optimal habitats for prickly lettuce, like ruderal places (Brant and Holec, 2004; Feráková, 1977; Hooftman et al., 2006).

Prickly lettuce is spread by achenes (cypselae). They are relatively small, mostly 3–4 mm long, ±1 mm wide, oblong-ovate, usually gray-brown in colour with a white filiform beak equalling or slightly longer than the achene. On both sides, there are 5–10 ribs with simple bristles mainly close to the beak (Dostál, 1989; Feráková, 1977; Grulich, 2004; Prince and Carter, 1977).

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According to the achene wall anatomy, Zhu et al. (2006) characterize achenes of *Lactuca* L., *Pterocypsela* Shih, *Cicerbita* Wallr., *Chaetoseris* Shih and *Stenoseris* Shih as a winged type, which is characterized by its protruding wings and costae in transverse section. Achenes of some *Lactuca* species, e.g. *L. virosa* have broad, wing-like margins; however achenes of *L. serriola* have very narrow margins (Prince and Carter, 1977). Weight of 1000 achenes is approximately 0.494 g (Brant and Holec, 2004). Under field conditions of Central Europe, the mean number of heads for a normal plant is 1057, and the mean number of achenes per capitulum is 16 (Brant et al., 2002). Under field conditions, the capitula produce ripened achenes for approximately 2 months, while in the glasshouse this lasts for approximately 6 weeks (Doležalová, 2009, personal communication). Flowering period and ripening time differ significantly between genotypes from various eco-geographic regions (Křístková et al., 2007).

Achenes of *L. serriola* are spread mostly by wind (Brant and Holec, 2004), because they have a pappus that is always monomorphic, consisting of two equal rows of whitish bristles, which are longer than the involucral bracts (Feráková, 1977). On the top of the pappus bristles, there are fine hooks of different sizes and shapes. Pappus bristles of *L. serriola* consist of two or three vertical rows of cells (Feráková, 1977).

Mature achenes provide an easy and reliable means of identification (Prince and Carter, 1977). Many authors (e.g. Feráková, 1977) have recognized the fruit of *Lactuca* as diagnostically the most important organ for specific or subspecific identification. Using the colour, size, bristles, and beak-length, it is possible to identify the different wild species (Prince and Carter, 1977). Morphology of achenes was used among others to distinguish *L. serriola* f. *integrifolia* from *L. virosa* (Carter and Prince, 1982). Distinctive features such as the basic shape of the achene and the ratio of the beak to the body of the achene have been used to determine sectional levels in species of the globally distributed genus *Lactuca* L. (Brant and Holec, 2004; Feráková, 1977; Lebeda and Astley, 1999).

Lactuca serriola is considered a direct progenitor of cultivated lettuce (*Lactuca sativa* L.) (De Vries, 1997; Lebeda et al., 2007b). Due to their broad genetic variability, progenitors of the cultivated crop possess genes for resistance to diseases, pests, and abiotic factors, as well as genes for physiological and quality characters (Křístková and Lebeda, 1999; Lebeda et al., 2007b). Wild *Lactuca* species, including *L. serriola*, are sources of race-specific resistance genes against lettuce downy mildew (*Bremia lactucae* Regel): Lebeda et al. (2002, 2007a). *L. serriola* has been used in commercial lettuce breeding for more than 60 years (Lebeda et al., 2004a,b, 2007b, 2009a; Mou, 2008).

Because of the under-representation of *Lactuca* spp. germplasm accessions in genebanks (Lebeda et al., 2004a, 2007b) and the need to increase our knowledge about global biodiversity and the distribution of native *L. serriola* populations, explorations to collect wild lettuce in Central and North-western European countries – Czech Republic, Germany, the Netherlands and the United Kingdom – were undertaken (Lebeda et al., 2007a). During the explorations, 50 populations of *L. serriola* were located and evaluated *in situ*, and achenes of each population were collected (Lebeda et al., 2007b).

Quantitative differences in the fruit size have been in the centre of general attention of botanists for centuries. The present study deals with the morphological variability of *L. serriola* achenes at the subspecific level of classification, geographical distribution, and ecobiology (Lebeda et al., 2007b). The objectives of this study were: (1) to obtain detailed data about morphology of *L. serriola* achenes, and their variation at the subspecific level; (2) to confirm the existence of morphological differences between populations, and their relation to eco-geographic features. The results of this study will enhance the utilization of *L. serriola* by helping to clarify its taxonomic status, and increase our knowledge of the biodiversity, ecobiology, and the structure and dynamics of natural populations in Europe.

Materials and methods

Plant material

A total of 800 achene samples of *L. serriola* were collected from 50 populations/locations (each represented by 16 plants) during explorations conducted in August and September, 2001 in four European countries including the Czech Republic (CZ), Germany (D), the Netherlands (NL) and United Kingdom (UK): Fig. 1 – Lebeda et al. (2007a). The achenes were collected along an east–west transect between 2°34′50″W–17°32′46″E and 47°40′42″–54°04′19″N (Lebeda et al., 2007a). Achenes of 761 *L. serriola* plants originating from 50 populations were morphologically evaluated. The *L. serriola* plants were regenerated in the glasshouse of the Department of Botany at the Faculty of Science of Palacký University in Olomouc (Czech Republic) from the beginning of March until the end of October 2002. After germination, the plants were transplanted to plastic pots with garden soil. They were grown under long-day conditions with temperatures during the day at 18–30 °C and 12–16 °C during the night. Each population was represented by 16 plants. The minimum distance between individual accessions was 0.75 m in the glasshouse. The regeneration followed the international standards for *Lactuca* genetic resources (Boukema et al., 1990; Hintum and Boukema, 1999; Lebeda et al., 2007b). The achenes (fruits) were harvested from single plants from June to October 2002 from 3 to 4 post-blossoming heads, each containing around 60 achenes. The achenes were analyzed according the following methodology.

Measurement of achene characters

Achenes were measured using the ImageJ computer program (ImageJ 1.32j) after being scanned as JPGs at a resolution of 400 dpi. Calibration was done such that the distance of 20 mm was determined by the program on a scanned ruler. Another measurement of the distance was converted into mm with an accuracy of 0.01 mm.

Fifty achenes per plant were randomly chosen to determine their shape. Following the descriptor list for wild *Lactuca* L. spp. (Doležalová et al., 2003), five morphological characters were studied: length (Lab) and width of the achene's body (Wab), length of beak (Lb), number of ribs (Nr – Fig. 2) and length/width index (L/W index). The length and width were measured at the longest and widest point of the achene, while the length of beak was the distance from an achene's body to the discus (Figs. 2 and 4). Ten achenes of each plant were randomly chosen to determine the number of ribs, using a magnifying glass where the ribs were quantified separately for each side of the achene. The shape of achene was determined by L/W index.

Statistical analyses

Data were analyzed using mean values for each character. All data were analyzed using the STATISTICA Cz program (StatSoft, 2007). Morphological differences between achenes of *L. serriola* forms were evaluated using the Mann–Whitney *U* test. To determine significant differences within the populations between countries for morphological characteristics, an ANOVA, Scheffé test, and Tukey HSD test (Honest Significant Difference test) were used. Non-parametric correlation analyses (Spearman's rank correlation coefficient – r_s) were used to reveal associations between morphological characters of the achenes and eco-geographic parameters of the collection sites.

Three geographical features – latitude, longitude, altitude – and two ecological – population size and substrate characteristics (sand,

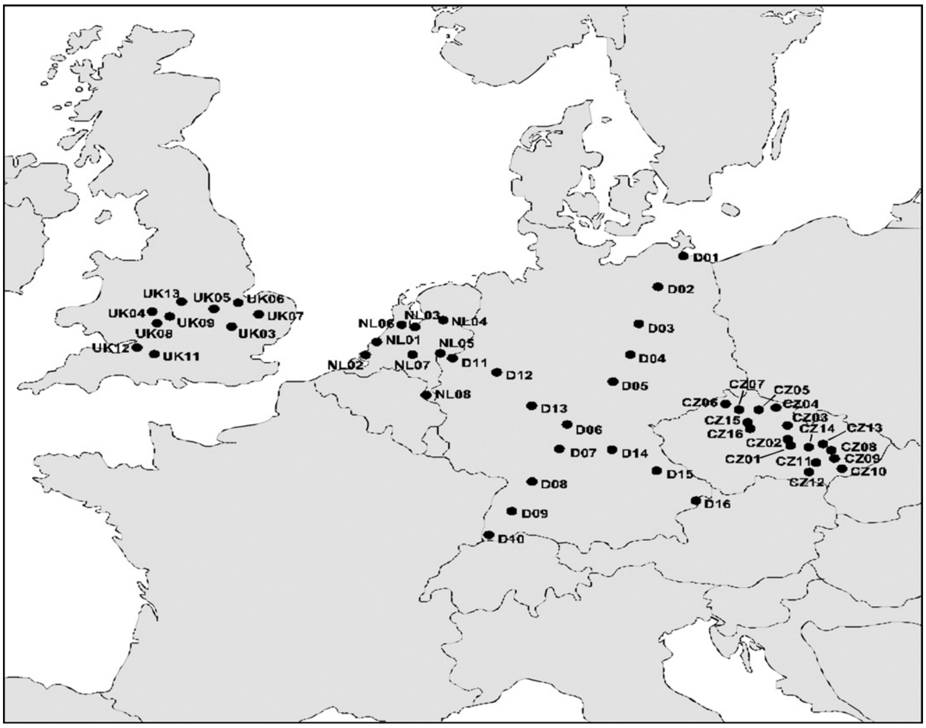

Fig. 1. Map showing the geographical distribution of *L. serriola* populations recorded in the Czech Republic (CZ), Germany (D), the Netherlands (NL) and United Kingdom (UK) (Lebeda et al., 2007a).

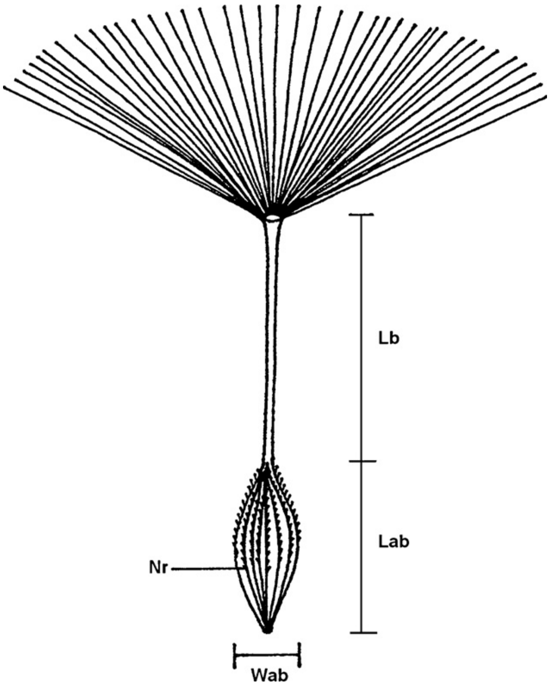

Fig. 2. Schematic illustration of *L. serriola* achene with the evaluated morphological features Lab – length of achene body, Lb – length of beak, Wab – width of achene body, Nr – number of ribs.

loamy sand, sandy loam, loam, clay loam, clay, gravels, stony, basalt blocks) – factors were analyzed (Lebeda et al., 2007a). All analyses were conducted using CANOCO for Windows 4.5 and CanoDraw for Windows 4.5 (Ter Braak and Šmilauer, 2002). The species data was logarithmically transformed. Direct gradient analysis (RDA, redundancy analysis) was used according to the gradient length (the highest value 0.124) from Detrended Correspondence Analysis (DCA). DCA is an indirect gradient analysis in which ecological gradients are derived from species composition. RDA is a direct gradient analysis, relating achene characters to habitat factors. To find the influence of geographic factors, ecological factors (population size and substrate characteristics) were used as covariables and *vice versa*. Their significance was determined using the method 'forward selection', sequentially choosing the best variables, as seen in Table 6. Finally, to test the significance of the environmental factors used in RDA, a Monte-Carlo permutation test with 999 permutations was used.

Results

Characters of the Lactuca serriola populations

Original site/habitat data of the *L. serriola* populations including leaf form, location with site description, geographic features (latitude, longitude, altitude), and ecological factors of population size (number of plants), landform, soil texture and site characteristics have been described elsewhere (Lebeda et al., 2007a). Individual soil textures were described using the soil texture triangle (Troeh and Donahue, 2003).

Here, morphological characters of *L. serriola* achenes were evaluated from a total of 761 plants (50 achenes per plant). The highest number of achenes evaluated was from 251 plants originating from the Czech Republic, whereas the lowest num-

Table 1
Abundance and frequency (%) of morphologically evaluated plants of *Lactuca serriola* leaf forms from the Czech Republic, Germany, the Netherlands and United Kingdom.

Country	Abundance		Total	% per country		% within all countries	
	f.s.	f.i.		f.s.	f.i.	f.s.	f.i.
CZ	251	0	251	100.00	0.00	48.46	0.00
D	209	36	245	85.31	14.69	40.35	14.81
NL	56	66	122	45.90	54.10	10.81	27.16
UK	2	141	143	1.40	98.60	0.39	58.02
Total	518	243	761				

CZ – Czech Republic; D – Germany; NL – the Netherlands; UK – United Kingdom; f.s. – *L. serriola* f. *serriola*; f.i. – *L. serriola* f. *integrifolia*.

ber of achenes originated from 122 plants collected in the Netherlands (Table 1). The highest frequency of *L. serriola* f. *serriola* populations was in the Czech Republic and Germany, while to the west (the Netherlands and the United Kingdom) *L. serriola* f. *integrifolia* was the dominant form (Table 1). *L. serriola* populations occurred on different soil textures, from sandy to stony soils (Lebeda et al., 2007a). Preference of both *L. serriola* forms for soil textures in all studied countries is shown in Fig. 3.

Morphological variation of Lactuca serriola achenes

Data on the investigated morphological parameters of *L. serriola* achenes are given in Table 2. Achene characters were evaluated in all 761 plants (Lb: 760, due to mechanical seed damage). Mean of Lab was 3.09 mm. A minimum mean Lab of 2.44 mm was observed in population D14 collected in Bavaria, Germany. The maximum mean Lab value was 4.20 mm found in population CZ4 originating from the province of Hradec Králové, Czech Republic (Lebeda et al.,

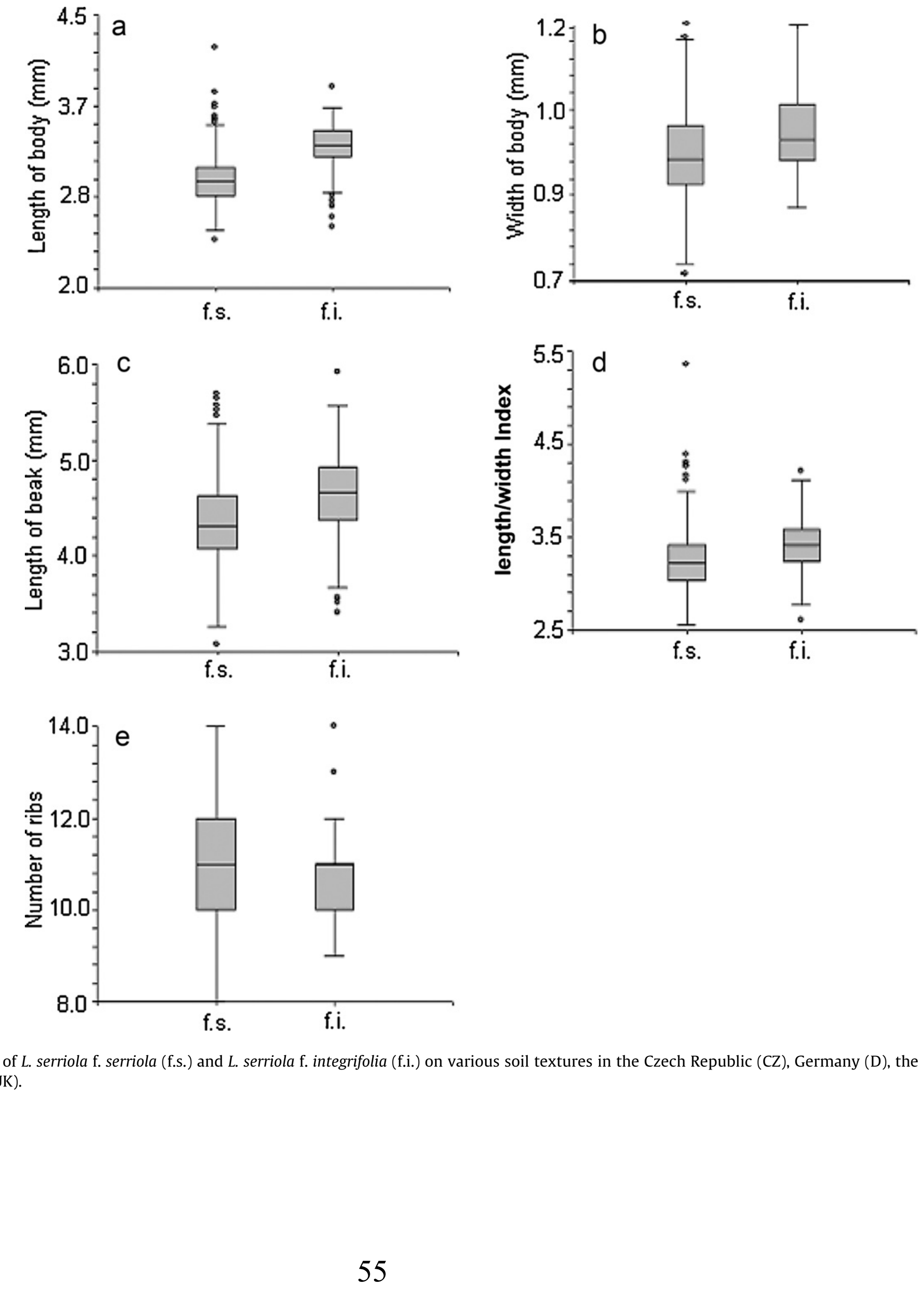

Fig. 3. Occurrence of *L. serriola* f. *serriola* (f.s.) and *L. serriola* f. *integrifolia* (f.i.) on various soil textures in the Czech Republic (CZ), Germany (D), the Netherlands (NL) and United Kingdom (UK).

Table 2
Morphological data of achenes of *Lactuca serriola* plants.

Morphological characters	*L. serriola*				
	N	Mean	SD	min	max
Lab	761	3.09	0.25	2.44	4.20
Wab	761	0.96	0.09	0.71	1.20
Lb	760	4.44	0.42	3.07	5.92
L/W index	761	3.23	0.30	2.50	5.18
Nr	761	10.95	0.92	8.00	14.00

Lab – length of achene's body; Wab – width of achene's body; Lb – length of beak; L/W index – length/width index; Nr – number of ribs; *N* – total number of evaluated *L. serriola* plants; SD – standard deviation; min, max – minimum and maximum mean value.

2007a). The Wab mean value was 0.96 mm. Population CZ2 from Pardubice province had a minimum value of 0.71 mm, whereas the maximum value of 1.20 mm was observed in the UK3 population from Bedfordshire, UK.

The average Lb was 4.44 mm. A minimum Lb of 3.07 mm was observed in population CZ4 originating from the province of Hradec Králové, while a maximum of 5.92 mm was reported in the UK3 population from Bedfordshire, UK.

Mean value of the L/W index was a 3.23 ratio. A minimum ratio of 2.50 was observed in population D16 from Bavaria, and a maximum value of 5.18 in population CZ4 from the province Hradec Králové.

The mean number of ribs (Nr) was 10.95. A minimum of 8 ribs was found in populations CZ9 and CZ10 from the eastern part of the Czech Republic, in the Zlín and Olomouc provinces, while the maximum number of 14 ribs was recorded for populations D5 and D9 from Germany, from the Thuringia and Baden-Württemberg regions (Table 2).

Comparison of achenes from both Lactuca serriola forms (L. serriola f. serriola and L. serriola f. integrifolia)

The Mann–Whitney *U* test showed that achenes of *L. serriola* f. *serriola* differ significantly ($P < 0.001$) from achenes of *L. serriola* f. *integrifolia* for all morphological characters (Table 3 and Figs. 4 and 5). In case of Lab, achenes of f. *serriola* are significantly shorter (2.98 mm) than achenes of f. *integrifolia* (3.31 mm). Comparison of Wab showed that achenes of f. *serriola* were thinner (0.95 mm) than those of f. *integrifolia* (0.99 mm). Achenes of f. *serriola* are characterized by shorter beaks (4.35 mm) than achenes of f. *integrifolia* (4.63 mm). *L. serriola* f. *integrifolia* achenes were more rounded with a L/W index ratio of 3.40 and having less ribs (10.72) compared to f. *serriola* with a L/W index ratio of 3.24 and 11.05 ribs (Table 3).

Non-parametric correlation analysis of the Spearman's correlation coefficient (r_s) was calculated between morphological characters and eco-geographic features (latitude, longitude, altitude) and population size. Significant positive correlations were found between Lab and the L/W index of both of *L. serriola* forms

Table 3
Differences between *L. serriola* f. *serriola* and *L. serriola* f. *integrifolia* in achene characters and their significance (Mann–Whitney *U* test, $P < 0.001$).

Morphological characters	f. *serriola*			f. *integrifolia*		
	N	Mean	SD	*N*	Mean	SD
Lab	518	2.98	0.21	243	3.31	0.19
Wab	518	0.95	0.09	243	0.99	0.08
Lb	517	4.35	0.40	243	4.63	0.39
L/W index	518	3.24	0.31	243	3.40	0.27
Nr	518	11.05	0.95	243	10.72	0.77

Lab – length of achene's body; Wab – width of achene's body; Lb – length of beak; L/W index – length/width index; Nr – number of ribs; *N* – total number of plants evaluated; SD – standard deviation.

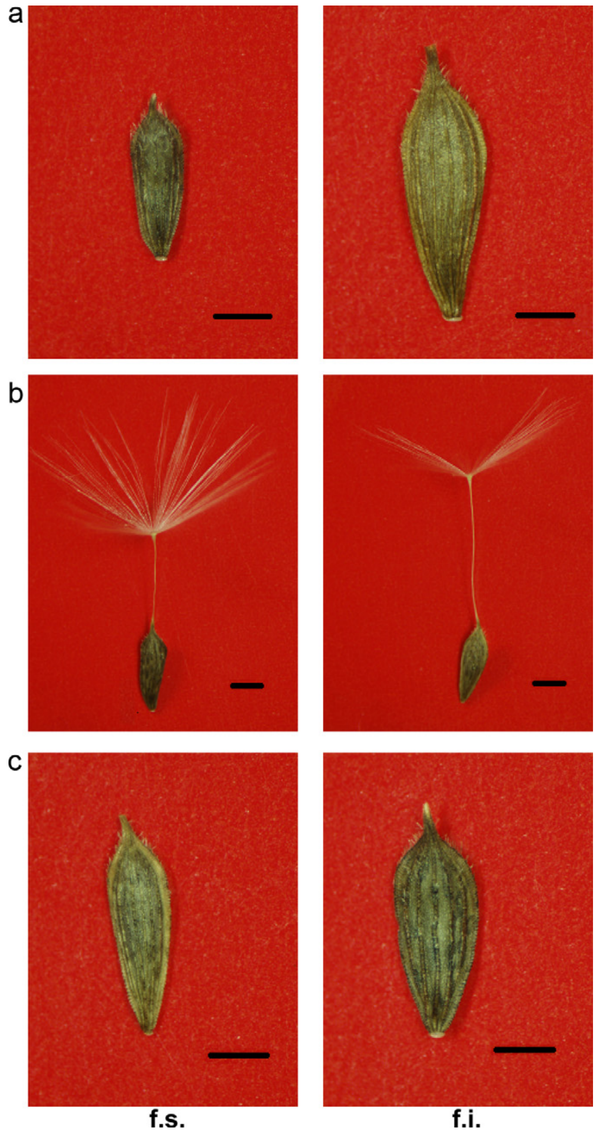

Fig. 4. Differences between *L. serriola* f. *serriola* (f.s.) and *L. serriola* f. *integrifolia* (f.i.) in achene characters: (a) length of body, (b) width of body, (c) length of beak, (d) length/width Index (e) number of ribs (expressed by box and whisker plots).

and latitude, and Nr of f. *integrifolia* and longitude (Table 4). In case of f. *serriola* significant negative correlations were found between Lab, Wab, Nr, and longitude; Lab and Lb and altitude. In the case of f. *integrifolia*, significant negative correlations were found between Lab, Lb and L/W index and longitude, and Lab and L/W index and altitude. Morphological characters of f. *integrifolia* achenes, such as Lab and Wab and Lb were negatively correlated with population size (Table 4).

Correlations between eco-geographic features and morphology of L. serriola achenes

Significant positive Spearman's correlations were observed between basic achene variables and latitude (Lab $r_s = 0.473$ and Wab $r_s = 0.134$, respectively) (Table 5). Beak length and latitude was also positively correlated ($r_s = 0.198$) while L/W index and latitude

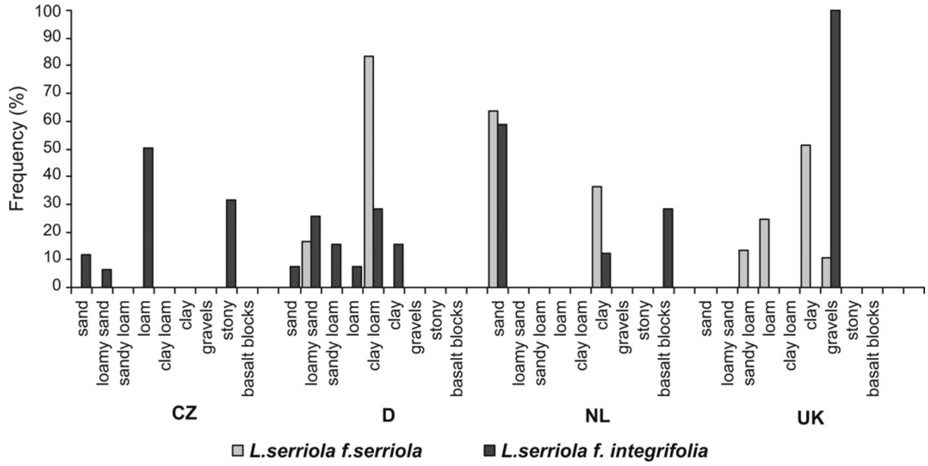

Fig. 5. *L. serriola* f. *serriola* (f.s.) and *L. serriola* f. *integrifolia* (f.i.) achene variation in observed morphological characters: a) length and width of achene body; b) length of beak; c) number of ribs (f.s. – 6 ribs, f.i. – 5 ribs). Scale bar = 1 mm.

Table 4
Relationships between eco-geographic features and evaluated morphological characters of achenes of *L. serriola* f. *serriola* and *L. serriola* f. *integrifolia* according to the Spearman rank correlation (r_s).

Eco-geographic factors	f.s.					f.i.				
	Lab	Wab	Lb	L/W index	Nr	Lab	Wab	Lb	L/W index	Nr
Latitude	0.180*	0.025	−0.015	0.105*	0.034	0.273*	−0.045	0.111	0.252*	−0.043
Longitude	−0.181*	−0.194*	0.010	0.082	−0.169*	−0.250*	−0.078	−0.194*	−0.145*	0.190*
Altitude	−0.114*	−0.084	−0.140*	0.014	−0.067	−0.213*	0.003	−0.126	−0.185*	−0.035
Population size	0.022	0.02	−0.057	0.003	0.034	−0.141*	−0.184*	−0.183*	0.052	0.099

Lab – length of achene's body; Wab – width of achene's body; Lb – length of beak; L/W index – length/width index; Nr – number of ribs; f.s. – *L. serriola* f. *serriola*; f.i. – *L. serriola* f. *integrifolia*
* Indicates a significant trend at $P < 0.05$.

Table 5
Spearman rank correlations (r_s) between eco-geographic factors and characters of *L. serriola* achenes.

Eco-geographic factors	r_s				
	Lab	Wab	Lb	L/W index	Nr
Latitude	0.473*	0.134*	0.198*	0.278*	−0.095*
Longitude	−0.572*	−0.290*	−0.278*	−0.214*	0.077*
Altitude	−0.480*	−0.195*	−0.276*	−0.225*	0.050
Population size	0.029	−0.023	−0.069	0.047	0.038

Lab – length of achene's body; Wab – width of achene's body; Lb – length of beak; L/W index – length/width index; Nr – number of ribs.
* Indicates a significant trend at $P < 0.05$.

has a significant correlation of $r_s = 0.278$). Longitude and Nr had a correlation of $r_s = 0.077$ (Table 5). Close negative correlations were found between Lab, Wab, Lb, L/W index, and longitude and altitude. Non-significant correlations were found between number of ribs and altitude, and between all evaluated morphological characters and population size.

The geographic features selected by forward selection (RDA), for *L. serriola* were longitude and latitude ($P = 0.002$, $P = 0.004$) (Table 6).

Table 6
Geographic (A) and substrate (B) factors selected by forward selection (RDA).

Factor	Variables	*F*-ratio	*P*
A	Longitude	48.863	0.002
	Latitude	5.808	0.004
B	Stony	4.613	0.002
	Basalt	4.592	0.002
	Sand	4.504	0.003
	Loamsand	2.939	0.021

Basalt – basalt blocks; Loamsand – loamy sand.

According to Fig. 6, with increasing latitude *L. serriola* achenes were mainly longer and slimmer (L/W index is increasing), with longer beaks, however, mostly narrower together with a low number of ribs (see also Table 5). The opposite was true with an increase in longitude, where all morphological characters were decreasing, with the exception of NR (Table 5 and Fig. 6). The ecological factors selected by forward RDA showed high significance ($P < 0.05$), were only four soil textures (stony, basalt blocks, sand and loamy sand) were selected (Table 6 and Fig. 7). Achenes from plants grown on sand substrate were longer, wider, and with longer beaks compared to those from loam-sand soil. Those had shorter Lab together with shorter beaks. In stony soil and places with basalt blocks, plants with 'thinner' achenes and higher number of ribs were found.

Comparison of achenes variability between studied countries

Using parametric Scheffé test and HSD test, significant differences in morphological characters and geographic origin of achenes

Table 7
Differences in achene morphology [(a) length of achenes body, (b) width of achenes body, (c) length of beak, (d) length/width index and (e) number of ribs] of *L. serriola* populations from the Czech Republic, Germany, the Netherlands and United Kingdom. Significant differences were expressed by using parametric Scheffé test and HSD test.

(a)

Scheffé							HSD				
Country	Mean	SD	Homologous groups				Country	CZ	D	NL	UK
			1	2	3	4					
CZ	2.95	0.22	+++				CZ				
D	3.03	0.22		+++			D	***			
NL	3.17	0.21			+++		NL	***	***		
UK	3.35	0.15				+++	UK	***	***	***	

(b)

Country	Mean	SD	Homologous groups		Country	CZ	D	NL	UK
			1	2					
CZ	0.93	0.08		+++	CZ				
D	0.97	0.09	+++		D	***			
NL	0.98	0.08	+++		NL	***	–		
UK	1.00	0.08	+++		UK	***	–	–	

(c)

Country	Mean	SD	Homologous groups			Country	CZ	D	NL	UK
			1	2	3					
CZ	4.38	0.43	+++			CZ				
D	4.33	0.40	+++			D	–			
NL	4.52	0.38		+++		NL	*	***		
UK	4.68	0.34			+++	UK	***	***	**	

(d)

Country	Mean	SD	Homologous groups			Country	CZ	D	NL	UK
			1	2	3					
CZ	3.21	0.31	+++			CZ				
D	3.14	0.28	+++	+++		D	–			
NL	3.27	0.27		+++		NL	–	**		
UK	3.39	0.27			+++	UK	***	***	**	

(e)

Country	Mean	SD	Homologous groups			Country	CZ	D	NL	UK
			1	2	3					
CZ	10.89	0.99	+++			CZ				
D	11.05	0.89	+++	+++		D	–			
NL	11.28	0.92		+++	+++	NL	**	–		
UK	10.59	0.65			+++	UK	–	***	***	

CZ – Czech Republic; D – Germany; NL – the Netherlands; UK – United Kingdom; SD – standard deviation; +++ – competence of countries to harbour homologous groups; — – indicates no statistically significant trend at $P > 0.05$.
* Indicates a significant trend at $P < 0.05$.
** A significant trend at $P < 0.01$.
*** A significant trend at $P < 0.001$.

of *L. serriola* were detected. According to mean values of Lab, variability of achenes of *L. serriola* populations from different countries was highly significant ($P < 0.001$). Each country can be considered as an individual group (Table 7a: "homologous groups"; Fig. 8a). In Wab *L. serriola* achenes originating from Czech populations were totally different from those of other countries (Table 7b and Fig. 8b). In case of Lb, no significant difference was found between the achenes of *L. serriola* populations from the Czech Republic and Germany, whereas the achenes from the Netherlands and United Kingdom formed individual groups (Table 7c and Fig. 8c). Achenes of *L. serriola* populations originating from the United Kingdom were significantly different from those from other countries in the L/W index ratio ($P < 0.001$) (Table 7d and Fig. 8d). This would also confirm the subspecific taxonomical difference of *L. serriola* populations occurring in continental Europe and at the British Islands (see above comparison of *L. serriola* f. *serriola* and f. *integrifolia*). In Nr, there was no significant difference between the achenes from the Czech Republic and Germany, contrary to the comparison of achenes from the Netherlands and the United Kingdom according to the Scheffé test (Table 7e and Fig. 8e).

Discussion

Lactuca serriola L. displays a large morphological, geographic, and genetic variation over a wide spectrum of different habitats (Feráková, 1977; Lebeda et al., 2001, 2004b, 2007a,b, 2009a,b). Within the taxon *L. serriola,* two different forms are recognized based on the leaf morphology and geographic distribution. *L. serriola* f. *serriola* with runcinate-pinnatifid cauline leaves is distributed mostly in continental Europe, and especially in Central and North Europe (Doležalová et al., 2001; Lebeda et al., 2001, 2004b, 2007a), whereas *L. serriola* f. *integrifolia* with non-lobed leaves is

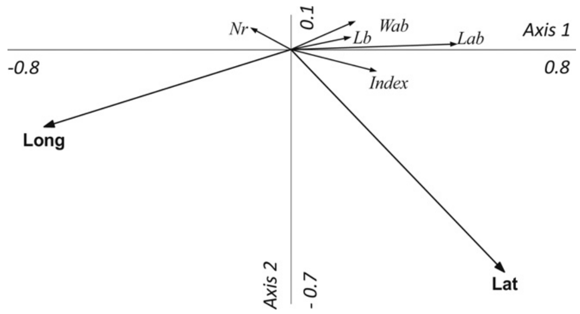

Fig. 6. Correlation of morphological characters of *L. serriola* achenes with geographical factors, which were selected by forwarded RDA. First and second axes account for 6.9% of the variability in species data. Lat – latitude; Long – longitude; Lab – length of body; Wab – width of body; Lb – length of beak; –length/width Index; Nr – number of ribs.

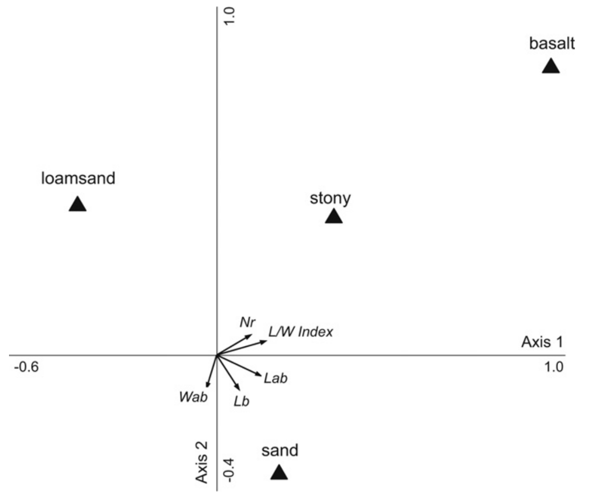

Fig. 7. Correlation of morphological characters of *L. serriola* achenes with substrate factors, which were selected by forwarded RDA. First and second axes account for 1.8% of the variability in species data. Soil textures: basalt – basalt blocks; loamsand – loamy sand; Lab – length of body; Wab – width of body; Lb – length of beak; L/W Index –length/width Index; Nr – number of ribs.

more common in Great Britain (Lebeda et al., 2004b, 2007a; Prince and Carter, 1977). The distribution of *L. serriola* in British Islands is restricted to the southeastern part (Carter and Prince, 1985; Prince and Carter, 1977). This distribution can be explained by the climatic conditions, mainly the limited summer rainfall (Carter and Prince, 1985). The frequency of both *L. serriola* forms is shown in Table 1.

In many cases the achenes of the Cichorieae, including *Lactuca* spp., are indispensable for the identification of the genera and

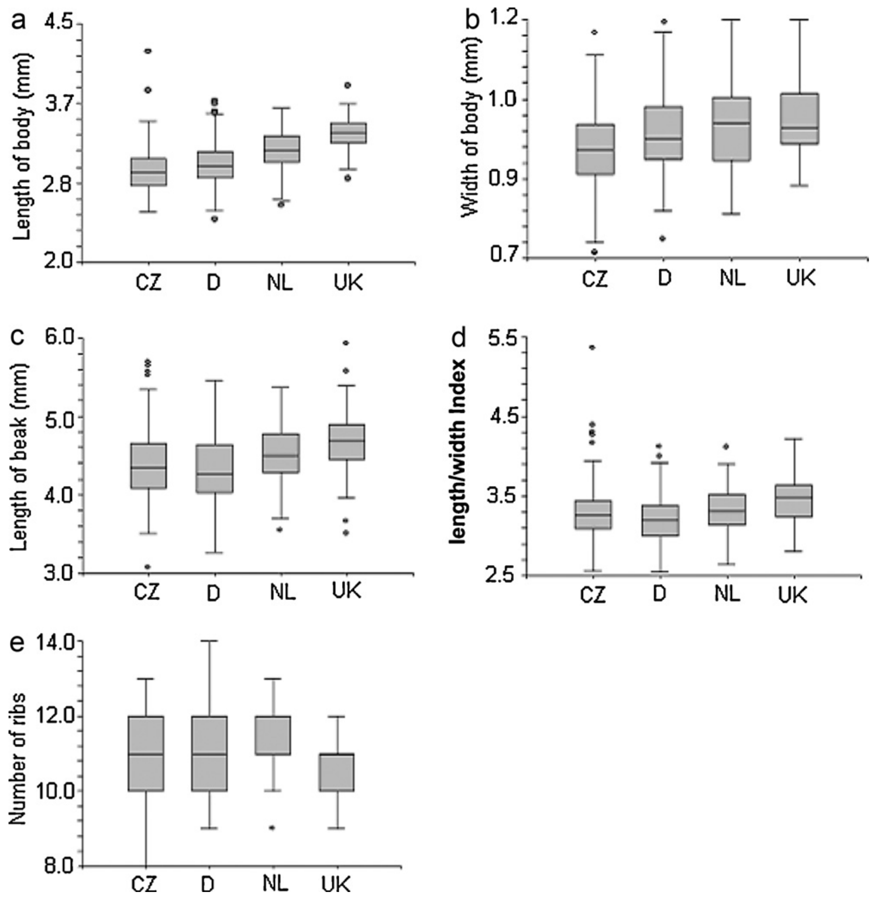

Fig. 8. Differences in achene morphology of *L. serriola* populations from the Czech Republic (CZ), Germany (D), the Netherlands (NL) and United Kingdom (UK): (a) length of body, (b) width of body, (c) length of beak, (d) length/width Index (e) number of ribs (expressed by box and whisker plots).

species; they are the most valuable taxonomic feature for taxon identification. Their variation may involve size, ribbing pattern, base, apex, shape, surface and anatomy, separately or in combination (Funk et al., 2009). In Floras of individual countries, there is only basic information about the shape, colour, and size of *Lactuca* spp. achenes, but detailed information about their morphology is very limited (e.g. Funk et al., 2009). Carter and Prince (1982) and Prince and Carter (1977) reported that the morphology of *L. serriola* achenes are used to distinguish them from achenes of other *Lactuca* spp. (e.g. *L. virosa*). However, no detailed comparative morphometric studies were reported by Feráková (1970, 1976, 1977) when treating all European species of *Lactuca* L. All these papers did not mention the existence of the two forms of *L. serriola* based on achene morphology.

Both *L. serriola* forms differ not only in leaf shape and geographic distribution, but also in achene morphology. *L. serriola* f. *serriola* achenes are shorter, thinner, shorter beaked, and have a lower L/W index ratio compared to *L. serriola* f. *integrifolia*. On the contrary, achenes of f. *serriola* have significantly higher Nr than f. *integrifolia* (Table 3; Figs. 4 and 5). These differences support the validity of previously described forms of *L. serriola* (Carter and Prince, 1982), as well as their natural geographic circumscription in Europe (Doležalová et al., 2001; Lebeda et al., 2001, 2004b, 2007a). Achenes of f. *serriola* originating from Central Europe (Czech populations) (Table 1) are significantly shorter and narrower than the other forms (Table 7a and b). In case of German *L. serriola* populations, where both leafy forms occur (Table 1), the achenes are significantly longer and wider than the Czech ones (Table 7a and b). Achenes from maritime populations from the southern country parts of the United Kingdom, where *L. serriola* f. *integrifolia* is the predominant form (Lebeda et al., 2007a; Table 1), have the longest and the widest achenes of all samples evaluated (Table 7a and b). For populations of *L. serriola* f. *integrifolia*, a higher mean L/W index ratio was found (Table 3 and Fig. 4d). According to the shape index, it is possible to say that achenes of f. *integrifolia* are thinner and achenes of f. *serriola* are rounder. The mean value of the L/W index ratio decreases along a west to east transect of Europe with the exception of the German populations that show a lower average ratio than the Czech populations (Table 7d and Fig. 8d). Thus, L/W index is low in the eastern *L. serriola* populations, while in the British populations the opposite is the case (Fig. 6). Clear differences in the achene morphology between the *Lactuca serriola* forms support recent taxonomic treatment of this species based on leaf morphology. This indicates a genetic background causing differences in the morphology of *Lactuca serriola* achene forms.

Significant differences in the mean size (mean length and width) of achenes between the countries sampled in this study could be explained using the island biogeography theory relating to plant populations in their dispersal ability. Generally, species living on islands have reduced dispersal ability compared to species from the mainland (Cody and Overton, 1996; Fresnillo and Ehlers, 2008; Harper et al., 1970). Reduction in dispersal potential increases with the age of island's populations (Cody and Overton, 1996). This evolutionary trend may also involve a reduction of the pappus in wind-dispersed species and an overall increase in achene size. Gravuer et al. (2003) performed a detailed study of the dispersal ability of achenes of *Liatris scariosa* var. *novae-angliae* from the Asteraceae family. They found that propagule mass was the strongest predictor of dispersal ability, whereas heavy propagules had a reduced dispersal potential. Dispersal capability was also reduced for long achenes, but increased for wide achenes. The results of the current study are more or less in agreement with this. The *L. serriola* achenes originating from the inland populations (from the Czech Republic and Germany) are significantly smaller than achenes from coastal or island populations (Dutch and United Kingdom, respectively) – Table 7a and b; Fig. 8a and b. Even if the pappus characters were not evaluated in this study, it is possible to assume that the Dutch and United Kingdom populations would have reduced dispersal ability. It means that these diaspores will fall much faster and reach higher terminal velocity (Chmielewski and Strain, 2007; Cody and Overton, 1996; Sheldon and Burrows, 1973). This phenomenon is probably one of the causes responsible for differences in genetic polymorphism of European populations of *L. serriola*. I.e. populations from Scandinavia and British Isles seem to be more homogeneous, in contrast to populations occurring in Central Europe which are very diverse and genetically sympatric (Lebeda et al., 2008, 2009b).

In case of Lb, achenes of *L. serriola* f. *serriola* have significantly shorter beaks than achenes of f. *integrifolia* (Table 3; Figs. 4 and 5). The statistically significant longer beak in achenes of f. *integrifolia* can be explained as the taxonomic feature typical for this form. The current massive expansion of *L. serriola* in Europe, including United Kingdom and the Netherlands (D'Andrea et al., 2009; Hooftman et al., 2006) is probably caused by the spreading of *L. serriola* f. *integrifolia*. Population genetic analysis by D'Andrea et al. (2009) revealed that the British populations were mainly dominated by one single genotype. This also strongly supports data about variability of European *L. serriola* populations expressed by AFLP (Lebeda et al., 2009b) and the distribution of race-specific resistance to *Bremia lactucae* (Lebeda and Petrželová, 2007; Lebeda et al., 2008; Petrželová and Lebeda, 2011). In relation to the studied countries, achenes from inland (Czech and German populations) create one homological group, which is identified by shorter beaks than achenes from the Dutch and United Kingdom populations (Table 7c and Fig. 8c). However, in comparing the LB within Czech and German populations – where only f. *serriola* occurs, the longer beaks were observed within Czech populations (Table 7c and Fig. 8c). This phenomenon could be partly influenced by landform. Achenes of plants from the Czech Republic were collected in hilly areas and lowlands, while those from Germany were collected in plain fields or undulating plains. Cody and Overton (1996) reported that dispersal ability reached higher values in the longer-beaked populations, and diaspores with beaked achenes have significantly lower settling velocities than diaspores with unbeaked achenes (Andersen, 1993). According to the 'model of parachute' (Gravuer et al., 2003), achenes from lowlands have developed a pappus with a significantly smaller surface and shorter beaks. They do not need to overcome higher vertical intervals. Mostly, this phenomenon was observed in German achenes (see Lebeda et al., 2007a).

Achenes from *L. serriola* plants collected in Great Britain are characterized by significantly lower number of ribs in contrast to those from continental Europe (Table 7e and Fig. 8e). If we compare both *L. serriola* forms, the achenes of f. *integrifolia* have significantly lower Nr (Table 3; Figs. 4e and 5). This fact can be explained as well by the reduction of dispersal ability in coastal or island plant populations (Cody and Overton, 1996; Fresnillo and Ehlers, 2008; Harper et al., 1970). Also, some insular species of *Asteraceae* from the Pacific Islands are distinguished by reduction of dispersial mechanisms (Carlquist, 1966). We hypothesize that the higher number of ribs creates a larger achene surface providing for better dispersion. However, this hypothesis must be critically tested in future studies.

Statistical analyses showed that the observed morphological characters of *L. serriola* achenes were correlated with environmental factors. *L. serriola* grows mostly in sunny habitats, with dry, fertile, and carbon rich soil. However, its ecological amplitude, including range of soil, is rather wide (Brant and Holec, 2004; Carter and Prince, 1985; D'Andrea et al., 2009; Feráková, 1977; Lebeda et al., 2007a). Hooftman et al. (2006) reported that in the Netherlands *L. serriola* now also occurs in habitats with low pH and high humidity. According to our observations (Lebeda et al., 2007a), *L. serriola* can occur on quite various soils, from sand to basalt blocks

(Fig. 3). Under conditions of continental Europe, prickly lettuce prefers drier soils such as sand, loam, stony substrates, and clay loam. However, in maritime areas (the Netherlands and the United Kingdom), *L. serriola* grows on sandy and clay soils and gravels (Fig. 3). This is also related to the two different *L. serriola* forms and their eco-geographical requirements (Lebeda et al., 2007a). Recently, we investigated the influence of different soil textures on morphological features of *L. serriola* achenes. Generally, the largest achenes with the longest beaks were found on sandy substrata. Achenes from sandy loam habitats were shorter and with shorter beaks. *L. serriola* achenes from stony substrata were 'thinner' and possessed higher Nr (Fig. 7). These relations can be explained by an increased distribution ability on non-optimal *L. serriola* habitats (D'Andrea et al., 2009; Hooftman et al., 2006), including stony or basalts blocks.

This study demonstrates that the morphological features of the achene and principles of geographic distribution, ecology, and interpopulation variability can be useful for better understanding subspecific taxonomy of *L. serriola*. It is evident that more detailed studies a larger number of populations from a wider range distribution range (Southern Europe!) and more heterogeneous eco-geographic conditions should render a still higher variability from which again a better understanding might be obtained of the micro-evolutionary processes involved in the spread and diversification of *L. serriola*.

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References

Andersen, M.C., 1993. Diaspore morphology and seed dispersal in several wind-dispersed Asteraceae. Am. J. Bot. 80, 487–492.

Boukema, I.W., Hazekamp, Th., van Hintum, Th.J.L., 1990. The CGN Collection Reviews: The CGN Lettuce Collection. Centre for Genetic Resources, Wageningen, Netherlands, pp. 2–5.

Brant, V., Bělka, J., Svobodová, M., 2002. Einfluss des Schnittes auf Wachstum und Reproduktion des Kompass-Lattichs (*Lactuca serriola* L.). J. Plant Dis. Protect. 18, 287–291.

Brant, V., Holec, J., 2004. Locika kompasová (*Lactuca serriola* L.). Rostlinolékař 15/5, 24–27.

Carlquist, S., 1966. The biota of long distance dispersal. Part 2. Loss of dispersibility in Pacific compositae. Evolution 20, 30–48.

Carter, R.N., Prince, S.D., 1982. A history of the taxonomy treatment of unlobed-leaved prickly lettuce, *Lactuca serriola* L., in Britain. Watsonia 14, 59–62.

Carter, R.N., Prince, S.D., 1985. The geographical distribution of prickly lettuce (*Lactuca serriola*). I. A general survey of its habitats and performance in Britain. J. Ecol. 73, 27–38.

Chmielewski, J.G., Strain, R.S., 2007. Achene aerodynamics in species of *Doellingeria*, *Eurybia*, *Oclemena*, and *Symphyotrichum*. J. Agric. Food Environ. Sci. 1, 1–10.

Cody, M.L., Overton, J.McC., 1996. Short-term evolution of reduced dispersal in island plant populations. J. Ecol. 84, 53–61.

D'Andrea, L., Broennimann, O., Kozlowski, G., Guisan, A., Morin, X., Keller-Senften, J., Felber, F., 2009. Climate change, anthropogenic disturbance and the northward range expansion of *Lactuca serriola* (Asteraceae). J. Biogeogr. 36, 1–15.

De Vries, M., 1997. Origin and domestication of *Lactuca sativa* L. Genet. Res. Crop Evol. 44, 165–174.

Doležalová, I., Křístková, E., Lebeda, A., Vinter, V., Astley, D., Boukema, I.W., 2003. Basic morphological descriptors for genetic resources of wild *Lactuca* spp. Plant Genet. Resour. Newsl. 134, 1–9.

Doležalová, I., Lebeda, A., Křístková, E., 2001. Prickly lettuce (*L. serriola* L.) germplasm collecting and distribution study in Slovenia and Sweden. Plant Genet. Resour. Newsl. 128, 41–44.

Dostál, J., 1989. Nová květena ČSSR, 2. díl. Academia Praha, pp. 1112–1115.

Feráková, V., 1970. A biosystematic study of critical species of *Lactuca* sect. Lactucopsis. Folia Geobot. Phytotax. 5, 401–427.

Feráková, V., 1976. *Lactuca* L. In: Tutin, T.G. (Ed.), Flora Europaea, vol. 4. Cambridge University Press, Cambridge, pp. 328–331.

Feráková, V., 1977. The Genus *Lactuca* L. in Europe. Komenský University Press, Bratislava, Czechoslovakia.

Fresnillo, B., Ehlers, B.K., 2008. Variation in dispersability among mainland and island populations of three wind dispersed plant species. Plant Syst. Evol. 270, 243–255.

Funk, V.A., Susanna, A., Stuessy, T.F., Bayer, R.J. (Eds.), 2009. Systematics, Evolution and Biogeography of Compositae. International Association for Plant Taxonomy, Vienna, Austria.

Gravuer, K., Von Wettberg, E.J., Schmidt, J., 2003. Dispersal biology of *Liatris scariosa* var. *novae-angliae* (*Asteraceae*), a rare New England grassland perennial. Am. J. Bot. 90, 1159–1167.

Grulich, V., 2004. *Lactuca* L. In: Slavík, B., Štěpánková, J. (Eds.), Květena České Republiky, vol. 7. Academia, Praha, pp. 487–497.

Harper, J.L., Lovell, P.H., Moore, K.G., 1970. The shapes and sizes of seeds. Ann. Rev. Ecol. Syst. 1, 327–356.

Van Hintum, Th.J.L., Boukema, I.W., 1999. Genetic resources of leafy vegetables. In: Lebeda, A., Křístková, E. (Eds.), Eucarpia Leafy Vegetables' 99. Palacký University, Olomouc, Czech Republic, pp. 59–74.

Hooftman, D.A.P., Oostermeijer, J.G.B., den Nijs, J.C.M., 2006. Invasive behaviour of *Lactuca serriola* (Asteraceae) in the Netherlands: spatial distribution and ecological amplitude. Bas. Appl. Ecol. 7, 507–519, http://linnaeus.nrm.se/botany/fbo/welcome.html.en ImageJ 1.32j, Wayne Rasband, National Institutes of Health, USA.

Křístková, E., Lebeda, A., 1999. Collection of *Lactuca* spp. genetic resources in the Czech Republic. In: Lebeda, A., Křístková, E. (Eds.), Eucarpia Leafy Vegetables' 99. Palacký University, Olomouc, Czech Republic, pp. 109–116.

Křístková, E., Lebeda, A., Doležalová, I., Vinter, V., Křístková, A., 2007. Variation in developmental stages of *Lactuca serriola* (prickly lettuce) germplasm from different European countries. In: Eucarpia Leafy Vegetables 2007, Conference Abstracts , University of Warwick, Warwick HRI, UK, Poster Presentations, 18–20 April 2007, p. 16.

Lebeda, A., Astley, D., 1999. World genetic resources of *Lactuca* spp., their taxonomy and biodiversity. In: Lebeda, A., Křístková, E. (Eds.), Eucarpia Leafy Vegetables' 99. Univerzita Palackého, Olomouc (Česká republika), pp. 81–94.

Lebeda, A., Petrželová, I., 2007. Comparison of resistance to *Bremia lactucae* in populations of *Lactuca serriola* occurring in Central Europe (Czech Republic) and the British Isles (England, U.K.). In: Bullitta, S. (Ed.), Plant genetic resources of geographical and other "islands (conservation, evaluation and use for plant breeding). Proceedings of the XVII Eucarpia Genetic Resources Section Meeting; 30 March–2 April 2005, Castelsardo (Italy). CNR-ISPAAM sez. Sassari Publisher, Sassari, Italy, pp. 59–62.

Lebeda, A., Doležalová, I., Křístková, E., Mieslerová, B., 2001. Biodiversity and ecogeography of wild *Lactuca* spp. in some European countries. Genet. Res. Crop Evol. 48, 153–164.

Lebeda, A., Pink, D.A.C., Astley, D., 2002. Aspects of the interactions between wild *Lactuca* spp. and related genera and lettuce downy mildew (*Bremia lactucae*). In: Spencer-Phillips, P.T.N., Gisi, U., Lebeda, A. (Eds.), Advances in Downy Mildew Research. Kluwer, Dordrecht, pp. 85–117.

Lebeda, A., Doležalová, I., Astley, D., 2004a. Representation of wild *Lactuca* spp. (Asteraceae, Lactuceae) in world genebank collections. Genet. Res. Crop Evol. 51, 167–174.

Lebeda, A., Doležalová, I., Feráková, V., Astley, D., 2004b. Geographical distribution of wild *Lactuca* species (Asteraceae, Lactuceae). Bot. Rev. 70, 328–356.

Lebeda, A., Doležalová, I., Křístková, E., Dehmer, K.J., Astley, D., Van de Wiel, C.C.M., Van Treuren, R., 2007a. Acquisition and ecological characterization of *Lactuca serriola* L. germplasm collected in the Czech Republic, Germany, the Netherlands and United Kingdom. Genet. Res. Crop Evol. 54, 555–562.

Lebeda, A., Ryder, E.J., Grube, R., Doležalová, I., Křístková, E., 2007b. Chapter 9: Lettuce (Asteraceae; *Lactuca* spp.). In: Singh, R. (Ed.), Genetic Resources, Chromosome Engineering, and Crop Improvement Series. Vegetable Crops, vol. 3. CRC Press, Boca Raton, pp. 377–472.

Lebeda, A., Petrželová, I., Maryška, Z., 2008. Structure and variation in the wild-plant pathosystem: *Lactuca serriola*–*Bremia lactucae*. Eur. J. Plant Pathol. 122, 127–146.

Lebeda, A., Doležalová, I., Křístková, E., Kitner, M., Petrželová, I., Mieslerová, B., Novotná, A., 2009a. Wild *Lactuca* germplasm for lettuce breeding: current status, gaps and challenges. Euphytica 170, 15–34.

Lebeda, A., Kitner, M., Dziechciarková, M., Doležalová, I., Křístková, E., Lindhout, P., 2009b. An insight into the genetic polymorphism among European populations of *Lactuca serriola* assessed AFLP. Biochem. Syst. Ecol. 37, 597–608.

Mou, B., 2008. Lettuce. In: Prohens, J., Nuez, F. (Eds.), Handbook of Plant Breeding. Vegetables I. Asteraceae, Brassicaceae, Chenopodiaceae, and Cucurbitaceae. Springer, New York, pp. 75–116.

Petrželová, I., Lebeda, A., 2011. Distribution of race-specific resistance against *Bremia lactucae* in natural populations of *Lactuca serriola*. Eur. J. Plant Pathol. 129, 233–253.

Prince, D.S., Carter, R.N., 1977. Prickly lettuce (*Lactuca serriola* L.) in Britain. Watsonia 11, 331–338.

Sheldon, J.C., Burrows, F.M., 1973. The dispersal effectiveness of the achene-pappus units of selected compositae in steady winds with convection. New Phytol. 72, 665–675.

StatSoft CR s.r.o., 2007. STATISTICA Cz (softwarový systém pro analýzu dat), verze 8.0. Available at www.statsoft.cz.
Ter Braak, C.J.F., Šmilauer, P., 2002. CANOCO 4.5–CANOCO Reference Manual and CanoDraw for Windows. User's Guide. Biometrics, Wageningen.
Troeh, F.R., Donahue, R.L., 2003. Dictionary of Agriculture and Environmental Science. Iowa State Press, Ames, Iowa.
Zhu, S.X., Qin, H.N., Shih, C., 2006. Achene wall anatomy and surface sculpturing of *Lactuca* L. and related genera (Compositae: Lactuceae) with notes on their systematic significance. J. Integr. Plant Biol. 48, 390–399.

Morphology of achenes of *Lactuca serriola* from Slovenia and Sweden

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Abstract

The morphological variability of achenes of *Lactuca serriola* representing 34 populations from Slovenia and 12 populations from Sweden was studied with regard to the eco-geographical conditions of both countries. Totally eight quantitative morphological characters were evaluated: length and width of achene body, length of beak, number of ribs, index length/width of achene body, length of pappus bristles, pappus area and diameter of discus. Statistical method of nested ANOVA proved significant differences within the studied morphological characters between Slovene and Swedish populations for length and width of achene body, length of pappus bristles and pappus area. Generally, *L. serriola* achenes from Slovenia were longer, wider and with longer pappus than achenes from Sweden. Among geographical factors, latitude expressed the highest impact to the evaluated morphological characters. To the North, index length/width of achene body, and length of beak were getting longer, conversely length and width of achene body, length of pappus bristles and pappus area were getting shorter.

Keywords: *Lactuca serriola*, prickly lettuce, compass lettuce, achene, pappus, morphology, variability

Introduction

Lactuca serriola L. (prickly lettuce, compass lettuce, fam Asteraceae) is highly polymorphic species and two forms are distinguished according to the shape of cauline leaves, f. *serriola* and f. *integrifolia* (Feráková 1977).

Lactuca serriola is considered as one of the direct progenitors of cultivated lettuce *Lactuca sativa* L. (De Vries 1997, Lebeda et al. 2007). It belongs to the primary gene-pool of lettuce and play an important role in moder breeding programes of lettuce as a source of race-specific resistance genes against lettuce downy mildew (*Bremia lactucae*) (Lebeda et al. 1999, 2007).

Prickly lettuce is a ruderal species, growing preferably on disturbed soil. From the ecological viewpoint this species is „r" strategist with short life cycle (D'Andrea et al. 2009). *L. serriola* is a annual or biennial therophyte which can be reproduced only by seeds (D'Andrea et al. 2009, Feráková 1977). Originaly the meridional-temperate, western Euroasian species, it has nowadays a worldwide distribution (Lebeda et al. 2004b). The spreading of this species is very closely related with human activities, mainly with transport and building constructions, and climate changes, specially climate warming (D´Andrea et al., 2009). It expands along roads, highways, railways and embankments (Lebeda et al. 2001). Recently, *L. serriola* has spread throught Europe as an invasive weed (Lebeda et al. 2001, 2004b, Hooftman et al. 2006, D' Andrea et al. 2009).

Spreading of *L. serriola* is provided with transport of plumed (fluffy) reproductive propagules, the achenes. The propagules of this taxon are monomorphic, in contrast to many other members of the family *Asteraceae* where the dimorphism or polymorphism in achenes is typical (Imbert et al. 1996, Baker and Dowd 1982, Harper et al. 1970). Pappus of *L. serriola*, in witness the genus *Lactuca* L., is always monomorphic, consisting of 2 rows of whitish hairs, which exceed the involucral bracts (Feráková 1977). Pappus bristles of *L. serriola* are smooth, consisting of two or three vertical rows of cells (Tuisl 1968).

Fruits and seeds possess many morphological traits important for taxonomical classification. Within the genus *Lactuca* L. the traits on fruit (achene) are in many cases sufficient for specific or subspecific identification (Feráková 1977). Morphological and anatomical study of fruits together with molecular and ecobiogeographical differences have also important role for delimitation of sections in currently accepted classification of the genus *Lactuca* L. (Lebeda and Astley 1999).

Achenes of *L. serriola* are relatively small. The length of achene body is 3 mm and together with beak is 6-8 mm (Dostál 1989, Grulich 2004). They are ±1 mm broad, oblong-ovate, moderately flattened, light brown to greyish. On the surface, there are 5-10 ribs with short fine bristles towards the apex. The beak is white, filiform, and as long as or longer than the achene body. Pappus is 3-4,5 mm long, white and deciduous (Feráková 1977, Dostál 1989, Grulich 2004).

First complex data on morphological parameters of *L. serriola* achenes from the Czech Republic, Germany, the Netherlands and the United Kingdom presented by Novotná et al. (2011) showed that both leafy forms of *L. serriola* can be distinquished also by achene morphology. Achenes of *L. serriola* f. *serriola* are shorter, thinner, with shorter beak, lower length/width index and higher number of ribs when compared to those of *L. serriola* f. *integrifolia*. In relation to studied eco-geographical features achene morphology was significantly correlated with longitude, latitude and soil texture of habitats. With increasing latitude *L. serriola* achenes were longer, narrower (slimmer), with lower number of ribs and longer beaks. With increasing longitude almost all studied morphological characters were decreasing except of number of ribs. *L. serriola* plants growing on sand substrate had longer, wider and longer beaked achenes compared in comparison with plants from loam-sand substrate. In extreme conditions such as stony substrate and basalt blocks *L. serriola* plants were characterized by thinner achenes with higher number of ribs.

The aim of recent study was to compare morphological parameters on achenes from ecogeographically different areas from Slovenia and Sweden. Slovenia is close to the centre of diversity of European wild *Lactuca* spp., and the mean year temperature in Ljubljana in the period of 1991-2000 was 10,9 °C (http://pxweb.stat.si/pxweb/Dialog/Saveshow.asp). The northern boundary of the distribution of *L. serriola* in Europe is situated in the territory of Sweden, and the mean year temperaturte in Stockolm is 6,6 °C (http://www.climatetemp.info/sweden/).

Obtained data will be compared to those on *L. serriola* achenes from other European countries (Czech Republic, Germany, the Netherlands and the United Kingdom) published by Novotná et al. (2011). Results of this study can contribute to better understand the role of environmetal (eco-geographical) conditions in relation to morphology of plant propagules and to plant dispersal.

Material and methods

Plant material

Initial experimental material was collected during the collecting and exploration missions to Slovenia and Sweden in 2000 (Doležalová et al. 2001). The set of *L. serriola* samples under study consisted of 72 seed samples from 34 populations in Slovenia (SVN) and 47 seed samples from 12 populations in Sweden (SWE) (Table 1, Figure 1a, b). Detail passport data on collected seed samples are available by authors of this paper.

The regeneration of samples was performed in the greenhouses of the Department of Botany, Faculty of Science, Palacký University in Olomouc (Czech Republic) in 2006. Each sample was represented by 16 plants. They were cultivated in plastic pots with garden soil under standard protocol for regeneration of plant genetic resources of *Lactuca* spp. (Boukema et al. 1990). During vegetative growth, plants were assessed for morpholocical traits on stem, leaves, inflorescence and for developmental stages according to descriptor lists of Doležalová et al. (2002, 2003).

Achenes were collected from five plants per each sample. Around 60 mature achenes were collected from 3 - 4 heads from each plant. These samples of *L. serriola* achenes are maintained on the Department of Botany (faculty of Sciencer, Palacký University in Olomouc, Czech Republic).

Morphological evaluation and measurements of achenes

Fifty achenes per plant were randomly chosen to determine their shape. Eight morphological characters were studied: length (Lab) and width of the achene's body (Wab), length/width index (Lab/Wab index) of achene body, length of beak (Lb), number of ribs (Nr), length of pappus bristles (Lbr), pappus area (Paparea) and diameter of discus (Discus). Achenes were measured using the ImageJ computer program (ImageJ 1.32j) after being scanned as JPGs at a resolution of 400 dpi. Calibration was done such that the distance of 20 mm was determined by the program on a scanned ruler. Another measurement of the distance was converted into mm with an accuracy of 0.01 mm. The shape of achene body given by Lab/Wab index was counted from corresponding values. Length and width of achene were measured at the longest and widest point of the achene body. Length of beak was given by the distance from the apical point of achene body to the discus, length of pappus bristles was the distance from the discus to the end of the bristle. Diameter of discus was measured from one to the second edge of discus. Area of pappus was calculated as a surface of circle, where the radius is given by the length of bristle. For this purpose totally five bristles per each achene were measured.

Ten achenes of each plant were randomly chosen to determine the number of ribs, using a magnifying glass where the ribs were quantified separately for each side of the achene. Statistically analyzed character "number of ribs" (Nr) is the sum of all ribs from both side of achene body.

Statistical analysis

To determine variation and significance of differences in morphological characters of achenes within the studied set of *L. serriola* populations, significance was analysed by nested ANOVA General Linear Models (GLM), NCSS verze 2007 (Hintze 2001). Associations between morphological characters of achenes and geographical parameters of the plant populations/collection sites were revealed with analyses conducted with CANOCO for Windows 4.5 and CanoDraw for Windows 4.5 (ter Braak and Šmilauer 2002). Totally 3 geographical characteristics (latitude, longitude, altitude) were in the set of factors. According to the gradient length from Detrended Correspondence Analysis (DCA, the highest value 0.914) direct gradient analysis (RDA, redundancy analysis) was used. RDA relates evaluated morphological characters of *L. serriola* achenes to habitat factors. The significance of studied geographical factors was found using the method forward selection (RDA). Monte-Carlo permutation test with 999 permutations was used to test the significance of the explaining environmental factors.

Results

Data on morphological characters of *L. serriola* achenes from Slovenia were obtained by measuring achenes from 304 plants, representing 72 seed samples from 34 populations. According to the shape of cauline leaves, all plants were determined as *Lactuca serriola* L. f. *serriola*. Basic characteristics of this set are given in the Table 1. Corresponding data on achenes from Sweden were obtained by measuring achenes from 186 plants representing 47 seed samples from 12 populations. Sample 192/00-3 was not analyzed for four parameters on the achene body (Lab, Wab, Lb, Lab/Wab index). Within samples from Sweden, *L. serriola* f. *serriola* was dominating, occurrence of *L. serriola* f. *integrifolia* was determinated only in 3 plants within one seed sample (Table 1).

Descriptive statistics of evaluated morphological characters of achenes are summarized in the Table 2. The mean value of length of achene body (Lab) within samples from Slovenia was 3.06 mm. The minimum value (2.12 mm) was observed within the population 5 from Gornja Radgona and maximum value (4.01 mm) was found in population 17 from Preloge (Table 2, Figure 1a). The mean value of length of achene body (Lab) within samples from Sweden was 2.89 mm. Minimum value of 1.93 mm recorded in population 42 from Linköping and maximum value 3.82 mm observed in population 46 from Malmö (Table 2, Figure 1b).

The mean value of width of achene body (Wab) within samples from Slovenia was 1.04 mm, the minimum value (0.48 mm) was recorded in population 2 from Pesnica and maximum value (1.61 mm) was recorded in population 4 from Spodnja Ščavnica (Table 2, Figure 1a). The mean value of width of achene body (Wab) for samples from Sweden was 0.96 mm. The minimum value of 0.54 mm was found in population 38 from Högsta and maximum of 3.03 was recorded in population 36 from Stockholm (Table 2, Figure 1b).

The mean value of length of beak (Lb) of samples from Slovenia was 4.2 mm. The minimum value 1.73 mm was observed in population 14 from Šikole and the maximum value 6.52 mm in population 2 from Pesnica (Table 2, Figure 1a). Corresponding mean value of samples from Sweden was 4.35 mm, the minimum value of 1.89 mm was observed in population 44 from Kristianstad and the maximum of 5.99 mm was recorded in population 38 from Högsta (Table 2, Figure 1b).

The mean value of length/width index (Lab/Wab index), i.e. length of achene body to width of achene body for Slovenian samples was 2.99 mm. The minimum value (1.72) was found in population 5 from Gornja Radgona and the maximum value (5.77) was found in population 2 from Pesnica (Table 2, Figure 1a). The mean value of length/width index for Swedish samples was 3.04. Minimum value (0.97) was recorded in population 36 from Stockholm and maximum value (5.19) was observed in population 38 from Högsta (Table 2, Figure 1b).

The mean length of pappus bristles (Lbr) for samples from Slovenia was 5.07 mm. The minimum value (3.18 mm) was recorded in population 9 from Žerovinci and the maximum (6.24 mm) was recorded in population 30 from Brezovica (Table 2, Figure 1a). The mean length of pappus bristles for samples from Sweden was 4.83 mm;

minimum value was 2.64 mm recorded in population 36 from Stockholm and maximum value was 5.81 mm found in population 41 from Norrköping (Table 2, Figure 1b).

The mean value of pappus area (Paparea), as derived from the length of pappus bristles was established for samples from Slovenia was 81.08 mm2. The minimum value of 31.71 mm2 was observed in population 9 from Žerovinci and the maximum 122.34 mm2 in population 30 from Brezovica (Table 2, Figure 1a). The mean area of pappus for samples from Sweden was 73.7 mm2 with minimum 21.88 mm2 in population 36 from Stockholm and maximum 105.85 mm2 in population 41 from Norrköping (Table 2, Figure 1b).

The mean diameter of discus (Discus) for samples from Slovenia was 0.27 mm. The minimum value (0.15 mm) was recorded in populations 14 from Šikole and 24 from Vransko. The maximum value (0.44 mm) was found in population 25 from Zavrh pri Trojanah (Table 2, Figure 1a). Mean diameter of discus for samples from Sweden was 0.27 mm. The minimum value was 0.15 mm recorded in population 36 from Stockholm and maximum value 0.41 mm was recorded in population 37 from Uppsala (Table 2, Figure 1b).

The mean number of ribs (Nr) for Slovenia samples was 11.71. The minimum number of 8 ribs was observed in populations 1 (Šentilj), 5 (Gornja Radgona), 15 (Maribor Stari Log), 18 (Slovenske Konjice), 23 (Prekopa), 24 (Vransko), 29 (Trzin) and 31 (Dragomer). The maximum number of 16 ribs was recorded in populations 1 (Šentilj), 10 (Pavlovci), 15 (Maribor Stari Log), 19 (Vojnik), 20 (Levec), 21 (Žalec), 25 (Zavrh pri Trojanah) (Table 2, Figure 1a). Mean number of ribs for samples from Sweden was 11.7. The minimum number of 7 ribs was recorded in population 45 from Landskrona and maximum number of 16 ribs was observed in populations 41 (Norrköping), 42 (Linköping) and 43 Jönköping (Table 2, Figure 1b).

Significant differences in mean values of the length (Lab) of width (Wab) of achene body of *L. serriola* from Slovenia and Sweden were proved (Table 3). Achenes from Slovenia were longer and wider when compared to those from Sweden (Table 2, Figures 2a, b). Within countries populations and seed samples were in these characters significantly different (Table 3).

No significant difference in the index of the length/width of achene body (index Lab/Wab) and in the length of beak (Lb) between samples from Slovenia and Sweden was proved (Table 3). Mean values are recorded in Table 2 and the Figures 2 c, d.

However, significant differences of Lb and Lab/Wab index were detected among populations and seed accessions within countries ($p<0.05$) (Table 3).

Comparison of mean values of length of pappus bristles (Lbr) and pappus area (Paparea) showed significant differences between countries, populations within countries and seed accessions within countries ($p<0.05$) (Table 4). Slovene populations had higher estimates of these morphological characters than Swedish populations (Table 2, Figures 3a, b).

No significant differences were found among countries in diameter of discus (Discus) and number of ribs (Nr) (Table 4). Mean values are recorded in Table 2 and Figures 3c, d. On the other hand, comparison of populations and seed accessions within countries showed significant differences ($p<0.05$) (Table 4).

Associations of evaluated morphological characters with geographical factors

Associations between measured morphological parameters of *L. serriola* achenes and geographical factors of collecting sites/locations were evaluated by redundancy analysis (RDA) (Figures 4, 5). Latitude had the significant influence on the morphological characters of *L. serriola* achene body ($F=665.66$, $p<0.001$) and also on morphological characters of pappus ($F=240.47$, $p=0.002$) (Table 5). To the North, length/width index of achene body (Lab/Wab index) and length of beak (Lb) were getting longer, conversely length (Lab) and width (Wab) of body were getting shorter (Figure 4). Length of pappus bristles (Lbr) and pappus area (Paparea) reached lower values on the places of higher latitude. For discus diameter (Discus) and number of ribs (Nr) likely no relation with geografical position of collecting sites of samples was found (Figure 5).

Longitude and altitude expressed lower impact on morphological parameters of *L. serriola* achenes (Table 5). To the West direction, achenes were characterized by shorter but wider bodies, longer beaks and lower length/width index of achene body (Figure 4). With increasing longitude all characters of pappus were getting longer (Figure 5). In the places of higher altitude, longer and wider *L. serriola* achenes with shorter beaks, longer pappus, wider discus and higher number of ribs occurred (Figures 4, 5).

Discussion

L. serriola is the most widely distributed species of the genus *Lactuca* L. with synanthropic worldwide occurence (Lebeda et al. 2004b, Brant and Holec 2004, Weaver and Downs 2003). According to many previous studies (Lebeda et al. 2001, Doležalová et al. 2001, Lebeda et al. 2007, Hooftman et al. 2006), during last 20 years prickly lettuce has shown an enormous range expansion and population increase in Europe and in some parts of Scandinavia (D'Andrea et al. 2009). In The Netherlands, the occurrence of *L. serriola* increased significantly since 1940, indicating that the species currently occurs in a broader range of vegetation types. Except of its original ruderal habitats, *L. serriola* was currently noted in more closed vegetation types, which are less continental and more humid (Hooftman et al. 2006).

Both leaf forms of *L. serriola* are not distributed equally (proportionally) througout Europe. Detail study of 50 populations from four European countries performed by Lebeda et al. (2007) revealed that only *L. serriola* f. *serriola* was recorded in the Czech Republic; in Germany there were 91% of plants form *serriola*; both forms were represented equally in the Netherlands, and *L. serriola* population in the United Kingdom was represented by form *integrifolia* in 98%. *Lactuca serriola* f. *integrifolia* was identified within population from Landskrona (Table 1, Figure 1b), geografically very close to area where in European continent this form was recorded.

Spreading of *L. serriola* is performed by the transport of achenes. The production of diaspores with plumose or comose structures that act as drag-enhancing parachutes is typical for many members of the *Asteraceae* (Andersen 1993). But not always, the pappus was understood as the primary instrument for long-distance seed dispersal. Goebel (1905, in: Sheldon and Burrows, 1973) suggested that the primary function of the pappus is as a transpiration apparatus for the fruit (Sheldon and Burrows, 1973).

Green (1980), Augspurger (1986), Matlack (1987), Andersen (1993), Gravuer et al. (2003), Chmielewski and Strain (2008) investigated fall speed (terminal velocity) and plume loading of wind-dispersed diaspores of many herbaceous members of family *Asteraceae* and trees of different families in horizontal still air. Horizontal winds spread diaspores over a broad area and carry them away from the parent (Augspurger 1986).

The aim of recent study was compare morphological traits of achenes from *L. serriola* originating from eco-geographically distinct countries, Slovenia and Sweden. These countries differ not only in geographical position but also in environmental conditions. The Mediterranean region including Slovenia is characterized by the highest diversity of European *Lactuca* spp. (Lebeda et al. 2004a) and it is considered as probable domesticated area of lettuce (De Vries 1997, Lebeda et al. 2004b, Lebeda et al. 2007). By contrast, the northmost European localities of *L. serriola* were found in Norway and Sweden at 60° N (Feráková 1977).

The results show that samples of *L. serriola* from Slovenia differ significantly to those from Sweden in length and width of achene bodies (Table 3). Generally, achenes of prickly lettuce were „bigger“ (longer and wider) in Slovenia than in Sweden (Table 2, Figures 2a, b). It is in agreement with RDA analysis showing shorter length and width of body to the north direction (Figure 4). Also the resulsts of the extensive research of morphology of *L. serriola* achenes from 4 countries of Central and West Europe (Czech Republic, Germany, The Netherlands and United Kingdom) (Novotná et al. 2011) showed significant differences in length of achene body. The shortest achenes were found in the Czech Republic, and to the west direction they were getting longer. In width of achene body the trend was similar. *L. serriola* achenes from the Czech populaltions were completely different to those of other three countries. This difference is caused by definite prevalence of *L. serriola* f. *serriola* populations in the Czech Republic than in other countries, where the form *integrifolia* was predominated. It was found that *L. serriola* f. *serriola* is determined by smaller achenes (with shorter lenght and width of achenes body), shorter beak and lower mean value of index length/width (Novotná et al. 2011).

Influence of other geographical factors such as longitude and altitude on length and width of achene body was weaker than in case of latitude (Table 5). Despite of that fact in the places of higher altitude longer and wider achenes were found (Figure 4). Gravuer et al. (2003) investigated the dispersal capability of a rare grassland species *Liatris scariosa* var. *novae-angliae* in New England. They found that dispersal ability of that taxon was reduced for longer and heavier achenes and it increased for wider achenes. According to their study, the propagule mass was the strongest predictor of dispersal ability. Our results also revealed that greater width of achene body facilitates the dispersability. In higher altitude wider achenes are prefered because their dispersal ability increases.

No significant differences were found in length of beak and index length/width of achene body between Slovene and Swedish populations (Table 3). This is in contrast with previously obtained results on *L. serriola* populations from some other European countries (Czech Republic, Gernamy, the Netherlands and United Kingdom) (Novotná et al. 2011). Highly significant differences were revealed between the Central European populations (from the Czech Republic) and populations from western Europe (The Netherlands, United Kingdom). Generally, to the West and to the North, length of beak and index length/width are getting higher (Novotná et al. 2011). According to our recent results, length of beak is getting longer with growing longitude and latitude and conversaly it is getting shorter with growing altitude (Figure 4).

Andersen (1993) made a study of morphology and settling velocity of some wind-dispersed species of *Asteraceae*, including *L. serriola*. Among others he found, that diaspores with beaked achenes have significantly lower settling velocities than diaspores with unbeaked achenes, even though beaked and unbeaked achenes do not differ in plume loading, which is the ratio of diaspore weight/plume area (Matlack 1987).

However, if we compared the studied *L. serriola* populations and seed accessions from Slovenia and Sweden, high significant differences within all evaluated morphological features of achenes were found.

Our recent data show that pappus bristles were longer in Slovene populations than in Sweden ones and the same trend was evident for the pappus area (Table 2, Figure 4). According to Sheldon and Burrows (1973) the efficiency of dispersal is determined more by the fine details of the pappus geometry, which directly affects its aerodynamic properties, than by the size ratio of pappus to achene. Fresnillo and Ehlers (2008) compared the dispersal ability of three wind dispersed plant species (*Cirsium arvense*, *Epilobium angustifolium* and *E. hirsutum*) from populations on mainland and three islands. They found that the achenes of *C. arvense* (*Asteraceae*) from mainland had significantly longer pappus than the achenes from the island populations. Generally, the achenes from islands have shorter pappus and lower dispersal ability than achenes from mainland (Harper et al. 1970), which is in accordance with our results.

In contrast, Gravuer et al. (2003) did not find the reduced dispersal ability for norther blazing star achenes of island populations relative to their mainland coutnerparts. Only studied features such as achene width and propagule mass were significantly greater in costal populations in comparison to inland and island populations.

Dispersal ability of wind-dispersed plants in island populations is influenced also by the age of those populations. Older island populations show increasingly reduced dispersal potential relative to mainland populations or to young island populations (Cody and Overton 1996). In older populations of *Lactuca muralis* (recently *Mycelis muralis*) the lower proportion of pappused achenes were found compared with newer colonies (Cody and Overton 1996). It is, however, unclear whether the observations were due to genetic differences or phenotypic plasticity, nevertheless, the existence of variation between populations has been established.

The evaluted achenes of Sweden *L. serriola* populations originate from the southern part of the country (Doležalová et al. 2001), which is strongly influenced by the sea. Considering that fact, the environmental conditions are very similar like in an island. Results of our study are in agreement of Fresnillo and Ehlers (2008), and Cody and Overton (1996). Sheldon and Burrows (1973) also recorded that a reduction in the weight of the pappus in relation to the achene weight increases the terminal velocity.

Very detailed comparing study of the pappus characters, especially of the pappus bristles of weedy and non-weedy aster species was done by Chmielewski and Strain (2007). They conclude that the achenes of weedier aster species have the potential to remain in the air longer and thus be dispersed further on average than achenes of the non-weedy aster species. The better dispersal ability of weedy species is influenced mainly by plant height, comparatively lower values of terminal velocity and comparatively lesser values of achene mass.

For discus diameter between Slovene and Swedish populations, no significant difference was found either (Table 4). The mean value of that trait from both countries is 0.27 mm (Table 2). According to correlation analysis, weak correlation was found in latitude and longitude.

Number of ribs between populations from Slovenia and Sweden was not significantly different as well (Table 4). In both countries, the mean value of that character was 11.7 ribs (Table 2). However, the achenes from central European populations (from the Czech Republic and Germany) created a distinct group, significantly different from the group of Dutch and English populations (Novotná et al. 2011).

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Literature

Andersen, M.C. (1993) Diaspore morphology and seed dispersal in several wind-dispersed Asteraceae. Am. J. Bot. 80(5): 487-492.

Augspurger, C.K. (1986) Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. Am. J. Bot. 73(3): 353-363.

Baker, G.A., Dowd, D.J. (1982) Effect of parent plant density on the production of achene types in the annual *Hypochoeris glabra*. J. Ecol. 70: 201-215.

Boukema, I.W., Hazenkamp, Th., van Hintum, Th.J.L. (1990) CGN Collection Reviews: The CGN Lettuce Collection. December 1990, Centre for Genetic Resources, The Netherlands (CGN), Wageningen, The Netherlands.

Brant, V., Holec, J. (2004) Locika kompasová (*Lactuca serriola* L.). Rostlinolékař 15/5: 24-27.

Chmielewski, J.G., Strain, R.S. (2007) Achene aerodynamics in species of *Doellingeria*, *Eurybia*, *Oclemena*, and *Symphyotrichum*. J. Agric. Food Environ. Sci. 1:1-10.

Cody, M.L., Overton, J. McC. (1996) Short-term evolution of reduced dispersal in island plant populations. J. Ecol. 84: 53-61.

Corel PHOTO-PAINT X3 (2005) version 13.0.0.739.

D'Andrea, L., Broennimann, O., Kozlowski, G., Guisan, A., Morin, X., Keller-Senften, J. and Felber, F. (2009) Climate change, anthropogenic disturbance and the northward range expansion of *Lactuca serriola* (Asteraceae). J. Biogeogr. 36: 1-15.

De Vries, M. (1997) Origin and domestication of *Lactuca sativa* L. Genet. Resour. Crop Evol. 44: 165-174.

Doležalová, I., Křístková, E., Lebeda, A., Vinter, V. (2002) Description of morphological characters of wild *Lactuca* L. spp. genetic resources (English-Czech version). Hort. Sci. (Prague), 29 (2): 56-83.

Doležalová, I., Křístková, E., Lebeda, A., Vinter, V., Astley, D., Boukema, I.W. (2003) Basic morphological descriptors for genetic resources of wild *Lactuca* spp. Plant Genet. Resour. Newsl. 134: 1-9.

Doležalová, I., Lebeda, A., Křístková, E. (2001) Prickly lettuce (*L. serriola* L.) germplasm collecting and distribution study in Slovenia and Sweden. Plant Genet. Resour. Newsl. 128: 41-44.

Dostál, J. (1989) Nová květena ČSSR, 2. díl. Academia Praha, pp. 1112-1115.

Feráková, V. (1977) The genus *Lactuca* L. in Europe. Komenský University Press, Bratislava (Czechoslovakia).

Fresnillo, B., Ehlers, B.K. (2008) Variation in dispersability among mainland and island populations of three wind dispersed plant species. Plant Syst. Evol. 270: 243-255.

Goebel, K. (1905) Organography of Plants, Vol. II. Clarendon Press, Oxford. Cited in: Sheldon, J.C., Burrows, F.M. (1973) The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. New Phytol. 72: 665-675.

Gravuer, K., Von Wettberg, E.J, Schmitt, J. (2003) Dispersal biology of *Liatris scariosa* var. *novae-angliae* (*Asteraceae*), a rare New England grassland perennial. Am. J. Bot. 90: 1159-1167.

Green, D.S. (1980) The terminal velocity and dispersal of spinning samaras. Am. J. Bot. 67(8): 1218-1224.

Grulich, V. (2004) *Lactuca* L. In: Slavík, B., Štěpánková, J. (Eds.) Květena České republiky 7. Academia, Praha, pp. 487-497.

Harper, J.L., Lovell, P.H., Moore, K.G. (1970) The shapes and sizes of seeds. Annu. Rev. Ecol. Syst. 1: 327-356.

Hintze, J.L. (2001) NCSS Statistical system for windows. NCSS, Dr. J.L: Hintze, Kaysville, Utah, USA.

Hooftman, D.A.P, Oostermeijer, J.G.B., den Nijs, J.C.M. (2006) Invasive behaviour of *Lactuca serriola* (Asteraceae) in the Netherlands: Spatial distribution and ecological amplitude. Basic Appl. Ecol. 7: 507-519.

ImageJ 1.32j, Wayne Rasband, National Institutes of Health, USA.

Imbert, E., Escarré, J., Lepart, J. (1996) Achene dimorphism and among-population variation in *Crepis sancta* (Asteraceae). Int. J. Plant Sci. 157: 309-315.

Křístková, E., Lebeda, A. (1999) Collection of *Lactuca* spp. genetic resources in the Czech Republic. In: Lebeda, A., Křístková, E. (Eds.) Eucarpia Leafy Vegetables '99. Univerzita Palackého, Olomouc (Česká republika), pp. 109-116.

Lebeda, A., Astley, D. (1999) World genetic resources of *Lactuca* spp., their taxonomy and biodiversity. In: Lebeda, A., Křístková, E. (Eds.) Eucarpia Leafy Vegetables '99. Univerzita Palackého, Olomouc (Česká republika), pp. 81-94.

Lebeda, A., Doležalová, I., and Astley, D. (2004a) Representation of wild *Lactuca* spp. (Asteraceae, Lactucae) in world genebank collections. Genet. Resour. Crop Evol. 51: 167-174.

Lebeda, A., Doležalová, I., Feráková, V., Astley, D. (2004b) Geographical distribution of wild *Lactuca* species (Asteraceae, Lactuceae). Bot. Rev. 70: 328-356.

Lebeda, A., Doležalová, I., Křístková, E., Kitner, M., Petrželová, I., Mieslerová, B., Novotná, A. (2008) Wild *Lactuca* germplasm for lettuce breeding: recent status, gaps and challenges. In: Prohens, J. and Badenes, M.L. (Eds.) Modern Variety Breeding for Present and Future Needs. Universidad Politécnica de Valencia, Valencia, Spain.

Lebeda, A., Doležalová, I., Křístková, E., Mieslerová, B. (2001) Biodiversity and ecogeography of wild *Lactuca* spp. in some European countries. Genet. Resour. Crop Evol. 48: 153-164.

Lebeda, A., Doležalová, I., Křístková, E., Vinter, V., Vránová, O., Doležal, K., Tarkowski, P., Petrželová, I., Trávníček, B., Novotný, R., Janeček, J. (1999) Complex research of taxonomy and ecobiology of wild *Lactuca* spp. genetic resources. In: Lebeda, A., Křístková, E. (Eds.) Eucarpia Leafy Vegetables '99. Univerzita Palackého, Olomouc (Česká republika), pp.117-131.

Lebeda, A., Ryder, E.J., Grube, R., Doležalová, I., Křístková, E. (2007) Lettuce (Asteraceae; *Lactuca* spp.), Chapter 9. In: Singh, R.J. (Ed.) Genetic Resources, Chromosome Engineering, and Crop Improvement, Vol. 3, Vegetable Crops. Boca Raton, CRC Press, Boca Raton, Tailor and Francis Group, pp. 377-472.

Matlack, G.R. (1987) Diaspore size, shape, and fall behaviour in wind-dispersed plant species. Am. J. Bot. 74(8): 1150-1160.

Novotná, A., Doležalová, I., Lebeda, A., Kršková, M., Berka, T. (2011) Morphological variability of achenes of some European populations of *Lactuca serriola* L., Flora 206:473-483.

Sheldon, J.C., Burrows, F.M. (1973) The dispersal effectiveness of the achene-pappus units of selected Compositae in steady winds with convection. New Phytol. 72: 665-675.

ter Braak, C.J.F., Šmilauer, P. (2002) CANOCO 4.5 – CANOCO reference manual and CanoDraw for Windows. User's Guide. – Biometrics, Wageningen.

Tuisl, G. (1968) Der Verwandtschaftskreis der Gattung *Lactuca* L. im iranischen Hochland und seinen Randgebieten. Selbstverlag Naturhistorisches Museum Wien, Vienna.

Weaver, S.E., Downs, M.P. (2003) The biology of Canadian weeds. 122. *Lactuca serriola* L. Can. J. Plant Sci. 83: 619-628.

Cited web sites:

Anonym (2011) Climate and Temperature Information, Sweden. [cit. 22nd June 2011]. Available from www: <http://www.climatetemp.info/sweden/>.

Anonym (2011) Statični urad republike slovenije. [cit. 22nd June 2011]. Available from www: <http://pxweb.stat.si/pxweb/Dialog/Saveshow.asp>.

Anonym (2011) ISO 3166-1 alpha-3. [cit. 1st July 2009]. Available from www: <http://en.wikipedia.org/wiki/ISO_3166-1_alpha-3>.

Table 1. List of *L. serriola* samples from Slovenia and Sweden used in the study.

Population number	Sample number	Location	Geographical position Latitude [N]	Longitude [E]	Altitude [m a.s.l.]
Slovenia					
1	1/00 - 4/00	Šentilj	46°40'50"	15°39'11"	299
2	5/00 - 6/00	Pesnica	46°36'45"	15°40'13"	258
3	9/00	Lenart	46°35'00"	15°51'0"	251
4	10/00 - 12/00	Spodnja Ščavnica	46°37'44"	15°56'22"	221
5	14/00 - 15/00	Gornja Radgona	46°40'41"	15°59'25"	218
6	16/00	Radenci	46°38'18"	16°03'01"	201
7	21/00	Iljaševci	46°34'28"	16°07'50"	187
8	22/00 - 23/00	Ljutomer	46°31'38"	16°11'35"	220
9	24/00 - 25/00	Žerovinci	46°29'15"	16°08'30"	286
10	26/00 - 27/00	Pavlovci	46°26'07"	16°08'03"	212
11	28/00 - 29/00	Dobrava	45°51'24"	14°58'05"	249
12	35/00	Ptuj	46°25'07"	15°52'18"	225
13	36/00	Gaj	46°27'05"	15°41'00"	259
14	41/00 - 43/00	Šikole	46°24'18"	15°42'11"	243
15	44/00 - 48/00	Maribor Stari Log	45°43'29"	14°55'18"	395
16	51/00	Slovenska Bistrica	46°23'34"	15°34'24"	273
17	52/00 - 54/00	Preloge	46°13'34"	15°33'53"	221
18	55/00 - 57/00	Slovenske Konjice	46°20'13"	15°25'10"	348
19	58/00 - 60/00	Vojnik	46°17'29"	15°17'55"	270
20	61/00 - 62/00	Levec	46°14'34"	15°13'10"	242
21	63/00	Žalec	46°15'03"	15°10'13"	256
22	64/00 - 67/00	Šempeter	46°15'36"	15°07'12"	271
23	68/00 - 69/00	Prekopa	46°15'0"	14°59'0"	319
24	70/00, 72/00 - 73/00	Vransko	46°14'56"	14°57'45"	346
25	74/00 - 78/00	Zavrh při Trojanah	45°49'52"	14°30'08"	786
26	79/00	Žirovše	46°10'14"	14°47'46"	392
27	80/00 - 81/00	Lukovica	46°10'30"	14°41'00"	337
28	82/00 - 83/00	Dob	46°09'03"	14°37'45"	305
29	84/00 - 85/00	Trzin	46°08'57"	14°33'57"	298
30	86/00	Brezovica	46°02'02"	14°23'59"	424
31	87/00	Dragomer	46°01'12"	14°22'48"	301
32	89/00	Logatec	46°23'00"	13°45'00"	624
33	90/00 - 91/00	Kalce	45°53'42"	14°11'23"	494
34	96/00	Postojna	45°46'31"	14°12'51"	594
Sweden					
35	171/00 - 173/00	Farstanäs	59°05'49"	17°38'59"	21
36	174/00 - 178/00	Stockholm	59°19'57"	18°03'52"	15
37	179/00	Uppsala	59°51'29"	17°38'40"	35
38	180/00 - 182/00	Högsta	59°58'16"	17°34'12"	27
39	183/00 - 185/00	Uppsala	59°51'29"	17°38'40"	35
40	186/00 - 189/00	Stockholm	59°19'57"	18°03'52"	15
41	190/00 - 192/00	Norrköping	58°35'40"	16°11'01"	62
42	193/00 - 197/00	Linköping	58°24'06"	15°03'58"	118
43	198/00 - 200/00	Jönköping	57°46'54"	14°09'30"	158
44	203/00 - 204/00	Kristianstad	56°01'52"	14°09'17"	7
45	205/00* - 209/00	Landskrona	55°52'13"	12°49'48"	3
46	210/00 - 215/00, 217/00 – 220/00	Malmö	55°36'11"	13°00'04"	8

* 3 plants of sample 205/00 (205/00-1, 205/00-2, 205/00-3) - *L. serriola* f. *integrifolia*, all other plants in the studied set – *L. serriola* f. *serriola*

Table 2. Descriptive statistics of morphological characters of *L. serriola* achenes from Slovenia (SVN) and Sweden (SWE)

Morphological character	Parameters of *L. serriola* achenes from											
	Slovenia (SVN)						Sweden (SWE)					
	N	No. of plants	Mean	SD	min	max	*N*	No. of plants	Mean	SD	min	max
Lab	15178	304	3.06	0.26	2.12	4.01	9236	185	2.89	0.24	1.93	3.82
Wab	15178	304	1.04	0.13	0.48	1.61	9236	185	0.96	0.12	0.54	3.03
Lb	15178	304	4.20	0.53	1.73	6.52	9236	185	4.35	0.51	1.89	5.99
Lab/Wab index	15178	304	2.99	0.39	1.72	5.77	9236	185	3.04	0.39	0.97	5.19
Lbr	3040	304	5.07	0.38	3.18	6.24	1858	186	4.83	0.37	2.64	5.81
Paparea	3040	304	81.08	11.99	31.71	122.34	1858	186	73.7	10.9	21.88	105.85
Discus	3040	304	0.27	0.04	0.15	0.44	1858	186	0.27	0.04	0.15	0.41
Nr	3040	304	11.71	1.36	8.00	16.00	1858	186	11.7	1.25	7.00	16.00

Lab – length of achene body (mm), Wab – width of achene body (mm), Lb – length of beak (mm), Lab/Wab index – index length/width of achene body, Lbr – length of bristles (mm), Paparea – pappus area (mm2), Discus – diameter of discus (mm), Nr – number of ribs
N - number of *L. serriola* achenes measured
SD - standard deviation
min, max – minimum and maximum value

Table 3. Morphological characters of *L. serriola* achene bodies in 119 seed samples and 46 populations from Slovenia and Sweden as analysed by Nested ANOVA.

Morphological character	Source of variation	df	SS	F
Lab	Country	1	167.34	28.97***
	Populations within countries	44	254.14	2.27***
	Seed samples within countries	73	185.83	56.04***
Wab	Country	1	31.15	29.42***
	Populations within countries	44	46.59	3.8***
	Seed samples within countries	73	20.36	21.28***
Lb	Country	1	138.75	2.56 ns
	Populations within countries	44	2388.87	5.04***
	Seed samples within countries	73	786.58	75.61***
Lab/Wab index	Country	1	13.73	1.3 ns
	Populations within countries	44	463.52	5.43***
	Seed samples within countries	73	141.64	15.41***

Lab - length of achene body, Wab - width of achene body, Lb - length of beak,
Lab/Wab index - index length of achene body/width of achene body
df – degrees of freedom
SS – Sum of Squares
F – F-ratio
***$p < 0.05$; ns - not significant

Table 4. Morphological characters of pappus of *L. serriola* achenes in 119 seed samples and 46 populations from Slovenia and Sweden as analysed by Nested ANOVA.

Morphological character	Source of variation	df	SS	F
Lbr	Country	1	64.32	18.31***
	Populations within countries	44	154.57	2.85***
	Seed samples within countries	73	89.92	13.25***
Paparea	Country	1	62664.8	18.11***
	Populations within countries	44	152252	3.00***
	Seed samples within countries	73	84141.5	13.08***
Discus	Country	1	0	0 ns
	Populations within countries	44	0.45	2.15***
	Seed samples within countries	73	0.35	3.87***
Nr	Country	1	0.34	0.01 ns
	Populations within countries	44	1302.32	3.22***
	Seed samples within countries	73	671.89	6.75***

Lbr - length of bristles, Paparea – area of pappus, Discus - diameter of discus,
Nr - number of ribs
df – degrees of freedom, SS – Sum of Squares, F – F-ratio
***$p < 0.05$; ns - not significant

Table 5. Impact of geographical factors affecting evaluated morphological characters of *L. serriola* achene body (Lab, Wab, Lb, Lab/Wab index) and pappus (Lbr, Paparea, Discus, Nr) selected by forward selection method (RDA).

Variables	Achene body		Pappus	
	F-ratio	p	F-ratio	p
Latitude	665.66	< 0.001	240.47	0.002
Longitude	314.87	< 0.001	39.64	0.002
Altitude	150.70	< 0.001	11.22	0.002

p - probability

Figure 1a. Map of geographical distribution of *L. serriola* populations in Slovenia

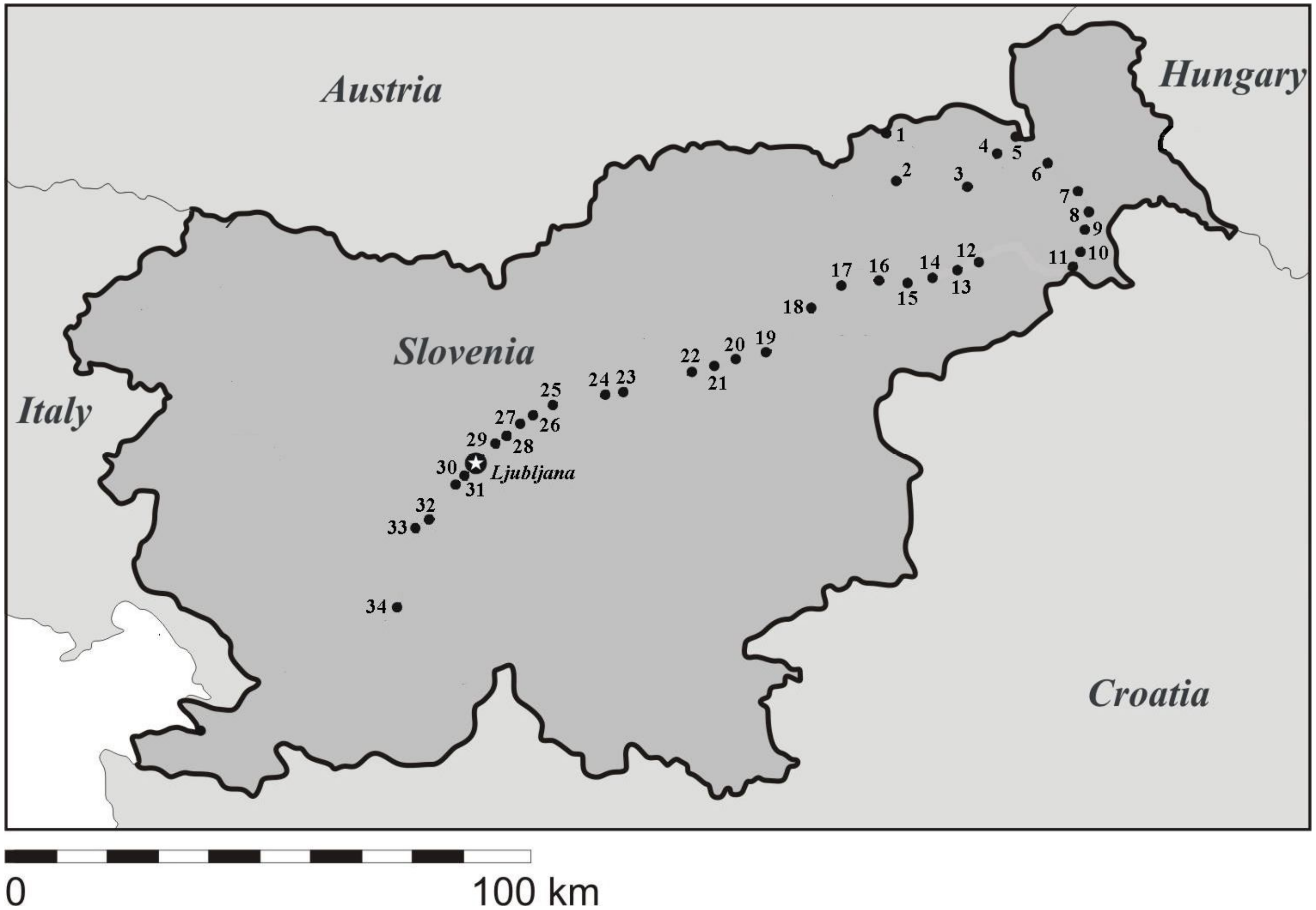


Figure 1b. Map of geographical distribution of *L. serriola* populations in Sweden

Figure 2. Morphology of achene bodies of *L. serriola* from Slovenia (SVN) and Sweden (SWE): a) length of achene body (Lab), b) width of achene body (Wab); c) length of beak (Lb); d) index of length/width of achene body (Lab/Wab index).

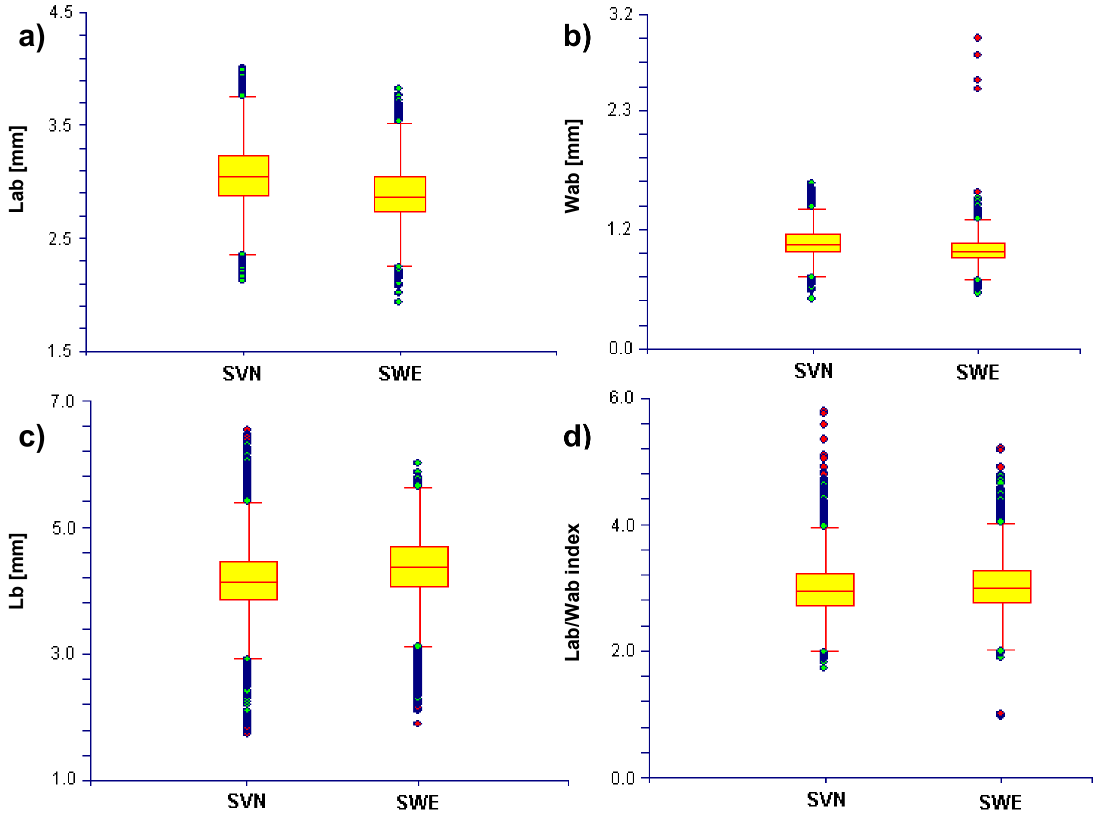


Figure 3. Morphology of pappus and achenes of *L. serriola* achenes from Slovenia (SVN) and Sweden (SWE): a) length of bristles (Lbr), b) pappus area (Paparea), c) diameter of discus (Discus), d) number of ribs (Nr).

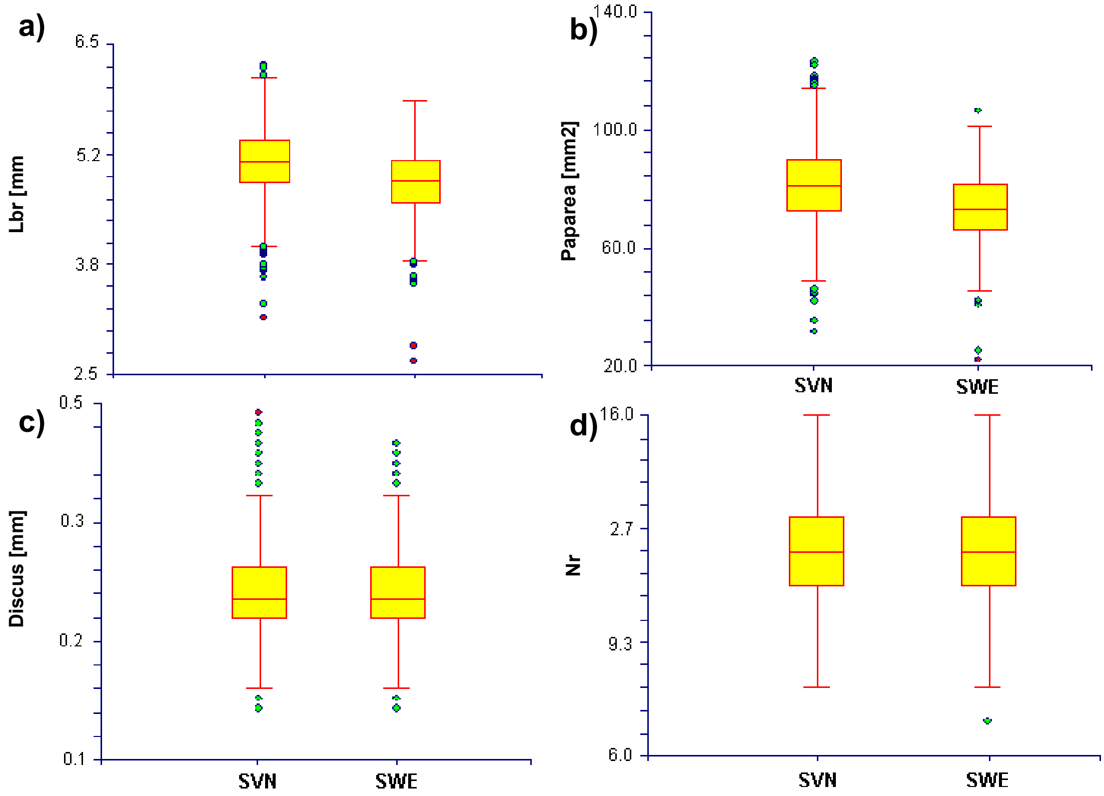


Figure 4. Correlation of morphological characters of achene body of *L. serriola* from Slovenia and Sweden with geographical factors selected by forward selection RDA. Axis 1 and Axis 2 account for 4.5% of the variability in species data.

Lab – length of achene body; *Wab* – width of achene body; *Lb* – length of beak; *Lab/Wab index* – index length/width of achene body

lat – latitude, long – longitude, alt (m) - altitude

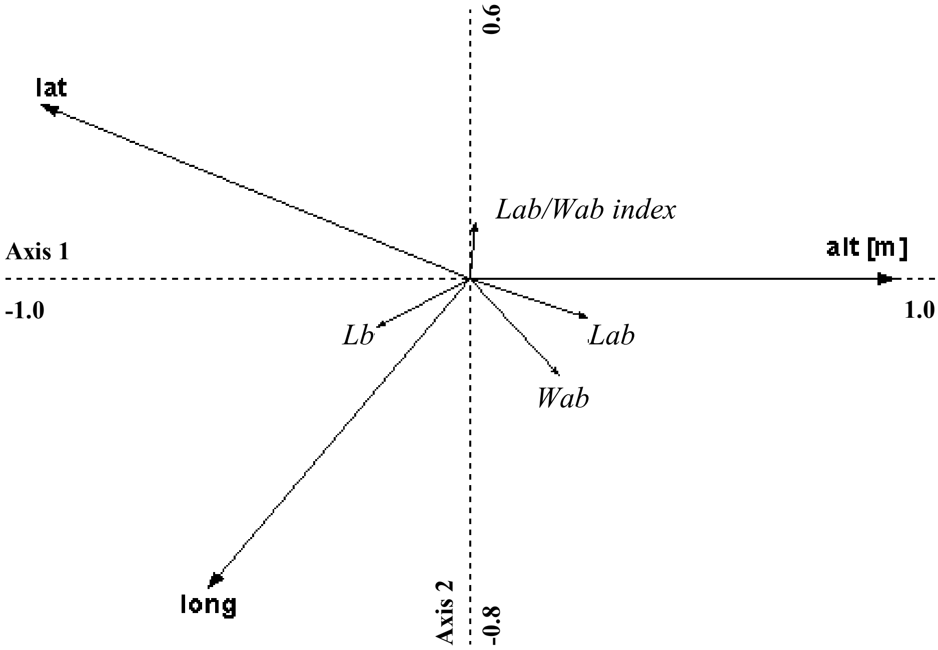
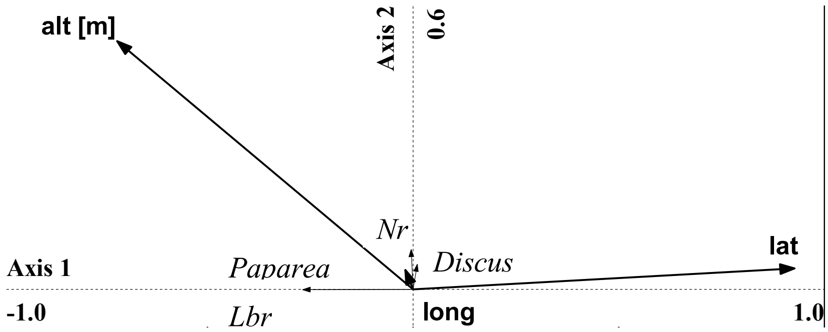


Figure 5. Correlation of morphological characters of pappus of *L. serriola* achenes from Slovenia and Sweden with geographical factors selected by forwarded selection RDA. Axis 1 and Axis 2 account for 6.6% of the variability in species data.

Lbr – length of bristles; *Paparea* – area of pappus; *Discus* – diameter of discus; *Nr* – number of ribs

lat – latitude, long – longitude, alt (m) - altitude



4.3. Morphological variability of *Lactuca serriola* leaves

Comparative study of variation of some morphological and developmental characteristics of *Lactuca serriola* germplasm collected in Central Europe (Czech Republic) and the British Isles (England, U.K.)

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Key words: biodiversity, flowering phenology, leaf morphology, prickly lettuce.

Abstract

Genetic resources of wild *Lactuca* species, including *L. serriola*, have been used in commercial lettuce breeding for more than sixty years (Lebeda *et al.*, 2004 a,b). Generally *L. serriola* is assumed to be a direct progenitor of cultivated lettuce (*L. sativa*) (de Vries, 1997). *L. serriola* has spread as an invasive weed almost throughout Europe, occurring mostly in synanthropic habitats (Lebeda *et al.*, 2001). Twenty six *L. serriola* populations (16 individuals of each) collected in Czech Republic (16 popns.) and the U.K. (10 popns.) were grown in a glasshouse under controlled conditions and morphologically characterised following the descriptor list of wild *Lactuca* germplasm (Doležalová *et al.*, 2003). The assessment included 26 quantitative and qualitative characters of stems, rosette and cauline leaves, inflorescences and flowers and an evaluation of flowering stage. Significant differences in mean stem length were found between populations collected in the Czech Republic (CZ) and the United Kingdom (UK) (1.49 m and 1.54 m, respectively). The morphology of rosette and cauline leaves including their apices, showed that only *L. serriola* f. *serriola* was recorded in the CZ (100% of plants), while 98% of plants from populations collected in the UK were determined as f. *integrifolia*. Plants from the UK possessed anthocyanin in the apex in 99.3% of individuals, but anthocyanin presence in the stripes in only 0.7% of the individuals. In the Czech populations the presence of anthocyanin was distributed in the apex in 32.14%, of plants, in stripes in 28.97%, and in the apex and spots together in 29.37%. Both corymbose (50.40%) and pyramidal panicles (49.60%) were presented more or less equally in populations from the CZ. The corymbose panicle was characteristic of the majority (71.13%) of plants collected in the UK. Intermediate flowering phenology was recorded in the majority of plants in both countries (CZ 58%; UK 64%), but 35% of plants from the CZ flowered early and 7% exhibited late flowering. *Lactuca serriola* plants from the UK exhibited early flowering in 15% of the plants and late flowering in 21% of individuals.

Acknowledgements

Lactuca serriola seed samples originating from U.K. were collected by Dr. Dave Astley (Warwick HRI, Wellesbourne, U.K.), his generous help and support is greatly acknowledged. Research was supported by project of EU GENE-MINE (Contract No. QLK5-2000-00722), and project "Variability of components and interactions in plant pathosystem and impact of environmental factors on their expression" (MŠMT Praha).

References

Doležalová I., Krístková E., Lebeda A., Vinter V., Astley D. and Boukema I.W. 2003. Basic morphological descriptors for genetic resources of wild *Lactuca* spp. Plant Genet. Resour. Newsl. 134, 1-9.

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Vries I.M. de 1997. Origin and domestication of *Lactuca sativa* L. Genet. Resour. Crop Evol. 44, 165-174.

Comparative study of variation of some morphological and developmental characteristics of *Lactuca serriola* germplasm collected in Central Europe (Czech Republic) and the British Isles (England, U.K.)

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INTRODUCTION

Genetic resources of wild *Lactuca* species, including *L. serriola*, have been used in commercial lettuce breeding for more than sixty years (Lebeda et al., 2004 a,b). Generally *L. serriola* is assumed to be a direct progenitor of cultivated lettuce (*L. sativa*) (de Vries, 1997). *L. serriola* has spread as an invasive weed almost throughout Europe and occures mostly in synanthropic habitats (Lebeda et al., 2001).

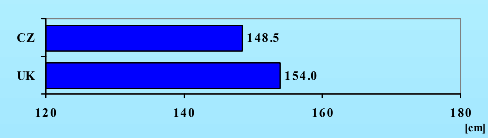
MATERIAL AND METHODS

Twenty six *L. serriola* populations (16 individuals of each) collected in Czech Republic (16 popns.) and the U.K. (10 popns.) were grown in a glasshouse under controlled conditions and morphologically characterised following the descriptor list of wild *Lactuca* germplasm (Doležalová et al., 2003). The assessment included 26 quantitative and qualitative characters of stems, rosette and cauline leaves, inflorescences and flowers and an evaluation of flowering stage.

RESULTS

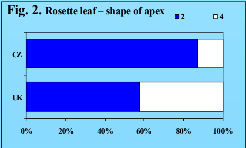
Significant differences were found in mean stem length between populations collected in the Czech Republic (CZ) and the United Kingdom (UK) (149 cm and 154 cm, respectively) (Figure 1).

Fig. 1. Mean stem lenght



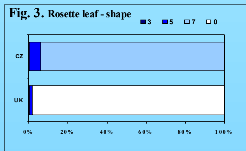
The morphology of rosette and cauline leaves including their apices, showed that only *L. serriola* f. *serriola* was recorded in the CZ (100% of plants), while 98% of plants from populations collected in the UK were determined as f. *integrifolia* (Figures 2, 3, 4, 5).

Fig. 2. Rosette leaf – shape of apex



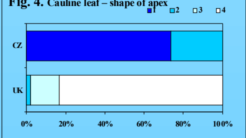
2 subacute 4 obtuse

Fig. 3. Rosette leaf - shape



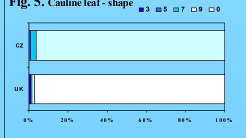
3 pinnatilobed 5 pinnatipart 7 pinnatifid 0 entire

Fig. 4. Cauline leaf – shape of apex



1 acute 2 subacute 3 rounded 4 obtuse

Fig. 5. Cauline leaf - shape

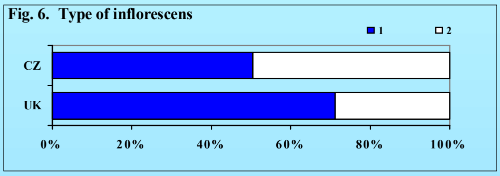


3 pinnatilobed 5 pinnatipart 7 pinnatifid

9 pinnatisect 0 entire

Both corymbose (50.40%) and pyramidal panicles (in 49.60%) were presented more or less equally in populations from the CZ. The corymbose panicle was characteristic of the majority (71.13%) of plants collected in the UK (Figure 6).

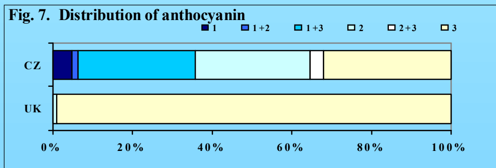
Fig. 6. Type of inflorescens



1 corymbose panicle 2 pyramidal panicle

Plants from the UK possessed anthocyanin in the apex in 99.3% of individuals, but anthocyanin presence in the stripes in only 0.7% of the individuals. In the Czech populations the presence of anthocyanin was distributed in the apex in 32.14%, of plants, in stripes in 28.97%, and in the apex and spots together in 29.37% (Figure 7).

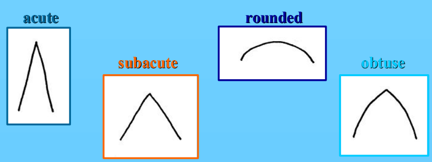
Fig. 7. Distribution of anthocyanin



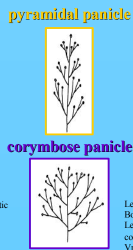
1 in spots 2 in stripes 3 in the apex

Intermediate flowering phenology was recorded in the majority of plants in both countries (CZ 58%; UK 64%), but 35% of plants from the CZ flowered early and 7% exhibited late flowering. *Lactuca serriola* plants from the UK exhibited early flowering in 15% of the plants and late flowering in 21% of individuals.

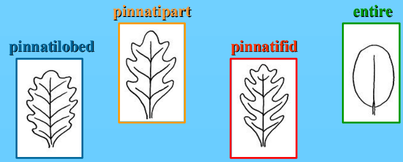
Rosette (cauline) leaf – shape of apex



Inflorescens of heads - type



Rosette (cauline) leaf – depth of incisions



REFERENCES

Doležalová I., Krístková E., Lebeda A., Vinter V., Astley D. and Boukema I.W. 2003. Basic morphological descriptors for genetic resources of wild *Lactuca* spp. Plant Genet. Resour. Newslet. 134, 1-9.

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ACKNOWLEDGEMENTS

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4.4. Distribution, ecogeography and ecobiology of germplasm accessions of wild *Lactuca* species from USA and Canada

Wild and weedy *Lactuca* species, their distribution, ecogeography and ecobiology in USA and Canada

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Abstract During 2002, 2004, 2006 and 2008, trips were undertaken in the United States and Canada by members of Department of Botany, Palacký University in Olomouc (Czech Republic) to record distribution and sample the diversity of wild and weedy *Lactuca* species. In that period, 16 states in the USA (Arizona, California, Colorado, Idaho, Iowa, Minnesota, Montana, Nevada, New York, North Carolina, Oregon, South Dakota, Utah, Washington, Wisconsin, Wyoming) and two provinces in Canada (Ontario, Quebec) were visited. Seven wild and weedy *Lactuca* species (*L. serriola*, *L. saligna*, *L. virosa*, *L. canadensis*, *L. biennis*, *L. floridana*, *L. ludoviciana*), an interspecific hybrid (*L. canadensis* × *L. ludoviciana*), and an undetermined *Lactuca* species were recorded, and 343 seed samples were collected from 200 locations. The largest number of wild *Lactuca* species that we observed was recorded in Iowa and the largest number of samples was collected in California. The most common habitats of weedy species (*L. serriola*, *L. saligna* and *L. virosa*) were along transport corridors, such as roadsides, road ditches, parking sites and petrol stations, grassy slopes and ruderal places. The most frequent species was *L. serriola*, an Old World introduction, which we observed in all states and provinces visited, except for New York, and in broad range of elevations (up to 2358 m a.s.l.). *Lactuca saligna* was recorded only one time in Salinas, California. *Lactuca virosa* was found repeatedly in Washington State along the road to the Mt. St. Helens and in Redwoods, California. Native North American taxa (*L. canadensis*, *L. floridana*, *L. ludoviciana*) were recorded only in Iowa. *Lactuca biennis* was found only in Canada in the southern part of Quebec. Records of diseases and pests showed only occasional occurrences of downy mildew (*Bremia lactucae*) and powdery mildew (*Golovinomyces cichoracearum*). Most plant-disease findings were made in Canada. Results of these efforts enrich our knowledge of the distribution, ecogeography and ecobiology of *Lactuca* species occurring spontaneously

in North America. Seed collections (accessions) will be conserved in the working collection of the genebank at Palacký University for use in future research in ecogeography, ecobiology, resistance and genetic polymorphisms, and to enrich of germplasm diversity available for lettuce breeding.

Keywords Habitats · Distribution · Disease occurrence · Downy mildew · Ecology · Geography · Lettuce · Morphological variation · Powdery mildew

Introduction

The progenitors of lettuce and its other wild and weedy relatives have become very important in lettuce breeding (Mou 2008; Lebeda et al. 2009a), serving as donors of new resistance genes against diseases, pests, and abiotic stresses, as well as of genes for improving physiological and quality traits (Lebeda and Křístková 1995; Lebeda et al. 2007b). Significant progress in the collection, characterization, and practical application of *Lactuca* germplasm has been achieved during the last 25 years (Lebeda et al. 2009a). Despite this, basic data about the biology and ecology of most *Lactuca* L. species are still lacking (Lebeda et al. 2007b). In response to this, a comprehensive research program on wild and weedy *Lactuca* taxa was initiated in the early 1990s in the Czech Republic (Lebeda et al. 1999).

In 1995, intensive missions to observe and collect wild *Lactuca* species in Europe were initiated by the Department of Botany, Palacký University in Olomouc (Czech Republic) (Lebeda et al. 1999). From 1995 to 2008, several expeditions to Europe (including 14 countries), and to the United States and Canada were undertaken by members of that institution (Lebeda et al. 2009a). In the United States, Department of Botany, Palacký University in Olomouc cooperates in this area with the USDA-ARS North Central Regional Plant Introduction Station in Ames, Iowa and the Department of Horticulture, Iowa State University. Field studies and collections were also made in Turkey, Israel, Jordan, South Korea, New Zealand and China (Beharav et al. 2008; 2009; Lebeda et al. 2009a). Recent knowledge about geographic distribution of wild *Lactuca* spp. in North America is rather limited (Funk et al. 2009; Lebeda et al. 2004b), and also genetic resources of *Lactuca* spp. from this geographic area are limited (Lebeda et al. 2004a). For these reasons, exploration missions to the United States and

Canada were conducted (mostly by A. Lebeda) in the years 2002, 2004, 2006 and 2008, to 16 states if the USA (Arizona, California, Colorado, Idaho, Iowa, Minnesota, Montana, Nevada, New York, North Carolina, Oregon, South Dakota, Utah, Washington, Wisconsin, Wyoming) and two provinces in Canada (Ontario, Quebec).
Systematic relationships and geographic distribution of the genus *Lactuca*

Following currently accepted taxonomic concepts, the genus *Lactuca* is considered as a member of the family Compositae (Asteraceae), subfamily Cichorioideae, tribe Lactuceae (recently treated as a tribe Cichorieae (Funk et al. 2009)), subtribe Lactucinae (Bremer et al. 1994) (recently treated as a subclade Lactucinae (Funk et al. 2009)). The family Compositae has a worldwide distribution (Heywood 1978) and is one of the largest families of flowering plants, including about 1,600-1,700 genera with about 30,000 species (Funk et al. 2009). According to Funk et al. (2009), Cichorieae are mainly distributed in the temperate zone of the northern hemisphere, both in the Old and New Worlds. They reported three main centers of diversity: Central to Eastern Asia; the Mediterranean Basin, including SW Asia and, to lesser extent, western North America. Some genera (e.g. *Lactuca*, *Launaea*) are found in semiarid and arid environments.

A careful search of available literature showed that the genus comprises 98 wild *Lactuca* species, mainly occurring in Asia (51), Africa (43) and Europe (17). In the New World, 12 wild and weedy *Lactuca* species can be found, with 10 of them described from North America (Lebeda et al. 2004b). This group of *Lactuca* species is classified as the North American group (Lebeda and Astley 1999) and includes species originating and distributed in North America (from Canada to Florida), as well as species which are synanthropic and cosmopolitan (*L. serriola*, *L. saligna, L. virosa*) (Steyermark 1963; Nessler 1976; Strausbaugh and Core 1978; Cronquist 1980; McGregor et al. 1986). Several *Lactuca* spp. in North America have been reported as autochthonous e.g. *L. canadensis*, *L. graminifolia*, *L. biennis*, *L. floridana*, *L. ludoviciana*, *L. hirsuta* and *L. terrae-novae* (Lebeda et al. 2004b) and *L. tatarica* subsp. *pulchella* (Hultén 1968).

A key difference between North American and European wild *Lactuca* species is their haploid chromosome number. By this character, the genus can be divided into three main groups. The first two groups include Eurasian, African, Middle Eastern and Indian species with base chromosome numbers of n=8 or n=9. The third group includes species native to North America from Canada to Florida (Lebeda and Astley 1999). This group is characterized by the consistent presence of the haploid chromosomes number, n=17 (Babcock et al. 1937). In these species, higher contents of nuclear DNA have been established in comparison with Eurasian taxa (Doležalová et al. 2002). They are of amphidiploid origin, resulting from interspecific crossing, chromosome doubling (perhaps through unreduced-gamete formation), and subsequent hybrid stabilization (or diploidization) (Feráková 1977). This third group is rather geographically and genetically isolated (Lebeda et al. 2007b). Species of this group are annual or biennial with relatively high morphological variability, particularly in terms of leaf shape (Lebeda and Astley 1999). *Lactuca canadensis*, *L. graminifolia* and *L. biennis* are the most common species from the viewpoint of their occurrence in individual states of USA. *Lactuca canadensis* occurs throughout a great part of the northeastern and northcentral USA and southern Canada in thickets, at the edges of woods and in forest clearings (Fernald 1950; Cronquist 1980; McGregor et al.1986; Hickman 1993; Kartesz 1994). *Lactuca graminifolia* is widespread in sandy fields, open woods and clearings mainly in North and South Carolina, Arizona, Texas, Florida and Mexico (Cronquist 1980). *Lactuca hirsuta* occurs in similar habitats. *Lactuca biennis* is scattered throughout the Great Plains (USA) in forest clearings, along streams and lake shores (McGregor et al. 1986). Typical habitats for *L. floridana* are along streams with rich, moist soil, and in woods (Cronquist 1980; McGregor et al. 1986). *Lactuca ludoviciana* occurs in open habitats, prairies, waste, rather moist places, low grounds, and roadsides (Cronquist 1980; McGregor et al. 1986; Hickman 1993; Lebeda and Astley 1999). *Lactuca terrae-novae* is a characteristic element of calcareous subalpine meadows of Newfoundland (Fernald 1950).

The main purposes of this study were: 1) to expand and clarify our knowledge about the distribution and eco-geography of wild *Lactuca* species in North America; 2) to collect representative seed samples of *Lactuca* populations; and 3) to establish a basic germplasm collection for future research and exploitation of North American, wild *Lactuca* species. Subsequently the paper is also focused on elucidation the knowledge about the biodiversity, geographical distribution, ecobiology and occurrence of fungal parasites on wild and weedy populations of *Lactuca* spp. throughout the United States and Canada.

Material and methods

To assess the distribution and ecogeography of wild and weedy *Lactuca* in North America, extensive parts of the United States and Canada were explored. In the United States, 16 states representing the Northeast (New York), Midwest (Wisconsin, Iowa, Minnesota, South Dakota), West (Wyoming, Montana, Idaho, Utah, Colorado, Arizona, Nevada, California, Oregon, Washington) and South (North Carolina) were surveyed (Fig. 1). Trips focused mostly heavily on the West, whereas in the South and the Northeast only two states were visited. In Canada, expeditions were made only in 2 provinces (Quebec, Ontario) (Fig. 2). Missions were undertaken between July and October in 2002 (Canada, USA), 2004 (Canada, USA), 2006 (USA) and 2008 (twice USA). Details on all missions and maps of the most important visited and collection sites are presented in Figures 1 and 2 and Table 1. In total, 343 seed samples of seven wild and weedy *Lactuca* species, along with an interspecific hybrid and some undetermined taxa were recorded and collected from 200 locations (Tables 2 and 3; detailed list of locations is available from authors). There were mostly collected one to two seed samples at each locality, only in few localities with high density of plants seeds from three to four plants were sampled. Seed samples (20-30 seeds per plant) were typically kept separate by mother plant. Only in rare cases with few seeds per plant, was material bulked together from neighboring mother plants.

Information about the seed samples, including name of collector(s), sample number, collection date, botanical name, population size, geographic and ecological characteristics of the collection site (country, state/province, type of habitat, location, latitude, longitude, elevation, soil texture), and the occurrence of downy (*Bremia lactucae* Regel) and powdery (*Golovinomyces cichoracearum* (DC.) V.P. Gelyuta) mildews were recorded. The degree of infection (DI) for *B. lactucae* was evaluated on a scale of 0 to 3 (Petrželová and Lebeda 2004), and for *G. cichoracearum* on a scale of 0 to 4 (Lebeda 1994) (Table 5). The geographical characteristics of many collection sites were obtained from the database, (http://www.geonames.org/). Additional details about the routes and collection sites are available from authors at the Department of Botany, Palacký University in Olomouc, Czech Republic.

Collected seed samples have been incorporated into the working collection of *Lactuca* germplasm in the Department of Botany, Palacký University in Olomouc, Czech Republic (http://botany.upol.cz/).

Results of the searching and collection trips

Data about the occurrence of North American *Lactuca* spp. are presented as follows. Geographic and ecological characteristics of habitats and population sizes are summarized for each taxon in individual US states and two Canadian provinces, arranged in the following order: USA (Northeast, Midwest, West and South) and Canada (Fig. 1, 2). Developmental characteristics (flowering time, time of seeds maturity) and records on occurrence of downy and powdery mildews infection are also given. Phytocenological (vegetation) characteristics are not reported herein.

United States of America

Northeast

New York

Two dry plants of an unidentified *Lactuca* species at the end of their life cycle but without obvious disease infection (Table 5) were observed near pavement at the New York Botanical Garden in Bronx (40°51‘N, 73°52‘W and 16 m a.s.l.) in the beginning of October 2006 (Table 3, 4). These plants were growing as weeds and were not a part of botanical garden collections. A single accession was collected (Fig. 1 and Table 1, 2, 3).

Midwest

Wisconsin

During August 2002, a mission to Wisconsin was realized and only *L. serriola* f. *serriola* was recorded. *Lactuca serriola* populations were observed along roadsides and near petrol stations (Table 4). Four accessions were collected from two sites (Madison and Dodgeville) (Fig. 1 and Table 1, 2, 3), located between 42°57‘and 43°04‘N, 89°24‘and 90°07‘W with elevations from 267 to 369 m a.s.l. At the collection site in Dodgeville, there was a low incidence of both downy and powdery mildews (DI=1) (Table 5).

Iowa

In Iowa, expeditions were conducted in 2002 and 2008 (Fig. 1 and Table 1). In 2002, the mission started in the east, close to Cedar Rapids and proceeded to west near Ames and Des Moines to Carroll and Denison. The 2008 trip focused on the distribution of wild *Lactuca* species in central Iowa and captured considerable species diversity with a total of four species and an interspecific hybrid (Table 2), including *L. serriola* f. *serriola* (30 accessions), *L. canadensis* L. (25 accessions), *L. floridana* (L.) Gaertn. (9 accessions), *L. ludoviciana* (Nutt.) Rieddl (4 accessions), and *L. canadensis* × *L. ludoviciana* (2 accessions). Across Iowa, 20 localities were visited between 41°36‘and 42°04‘N; 91°38‘ and 95°42‘W, with elevation from 218 to 391 m a.s.l. The most common habitats were margins and ditches along roads and ruderal places, with the exception of *L. floridana* which was found in mesic riverine forests (Table 4). Population size ranged from 10 to 50 plants of all recorded species. The occurrence of diseases was limited; only powdery mildew was recorded on *L. serriola* f. *serriola* (DI=1). Downy mildew (*B. lactucae*) was not observed (Table 5).

Minnesota

One short misssion was realized to Minneapolis in August 2008. Three sites with occurrence of *L. serriola* f. *serriola* were located in Minneapolis (Fig. 1 and Table 1, 2, 3). These sites were all near 44°59‘N; 93°16‘W and 258 m a.s.l. Plants were growing in grassy places near pavement and in cracks in asphalt near walls in the city center (Table 4). Size of populations were limited and varied between 5 to 15 plants. Infections of powdery mildew on these plants varied between DI= 1-4 (Table 5).

South Dakota

The distribution of *Lactuca* was recorded in southern South Dakota in August 2002 (Fig. 1 and Table 1). The mission started in the southeast in Sioux Falls and continued west through Chamberlain to Kyle and Wounded Knee, finishing in Hot Springs near the Wyoming border. Only *L. serriola* f. *serriola* was observed. Population sizes were not recorded in detail during this mission; however, most of the populations ranged between one to ten plants. The most common habitats were places along transport corridors, such as road margins, ditches and parking sites. Two localities were also noted at a prairie, in the vicinity of Kyle (Table 4). Infections of downy or powdery mildew were not observed (Table 5). Altogether ten samples of *L. serriola* f. *serriola* were collected from seven locations (43°08‘ and 43°49‘N, 96°42 and 103°28‘W at elevations from 448 (Hot Springs) to 1051 m a.s.l. (Sioux Falls) (Table 2, 3).

West

Wyoming

Missions in August 2002 and September 2008 visited the northern part of Wyoming, including Gillette, Buffalo, Ten Sleep, Manderson, Cody, Elk Creek, Grand Teton National Park, Alpine and Yellowstone National Park (Fig. 1 and Table 1). At 12 different sites (between 43°10‘ and 46°34‘N, 104°07‘and 111°55‘W, at elevations from 1041 m a.s.l. at Elk Creek to 2358 m a.s.l. at Yellowstone Lake) *L. serriola* f. *serriola* (15 accessions) and *L. serriola* f. *integrifolia* (2 accessions) were found. *Lactuca serriola* f. *serriola* was commonly grown along roadsides and in gravelly and ruderal places (Table 4). Interestingly, we also found one plant on a stony slope by Yellowstone Lake very close to sulfur steam. *Lactuca serriola* f. *integrifolia* was observed in a flower bed and along the road. No diseases were recorded on *L. serriola* in Wyoming (Table 5).

Montana

The expedition in 2008 started in Osburn, in northwestern Montana, continued southeast through Lozeau, Missoula, Drummond and Frontier Town, and ended in Bozeman in the southwest (Fig. 1 and Table 1). Only *L. serriola* f. *serriola* was recorded. From six sites, between 45°43‘ and 47°30‘N; 111°04‘ and 115°59‘W at elevations of 768 (Osburn) to 1921 m a.s.l. (Frontier Town), ten seed samples were collected (Table 2, 3). The most common habitats of this taxon were grassy slopes, parking areas of petrol stations, and the margin of pavement (Table 4). The number of plants in populations varied from one to nearly 100. The occurrence of powdery mildew (DI=2) was observed only in one population near Missoula (Table 5).

Idaho

Bonneville County (Idaho Falls) and Bannock County (Downey) in southeastern Idaho were visited and searched repeatedly during 2002 and 2008 (Fig. 1 and Table 1); only *L. serriola* was recorded. The distribution of *L. serriola* populations was recorded from 1434 to 1483 m a.s.l., bounded by the following geographical coordinates: 42°21‘ and 43°37‘N; 111°41‘ and 112°14‘W. Many *L. serriola* populations were found in gravelly and stony places along roads (38%) or in grassy and ruderal communities (25%) (Table 4). In total, eight *L. serriola* f. *serriola* seed samples from four locations were collected (Table 2, 3). The size of populations, recorded only during the 2008 mission, was extremely variable and ranging from ca 20 plants (in Downey) to more than 1000 dry plants close to Idaho Falls. Powdery mildew was recorded in two locations in 2008. The population in Idaho Falls has serious infection (DI=3), and, conversely, the population in Downey expressed a very low degree of infection (DI=1) (Table 5).

Utah

Utah was visited repeteadly in August 2002, in September 2006 and 2008 (Table 1). The distribution of *Lactuca* was studied mostly in the southern part, but some observations and seed collections were realized in northern and central Utah (Fig. 1). Only *L. serriola* f. *serriola* was recorded. Observation and collection sites were situated between 37°06‘ and 42°01‘N, 109°21‘ and 113°35‘W, at 823 (Saint George) to 2155 m a.s.l. (Monticello). In total, 29 seed samples of *L. serriola* f. *serriola* were collected from 25 locations (Table 2, 3). Some places, e.g. Moab, Monticello, Orderville and Spring Dale, were visited repeatedly (Table 1). Two accessions were bulked population samples. In Utah, the populations of *L. serriola* were rather rare, and they were mostly observed in ruderal and grassy places, along roads and pavement and near walls. Two accessions were also collected from fields and gravelly habitats (Table 4). The sizes of populations observed in 2006 and 2008 varied from one individual to more than 100 plants. Generally, these plants were dry; only in Zion National Park were green and flowering plants recorded. Powdery mildew infection was seldom recorded; during 2002 and 2006 missions, it was observed at one site in the center of Monticello (DI=3, 1, respectively) (Table 5).

Colorado

Southwestern Colorado was visited in the end of September during 2008, including Dove Creek, Yellow Jacket, Mesa Verde National Park, Cortez and Towaoc (Fig. 1 and Table 1). Only populations of *L. serriola* were observed at elevations ranging from 1802 (Towaoc) to 2325 m a.s.l. (Mesa Verde National Park, Visitor Center) between the coordinates 37°07‘ and 37°49‘N; 108‘29‘ and 109°03‘W. Seven seed samples of *L. serriola* f. *serriola* from 4 locations and one of *L. serriola* f. *integrifolia* (Table 2, 3) were collected. Most records of *L. serriola* were along pavement and in grassy places (Table 4), and the size of populations varied from five to 30 plants. No infections of downy or powdery mildew or any other diseases were recorded (Table 5).

Arizona

Missions were undertaken in the end of August 2002, and in the end of September 2006 and 2008 (Fig. 1 and Table 1), resulting in the recording and acquisition of eleven *L. serriola* f. *serriola* seed samples and one *L. serriola* f. *integrifolia* sample from ten locations (Table 2, 3). In general, only *L. serriola* was recorded in Arizona. No other *Lactuca* species were observed. The plants were located in an area bounded by 35°11‘ and 36°08‘N, 111°14‘and 114°71‘W with elevations between 1019 (Kingman) and 2279 m a.s.l. (Grand Canyon National Park). Most observations of single plants or larger populations were recorded in habitats influenced by man. Populations of *L. serriola* f. *serriola* were observed mostly in parking sites, petrol stations and ruderal places (27%), and other common habitats were grassy slopes and pavements (18%) and roadsides (~ 9%). *Lactuca serriola* f. *integrifolia* plants were only found near pavement (Table 4). The size of populations varied from one to 70 plants. Desert areas were free of *L. serriola*. In the majority of populations, the plants, at the time of observation, were at the seed stage of their reproduction cycle although three plants in the vicinity of Grand Canyon National Park had completely senesced. In 2002, four seed samples of *L. serriola* f. *serriola* were obtained from three locations in the northern and western part of the state (near Tuba City, Williams and Kingman). In 2006, collections were again made near Tuba City and Williams, with two seed samples of *L. serriola* f. *serriola* collected. The most recent mission (2008) visited Grand Canyon National Park and the surroundings of Kingman. On that trip, five accessions of *L. serriola* f. *serriola* and one of f. *integrifolia* were collected from five locations. In Arizona, the occurrence of downy or powdery mildew was not recorded (Table 5).

Nevada

Expeditions in Nevada took place in the end of August 2002, in the middle of October 2004, and in the end of September 2006 and 2008 (Fig. 1 and Table 1). *Lactuca serriola* f. *serriola* was the only taxon recorded and was extremely rare. Only in Las Vegas (36°10‘N, 115°08‘W and 610 m a.s.l.) and Mesquite (36°48‘N, 114°04‘W and 486 m a.s.l.), were individual plants observed (Table 2, 3). In Las Vegas, a population of five plants was recorded in a bed with palms; in Mesquite, a lone plant was growing in a ruderal place (Table 4). Powdery mildew infection (DI=3) was recorded in Las Vegas (Table 5).

California

Our most extensive survey of the distribution and ecogeography of wild and weedy *Lactuca* was conducted in California. The most frequent species was *L. serriola*. In total, 72 seed samples of three weedy *Lactuca* spp. (*L. serriola*, *L. saligna*, *L. virosa* and *L. floridana*) (Table 2). One accession of *L. serriola* f. *serriola* was a bulk made from five mother plants. Fifty locations with occurrence *Lactuca* spp. were visited (Table 3), distribution was recorded at elevations ranging from 11(Santa Cruz) to 1902 (Lake Tahoe) m a.s.l. in the area between 35°38‘ and 41°46‘N; 118°24‘ and 124°12‘W. The expeditions took place in all four years of this study, between August and October (Fig. 1 and Table 1). In 2002, the mission passed through the central part of California, from the east (Sequoia National Park) to the Pacific coast (Salinas). On this trip, twelve samples of *L. serriola* f. *serriola* were collected at nine locations, and. *L. serriola* f. *integrifolia* was found at two locations (Exeter and Fresno).

In 2004, the mission started in El Dorado Hills, in the Sacramento River valley and continued northeast to Lake Tahoe via Coalinga, Lemoore and Visalia, then to the southeast to Yosemite Forks, and, finally, along the northwest coast through Redwood National Park and Crescent City and back to central California at Calistoga. Twenty-seven seed samples of *L. serriola* f. *serriola*, *L. serriola* f. *integrifolia* and *L. virosa*, along with one sample of *L. floridana* were collected at 16 locations. One plant of *L. floridana* occurred together with *L. serriola* f. *serriola* at El Dorado Hills (near road US 50, ca 3 miles before Silver Fork, 1190 m a.s.l.). *Lactuca virosa* was also found only in one location at Redwood National Park, along the northwest coast.

During the 2006 mission, the central part of California was again visited, starting in Salinas on the Pacific coast. It continued east towards Yosemite National Park in the Sierra Nevada and then returned to Salinas. *Lactuca saligna* was found in two locations in Salinas, *L. serriola* f. *integrifolia* once in Santa Cruz, and *L. serriola* f. *serriola* at 8 sites.

The most recent mission in 2008 headed from Herlong Junction and Susanville in norteastern California to Mt. Shasta in the north and then to the southeast to Yosemite National Park, continuing to the west to San Juan Bautista. On this occassion, only *L. serriola* f. *serriola* (14 seed samples) was recorded at 12 locations.

In California, most common distribution of *L. serriola* was recorded along roads, near pavement, parking sites, walls or petrol stations, or in ruderal communities, field margins, grassy places, or road ditches. *Lactuca saligna* was observed at the margins of the fields and in ruderal places and is very rare in California. *L. virosa* was recorded only in one locality collected in pavement close to roadways in Redwoods. One an unidentified *Lactuca* was recorded in a more or less natural habitat close to the Silver Fork American River in El Dorado Hills (Table 4). Populations of *L. serriola* were composed up of one to nearly 100 plants. At the time of observation the plants were mostly dry and at the end of their life cycle. Only at Calistoga and Salinas were young green plants of *L. serriola* found. Two young green plants of *L. virosa* in flower were observed at a site in Redwood National Park at the end of October, 2004. Infection of downy mildew was recorded from only two locations. One of them was found on *L. serriola* f. *integrifolia* in Fresno with DI=3 during 2002. The second record (with DI=3) was on *L. serriola* f. *serriola* in Squaw Valley during 2008. Powdery mildew was not observed on any location with occurrence of *Lactuca* spp. (Table 5).

Oregon

Collection missions in Oregon were conducted in October 2004 and September 2008 (Table 1), with a focus on the western and southwestern parts of the state (Fig. 1). Only populations of *L. serriola* (both forms, i.e. f. *integrifolia* and f. *serriola*) were recorded. Observation and collection sites were situated between 42° and 46°11‘N, 121°47‘ and 123°50‘W with elevations from 7 m a.s.l. at Astoria to 1252 m a.s.l. at Klamath Falls. Typical habitats of *L. serriola* included roadway and pavement margins, ruderal places, gravelly and stony places, petrol stations, parking lots, and disturbed areas near walls (Table 4). The number of mostly dry plants in observed populations varied from one to nearly 100. Altogether we collected seven samples of *L. serriola* f. *serriola* from five locations and five samples of *L. serriola* f. *integrifolia* from four locations (Table 2, 3). The occurrence of powdery mildew was recorded during both missions at two locations (Medford and Salem), where the host plants were *L. serriola* f. *serriola* (DI=2 and 3, respectively) (Table 5).

Washington

Expeditions were conducted in October 2004 and September 2008 (Table 1). During the first mission, Longview and Hoffstadt Creek Park were visited, and the second expedition began in Spirit Lake, continued to Hoffstadt Creek Park, and then to Ethel, Tieton Dam, and Rimrock northeast to Spokane (Fig. 1). Occurrence of *L. serriola*, *L. virosa* and an unidentified *Lactuca* spp. was recorded, resulting in total of 19 samples collected from 12 sites (46°08‘to 47°39‘N and 117°29‘ to 122°56‘W, ranging from 6 (Longview) to 1050 m a.s.l. (Spirit Lake) (Table 2, 3). Frequent *L. serriola* f. *serriola* populations were seen along the pavement and road margins and in grassy places and stony slopes. *Lactuca serriola* f. *integrifolia* occurred mainly in ruderal habitats. *Lactuca virosa* populations were recorded only along the Road No. 504 to Mt. St. Helens (Hoffstadt, above Hoffstad Bridge) on stony rubble below a road. Three plants of an undetermined *Lactuca* grew in a grassy habitat (Spokane) (Table 4). Population size of both species generally varied between one and ten plants, but there were more than 30 plants of *L. virosa* above Hoffstadt Bridge in 2004 and more than 500 plants of *L. serriola* at the Ryegrass Rest Area in 2008. *Lactuca serriola* plants were typically dry, while *L. virosa* plants were in rosette stage, bolting, in flower and seed maturity. In 2004, downy mildew (DI=2) was recorded on *L. serriola* f. *serriola* in Hoffstadt, Bluffus (Table 5).

South

North Carolina

In September 2006, during an expedition to North Carolina in the vicinity of Asheville (near 35°36‘N, 82°33‘W and 650 m a.s.l.) (Fig. 1 and Table 1, 2, 3) only *L. serriola* was recorded. However, twelve seed samples of an undetermined *Lactuca* species were collected at four locations. In each location, only a single plant was observed, growing mostly on grassy slopes but one plant was found on a forested slope (Table 4). At the North Carolina Arboretum on the Blue Ridge Parkway, at Mount Pisgah, we observed *L. serriola* plants in flower with some mature seeds. In the center of Asheville, *L. serriola* plants were dry at the end of their life cycle. All recorded plants were free of diseases (Table 5).

Canada

Quebec

In August 2004, our mission focused on the southern part of Quebec including Montreal city and Montérégie (Sainte-Clotilde-de-Châteauguay and Saint-Patrice-de-Sherrington). The genus *Lactuca* was represented by *L. serriola* (f. *serriola* and f. *integrifolia*) and *L. biennis* (Moench) Fern. Altogether 43 seed samples were collected between 45°09‘ and 45°31‘N, 73°39‘ and 73°41‘W, from 48 to 61 m a.s.l. Four of these samples were mixtures of both *L. serriola* forms. *Lactuca serriola* was mostly recorded in grassy and ruderal places, along house walls and in parking lots (Table 4). Of all the locations we visited in North America, Quebec had the most plants infected with powdery mildew (*G. cichoracearum*). In Montreal city, powdery mildew was observed in 24 locations involving both *L. serriola* f. *serriola* and f. *integrifolia*. Populations of *L. serriola* f. *integrifolia* had either low (DI=1) or high (DI=4) levels of infection, whereas in *L. serriola* f. *serriola*, populations displayed various infection levels (DI=1-4). In Sainte-Clotilde-de-Châteauguay, powdery mildew was recorded in two locations on *L. serriola* f. *serriola* (DI=1). In Saint-Patrice-de-Sherrington, there were two collecting sites with powdery mildew on *L. serriola* f. *serriola* (in one, it was also found on f. *integrifolia*) with DI=1-3. Moreover, downy mildew (DI=1) on *L. serriola* plants infected by powdery mildew was recorded in both Sainte-Clotilde-de-Châteauguay and Saint-Patrice-de-Sherrington. In Saint-Patrice-de-Sherrington we also noted natural infections of downy mildew on *L. biennis* (DI=3) (Table 5).

Ontario

In August 2002, six seed samples of *L. serriola* f. *serriola* were collected at 4 locations around Toronto (43°42‘N, 79°25‘W, 173 m a.s.l.). One seed sample was a mixture of *L. serriola* f. *serriola* and *L. serriola* f. *integrifolia*. Populations of *L. serriola* were observed near pavements, and curbs, along roadsides, and in ruderal places (Table 4). A high level of infection with powdery mildew (DI=3) was identified on *L. serriola* f. *serriola* at two sites (Table 5).

Discussion

Old World Weedy *Lactuca* spp.

Lactuca serriola

Lactuca serriola (prickly lettuce, compass plant) is annual, winter annual or biennial species (Nessler 1976; Feráková 1977; Strausbaugh and Core 1978; McGregor et al. 1986; Lebeda and Astley 1999). It is the most variable and widely distributed species of the genus *Lactuca* (Feráková 1977; Lebeda et al. 2004b, 2009a,b). Within *L. serriola*, two main botanical forms are recognized based on leaf shape. *Lactuca serriola* f. *serriola* is characterized by pinnately-lobed leaves and *L. serriola* f. *integrifolia* with entire rosette and cauline leaves (Prince and Carter 1977; Carter and Prince 1982).

Lactuca serriola is a temperate, western Eurasian species (Lebeda et al. 2004b). According to Clapham et al. (1962), it is „probably native" to England. In last decades it has spred throughout Europe as an invasive weed occupying ruderal places (Frietema de Vries et al. 1994; D'Andrea et al. 2009). Hooftman et al. (2006) reported that within Europe, native species may also become invasive, and concluded that *L. serriola* has broadened its ecological amplitude. *L. serriola* is also native to North Africa (Feráková 1977). It was introduced to North America where it became established as a weed (Feráková 1977; Alexander et al. 2009a,b). It is now widely distributed and abundant throughout much of the United States and Canada (Gleason and Cronquist 1963; Radford et al. 1968; Nessler 1976; Strausbaugh and Core 1978; Cronquist 1980; McGregor et al. 1986; Hickman 1993; Kartesz 1994). Nevertheless, detailed information about its distribution in many parts of USA is still fragmentary (Lebeda et al. 2004b). Our recent study represents contribution to this topic.

During our North American missions in the period 2002-2008, *L. serriola* was the most commonly recorded species. Its presence was confirmed in all visited states and provinces, except for New York. However, *L. serriola* has also been reported from that state (http://plants.usda.gov/java/county?state_name=New%20York&statefips=36&symbol=LASE). Untill now, most records of *L. serriola* in USA and Canada have not distinguished collections at the level of botanical form. Our recent observations showed that *Lactuca seriola* f. *integrifolia* was less frequent that was f. *serriola*, which supports the assertion of Hegi (1987), who considered f. *integrifolia* to be generally rare. A survey of wild *Lactuca* species in Europe also reported that f. *integrifolia* is marginal (Lebeda et al. 2001), except in the British Isles where it is the common form (Prince and Carter 1977; Lebeda et al. 2001, 2007a). In the present study, it was mainly observed in California, Oregon and Quebec. This is for the first time when geographic distribution of both *L. serriola* forms was recorded on North American continent (see Lebeda et al. 2004b). Whereas, in Flora of Missouri are treated both forms, under the names *Lactuca scarriola* f. *scarriola* and *L. scarriola* f. *integrifolia* (Steyermark 1963).

Consistent with its status as a weed in North America (Radford et al. 1968; Nessler 1976, Strausbaugh and Core 1978; Cronquist 1980; McGregor et al. 1986; Hickman 1993; Weaver and Downs 2003), in our recent study *L. serriola* was most frequently found in disturbed habitats including the margins of roads and pavement, at parking sites and around petrol stations, in road ditches and ruderal places with fertile soil. This suggests that *L. serriola* is spreading with human activities, namely with transport (Lebeda et al. 2001, 2004b, 2007a). Notably, the presence of *L. serriola* in field margins with rich soil was also reported from Great Britain and Central Europe (Lebeda et al. 2007a). In Sweden the majority of populations were noted a significant components of ruderal plant associations (Doležalová et al. 2001), what is in accordance with Frietema de Vries et al. (1994). A similar situation was observed in the Netherlands, where 62.5% of *L. serriola* populations were found in ruderal habitats (Lebeda et al. 2007a). Hooftman et al. (2005) reported that *L. serriola* currently ocupies at least 60% of the Netherlands and it is found in a wider range of plant communities at less continental and more humid habitats. During a study of the ecogeographical distribution of *L. serriola* in Slovenia, Doležalová et al. (2001) observed that about 16% of populations were growing in wet environments, e.g. wet grounds, ditches and drains. This contrasts with *L. serriola* populations in Sweden, where they were mostly found on gravel or among stones in dry, sunny exposures (Doležalová et al. 2001). Feráková (1977) mentioned that *L. serriola* prefers open habitats, such as screes, quarries and ruins, where it appears to be a pioneer plant. These habitat observations from the Old World are confirmed by our recent observations.

In Canada it occupies a variety of disturbed sites, and is becoming an increasing problem in crops grown with reduced tillage (Weaver and Downs 2003; Weaver et al. 2006). However, during our missions in North America, *L. serriola* was also found in some unusual habitats, with very demanding ecological conditions, such as asphalt cracks and along house walls in highly urbanized areas, such as Minneapolis, extreme desert conditions in Utah and Arizona, and stony slopes close to sulfur steam at Yellowstone National Park. These findings confirmed a broad ecological amplitude and plasticity of *L. serriola* and its high potential for adaptation under extreme conditions. This is also supported by recent conclusions of D'Andrea et al. (2009) regarding the spread of European populations of *L. serriola*. The similar conclusions were made by Alexander et al. (2009a) based on investigations of the distribution of *L. serriola* along the mountain roads in both their native (Valais, southern Swiss Alps) and introduced (Wallowa Mountains, northeastern Oregon, USA) ranges.

From an orographic viewpoint, *L. serriola* was recorded from 6 m a.s.l. (Longview, Washington) all the way up to 2325 (Mesa Verde National Park, Colorado) and 2358 m a.s.l. (Yellowstone Lake, Wyoming). Hickman (1993) reported *L. serriola* usually occurs up to 2000 m a.s.l. in California. According to Meusel and Jäger (1992), the northern boundary of *L. serriola* is limited by cool summers, which may result in significantly lower limits to its upper elevations in Europe. For example, Feráková (1977) noted that its optimal elevation range in Europe is between 200 and 600 m a.s.l., which was confirmed by Lebeda et al. (2001, 2007a) and Doležalová et al. (2001). Nevertheless, Lebeda et al. (2001) did find sporadic occurrence of *L. serriola* f. *serriola* at elevations of 1050 m a.s.l. in Switzerland and 1613 m a.s.l. in Italy. There the plants were significantly reduced in growth at the flowering stage, without well-developed seeds. From the results of our study in North America, there is some evidence for elevational differentiation between the two botanical forms of *L. serriola*. *Lactuca serriola* f. *serriola* was recorded more often from higher elevations, whereas f. *integrifolia* was common mostly in lower sites, the highest being at Chinquapin, California at 1830 m a.s.l. At that site, there was population of about 25 plants. Recently, Alexander et al. (2009a) suggested that changing climatic conditions along environmental gradients within the niche (i.e. the altitudinal range) are likely to pose only transitory and limited constraints to the spread of alien plants into high mountain areas. Our data about altitudinal distribution of *L. serriola* in USA showed great ecological amplitude of this species (higher than in Europe, see Lebeda et al. 2001). It was hypothetised by Alexander et al. (2009a) that the greater ecological amplitude of *L. serriola* in the introduced range raises the intriguing possibility that novel evolution may enable introduced populations to invade environments outside the niche in the native range.

Our observations showed that *L. serriola* was typically free of diseases (ca 90% of observed individuals and/or populations). When diseases were recorded, most records were made on *L. serriola* f. *serriola* which was the most common host species of downy mildew (*Bremia lactucae*) and, more frequently, powdery (*Golovinomyces cichoracearum*) mildew. This is in agreement with our observations in Europe (Czech Republic) where *G. cichoracearum* infection became more frequent in the warmer and drier summer months (July-September) (Mieslerová et al. 2007). These findings also showed that both pathogens can occurr together within the same population of *L. serriola* (Mieslerová et al. 2007). This phenomenon was also observed during our study expedition in Quebec (Canada) where both patogens were recorded on *L. serriola* plants. Downy mildew was found only in Wisconsin (USA) and Quebec (Canada). These records are one a few reports about *B. lactucae* naturaly infected *L. serriola* plants in North America (Lebeda et al. 2002). A low frequency of downy mildew infections was recorded during similar missions in some European countries (Lebeda et al. 2001, 2007a; Doležalová et al. 2001), where it was found in relatively high frequency in the Czech Republic (Lebeda et al. 2001, 2007a, 2008a). However, there were recorded significant differences in distribution and infection intensity of *B. lactucae* between different areas and habitats (Lebeda et al. 2008a; Petrželová and Lebeda 2004).

Our North American observations supported a general phenomenon, that *L. serriola* has spread rapidly not only northwards in Europe but also throught the North American continent. Climate changes and anthropogenic disturbance have contributed to the expanding of ruderal species, including *L. serriola*, outside their current distribution area (D'Andrea et al. 2009). Extension of *L. serriola* ecological amplitude (less continental and more humid) recorded by Hooftman et al. (2006) in the Netherlands is in accordance with our recent observations in the USA e.g. more humid grassy places and ditches in Minessota, Idaho, Montana, Utah and Colorado. Our current studies are focused on genetic polymorphism of North American *L. serriola* populations (Kitner et al. 2009) from the viewpoint of understanding their biogeographical structure and possible territorial expansion, analogous to our earlier research in Europe (Lebeda et al. 2009b).

Lactuca saligna

Lactuca saligna (willow-leaved lettuce) is a Eurasian species (Feráková 1977), widely distributed throughout the Mediterranean Basin (Beharav et al. 2008), extending to the Caucasus and parts of temperate Europe (Lebeda et al. 2004b). It was likely introduced to North America from Europe. As an adventive plant, it was reported in the northeastern part of the United States and Canada (Feráková 1977). In the first half of 20th Century, additional localities were reported around San Francisco Bay (Stebbins 1939) and from Colorado to Oregon (Cronquist 1955). During our expeditions, *L. saligna* var. *saligna* was recorded only one time at abandoned, small garden in Salinas (California), confirming the continued occurrence of this taxon in California (Stebbins 1939; Hickman 1993). It is evident that this species is very rare not only in California, but across the USA in contrast to the Mediterranean Basin or Middle East (Beharav et al. 2008; Lebeda et al. 2001, 2004b).

According to Feráková (1977), *L. saligna* prefers warm, fertile, semi-arid and slightly salty soils. Some, mostly historical, records from central Europe report this taxon from subhalophilic meadows (Lebeda et al. 2004b). Its most common habitats are waste and disturbed places, and borders of wooded areas, arable fields and river banks (Feráková 1977; McGregor et al. 1986; Hickman 1993; Lebeda et al. 2001, 2004b; Beharav et al., 2008). It can also be found quite often along railways and roadsides (Feráková 1977). From our recent survey in USA, we cannot draw any general conclusions, because of its rarity.

Lactuca saligna has a broad elevational range in Europe. In Italy, it can be found up to 1000 m a.s.l., in Cyprus up to 1680 m a.s.l., and in Turkey up to 2400 m a.s.l. (Hegi 1987; Meusel and Jäger 1992). Nevertheless, in Europe it is most frequently found between 0 and 300 m a.s.l. (Lebeda et al. 2001). The single site we recorded in California was located at 16 m a.s.l.

Lactuca virosa

Lactuca virosa (wild lettuce, bitter lettuce, opium lettuce) is native to Europe, mostly in the Mediterranean Basin (Mejías 1993, 1994). It was introduced as a medicinal plant into several European countries and also into North America, where it became naturalized (Feráková 1977). According to Stebbins (1939), it was found in the vicinity of Berkeley, California, in rocky crevices together with *L. serriola*. Hickman (1993) confirmed its occurrence in California, and according USDA PLANTS database is also known from Alabama and the District of Columbia. Our recent survey confirmed its continued and very rare presence in California (only one record in Redwoods). The only other observation of this species during our expeditions was made above Hoffstadt Bridge (780 m a.s.l.), under Forest Learning Centre, along the Road 504 to Volcano Mt. St. Helens, in the southern part of Washington. There, populations of about 30 plants were recorded repeteadly in 2004 and 2008 in stony rubble.

According to Hickman (1993) and Lebeda and Astley (1999), typical habitats for *L. virosa* include disturbed, shrubby and wooded slopes, ruderal habitats, roadsides and embankments. As for its natural habitats in Europe, sand dunes on rocks on seashores, screes, and clearing in woodlands are optimal (Feráková 1977). In the northwestern part of its native distribution range in eastern England, it can be found on limestone (Meusel and Jäger 1992). Lebeda et al. (2001, 2007a) noted that its occurrence was quite rare based on experiences from European field surveys.

From an orographic perspective, *L. virosa* is a thermophilous species distributed from lowland to submontane regions (Feráková 1977). Some records from higher elevations, such as 1560 m a.s.l. in Switzerland or 2300 m a.s.l. in Morocco, are perhaps exceptional (Feráková 1977; Hegi 1987; Meusel and Jäger 1992). In California, its occurrence was reported by Hickman (1993) at elevations ca 760 m a.s.l., which is consistent with our recent observations made in Redwoods National Park (California) where were recorded two flowering plants in wet pavement of road CA 128 between Navaro Head and Navaro Redwood (ca 450 m a.s.l.). Those plants were green and flowering at the end of October, near the end of a typical growing season. No incidence of disease on *L. virosa* was noted on our North American explorations. Because of two repeated records (2004 and 2008) in the same area, it seems that the population of *L. virosa* along the Road 504 near Hoffstadt Bridge is well established and expanding what is demonstrated by record (in 2008) of dense population of *L. virosa* at stony pavement above Castlelae viewpoint at an elevation 1050 m a.s.l.

North American Native Taxa

Lactuca canadensis

Annual or biennial *L. canadensis* (wild lettuce, Canada lettuce, horse-weed, devil weed) is considered as one of the most common, native *Lactuca* species in North America (Strausbaugh and Core 1978; Cronquist 1980; Lebeda and Astley 1999). It is a native plant throughout most of the northeastern and northcentral part of the United States and in the southern part of Canada (Lebeda and Astley 1999; Lebeda et al. 2007b). Cronquist (1980) and McGregor et al. (1986) also noted the southern extent of its range as extending from northern Florida to the eastern part of Texas. Hickman (1993) stated that it had also been recorded from northern California. Our records of *L. canadensis* were limited only to Iowa, where 12 locations were found. At those locations, we collected 25 seed samples of this species along with two from putative hybrids between *L. canadensis* and *L. ludoviciana*, in the presence of the parental taxa along a roadside.

Lactuca canadensis is typically found at the edges of woods, along roadsides, and in forest clearings and thickets, fields, waste and moist open places, and pastures (Radford et al. 1968; Strausbaugh and Core 1978; Cronquist 1980; McGregor et al. 1986; Hickman 1993; Lebeda et al. 2007b). In Iowa, *L. canadensis* plants were widely distributed along transport corridors, such as roadsides and ditches, and also in ruderal places where, generally, single plants were found. Populations were observed in Iowa at elevations from 281 (Ames) to 336 m a.s.l. (vicinity of Ames and Ledges Park).

However, in California, this species can be found at elevations up to 1050 m a.s.l. (Hickman 1993). Nevertheless, during our missions this species was not recorded in California. We recorded no diseases on this species.

Lactuca floridana

Lactuca floridana (woodland lettuce, Florida lettuce, Florida blue lettuce) is an annual or biennial species (Cronquist 1980; McGregor et al. 1986; Lebeda and Astley 1999) native to the eastern part of the United States, from Maine south to central Florida and Puerto Rico (Liogier 1997), and west to the eastern part of Great Plains, including Minnesota, Kansas and Texas (Cronquist 1980; Liogier 1997; McGregor et al. 1986). During our expeditions, *L. floridana* was recorded only on a limited scale in Ames (Iowa) with nine seed samples collected at Brookside Park along the banks of Squaw Creek (274 – 282 m a.s.l.). Other observations were made near the Des Moines River in Boone County. One plant of *L. floridana* was also recorded at Eldorado Hills (ca 3 miles before Silver Fork) in California at stony and sandy backround at an elevation 1190 m a.s.l. This is very surprising and probably the first record of this species in western coast of USA (http://plants.usda.gov/java/ profile?symbol=LAFLF). Habitats in woods, along streams with rich, moist soil, are typical for *L. floridana* (Cronquist 1980; Liogier 1997; McGregor et al. 1986). We observed this species in September at the full-flowering stage at the start of seed formation, and we recorded no incidence of plant diseases.

Lactuca ludoviciana

Lactuca ludoviciana (western wild lettuce) is a biennial or possibly short-lived perennial plant (Cronquist 1980; McGregor et al. 1986; Hickman 1993) native to the prairies and plains of central part of the United States and adjacent areas in Canada (Cronquist 1980; Hickman 1993). Its presence extends southeast to Arkansas and Louisiana, and casually it has spread elsewhere (Cronquist 1980). Current expeditions showed that this species was recorded only from Iowa, where four seed samples were collected along a roadside west of Ames (near Ledges Park), at an elevation of 326 m a.s.l. Generally it is found in open habitats, prairies, waste, rather moist places, low grounds, and roadsides (Cronquist 1980; McGregor et al. 1986; Hickman 1993; Lebeda and Astley 1999). Hickman (1993) noted that *L. ludoviciana* is found in California at elevations below 300 m a.s.l., however during our missions we have never recorded this species in California. No incidence of downy and powdery mildew was observed on population of this species in Iowa.

Lactuca biennis

Lactuca biennis (blue wood lettuce, tall blue lettuce) is an annual or biennial plant, common in northern parts of North America (Strausbaugh and Core 1978; Cronquist 1980; Lebeda and Astley 1999; Lebeda et al. 2007b) from Alaska east across Canada to the northeastern United States, and south to northern California, the Great Plains, Iowa, Illinois, Tennessee, and the northern parts of North Carolina and western Virginia (Radford et al. 1968; Hultén 1968; Nessler 1976; Cronquist 1980; McGregor et al. 1986; Hickman 1993; Kartesz 1994). On our missions, *L. biennis* was found only in Canada in Saint-Patrice-de-Sherrington, in the southern part of Quebec, at an elevation of 61 m a.s.l. Three seed accessions were taken from one population of 10 plants, which were growing in a grassy ditch near a water canal. Usually blue wood lettuce can be found in rich moist soil, forest clearings, woodlands, along streams and lakes and roadsides (Hultén 1968; Cronquist 1980; McGregor et al. 1986). Hickman (1993) mentioned that in California *L. biennis* can be found generally at elevations below 500 m a.s.l. At the site in Quebec, the plants were heavily infected by downy mildew (DI=3). This is probably the first record of *B. lactucae* on this species in Canada (Lebeda et al. 2002).

Conclusions

Those species most closely related to agronomically and horticulturally crops are considered as invaluable resources that underpin the food security of all humanity. These wild species constitute a broad genetic base and thus provide essential materials for plant breeding. Despite enormous progress in research on wild *Lactuca* germplasm achieved during last thirty years, there is lack of data representing some key topics for future research and their exploitation in lettuce breeding (Lebeda et al. 2009a). Studies of the distributions and ecogeography of wild and weedy *Lactuca* species in the North American continent provide new information on inter- and intrapopulation structure for taxonomists, plant-population biologists, weed scientists, ecologists, and curators of *Lactuca* germplasm collections, as well as for lettuce breeders. Our recent missions have substantially contributed to creation of a framework for future biodiversity research, as well as to increase the diversity of wild *Lactuca* germplasm to be conserved and exploited in lettuce breeding (Lebeda et al. 2007b; Mou 2008). The next phases of our research are aimed at adetailed characterization of this germplasm (at different levels from morphological to molecular) and should elucidate relationships among populations, increasing our knowledge about inter- and intraspecific variability of these species in North America (Kitner et al. 2009). Field observations and detailed surveys of naturally occurring diseases, especially of downy and powdery mildews, in wild and weedy *Lactuca* populations will be used to refine our understanding of intra- and interpopulation variability in disease resistance and its underlying mechanisms (cf. Lebeda et al. 2008b). Succeeding research on the detection and characterization of race-specific genes and related factors will aid in the selection of resistant genotypes for lettuce improvement.

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References

Alexander JM, Naylor B, Poll M, Edwards PJ, Dietz H (2009a) Plant invasions along mountain roads: the altitudinal amplitude of alien Asteraceae forbs in their native and introduced ranges. Ecography 32:334–344

Alexander JM, Poll M, Dietz H, Edwards PJ (2009b) Contrasting patterns of genetic variation and structure in plant invasions of mountains. Divers Distrib 15:502–512

Babcock EB, Stebbins GL, Jenkins JA (1937) Chromosomes and phylogeny in some genera of the *Crepidinae*. Cytologia (Tokyo) Fujii Jubilee Volume: 188-210

Beharav A, Ben-David R, Doležalová I, Lebeda A (2008) Eco-geographical distribution of *Lactuca saligna* natural populations in Israel. Israel J Plant Sci 56:195–206

Beharav A, Ben-David R, Doležalová I, Lebeda A (2009) Eco-geographical distribution of *Lactuca aculeata* natural populations in northeastern Israel. Genet Resour Crop Evol (in press). (DOI 10.1007/s10722-009-9503-6)

Bremer K, Anderberg AA, Karis PO, Nordenstam B, Lundberg J, Ryding O (1994) Asteraceae: Cladistics and Classification. Timber Press, Portland, OR

Carter RN, Prince SD (1982) A history of the taxonomy treatment of unlobed-leaved prickly lettuce, *Lactuca serriola* L., in Britain. Watsonia 14:59–62

Clapham AR, Tutin TG, Warburg EF (1962) Flora of the British Isles. Botanical Society of the British Isles, London.

Cronquist A (1955) Compositae. In: Hitchcock CL, Cronquist A, Owenby M, Thompson JW (eds) Vascular Plants of the Pacific Northwest. Part 5, University of Washington Press, Seattle, pp 1–343

Cronquist A (1980) Vascular Flora of the Southern United States. Vol. I, Asteraceae. The University of North Carolina Press, Chapel Hill

D'Andrea L, Broennimann O, Kozlowski G, Guisan A, Morin X, Keller-Senften J, Felber F (2009). Climate change, anthropogenic disturbance and the northward range expansion of *Lactuca serriola* (Asteraceae). J Biogeogr 36:1573–1587

Doležalová I, Lebeda A, Křístková E (2001) Prickly lettuce (*Lactuca serriola* L.) germplasm collecting and distribution study in Slovenia and Sweden. Plant Genet Resour Newsl 128:41–44

Doležalová I, Lebeda A, Janeček J, Číhalíková J, Křístková E, Vránová O (2002) Variation in chromosome numbers and nuclear DNA contents in genetic resources of *Lactuca* L. species (Asteraceae). Genet Resour Crop Evol 49:383–395

Feráková V (1977) The genus *Lactuca* L. in Europe. Komenský University Press, Bratislava (Czechoslovakia)

Fernald ML (1950) Gray's manual of botany, 8th ed, American Book Company, New York

Frietema de Vries FT, Van der Meijden R, Brandenburg WA (1994) Botanical files on lettuce (*Lactuca sativa*). Gorteria Suppl 2:1–34

Funk VA, Susanna A, Stuessy TF, Bayer RJ (eds) (2009) Systematics, Evolution and Biogeography of Compositae. International Association for Plant Taxonomy, Vienna, Austria

Gleason HA, Cronquist A (1963) Manual of Vascular Plants of Northeastern United States and Adjacent Canada. Van Nostrand, Princeton, N J

Hegi G (ed) (1987) Illustrierte Flora von Mitteleuropa, Vol 6, Part 4, Verlag Paul Parey, Berlin, pp 1113–1134

Heywood VH (1978) Flowering Plants of the World. Oxford University Press, Oxford

Hickman JC (ed) (1993) The Jepson Manual: Higher Plants of California. University of California Press, Berkeley

Hooftman DAP, Oostermeijer JGB, den Nijs JCM (2006) Invasive behaviour of *Lactuca serriola* (Asteraceae) in the Netherlands: Spatial distribution and ecological amplitude. Basic Appl Ecol 7:507–519

Hultén E (1968) Flora of Alaska and Neighboring Territories. Stanford University Press, Stanford, California

Kartesz TJ (1994) A Synonymized Checklist of the Vascular Flora of the United States, Canada and Greenland. Vol 1, 2nd ed, Timber Press, Portland, OR

Kitner M, Maras M, Lebeda A, Meglič V, Šmachová P, Novotná A, Doležalová I (2009) Genetic diversity analysis of wild *Lactuca serriola* germplasm collection from North America assessed by AFLP. In: Goličnik M, Bavec A (eds) Book of Abstracts of the Joint Congress of The Slovenian Biochemical Society and The Genetic Society of Slovenia with International Participation; Otočec, September 20-23, 2009, Slovenian Biochemical Society and Genetic Society of Slovenia, Ljubljana, p 175

Lebeda A (1994) Evaluation of wild *Lactuca* species for resistance of natural infection of powdery mildew (*Erysiphe cichoracearum*). Genet Resour Crop Evol 41:55–57

Lebeda A, Astley D (1999) World genetic ressource of *Lactuca* spp., their taxonomy and biodiversity. In: Lebeda A, Křístková E (eds) Eucarpia Leafy Vegetables ´99, Proceedings of the Eucarpia Meeting of Leafy Vegetables Genetics and Breeding. Palacký University, Olomouc, Czech Republic, pp 81–94

Lebeda A, Doležalová I, Astley D (2004a) Representation of wild *Lactuca* spp. (Asteraceae, Lactuceae) in world genebank collections. Genet Resour Crop Evol 51:167–174

Lebeda A, Doležalová I, Feráková V, Astley D (2004b) Geographical distribution of wild *Lactuca* species (Asteraceae, Lactuceae). Bot Rev 70:328–356

Lebeda A, Doležalová I, Křístková E, Dehmer KJ, Astley D, van de Wiel CCM, van Treuren R (2007a) Acquisition and ecological characterization of *Lactuca serriola* L. germplasm collected in the Czech Republic, Germany, the Netherlands and United Kingdom. Genet Resour Crop Evol 54:555–562

Lebeda A, Doležalová I, Křístková E, Kitner M, Petrželová I, Mieslerová B, Novotná A (2009a) Wild *Lactuca* germplasm for lettuce breeding: recent status, gaps and challenges. Euphytica 170:15–34 (DOI:10.1007/s10681-009-9914-7)

Lebeda A, Doležalová I, Křístková E, Mieslerová B (2001) Biodiversity and ecogeography of wild *Lactuca* spp. in some European countries. Genet Resour Crop Evol 48:153–164

Lebeda A, Doležalová I, Křístková E, Vinter V, Vránová O, Doležal K, Tarkowski P, Petrželová I, Trávníček B, Novotný R, Janeček J (1999) Complex research of taxonomy and ecobiology of wild *Lactuca* spp. genetic resources. In: Lebeda A, Křístková E (eds) Eucarpia Leafy Vegetables ´99, Proceedings of the Eucarpia Meeting of Leafy Vegetables Genetics and Breeding.. Palacký University, Olomouc, Czech Republic, pp 117–131

Lebeda A, Kitner M, Dziechciarková M, Doležalová I, Křstková E, Lindhout P (2009b) An insight into the genetic polymorphism among European populations of *Lactuca serriola* assessed by AFLP. Biochem Syst Ecol 37:597–608

Lebeda A, Křístková E (1995) Genetic resources of vegetable crops from the genus *Lactuca*. Hort Sci (Prague) 22:117–121

Lebeda A, Petrželová I, Maryška Z (2008a) Structure and variation in the wild-plant pathosystem; *Lactuca serriola* – *Bremia lactucae*. Europ J Plant Pathol 122:127–146

Lebeda A, Pink DAC, Astley D (2002) Aspects of the interactions between wild *Lactuca* spp. and related genera and lettuce downy mildew (*Bremia lactucae*). In: Spencer-Phillips PTN, Gisi U, Lebeda A (eds) Advances in Downy Mildew Research. Kluwer Academic Publishers, Dordrecht, pp 85–117

Lebeda A, Ryder EJ, Grube R, Doležalová I, Křístková E (2007b) Lettuce (Asteraceae; *Lactuca* spp.), Chapter 9, In: Singh R (ed) Genetic Resources, Chromosome Engineering, and Crop Improvement, Volume 3 – Vegetable Crops. CRC Press, Boca Raton, FL, pp 377–472

Lebeda A, Sedlářová M, Petřivalský M, Prokopová J (2008b) Diversity of defence mechanisms in plant-oomycete interactions: a case study of *Lactuca* spp. and *Bremia lactucae*. Europ J Plant Pathol 122:71–89

Liogier HA (1997) Descriptive Flora of Puerto Rico and Adjacent Islands. Spermatophyta-Dicotyledonae, Vol V, Acanthaceae to Compositae. Universidad de Puerto Rico, San Juan, Puerto Rico

McGregor RL, Barkley TM, Brooks RE, Schofield EK (1986) Flora of the Great Plains. University Press of Kansas, Lawrence

Mejías JA (1993) Cytotaxonomic studies in the Iberian taxa of the genus *Lactuca* (Compositae). Bot Helvet 103:113–130

Mejías JA (1994) Self-fertility and associated flower head traits in the Iberian taxa of *Lactuca* and related genera (Asteraceae: Lactuceae). Plant Syst Evol 191:147–160

Meusel H, Jäger EJ (1992) Vergleichende Chorologie der Zentraleuropäischen Flora. Gustav Fischer Verlag, Jena

Mieslerová B, Petrželová I, Lebeda A, Česneková E (2007) Occurrence of lettuce downy mildew and powdery mildew in natural populations of prickly lettuce. In: Lebeda A, Spencer-Phillips PTN (eds) Advances in Downy Mildew Research, Vol 3 Proceedings of The 2nd International Downy Mildews Symposium. Palacký University in Olomouc and JOLA, v.o.s., Kostelec na Hané (Czech Republic), pp 59–64

Mou B (2008) Lettuce. In: Prohens J, Nuez F (eds) Handbook of plant breeding. Vegetables I. Asteraceae, Brassicaceae, Chenopodiaceae, and Cucurbitaceae. Springer Science, New York, pp 75–116

Nessler CL (1976) A systematic survey of the tribe Cichorieae in Virginia. Castanea 41:226–248

Petrželová I, Lebeda A (2004) Occurrence of *Bremia lactucae* in natural populations of *Lactuca serriola*. J Phytopathol 152:391–398

Prince DS, Carter RN (1977) Prickly lettuce (*Lactuca serriola* L.) in Britain. Watsonia 11:331–338

Radford AE, Ahles HE, Bell CR (1968) Manual of the Vascular Flora of the Carolinas. The University of North Carolina Press, Chapel Hill

Stebbins GL (1939) Notes of *Lactuca* in western North America. Madroño 5:123–126

Steyermark JA (1963) Flora of Missouri. Iowa State University Press, Ames, Iowa

Strausbaugh PD, Core EL (1978) Flora of West Virginia, 2nd ed, Seneca Books Inc., Grantsville, WV

Weaver SE, Cluney K, Downs M, Page E (2006) Prickly lettuce (*Lactuca serriola*) interference and seed production in soybeans and winter wheat. Weed Sci 54:496–503

Weaver SE, Downs MP (2003) The biology of Canadian weeds. 122. *Lactuca serriola* L. Can. J Plant Sci 83:619–628

Table 1 Survey of mission´s terms realized in USA and Canada

		Terms of missions			
Country	State/ Province	2002	2004	2006	2008
USA	New York			October, 7	
	Wisconsin	August, 18 - 19			
	Iowa	August, 20 - 21			August, 23 - 31
	Minnesota				July, 28 - 30
	South Dakota	August, 21 - 22			
	Wyoming	August, 23 - 25			September, 21
	Montana				September, 20
	Idaho	August, 25			September, 22
	Utah	August, 25 - 26		September, 27 - 28	September, 22 - 25
	Colorado				September, 25 - 26
	Arizona	August, 26 - 27		September, 29; October, 2	September, 27 - 28
	Nevada	August, 27	October, 17	September, 27	September, 16, 28
	California	August, 28 - 29	October, 10 - 16; 21 - 22	September, 23 - 26	September, 16 - 17; September, 29 - October, 2
	Oregon		October, 18 - 21		September, 17 - 18
	Washington		October, 20		September, 18 - 19
	North Carolina			September, 19 - 21	
Canada	Quebec		August, 26 - September, 1		
	Ontario	August, 11 - 13			

Table 2 Number of *Lactuca* seed samples collected in USA and Canada

	Number of seed samples																		
	USA																Canada		
Taxon	NY	WI	IA	MN	SD	WY	MT	ID	UT	CO	AZ	NV	CA	OR	WA	NC	ON	QC	Total
L. serriola f. *serriola*		4	30	8	10	15	10	8	29	7	11	2	54	7	11		6	30	242
L. serriola f. *integrifolia*						2				1	1		12	5	1			10	32
L. saligna													3						3
L. virosa													2		6				8
L. canadensis			25																25
L. canadensis × *L. ludoviciana*			2																2
L. floridana			9										1						10
L. ludoviciana			4																4
L. biennis																		3	3
Lactuca sp.	1														1	12			14
Total	1	4	70	8	10	17	10	8		8	12	2	72	12	19	12	6	43	343

NY	New York	CO	Colorado
WI	Wisconsin	AZ	Arizona
IA	Iowa	NV	Nevada
MN	Minnesota	CA	California
SD	South Dakota	OR	Oregon
WY	Wyoming	WA	Washington
MT	Montana	NC	North Carolina
ID	Idaho	ON	Ontario
UT	Utah	QC	Quebec

Table 3 Quantitative expression of distribution (number of locations) of wild *Lactuca* spp. in the USA and Canada

Country	State/ province	*Lactuca* spp.									
		LSES	LSEI	LSAL	LVIR	LCAN	LCAN × LLUD	LBIE	LFLO	LLUD	LSP
USA	New York										1
	Wisconsin	2									
	Iowa	13				12	1		1	1	
	Minnesota	3									
	South Dakota	7									
	Wyoming	10	2								
	Montana	6									
	Idaho	4									
	Utah	25									
	Colorado	4	1								
	Arizona	9	1								
	Nevada	2									
	California	42	10	2	1						1
	Oregon	5	4								
	Washington	8	1		3						1
	North Carolina										4
Canada											
	Quebec	19	10					1			
	Ontario	4									

LSES	*L. serriola* f. *serriola*	LCAN x LLUD	*L. canadensis* × *L. ludoviciana*
LSEI	*L. serriola* f. *integrifolia*	LBIE	*L. biennis*
LSAL	*L. saligna*	LFLO	*L. floridana*
LVIR	*L. virosa*	LLUD	*L. ludoviciana*
LCAN	*L. canadensis*	LSP	*Lactuca* sp.

Table 4 Frequency (%) of most typical habitats of wild *Lactuca* spp. in USA and Canada

	Country																	
	USA																Canada	
Taxon/Habitat	NY	WI	IA	MN	SD	WY	MT	ID	UT	CO	AZ	NV	CA	OR	WA	NC	QC	ON
L. serriola* f. *serriola																		
Banks of a river																		
Flower beds, field margins									3			50	7				7	
Grassy slope and places, prairie					20		40		21	14	18		2	14	27		23	
Others (gravels, stony slopes)						33		38	7				2		18		7	
Parking sites, petrol stations		50			20	7	30				27		2				3	
Pavement, street curbs				50		7	30		14	71	18		28	14	36		13	50
Road ditch			47		30								2				3	
Road-side (road margin), highway		50	50		30	27		38	10		9		39	29	18		10	33
Ruderal			3			27		25	38	14	27	50	17	29			20	17
Walls				50					7				2	14			13	
L. serriola* f. *integrifolia																		
Banks of a river																		
Flower bed, field margins						50												
Grassy slope and places, prairie																	10	
Others (gravels, stony slopes)														20			10	
Parking sites, petrol stations													25				20	
Pavement, street curbs										100	100		17	60				
Road ditch																		
Road-side (road margin), highway						50							58	20				
Ruderal															100		20	
Walls																	40	
L. saligna																		
Flower bed, field margins													67					
Ruderal													33					
L. virosa																		
Others (gravels, stony slopes)															50			
Pavement, street curbs													100		50			
L. canadensis																		
Road ditch			26															
Road-side (road margin), highway			59															
Ruderal			15															
L. bienis																		
Flower bed, field margins																	100	
L. floridana																		
Banks of a river			100															
L. ludoviciana																		
Road-side (road margin), highway			100															
***Lactuca* sp.**																		
Grassy slope and places, prairie	100														100	100		
Road-side (road margin), highway													100					

NY	New York	CO	Colorado
WI	Wisconsin	AZ	Arizona
IA	Iowa	NV	Nevada
MN	Minnesota	CA	California
SD	South Dakota	OR	Oregon
WY	Wyoming	WA	Washington
MT	Montana	NC	North Carolina
ID	Idaho	ON	Ontario
UT	Utah	QC	Quebec

Table 5 Summary of powdery (*G. cichoracearum*) and downy (*B. lactucae*) mildews records on wild *Lactuca* spp. in USA and Canada in 2002-2008

Country	State/ Province	Host *Lactuca* spp.	*G. cichoracearum*		*B. lactucae*	
			No of location surveyed/ No of records	Degree of infection/ No of records	No of location surveyed/ No of records	Degree of infection
USA	Wisconsin	LSES	4/1	1	4/1	1
	Iowa	LSES	20/1	1		
	Minnesota	LSES	3/1	2		
	Montana	LSES	6/1	2		
	Idaho	LSES	4/2	1; 3		
	Utah	LSES	25/1	1 (2006); 3 (2002)		
	Nevada	LSES	2/1	3		
	California	LSES	38/1	3		
		LSEI	12/1	3		
	Oregon	LSES	5/2	2; 3		
	Washington	LSES			12/1	2
Canada	Quebec	LSES	21/16	1/5; 2/2; 3/3; 4/6	21/2	1
		LSEI	9/8	1/4; 4/4		
		LBIE			1/1	3
	Ontario	LSES	4/2	3		

LSES *L. serriola* f. *serriola*
LSEI *L. serriola* f. *integrifolia*
LBIE *L. biennis*

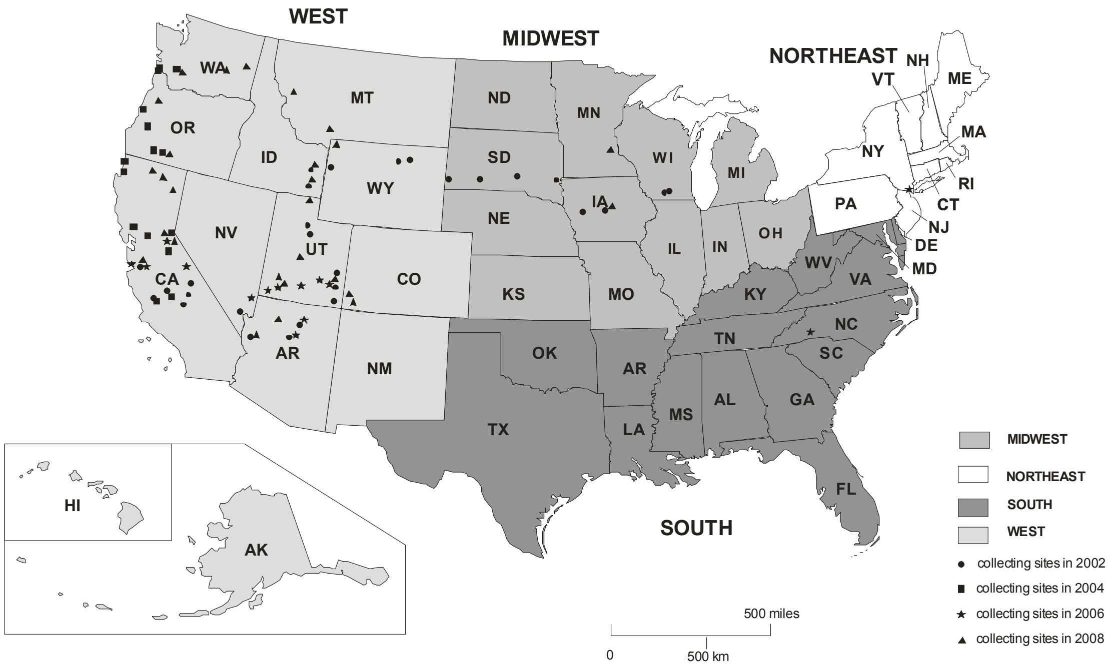

Fig. 1 Collecting sites of wild *Lactuca* spp. in USA

Fig. 2 Collecting sites of wild *Lactuca* spp. in Canada

North American Continent – a New Source of Wild *Lactuca* spp. Germplasm Variability for Future Lettuce Breeding

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Abstract
In the years 2002-2008, missions were undertaken in the USA and Canada to search for wild and weedy *Lactuca* species. Altogether, 16 states in the USA (Arizona, California, Colorado, Idaho, Iowa, Minnesota, Montana, Nevada, New York, North Carolina, Oregon, South Dakota, Utah, Washington, Wisconsin and Wyoming) and two provinces in Canada (Ontario and Quebec) were visited. In total, seven wild and weedy *Lactuca* spp. (*L. serriola*, *L. saligna*, *L. virosa*, *L. canadensis*, *L. biennis*, *L. floridana*, and *L. ludoviciana*), an interspecific hybrid (*L. canadensis* × *L. ludoviciana*), and an undetermined *Lactuca* species were observed and collected in 200 locations. In this paper, we present new data on the distribution and ecobiology of *Lactuca* naturally occurring in North America. Morphological assessment of *L. serriola* samples acquired from North America revealed considerable intraspecific phenotypic variation. Although *L. serriola* samples originating from various eco-geographical regions differed significantly in their genetic polymorphisms (based on AFLP markers), little variation was observed in their absolute DNA content.

INTRODUCTION

The wild relatives of agricultural crops conserved in genebank collections constitute a broad genetic base that can provide essential materials for plant breeding (Lebeda et al., 2007). In many cases, the primary genepools of cultivated crops have been carefully examined but have been found deficient as sources of specific traits important for breeding. Those deficiencies have motivated expeditions to regions of high agrobiodiversity and increased emphasis on the utilization of wild crop relatives (Hajjar and Hodgkin, 2007; Lebeda et al., 2009a). Newly collected germplasm accessions serve as donors of new resistance genes against diseases, pests, and abiotic stresses, as well as of genes for improving physiological and quality traits (Lebeda et al., 2007). During the last 30 years, there has been considerable progress in the collection, characterization, and practical application of *Lactuca* L. germplasm collections, as well as in filling in gaps in our knowledge about the biology and ecology of many *Lactuca* species (Lebeda et al., 2009a).

Current information about the geographic distribution of wild and weedy *Lactuca* species in North America is still incomplete (Funk et al., 2009; Lebeda et al., 2004b), and readily available genetic resources of *Lactuca* from this geographic area are limited (Lebeda et al., 2004a). For these reasons, exploration missions to the United

States and Canada were conducted in the years 2002, 2004, 2006 and 2008, to 16 states of the USA and two Canadian provinces (Lebeda et al., 2011).

The aim of the research described herein is to present information on the distribution, ecogeography and ecobiology of *Lactuca* species occurring spontaneously in North America. This paper summarizes preliminary results on phenotypic and genotypic variation of wild and weedy *Lactuca* accessions collected in North America, with a strong emphasis on *L. serriola* L. These accessions are currently maintained in the working collection of the genebank at Palacký University in Olomouc, Czech Republic to support research in ecogeography, plant biology, and genetic diversity, and to enrich the genetic resources available for lettuce breeding.

MATERIALS AND METHODS

Field studies and collecting missions

To study the distribution and ecogeography of wild and weedy *Lactuca* in North America, extensive parts of the United States and Canada were explored. In the United States, 16 states representing the Northeast (New York), Midwest (Wisconsin, Iowa, Minnesota, South Dakota), West (Wyoming, Montana, Idaho, Utah, Colorado, Arizona, Nevada, California, Oregon, Washington) and South (North Carolina) were surveyed. In Canada, expeditions were made only in two provinces (Quebec, Ontario). Detailed information about these expeditions and summaries of the passport and ecogeographic data of the seed samples collected is provided elsewhere (Lebeda et al., 2011). All seed samples have been incorporated into the working collection of *Lactuca* germplasm in the Department of Botany, Palacký University in Olomouc, Czech Republic (http://botany.upol.cz/).

Morphological characterization

Morphological assessments of 231 *L. serriola* seed samples were performed during the course of their regeneration (during the vegetative period from April to October 2009) in a greenhouse under controlled conditions (Lebeda et al., 2007). Assessments included 12 quantitative and qualitative characters of stems (e.g., form of branching, character of indumentum), rosette and cauline leaves (e.g., rosette formation, depth of leaf incisions), inflorescences and flowers (e.g., inflorescence type, anthocyanin presence in bracts), following published descriptor lists for wild *Lactuca* species (Doležalová et al., 2002a; 2003).

Analysis of absolute DNA contents in *L. serriola*

Absolute content of nuclear DNA was measured in ten genotypes of *L. serriola* originating from USA and Canada. The measurements were done in two flow-cytometry labs (Department of Botany, Palacký University in Olomouc and Department of Botany, Charles University in Prague). The relative fluorescence of nuclei was measured with a CyFlow ML cytometer (Partec GmbH, Münster, Germany) equipped with an argon ion laser. The instrument was calibrated before each set of measurements with a standard of pea nuclei (*Pisum sativum* 'Ctirad'; 2C = 9.09 pg). The nuclei of *L. serriola* were isolated in OTTO I buffer and stained in OTTO II buffer supplemented with DNAse free RNase A (50 μg/ml) and propidium iodide (50 μg/ml) (http://www.ibot.cas.cz/fcm/suda/). At least 5,000 nuclei were analyzed in each sample.

AFLP polymorphisms in *L. serriola*

A subset of 92 accessions covering a broad transect of territory between the southwest (California, USA) and northeast (Quebec, Canada) was used for preliminary evaluation of genetic differentiation of *L. serriola* accessions. Genomic DNA was extracted from bulked leaf samples taken from ten individual plants of each accession by the CTAB method (Kump and Javornik, 1996). The integrity and quality of DNA were estimated on 0.8% agarose gels. Concentrations of DNA samples were determined by a NanoDrop ND-1000 Spectrophotometer (NanoDrop Technologies, Wilmington, Delaware, USA). Amplified Fragment Length Polymorphism (AFLP) analyses were conducted by using the original protocol of Vos et al. (1995), with modifications after Kitner et al. (2008). In total, ten primer combinations were used for AFLP analyses. Three primer combinations with 3+3 selective nucleotides were fluorescently labelled and amplicons detected on an automated ALFexpresII sequencer (Amersham-Pharmacia Ltd., Amersham, Buckinghamshire, England). The AFLP fragments of the other seven primer combinations with 3+4 selective nucleotides were separated on 6% polyacrylamide gel and visualised by silver staining. The fingerprints were scored manually, and resulting data subjected to statistical analysis with NTSYS-pc software (Rohlf, 1998) by using Jaccard´s coefficient of similarity and the Unweighted Pair Group Method with Arithmetic mean (UPGMA) clustering algorithm to construct dendrograms (with bootstrapping based on 1000 replicates).

RESULTS AND DISCUSSION

Field studies and collecting missions

In total seven wild and weedy *Lactuca* species (*L. serriola*, *L. saligna* L., *L. virosa* L., *L. canadensis* L., *L. biennis* (Moench) Fernald, *L. floridana* (L.) Gaertn., *L. ludoviciana* (Nutt.) Riddell), an interspecific hybrid (*L. canadensis* × *L. ludoviciana*), and an undetermined *Lactuca* species were observed and collected in 200 North American locations (Table 1). The largest number of localities was visited in California (56); nevertheless, the largest number of wild *Lactuca* species was recorded in Iowa (5). The most common taxon, *L. serriola,* was observed in all states and provinces visited, except for North Carolina and New York. From an orographic viewpoint, populations of *L. serriola* were recorded from 6 masl to 3524 masl. *L. saligna* was recorded only one time at abandoned, small gardens in Salinas, California. *L. virosa* was found in Washington State along the road to Mount Saint Helens on stony rubble, situated at ca. 1000 masl. Typical habitats of *L. serriola* were along transport corridors, including roadsides, ditches, parking lots and petrol stations, as well as on grassy slopes. Three native North American taxa, *L. canadensis*, *L. floridana*, and *L. ludoviciana*, were collected only in Iowa. *L. canadensis* populations were observed at elevations from 281 to 336 masl, where the plants were widely distributed along roadsides in ditches and ruderal places. *L. floridana* was recorded only on a limited scale in Ames, IA, along the banks of Squaw Creek. Plants of *L. ludoviciana* were grown along a roadside west of Ames, at an elevation of 326 masl. *Lactuca biennis* was found only in Canada in Saint-Patrice-de-Sherrington, in southern Quebec, at an elevation of 61 masl, in a grassy ditch near a water canal. In some locations, infections of downy mildew (*Bremia lactucae*) (on *L. serriola* and *L. biennis*) and powdery mildew (*Golovinomyces cichoracearum*) (on *L. serriola*) were observed. Most plant-disease findings were recorded in Canada (Lebeda et al., 2011).

There are reports of 12 wild and weedy *Lactuca* species from the New World, with 10 occurring in North America (Lebeda et al., 2004b). Into this group belong species native from Canada to Florida, which form a so-called "North American group" (Lebeda et al., 2007), as well as synanthropic and cosmopolitan species (*L. serriola*, *L. saligna, L. virosa*) (Cronquist, 1980; McGregor et al., 1986). The autochthonous *Lactuca* species in North America include *L. canadensis*, *L. graminifolia* Michx., *L.*

biennis, *L. floridana*, *L. ludoviciana*, *L. hirsuta* Muhl. ex Nutt., *L. terrae-novae* Fern. and *L. tatarica* (L.) C.A. Mey. subsp. *pulchella* (Pursh) Stebbins (Lebeda et al., 2004b). These species are annual, biennial or perennial with broad phenotypic variability, particularly in terms of leaf shape. An increasing interest in determining the geographic distribution of these wild *Lactuca* populations and sampling them from natural habitats resulted in the initiation of our collection expeditions. Field observations and detailed surveys of naturally occurring populations there provide new information on inter- and intrapopulation structure of *Lactuca* species. This can be useful for taxonomists, plant-population biologists, weed scientists, ecologists, and curators of *Lactuca* germplasm collections, as well as for lettuce breeders (Lebeda et al., 2007, 2009a; Mou, 2008).

Morphological variation in *Lactuca serriola*

Based on the morphology of rosette and cauline leaves, 80% of plants representing 231 North American accessions could be assigned to *L. serriola* f. *serriola*. Formation of basal rosettes was recorded in 77% of the plants, while the remaining ones quickly bolted. After bolting, all but one plant of *L. serriola* branched exclusively in the upper part of stem. The one exception branched along the whole stem. Basal branching was not observed. In 98% of the plants evaluated, we observed that stems were armed with prickly trichomes with rigid points, located mainly along the lower parts of the stem. In the majority of plants, small flexible trichomes, difficult to break, were recorded at a moderate density (Fig.1). Corymbose panicles were characteristic of all *L. serriola* plants. Anthocyanin in bracts was present in 80% of the plants, where a majority of those (43%) displayed anthocyanin at the apex. Other examples of anthocyanin distribution on the bracts included stripes (20%) and spots (3.5%) (Fig.1). Combinations of spots and stripes, or spots with the presence of anthocyanin at the apex were rarely recorded.

DNA content variation in *L. serriola*

The mean value of absolute 2C DNA content of *L. serriola* as determined in our laboratory was 5.86 pg and ranged from 5.79 to 5.89 pg. The lowest absolute 2C DNA value was found in a sample originating from Toronto, Ontario, the highest was in a sample from Dodgeville, Wisconsin. Differences within individual samples were low, ranging from 1.7% in a sample from Buffalo, Wyoming to 2.89% in a sample from Toronto. In an independent evaluation of absolute content of DNA conducted at the Department of Botany of Charles University, Prague, 2C DNA values ranged from 5.73 to 5.82 pg. The mean value was 5.77 pg. In the Charles University evaluation, the lowest and highest contents values were both found in samples originating from Toronto. Their differences within individual samples were low as well, ranging from 0.7% in a sample from Toronto to 2.77% in a sample originating from Dodgeville.

Although some works confirm the existence of noticeable intraspecific variability in the content of nuclear DNA (Ohri, 1998), other authors consider nuclear DNA content as a species-specific character (Greilhuber, 1998). Our data on nuclear DNA content in *L. serriola*, with such limited variation among 10 samples, tend to support the view of Greilhuber (1998).

A key difference between nearly all species of *Lactuca* native to North America and those of other regions is their haploid chromosome number. This group is characterized by the consistent presence of the haploid chromosome number, n = 17, making it both geographically and genetically isolated (Lebeda et al., 2007). These species are of amphidiploid origin, resulting from interspecific crossing, chromosome doubling (perhaps through unreduced-gamete formation), and subsequent hybrid stabilization (or diploidization) (Feráková, 1977). In these species, higher contents of nuclear DNA have been established in comparison with Eurasian taxa (Doležalová et al., 2002b). This is true for above mentioned species except for *L. tatarica* subsp. *pulchella* with a haploid chromosome number, n = 9 (Tomb et al., 1978).

AFLP polymorphism of *L. serriola*

In total, we detected 324 AFLP fragments with 268 (82.7%) polymorphic among 47 accessions analyzed. Bootstrapped UPGMA clustering distinguished accessions into four major groups with significant bootstrap values (Fig. 2). Group A represents an isolated cluster. Group B includes only 5 samples from Slovenia, which were used as an outgroup. There was a small cluster of three samples in group C, and a much larger one (group D) containing all remaining samples. There were no significant differences in morphological or provenance data for samples from groups A and C (Fig. 2). However, within cluster D one can distinguish two sub-clusters, which do correspond to some geographically distinct regions. Sub-cluster D1 represents samples collected exclusively in California, Nevada, Utah, Oregon, and Arizona, whereas samples from the northern part of the USA (Oregon, Wyoming, Wisconsin) and Canada (Quebec, Ontario) are present in sub-cluster D2. Evidently, the Sierra Nevada Mountains and other geographic barriers form a natural boundary between *L. serriola* populations collected along the Pacific coast and in the southwest and those populations sampled northward and eastward (Rocky Mts., Great Plains and Southeastern Canada). However, we should point out that the bootstrap values supporting the entire group D are relatively weak.

AFLP and isozyme studies conducted on European *L. serriola* populations showed that accessions originating in various eco-geographical conditions differed significantly in their genetic and protein polymorphisms (Lebeda et al., 2009b). AFLP and other molecular approaches should elucidate genetic relationships among all *L. serriola* populations, and increase our knowledge about intraspecific variability of those found in North America (Kitner et al., 2009).

CONCLUDING REMARKS

Our research has been investigating the North American continent as a new source of wild *Lactuca* germplasm variability, which should be conserved and evaluated, and then scientifically exploited in practical lettuce breeding. Initial morphological assessment of *L. serriola* samples acquired from North America revealed considerable intraspecific phenotypic variation. Morphological data obtained during the multiplication of seed samples under controlled conditions are important for future research aimed at clarifying relationships between quantitative and qualitative morphological traits and ecogeographic factors. Thus, we intend to conduct detailed morphological studies with this goal in mind, along with the application of AFLP and other molecular approaches to elucidate relationships among populations.

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Literature Cited

Cronquist, A. 1980. Vascular Flora of the Southeastern United States. Vol. I, Asteraceae. The University of North Carolina Press, Chapel Hill, NC, USA.

Doležalová, I., Křístková, E., Lebeda, A. and Vinter, V. 2002a Description of morphological characters of wild *Lactuca* L. spp. genetic resources (English-Czech version). Hortic. Sci. (Prague) 29:56–83.

Doležalová, I., Lebeda, A., Janeček, J., Číhalíková, J., Křístková, E. and Vránová, O. 2002b. Variation in chromosome numbers and nuclear DNA contents in genetic resources of *Lactuca* L. species (Asteraceae). Genet. Resour. Crop Evol. 49:383-395.

Doležalová, I., Křístková, E., Lebeda, A., Vinter, V., Astley, D. and Boukema I.W. 2003. Basic morphological descriptors for genetic resources of wild *Lactuca* spp. Plant Genet. Resour. Newsl. 134:1–9.

Feráková, V. 1977. The genus *Lactuca* L. in Europe. Univerzita Komenského, Bratislava, Slovakia.

Funk, V. A., Susanna, A., Stuessy, T.F. and Bayer R.J. (eds.) 2009. Systematics, Evolution and Biogeography of Compositae. International Association for Plant Taxonomy, Vienna, Austria.

Greilhuber, J. 1998. Intraspecific variation in genome size: A critical reassessment. Ann. Bot. 82 (Suppl. A):27-35.

Hajjar, R. and Hodgkin, T. 2007. The use of wild relatives in crop improvement: A survey of developments over the last 20 years. Euphytica 156:1-13.

http://www.ibot.cas.cz/fcm/suda/

Kitner, M., Lebeda, A., Doležalová, I., Maras, M., Křístková, E., Beharav, A., Nevo, E., Pavlíček, T. and Meglic, V. 2008. AFLP analysis of *Lactuca saligna* germplasm collections from four European and three Middle East countries. Isr. J. Plant Sci. 56:185–193.

Kitner, M., Maras, M., Lebeda, A., Meglič, V., Šmachová, P., Novotná, A. and Doležalová, I. 2009. Genetic diversity analysis of wild *Lactuca serriola* germplasm collection from North America assessed by AFLP. In: M. Goličnik and A. Bavec (eds.), Book of Abstracts of the Joint Congress of The Slovenian Biochemical Society and The Genetic Society of Slovenia, Otočec, September 20-23, 2009, p. 175. Slovenian Biochemical Society and Genetic Society of Slovenia, Ljubljana.

Kump, B. and Javornik, B., 1996. Evaluation of genetic variability among common buckwheat (*Fagopyrum esculentum* Moench) populations by RAPD markers. Plant Sci. 114:149-158.

Lebeda, A., Doležalová, I. and Astley, D. 2004a. Representation of wild *Lactuca* spp. (Asteraceae, Lactuceae) in world genebank collections. Genet. Res. Crop. Evol. 51:167-174.

Lebeda, A., Doležalová, I., Feráková, V. and Astley, D. 2004b. Geographical distribution of wild *Lactuca* species (Asteraceae, Lactuceae). Botanical Review 70:328-356.

Lebeda, A., Doležalová, I., Křístková, E., Kitner, M., Petrželová, I., Mieslerová, B. and Novotná, A. 2009a. Wild *Lactuca* germplasm for lettuce breeding: Recent status, gaps and
challenges. Euphytica 170:15-34. doi:10.1007/s10681-009-9914-7.

Lebeda, A., Doležalová, I. and Novotná, A. 2011. Wild and weedy *Lactuca* species, their distribution, ecogeography and ecobiology in USA and Canada. (prepared for press)

Lebeda, A., Kitner, M., Dziechciarková, M., Doležalová, I., Křístková, E. and Lindhout, P. 2009b. An insight into the genetic polymorphism among European populations of *Lactuca serriola* assessed by AFLP. Biochem. Syst. Ecol. 37:597-608.

Lebeda, A., Ryder, E.J., Grube, R., Doležalová, I. and Křístková, E. 2007. Lettuce (Asteraceae; *Lactuca* spp.), Chapter 9, pp. 377-472. In: R. Singh (ed.), Genetic

Resources, Chromosome Engineering, and Crop Improvement, Volume 3 – Vegetable Crops. CRC Press, Boca Raton, FL, USA.
McGregor, R.L., Barkley, T.M., Brooks, R.E. and Schofield, E.K. (eds.) 1986. Flora of the Great Plains. University Press Kansas, Lawrence, KS, USA.
Mou, B. 2008. Lettuce. In: J. Prohens and F. Nuez (eds.), Handbook of Plant Breeding. Vegetables I. Asteraceae, Brassicaceae, Chenopodiaceae, and Cucurbitaceae. Springer Science, New York, pp. 75-116.
Ohri, D. 1998. Genome size variation and plant systematics. Ann. Bot. 82 (suppl. A):75-83.
Rohlf, F.J. 1998. NTSYS-pc. Numerical taxonomy and multivariate analysis system, Applied Biostatistics, New York.
Tomb, A.S., Chambers, K.L., Kyhos, D.W., Powell, A.M. and Raven, P.H. 1978. Chromosome numbers in the Compositae. XIV. Lactuceae. Amer. J. Bot. 65:717-721.
Vos, P., Hogers, R., Bleeker, M., Reijans, M., Vandelee, T., Hornes, M., Frijters, A., Pot, J., Peleman, J., Kuiper, M. and Zabeau, M. 1995. AFLP - a new technique for DNA-fingerprinting. Nucl. Acid Res. 23:4407-4414.

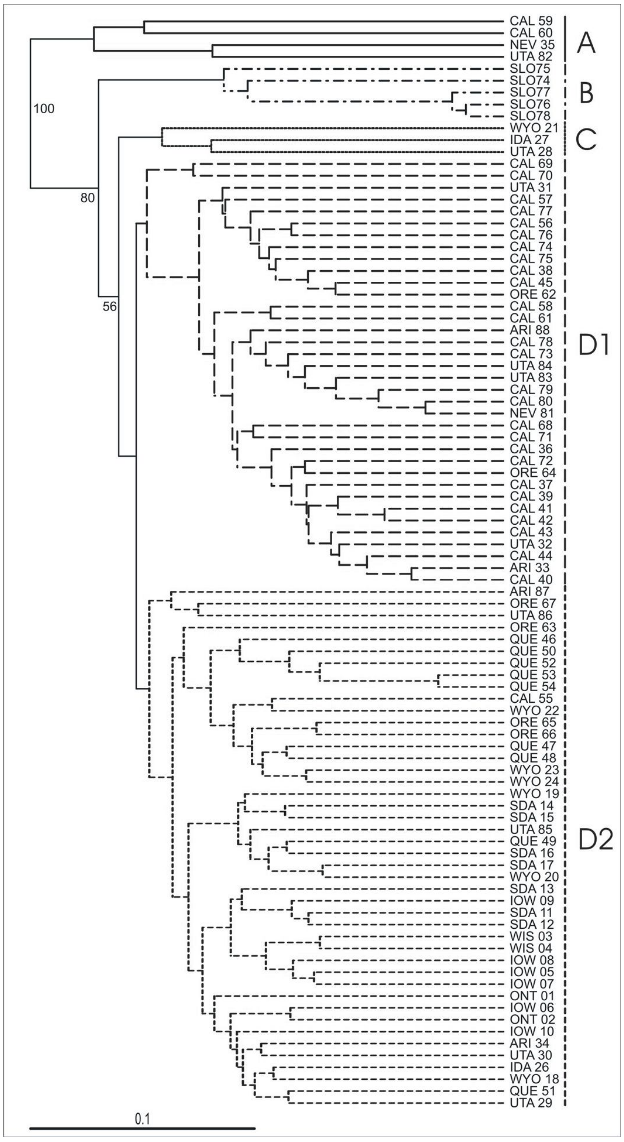
<u>Tables</u>

Table 1. Summary of locations and number of seed samples of wild and weedy *Lactuca* spp. collected in the USA and Canada (modified from Lebeda et al., 2011)

	No. of locations		No. of seed samples	
Taxon	USA	Canada	USA	Canada
L. serriola f. *serriola*	140	25	206	36
L. serriola f. *integrifolia*	19	10	22	10
L. saligna	2		3	
L. virosa	4		8	
L. canadensis	12		25	
L. canadensis × *L. ludoviciana*	1		2	
L. floridana	1		10	
L. ludoviciana	1		4	
L. biennis		1		3
Lactuca sp.	7		14	

Fig. 1. Phenotypic variation of *L. serriola*. Inflorescence without trichomes – A; spiny indumentum of the stem – B; absence of anthocyanin in involucral bracts – C; anthocyanin distribution in spots – D; anthocyanin distribution in stripes – E; anthocyanin distribution in the apex – F.

Fig. 2. UPGMA cluster analysis of within-population diversity among 47 *L. serriola* accessions using Jaccard´s similarity matrix. Numbers on branches are percentage values of bootstrap support (1000 replicates).



4.5. Genetic resources of wild *Lactuca* L. spp., their exploitation in lettuce breeding

Modern variety breeding for present and future needs

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Wild *Lactuca* germplasm for lettuce breeding: recent status, gaps and challenges

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ABSTRACT: Recent status, gaps and challenges regarding to wild *Lactuca* L. germplasm, their taxonomy, bio-geography, biology and ecology, gene pools, field explorations and collecting activities, germplasm collections, development of descriptors, characterization and evaluation, lettuce breeding and enhancement of *Lactuca* spp. are summarized and critically analysed. Future research and activities related to wild *Lactuca* germplasm are considered.

Keywords: biogeography, breeding, collecting, gene pools, genetic diversity, lettuce.

Introduction

Genetic resources of wild *Lactuca* species are an integral part of world plant heritage as conserved in gene bank system, and they play important role in recent lettuce breeding (Lebeda et al., 2007c; Mou, 2008). An enormous progress in theoretical research and practical applications of *Lactuca* germplasm was achieved during last 25 years (Lebeda et al., 2007c). Persisting gaps, problems and confusions in this area, with recent progress in their solving, are highlighted in this paper.

Taxonomy of *Lactuca* L.

Taxonomic and phylogenetic studies range the genus *Lactuca* L. to the Compositae (Asteraceae) (Funk et al., 2005), one of the largest plant families; subfamily Cichorioideae, tribe Lactuceae. Detailed search of available literature confirmed about 100 wild *Lactuca* spp. with the highest number of autochtonous species and species richness in Asia (51 species) and Africa (43 species) (Lebeda et al., 2004b). Latest molecular data on phylogenetic relationships among *Lactuca* species (Koopman et al., 1998) confirmed, with some modifications, a previously elaborated broader generic concept of this genus (summarized by Lebeda et al., 2007c). However, formal classification and the subgeneric division (Lebeda et al., 2007c) need critical reconsideration, further development and clarification.

Geographic distribution and hot-spots of diversity

Of late years the potential value of genes from wild species has for many times been stressed (Gass and Frese, 1999). Regarding the lettuce, the reasons are firstly the lost of genetic diversity and limited number of those species in current *ex-situ* germplasm collections (Lebeda et al., 2004a, 2007c). A primary objective is to concentrate the lettuce progenitors and/or wild relatives to world's collections from the areas of probable lettuce origin and those where the highest genetic diversity of *Lactuca* species occur (Lebeda et al., 2004c). The high levels of diversity of *Lactuca* species confined to the Mediterranean basin and southwest Asia indicate that those regions may be seriously considered as hot-spots for lettuce conservation priorities (Beharav et al., 2008; Lebeda et al., 2001). Future eco-geographic studies and collecting strategy must be more intensively oriented to the hot-spots in the Central and South Africa and North America as well (Lebeda et al., 2007c).

Biology and ecology

To the genus *Lactuca* belong annual, biennial or perennial herbs, rarely shrubs with abundant latex. In the sections Phoenixopus, Mulgedium, Lactucopsis, Tuberosae, Micranthae and Sororiae there are included mostly biennial or perennial species (Lebeda and Astley, 1999). The division of section Lactuca into two subsections Lactuca and Cyanicae is based on life cycle of their representatives (Feráková, 1977). Subsection Lactuca comprises annual, winter annual or biennial herbs; perennial species belong into subsection Cyanicae. The autochtonous North American species are biennial. The African species are annual or perennial herbs or sub-shrubs, rarely scandent. The genus *Lactuca* L. comprises species with wholly different ecological requirements occupying various habitats. The species of the lettuce genepool (those of the main breeder's interest) *L. serriola*, *L. saligna* and *L. virosa* are weedy and occur on waste places and ruderal habitats – mainly along roads, highways and ditches (Lebeda et al., 2001, 2004b, 2007a). The majority of *Lactuca* spp. like *L. perennis*, *L. viminea*, *L. graeca*, *L. tenerrima* are calciphilous plants and settle limestone and dolomite areas, mostly rocky slopes. Endemic lianalike species are found in rain forests of East Africa. A comprehensive survey regarding biology and ecology of European *Lactuca* species was done by Feráková (1977) and Lebeda et al. (2004b) who summarized available information about hundred *Lactuca* spp. from current world literature. However, basic data about biology and ecology in most of *Lactuca* spp. (esp. African and Asian origin) are still missing.

Gene pools and genetic diversity

Recent available knowledge concerning to exploitation of wild relatives in commercial lettuce breeding was specified by Lebeda et al. (2007c). In general, the primary gene pool comprises numerous cultivars and landraces of *L. sativa* and the wild ancestor *L. serriola.* The wild *serriola*-like species from Southwest Asia (*L. aculeata*, *L. altaica*, *L. azerbaijanica*, *L. georgica*, *L. scarioloides*) and African *L. dregeana*, which indicate very similar interfertility with the crop, belong to the primary gene pool as well (Lebeda et al., 2007c). Although *L. saligna* and *L. virosa* have been intensively studied by plant evolutionists and breeders, the categorization to secondary and tertiary gene pools has remained open to question. A view completely different from the previous conception was proposed by Koopman et al. (1998) who 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. However, categorization of many *Lactuca* spp. into gene pools is still questionable.

Germplasm collections - recent status and problems

Collections, their structure and gaps

Detailed information about wild *Lactuca* germplasm collections around the world was published by Lebeda et al. (2007c). From this survey it is evident that there are only few important collections in Europe (ca 5) and USA (ca 3). In the centres of high species richness and diversity there are no germplasm collections with local accessions. Analysis of ILDB (International Lactuca Database) showed that over 90% of the collections are represented by only three *Lactuca* species (*L. serriola, L. saligna, L. virosa*), mostly of European origin. The autochtonous species from other continents (Asia, Africa, America), which form ca 83% of known *Lactuca* species richness (Lebeda et al., 2004b), are represented in collections by ca 3% of accessions (Lebeda et al., 2004a). Broadening of the collecting activities in natural habitats of these areas is considered as a crucial point for future development of *Lactuca* spp. collections (Lebeda et al., 2007c).

Taxonomic status of accessions and duplicates

Correct taxonomic ranging of accessions is a base of all operations with plant material in gene banks, to prevent any genetic pollution and lost, to reduce redundancy within and among collections by eliminations of duplicates, and for correct interpretation of results of research work with germplasm material. Insufficient or incorrect passport data complicate evaluation of accessions morphologically, and by using biochemical and molecular markers (Hintum and Boukema, 1999).

Basic errors in taxonomic status of accessions as declared by gene banks were found during recent studies. When evaluating a set of 49 accessions of 24 wild *Lactuca* species by the mean of morphological characters, chromosome number, relative DNA content and isozyme polymorphism, a total of 17 accessions were reclassified and/or their taxonomic status was discussed (Doležalová et al., 2004).

Within a set of 95 *Lactuca* spp. accessions provided by gene banks in Czech Republic, Germany, Netherlands, UK and the USA, and represented by 12 *Lactuca* species (*L. aculeata, L. altaica, L. dentata, L. dregeana, L. indica, L. livida, L. perennis, L. quercina, L. saligna, L. serriola, L. tatarica* and *L. virosa*), morphologic assessment of plants confirmed taxonomic status declared only for 50 accessions. Other accessions were taxonomically re-determined (31 acc.); represented by mixtures of *L. serriola* forms, and/or different *Lactuca* species or interspecific hybrids of *Lactuca* (14 acc.) (Doležalová et al., 2007a).

Duplication of accessions is important problem of efficient genebanking. Comparison of passport data of four large collections (CGN, WRPIS, IPK and HRI) showed that 60% of the accessions are duplicated once, twice or in all studied collections (Hintum and Boukema, 1999). Morphologic assessment of the above mentioned set of 95 *Lactuca* spp. accessions forming 34 duplicate groups on the base of passport data, showed that 69 accessions can be considered as morphologic duplicates (Doležalová et al., 2007a).

Field studies and collecting activities

The increasing interest in sampling and study of geographic distribution of wild *Lactuca* populations in natural habitats resulted in collecting missions which have effectively been initiated in the early nineties at the Department of Botany, Palacký University in Olomouc (Czech Republic). In the years 1995-2008, expeditions were conducted in fourteen European countries (Austria, Croatia, the Czech Republic, France, Hungary, Germany, Greece, Italy, the Netherlands, Slovakia, Slovenia, Sweden, Switzerland, the United Kingdom), nine states of USA (Arizona, California, Idaho, Iowa, North Carolina, South Dakota, Utah, Wisconsin, Wyoming) and Canada. Field studies and collecting of *Lactuca* spp. germplasm were also made in Turkey, Israel, Jordan, South Korea and New Zealand. Almost 1300 seed samples of twelve wild *Lactuca* species were collected (Doležalová et al., 2001; Křístková and Lebeda, 1999; Křístková et al., 2001; Lebeda et al., 2001a; Lebeda, unpubl.).

Collecting expeditions of *L. serriola* germplasm in four European countries were conducted within the framework of the EU-funded project "GENE-MINE" (Lebeda et al., 2007a). The seed material (800 accessions originating from 50 locations) was used for regeneration, inclusion into the National Germplasm Collections of individual countries and for research purposes in follow-up studies (e.g. Lebeda and Petrželová, 2004).

In cooperation with the Institute of Evolution (Haifa University in Israel) searching and collecting trips of the wild species *L. saligna* (least lettuce, willow-leaf lettuce) were conducted in 2004-2007 to protect Israel and world lettuce crop (Beharav et al., 2008; Lebeda, unpubl.). In all cases the seed samples were harvested from individual plants following the international standards for germplasm acquisition (Guarino et al., 1995) and in order to avoid collection of duplicated material (Hintum and Boukema, 1999; Lebeda et al., 2004a). Basic passport data specifying the locality (sample identification, geographic coordinates, information on sampling, unique terms as an occurrence of diseases and pests, etc.) were recorded and are available in author's databases.

Descriptors development

An exact, detailed and distinct description of genetic resources serves as a tool for their correct taxonomic determination and a definition of both interspecific and intraspecific variations (Lebeda et al., 2007b). There are national descriptors elaborated for characterization of each national collections, e.g. those from the Centre for Genetic Resources (CGN, Wageningen, The Netherlands) (Boukema et al., 1990); the Western Regional Plant Introduction Station Pullman, Washington (USA) (McGuire et al., 1993).

An international minimum descriptor lists were elaborated for genetic resources of *L. sativa* and wild *Lactuca* spp. (*L. serriola* and related species from the primary gene pool) by the community of the representatives of European gene banks within a framework of the activities of the European Cooperative Programme (ECP/GR), Working Group of Leafy Vegetables (Lebeda and Boukema, 2005).

The descriptors and codes for genetic resources of cultivated lettuce (*Lactuca sativa* L.) (Křístková et al., 2008) and wild *Lactuca* spp. (English-Czech version) (Doležalová et al., 2002a) were developed as a basic rule for documentation of the characterization and evaluation of the Czech collection of lettuce accessions within the National Programme of Conservation and Utilization of Plant Genetic Resources of the Czech Republic. International list of the most important morphological characters of wild *Lactuca* species was created within the framework of the EU-funded project "GENE-MINE" (Fifth Framework Programme of the European Commission) (Doležalová et al., 2003).

Characterization and evaluation of wild *Lactuca* germplasm

Morphology

Morphologic assessment of each accession is performed during their regeneration by using descriptor lists (Doležalová et al., 2002a, 2003; Křístková et al., 2008). Detailed study of morphologic variation was performed for *L. serriola* and *L. saligna*. Fifty *L. serriola* populations collected in four European countries (Czech Republic, Germany, The Netherlands, United Kingdom) (Lebeda et al., 2007a) were cultivated in a greenhouse under controlled conditions. Assessment included 26 quantitative and qualitative characters of the stem (e.g. stem length), rosette and cauline leaves (e.g. depth of incisions), the inflorescence and flower (e.g. anthocyanin coloration on bracts) (summarized in Lebeda et al., 2007b) including the fruit morphology (e.g. length and width of achene body, length of achene beak and number of ribs) (Doležalová et al., 2007b). Similar morphologic assessment was performed for about 70 populations of *L. saligna* originated from Czech Republic, France, Italy, Portugal, Israel, Jordan and Turkey (Beharav et al., 2008; Křístková et al., 2007a).

Phenology

The genus *Lactuca* is extremely variable also from the phenological viewpoint. Among the developmental characteristics, substantial differences in the time of flowering were recorded between accessions originating from individual countries (Doležalová et al., 2005; Lebeda et al., 2007b, c). Substantial differences in developmental stages (beginnings of bolting and flowering) were recorded among 89 *L. serriola* samples originating from different eco-geographic conditions of Europe (Austria, Czech Republic, France, Germany, Italy, Slovakia, Switzerland, the Netherlands, the United Kingdom) when grown under unified conditions in a greenhouse. Developmental stages of plants, as being influenced (formed) by original eco-geographic conditions of samples (Lebeda et al., 2001), persist when plants are cultivated in unified environmental conditions and are fixed genetically (Křístková et al., 2007b).

Karyology and DNA content

Wild *Lactuca* species can be divided into three main groups, according to base chromosome number (Feráková, 1977). First group is relatively small and contains perennial species of

Europe and the Himalayas with haploid chromosome number n=8. The haploid chromosome number n=9, characterizes the majority of European and Mediterranean species, as well as species from the Middle East, Africa and India in the second group. The third group, containing of North American species distributed from Canada to Florida, is marked by a haploid chromosome number of n=17. It is of amphidiploid origin and somewhat geographically and genetically isolated. Our understanding of this genus remains incomplete, because the chromosome numbers of numerous *Lactuca* species are not known (Lebeda and Astley, 1999) or especially chromosome numbers of North American species may differ from the reported data (Doležalová et al., 2002b).

Until now, analyses of variation in nuclear DNA content have been performed on only a limited number of *Lactuca* species (*L. sativa, L. serriola, L. saligna, L. virosa*) (Bennett and Leitch, 1995; Koopman and De Jong, 1996; Koopman, 1999, 2000). Karyotype analysis and relative DNA content were used for characterization of *L. sativa, L. serriola, L. saligna,* and *L. virosa* and their evolutionary relationships (Koopman and De Jong, 1996). Flow cytometry was tested for reliability as a tool to distinguish some *Lactuca* species (Koopman, 1999, 2000). Doležalová et al. (2002b) analyzed fifty accessions of 25 *Lactuca* species (including hybrid *L. serriola* × *L. sativa* and *Mycelis muralis*) for chromosome number and relative DNA content variation. Later, Koopman (2002) showed that five *Lactuca* species (*L. viminea, L. virosa, L. serriola, L. sativa* and *L. sibirica*) have significant intraspecific variation in DNA content, but it was concluded that only the variation within *L. virosa* seems to have evolutionary significance. Recently, the studies are focused on intraspecific differences in DNA content in *L. serriola* germplasm, originating from the twelve European countries (Lebeda et al., 2004c, 2007c).

Resistance to diseases and pests

Recent advancement in research and breeding of lettuce for resistance to diseases and pests was summarized elsewhere (Lebeda et al., 2007c; Mou, 2008). Traditionally, *Bremia lactucae* is considered as the most important disease of cultivated lettuce. Limited availability of durable sources of resistance stimulates an increasing interest of breeders for new sources of resistance from wild *Lactuca* spp. (Lebeda et al., 2002). Current studies (Beharav et al., 2006; Lebeda et al., 2008; Lebeda and Zinkernagel, 2003; Petrželová et al., 2007) demonstrated that wild *Lactuca* (e.g. *L. saligna, L. serriola*) germplasm have enormous potential from this viewpoint. Their more intensive exploitation in resistance research and breeding is primarily based on increasing number of wild *Lactuca* accessions from various eco-geographical areas (Lebeda et al., 2004a, b).

Biochemical features (chemical compounds)

Current research of *Lactuca* germplasm is also focusing on detection and characterization of some chemical compounds (e.g. sesquiterpene lactones, phenolics and glucosides) of pharmacological importance (Kisiel and Barszcz, 1998; Kisiel and Zielinska, 2000). This aspect has been underestimated till now however that there is increasing potential for utilization, at least of some *Lactuca* germplasm, in further medicinal research and pharmacological purposes (Chen et al., 2007; Kim et al., 2007).

Protein and molecular polymorphism

The status of characterization of *Lactuca* spp. germplasm by protein and molecular markers was summarized by Dziechciarková et al. (2004a) and Lebeda et al. (2007b). Various methods and approaches have been applied for this purpose, however, only relatively limited number of species and accessions have been analysed (mostly same sets of accessions from a few germplasm collections) (e.g. Jansen et al., 2006). More detailed population studies are needed to define various relationships between eco-geographical distribution of *Lactuca* spp. and their genetic polymorphism. Recently some of these studies (e.g. for *L. saligna, L. serriola*) are in progress (Dziechciarková et al., 2004b; Kitner et al., 2008; Kuang et al., 2008).

Conclusions and future prospects

Despite enormous progress in research of wild *Lactuca* germplasm, the recent review demonstrated many gaps in our knowledge and understanding of various aspects related to this topic. As the most crucial points could be considered:

1) Complex taxonomic and phylogenetic treatment of the genus *Lactuca* L.;

2) Detailed floristic, bio-geographic and ecologic delimitation of distribution of known *Lactuca* spp.;

3) Clarification of the structure of *Lactuca* gene pools;

4) Reconsideration of germplasm collections structure from the viewpoint of quality and quantity;

5) Collecting and exploration missions, esp. to the areas of high species richness and diversity (e.g. South Africa and Asia);

6) Enlargement of activities focused on complex characterization and evaluation with importance not only for management of wild *Lactuca* gene bank collections, however also for their efficient utilization in lettuce breeding;

7) Broad international cooperation of different institutions, incl. Bioversity International.

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References

Beharav, A.; Lewinsohn, D.; Lebeda, A.; Nevo, E. 2006. New wild *Lactuca* genetic resources with resistance against *Bremia lactucae*. Genet. Res. Crop Evol. 53:467-474.

Beharav, A.; Ben-David, R.; Doležalová, I.; Lebeda, A. 2008. Eco-geographic distribution of *Lactuca saligna* populations in Israel: their collection and basic characterization for further research of intraspecific variability. Israel J. Plant Sci. (submitted)

Bennett, M.D.; Leitch, I.J. 1995. Nuclear DNA amounts in angiosperms. Ann. Bot. 76:113-176.

Boukema, I.W.; Hazekamp, Th.; van Hintum, T.J.L. 1990. The CGN Collections Reviews; The CGN Lettuce Collection. Centre for Genetic Resources, Wageningen, the Netherlands.

Chen, Y.H.; Chen, H.Y.; Hsu, C.L.; Yen, G.C. 2007. Induction of apoptosis by the *Lactuca indica* L. in human leukemia cellline and its active components. J. Agric. Food Chem. 55:1743-1749.

Doležalová, I.; Křístková, E.; Lebeda, A.; Vinter, V. 2002a. Description of morphological characters of wild *Lactuca* L. spp. genetic resources (English-Czech version). Hort. Sci. (Prague) 29:56-83.

Doležalová, I.; Křístková, E.; Lebeda, A.; Vinter, V.; Astley, D.; Boukema, I.W. 2003. Basic morphological descriptors for genetic resources of wild *Lactuca* spp. Plant Genet. Res. Newsl. 134:1-9.

Doležalová, I.; Lebeda, A.; Janeček, J.; Číhalíková, J.; Křístková E.; Vránová, O. 2002b. Variation in chromosome numbers and nuclear DNA contents in genetic resources of *Lactuca* L. species (Asteraceae). Genet. Resour. Crop Evol. 49:383-395.

Doležalová, I.; Lebeda, A.; Křístková, E. 2001. Prickly lettuce (*Lactuca serriola* L.) germplasm collecting and distribution study in Slovenia and Sweden. Plant Genet. Res. Newsl. 128:41-44.

Doležalová, I.; Lebeda, A.; Křístková, E.; Novotná, A. 2005. Morphological variation of *Lactuca serriola* populations from some European countries. In. Abstracts, p. 548. XVII International Botanical Congress, 17-23 July 2005,Vienna, Austria.

Doležalová, I.; Lebeda, A.; Křístková, E.; Novotná, A. 2007a. Relevance of morphologic assessment of wild Lactuca spp. germplasm for their taxonomic determination. Bulletin of Botanical Gardens, Museums & Collections, Polish Botanical Society 16A:22.

Doležalová, I.; Lebeda, A.; Novotná, A.; Kršková, M. 2007b. Variation in fruit morphology of *Lactuca serriola* populations from Czech Republic, Germany, Netherlands and United Kingdom, p. 8. In:Eucarpia Leafy Vegetables 2007 Conference Abstracts, 18-20 April 2007, Warwick HRI, Wellesbourne.

Doležalová, I.; Lebeda, A.; Tiefenbachová, I.; Křístková, E. 2004. Taxonomic reconsideration of some *Lactuca* spp. germplasm maintained in world genebank collections. Acta Hort. 634:193-201.

Dziechciarková, M.; Lebeda, A.; Doležalová, I.; Astley, D. 2004a. Characterization of *Lactuca* spp. germplasm by protein and molecular markers – a review. Plant Soil Environ. 50:47-58.

Dziechciarková, M.; Lebeda, A.; Doležalová, I.; Křístková, E., 2004b. Isozyme variation in European *Lactuca serriola* germplasm. pp. 103-107. In: Vollmann, J., Grausgruber, H., Ruckenbauer, P.(eds.), Genetic variation for plant breeding. Proceedings of the 17th Eucarpia General Congress, 8-11 September 2004, Tulln, Austria. BOKU-University of Natural Resources and Applied Life Sciences, Vienna, Austria.

Feráková, V. 1977. The genus *Lactuca* L. in Europe. Univerzita Komenského, Bratislava, Czechoslovakia.

Funk, V.A.; Bayer, R.J.; Keeley, S.; Chan, R.; Watson, L.; Gemeinholzer, B., Schilling, E.; Panero, J.L.; Baldwin, B.G.; Garcia-Jacas, N.; Susanna, A.; Jansen, R.K. 2005. Everywhere but Antarctica: Using a supertree to understand the diversity and distribution of the Compositae. Biol. Skr. 55:343-374.

Gass, T.; Frese, L. (eds.). 1999. Implementation of the global plan of action in Europe – Conservation and sustainable utilization of plant genetic resources for food and agriculture. Proc. of the European Symp., 1998, Braunschweig (Germany). Int. Plant Gen. Res. Ins. (IPGRI), Rome, Italy.

Guarino, L.; Rao, R.V.; Reid, R. (eds.). 1995. Collecting plant genetic diversity. Technical Guidelines. CAB International, Wallingford, UK.

Hintum, T.J.L.; Boukema, I.W. 1999. Genetic resources of leafy vegetables, pp. 59-72. In:Lebeda, A.; Křístková, E. (eds.), Eucarpia Leafy Vegetables ´99. Proceedings of the Eucarpia Meeting on Leafy Vegetables Genetics and Breeding. Palacký University Olomouc, Olomouc, Czech Republic.

Jansen, J.; Verbakel, H.; Peleman, J.; van Hintum, Th.J.L. 2006. A note on the measurement of genetic diversity within genebank accessions of lettuce (*Lactuca sativa* L.) using AFLP markers. Theor. Appl. Genet. 112:554-561.

Kim, K.H.; Kim, Y.H.; Lee, K.R. 2007. Isolation of quinic acid derivatives and flavonoids from the aerial parts of *Lactuca indica* L. and their hepatoprotective activity in vitro. Bioorg. Medic. Chem. Lett. 17:6739-6743.

Kisiel, W.; Barszcz, B. 1998. A germacrolide glucoside from *Lactuca tatarica*. Phytochemistry 48:205-206.

Kisiel , W.; Zielinska, K. 2000. Sesquiterpenoids and phenolics from *Lactuca perennis*. Fitoterapia 71:86-87.

Kitner, M.; Lebeda, A.; Doležalová, I.; Maras, M.; Křístková, E.; Beharav, A.; Nevo, E.; Pavlíček, T.; Meglic, V. 2008. AFLP analysis of *Lactuca saligna* germplasm collections from four European and three Middle East countries. Israel J. Plant Sci. (in press)

Koopman, W.J.M. 1999. Plant systematics as useful tool for plant breeders, examples from lettuce, pp. 95-105. In: Lebeda, A.; Křístková, E. (eds.), Eucarpia Leafy Vegetables ´99, Proceedings of the Eucarpia Meeting on Leafy Vegetables Genetics and Breeding, Palacký University in Olomouc, Olomouc, Czech Republic.

Koopman, W.J.M. 2000. Identifying lettuce species (*Lactuca* subs. *Lactuca*, Asteraceae). A practical application of flow cytometry. Euphytica 116:151-159.

Koopman, W.J.M. 2002. Zooming in on the lettuce genome: Species relationships in *Lactuca* s.l. inferred from chromosomal and molecular characters. Ph.D. diss., Wageningen University, The Netherlands.

Koopman, W.J.M.; Guetta, E.; Van de Wiel, C.C.M.; Vosman, B.; Van den Berg, R.G. 1998. Phylogenetic relationships among *Lactuca* (Asteraceae) species and related genera based on ITS-1 DNA sequences. Amer. J. Bot. 85:1517-1530.

Koopman, W.J.M.; De Jong, H.J. 1996. A numerical analysis of karyotypes and DNA amounts in lettuce cultivars and species (*Lactuca* subsp. *Lactuca*, Compositae). Acta Bot. Neerl. 45:211-222.

Křístková, E.; Doležalová, I.; Lebeda, A.; Vinter, V.; Novotná, A. 2008. Description of morphological characters of lettuce (*Lactuca sativa* L.) genetic resources. Hort. Sci. (Prague) (in press)

Křístková, E.; Lebeda, A. 1999. Collection of *Lactuca* spp. genetic resources in the Czech Republic. pp.109-116. In: Lebeda, A.; Křístková, E. (eds.), Eucarpia Leafy Vegetables '99. Proceedings of the Eucarpia Meeting on Leafy Vegetables Genetics and Breeding, Olomouc, Czech Republic, 8-11 June 1999, Palacký University Olomouc.

Křístková, E.; Lebeda, A.; Doležalová, I. 2001. Collecting and evaluating of *Lactuca serriola* germplasm in Europe, pp. 49-52. In: Swiecicki, W.; Naganowska, B.; Wolko, B. (eds.), Broad variation and precise characterization – Limitation for the future. Eucarpia, Section Genetic Resources, Poznań, Poland.

Křístková, E.; Lebeda, A.; Doležalová, I. 2007a. Phenotypic variability of *Lactuca saligna* germplasm collected in Italy and France. p.15. In: Eucarpia Leafy Vegetables 2007, Conference Abstracts, 18-20 April 2007, University of Warwick, Warwick HRI, UK, 2007; Poster Presentations.

Křístková, E.; Lebeda, A.; Doležalová, I.; Vinter, V.; Křístková, A. 2007b. Variation in developmental stages of *Lactuca serriola* L. (prickly lettuce) germplasm from different European countries. p. 16. In: Eucarpia Leafy Vegetables 2007, Conference Abstracts, 18-20 April 2007, University of Warwick, Warwick HRI, UK, 2007; Poster Presentations.

Kuang, H.; van Eck, H.J.; Sicard, D.; Michelmore, R.; Nevo, E. 2008. Evolution and genetic population structure of prickly lettuce (*Lactuca serriola*) and its *RGC2* resistance gene cluster. Genetics 178: (in press)

Lebeda, A.; Astley, D. 1999. World genetic resources of *Lactuca* spp., their taxonomy and biodiversity. pp. 81-94. In: Lebeda, A.; Křístková, E. (eds.), Eucarpia Leafy Vegetables '99. Proceedings of the Eucarpia Meeting on Leafy Vegetables Genetics and Breeding. Palacký University Olomouc, Olomouc, Czech Republic.

Lebeda, A.; Boukema, I.W. 2005. *Ad hoc* meeting on leafy vegetables. pp. 82-94. In: Thomas, G.; Astley, D.; Boukema, I.W; Daunay, M.C.; Del Greco, A.; Diez, M.J.; van Dooijweert, W.; Keller, J.; Kotlińska, T.; Lebeda, A.; Lipman, E.; Maggioni, L.; Rosa E. (comp.), Report of a Vegetable network. Joint Meeting with an *ad hoc* group of Leafy vegetables, 22–24 May 2003, Skierniewice, Poland. International Plant Genetic Resources Institute, Rome, Italy.

Lebeda, A.; Doležalová, I.; Astley, D. 2004a. Representation of wild *Lactuca* spp. (Asteraceae, Lactuceae) in world genebank collections. Gen. Resour. Crop Evol. 51:167-174.

Lebeda, A.; Doležalová, I.; Feráková, V.; Astley, D. 2004b. Geographical distribution of wild *Lactuca* spp. (Asteraceae, Lactuceae). The Botanical Rev. 70:328-356.

Lebeda, A.; Doležalová, I.; Janeček, J.; Gasmanová, N. 2004c. Differences in relative DNA content of *Lactuca serriola* germplasm collected in Europe, pp. 29-30. In:Summaries and

Program, 17th International Lettuce and Leafy Vegetable Conference, 28-31 August 2004, Sandman Hotel, Montreal-Longueuil. Agriculture and Agri-Food Canada.

Lebeda, A.; Doležalová, I.; Křístková, E.; Dehmer, K.J.; Astley, D.; Van de Wiel, C.C.M.; Van Treuren, R. 2007a. Acquisition and ecological characterization of *Lactuca serriola* L. germplasm collected in the Czech Republic, Germany, the Netherlands and United Kingdom. Gen. Resour. Crop Evol. 54:555-562.

Lebeda, A.; Doležalová, I.; Křístková, E.; Mieslerová, B. 2001. Biodiversity and ecogeography of wild *Lactuca* spp. in some European countries. Gen. Resour. Crop Evol. 48:153-164.

Lebeda, A.; Doležalová, I.; Křístková, E.; Novotná, A. 2007b. Comparative study of variation of some morphological characteristics of *Lactuca serriola* germplasm collected in Central Europe (Czech Republic) and the British Isles (England, U.K.). pp. 95-96 (Abstract). In:Bullitta, S. (ed.), Plant genetic resources of geographical and „other" islands (conservation, evaluation and use for plant breeding). Proceedings of the XVII Eucarpia Genetic Resources Section Meeting; 30 March – 2 April 2005, Castelsardo, Italy.

Lebeda, A.; Petrželová, I. 2004. Occurrence of race-specific resistance to *Bremia lactucae* in *Lactuca serriola* germplasm originating from four European countries, pp. 113-116. In:Vollmann, J., Grausgruber, H., Ruckenbauer, P. (eds.), Genetic variation for plant breeding. Proceedings of the 17th EUCARPIA General Congress, 8-11 September 2004, Tulln, Austria. BOKU-University of Natural Resources and Applied Life Sciences, Vienna, Austria.

Lebeda, A.; Petrželová, I.; Maryška, Z. 2008. Structure and variation in the wild-plant pathosystem: *Lactuca serriola - Bremia lactucae*. Europ. J. Plant Pathol. (in press)

Lebeda, A.; Pink, D.A.C.; Astley, D. 2002. Aspects of the interactions between wild *Lactuca* spp. and related genera and lettuce downy mildew (*Bremia lactucae*), pp. 85-117. In:Spencer-Phillips, P.T.N.; Gisi, U.; Lebeda, A. (eds.), Advances in downy mildew research. Dordrecht, Kluwer Academic Publishers.

Lebeda, A.; Ryder, E.J.; Grube, R.; Doležalová, I.; Křístková, E. 2007c. Lettuce (Asteraceae; Lactuca spp.), Chapter 9, pp. 377-472. In:Singh, R. (ed.), Genetic resources, chromosome engineering, and crop improvement Series, Volume 3 – Vegetable Crops. CRC Press, Boca Raton, FL, USA.

Lebeda, A.; Zinkernagel, V. 2003. Characterization of new highly virulent German isolates of *Bremia lactucae* and efficiency of resistance in wild *Lactuca* spp. germplasm. J. Phytopathol. 151: 274-282.

McGuire, P.E.; Ryder, E.J.; Michelmore, R.W.; Clark, R.L.; Antle, R.; Emery, G.; Hannan, R.W.; Kesseli, R.V.; Kurtz, E.A.; Ochoa, O.; Rubatzky, V.E.; Waycott, W. 1993. Genetic resources of lettuce and *Lactuca* species in California. An assessment of the USDA and UC collections and recommendations for long-term security. Report no. 12. University of California, Genetic Resources Conservation Program, Davis, USA.

Mou, B. 2008. Lettuce, pp. 75-116. In:Prohens, J., Nuez, F. (eds.), Handbook of plant breeding. Vegetables I. Asteraceae, Brassicaceae, Chenopodiaceae, and Cucurbitaceae. Springer Science, New York.

Petrželová, I.; Lebeda, A.; Nevo, E.; Beharav, A. 2007. Variation of response against *Bremia lactucae* in natural populations of *Lactuca saligna*, pp. 169-173. In:Lebeda, A.; Spencer-Phillips, P.T.N. (eds.), Advances in downy mildew research, Vol. 3. Proceedings of the 2nd International Downy Mildews Symposium. Palacký University in Olomouc and JOLA, v.o.s., Kostelec na Hané (Czech Republic).

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Wild *Lactuca* germplasm for lettuce breeding: current status, gaps and challenges

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Abstract In this review, we present a critical analysis of the current status of wild *Lactuca* L. germplasm in relation to its utility for lettuce breeding. We discuss wild *Lactuca* germplasm in ex situ collections from the perspectives of taxonomy, biogeography, biology and ecology, gene pools, field exploration and acquisition, descriptor development, characterization and evaluation, and enhancement. Future research and other activities related to wild *Lactuca* germplasm and their continued exploitation in lettuce breeding are considered.

Keywords Taxonomy · Biogeography · Ecology · Gene pools · Collecting · Gene banks · Duplicates · Descriptors · Genetic diversity · Phenology · DNA content · Disease resistance · Biochemical features · Molecular polymorphism

Introduction

Genetic resources of wild *Lactuca* species as conserved in the world's genebanks are an integral part of our global plant heritage, and they play important role in modern lettuce breeding (Lebeda et al. 2007c; Mikel 2007; Maggioni et al. 2008; Mou 2008). Considerable progress in both fundamental research on *Lactuca* germplasm and its practical applications has been achieved during last 25 years (Lebeda et al. 2007c). The most important remaining gaps, problems and sources of confusion related to the effective use of these key resources are highlighted in this paper along with a recent progress report.

Taxonomy of *Lactuca* L.

Taxonomic and phylogenetic studies clearly place the genus *Lactuca* L. in the tribe Lactuceae, subfamily Cichorioideae, of the Compositae (Asteraceae) (Funk et al. 2005), one of the largest plant families. A careful review of published literature confirmed the existence of about 100 wild *Lactuca* spp., with the highest number of autochthonous species and species richness in Asia (51 species) and Africa (43 species) (Lebeda et al. 2004b). The most recent molecular data on phylogenetic relationships among *Lactuca* species (Koopman et al. 1998) confirmed, with some modifications, a previously elaborated broader generic concept (summarized by Lebeda et al. 2007c). However, formal classification, including subgeneric divisions (Lebeda et al. 2007c), need critical reconsideration and further elaboration.

In addition, serious taxonomic discrepancies can be found in the main world collections of *Lactuca* L.

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germplasm. Doležalová et al. (2004) studied 49 accessions of 24 *Lactuca* species received from the main world genebanks. It was found, after taxonomic review, that 35% of accessions were wrongly taxonomically described and were redetermined (on the genus, species and subspecific level). Therefore, good knowledge of classical taxonomy combined with the comparative study of original herbarium specimens must be considered as a most important step for the efficient management and utilization of *Lactuca* genetic resources (Lebeda et al. 1999), and correct interpretation of experimental data (Lebeda et al. 2002).

Geographic distribution and hot-spots of diversity

There is increasing interest in the potential value of genes from wild species in crop improvement (Gass and Frese 1999). For lettuce, there are two crucial issues related to the utilization of genes from wild species: loss of genetic diversity in situ and limited access to wild *Lactuca* in current ex-situ germplasm collections (Lebeda et al. 2004a, 2007c). To overcome these challenges, genebanks should focus on rapidly acquiring lettuce progenitors and wild relatives from the probable center of origin of lettuce and from those areas with the highest genetic diversity of *Lactuca* species (Lebeda et al. 2004c). High levels of diversity of *Lactuca* species found in the Mediterranean basin and southwestern Asia indicate that those regions should be seriously considered as hot-spots for lettuce conservation (Beharav et al. 2008a, b; Kitner et al. 2008; Lebeda et al. 2001b, c, 2008d). Future ecogeographic studies should also focus on central and southern Africa, central Asia, and North America to determine if other hot-spots exist and to develop collecting strategies accordingly (Lebeda et al. 2007c) (Fig. 1).

Biology and ecology

The genus *Lactuca* includes annual, biennial and perennial herbs, and rarely shrubs, with abundant latex. Sections *Phoenixopus*, *Mulgedium*, *Lactucopsis*, *Tuberosae*, *Micranthae* and *Sororiae* (see Table 1) are mostly biennial or perennial (Lebeda and Astley 1999). The division of section *Lactuca* into two subsections, *Lactuca* and *Cyanicae*, is based on

Fig. 1 Geographical distribution of diversity hot-spots of wild *Lactuca* species

Table 1 Sections, subsections and geographical groups of *Lactuca* genetic resources (modified following Lebeda et al. 2004b, 2007c)

Sections/subsections
Lactuca
subsect. *Lactuca* (*L. aculeata*, *L. altaica*, *L. azerbaijanica*, *L. dregeana*, *L. georgica*, *L. livida*, *L. saligna*, *L. sativa*, *L. scarioloides*, *L. serriola*, *L. virosa*)
subsect. *Cyanicae* DC. (*L. perennis*, *L. tenerrima*)
Phaenixopus (Cass.) Bentham (*L. viminea*)
Mulgedium (Cass.) C.B. Clarke (*L. tatarica*, *L. sibirica*, *L. taraxacifolia*)
Lactucopsis (Schultz Bip. ex Vis. et Pančić) Rouy (*L. quercina*)
Tuberosae Boiss. (*L. indica*)
Micranthae Boiss. (*L. undulata*)
Sororiae Franchet (*L. sororia*)
Groups (geographical view)
North American (e.g. *L. biennis*, *L. canadensis*, *L. floridana*, *L. graminifolia*)
African (e.g. *L. capensis*, *L. dregeana*, *L. homblei*)

the life cycle of their members (Feráková 1977). Subsection *Lactuca* comprises annual, winter annual or biennial herbs; perennial species belong to subsection *Cyanicae*. The autochthonous North American species are mostly biennial; however, at least one perennial species, *L. tatarica* subsp. *pulchella* (syn. *L. oblongifolia*), is also reported (McGregor et al. 1986). The African species are annual or perennial herbs or sub-shrubs, rarely scandent (Lebeda et al. 2004b).

The genus *Lactuca* comprises species with various ecological requirements occupying diverse habitats. The species of lettuce's genepool (those of the breeders' main interest), *L. serriola*, *L. saligna* and *L. virosa*, are weedy and occur on waste places and ruderal habitats—mainly along roads, highways and ditches (Lebeda et al. 2001b, c, 2004b, 2007a) (Fig. 2). Most species, i.e. *L. perennis*, *L. viminea*, *L. graeca*, and *L. tenerrima*, are calciphilous plants found in limestone and dolomite areas, often on rocky slopes. Endemic, lianalike species are found in rain forests of East Africa. Comprehensive surveys regarding the biology and ecology of European *Lactuca* species were conducted by Feráková (1977) and Lebeda et al. (2004b), who summarized available information on about 100 species from current world literature. However, basic data about the biology and ecology of most species, especially those of African and Asian origin, are still unavailable.

Gene pools and genetic diversity

Human effort in the process of domestication probably involved selection of wild relatives for leaves that had a reduction in leaf spines, latex content and bitter flavor, and for plants with delayed bolting. Domestication has also led to a shortening of internodes, bunching of leaves, increased seed size and non-shattering (Fig. 3), and changes in photoperiodism (enabling cultivation under various daylengths). These processes have been accompanied by bottlenecks that restricted the genetic diversity available in the primary gene pool.

In general, the primary gene pool of cultivated lettuce comprises the numerous cultivars and landraces of *L. sativa* and its wild ancestor, *L. serriola*. The wild *serriola*-like species from southwestern Asia (i.e., *L. aculeata*, *L. altaica*, *L. azerbaijanica*, *L. georgica*, and *L. scarioloides*) and the African species, *L. dregeana*, all display similar levels of interfertility with the crop and belong to the primary gene pool as well (Lebeda et al. 2007c). Although *L. saligna* and *L. virosa* have been intensively studied by both evolutionary biologists and plant breeders, their categorization to the secondary or tertiary gene pools has remained an open question (Fig. 4). A view rather different from that outlined above was proposed by Koopman et al. (1998), who suggested that section *Lactuca* subsection *Lactuca* comprises the primary and secondary gene pools, while sections *Phaenixopus*, *Mulgedium* and *Lactucopsis* make up the tertiary gene pool. However, the categorization of many *Lactuca* species into gene pools is still unclear and needs additional attention.

Germplasm collections—recent status and problems

Collections, their structure and gaps

Data describing wild *Lactuca* germplasm collections in Europe and around the world were summarized by Lebeda and Boukema (2001) and Lebeda et al.

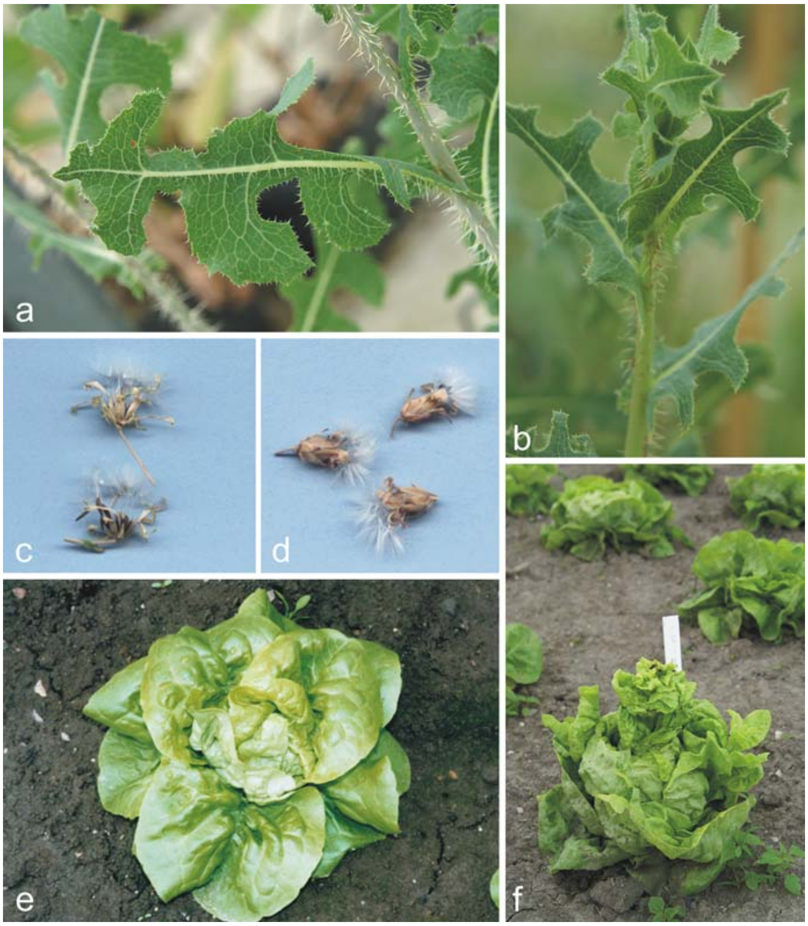
Fig. 2 Examples of *L. serriola* habitats: agricultural areas (**a**, **d**), piles of debris (**b**), urban areas—sterile substrate (**c**), pavement (**e**), along transport corridors—roadside (**f**), fallow lands—"*Lactuca* fields" (**g**)

(2007c), and information concerning the exploitation of these wild relatives in commercial lettuce breeding has been summarized by Lebeda et al. (2007c) and Mou (2008). From these reports, it is clear that there are only few important collections in Europe (ca. 5) and the USA (ca. 3). In geographic centres of high species richness and diversity there are no significant germplasm collections with local accessions. Analysis of the International *Lactuca* Database (ILDB) showed that over 90% of wild collections are represented by only three species, *L. serriola*, *L. saligna*, and *L. virosa*, mostly of European origin. The autochthonous species from other continents (Asia, Africa, and the Americas), which form ca. 83% of known *Lactuca* species richness (Lebeda et al. 2004b), are represented in collections by only about 3% of the accessions (Lebeda et al. 2004a). Recently, Pandey et al. (2008) collected 373 species of wild crop relatives representing 120 genera and 48 families in the Indian gene centre; however, they made no mention of lettuce nor of its wild relatives. This example illustrates the underrepresentation of wild *Lactuca* species in recent collecting activities, which is a crucial feature needing attention for the future development of these collections (Lebeda et al. 2007c; Beharav et al. 2008b).

Taxonomic status of accessions and duplicates

The correct use of botanical nomenclature and, more importantly, the accurate taxonomic identification of genebank accessions are core tasks for the effective

Fig. 3 Domestication of lettuce involved selection against latex content (**a**), leaf and stem spines (**a**, **b**), increase in seed size and non-shattering seeds (**c**, **d**), shortening of internodes, bunching of leaves (**e**), and selection for late bolting (**f**); **a**,**b**,**c** *L. serriola*; **d**,**e**,**f** *L. sativa*



management and utilization of plant genetic resources. Insufficient or incorrect passport data, including taxonomic identification, complicate the evaluation of accessions (van Hintum and Boukema 1999; Lebeda et al. 2007c; Rajicic and Dehmer 2008), and make it more difficult to preserve genetic integrity, reduce collection redundancy, and interpret research findings.

Basic errors in the taxonomic status of accessions as reported by genebanks have been found repeatedly. When evaluating a set of 49 accessions of 24 wild *Lactuca* species for morphological characters, chromosome number, relative DNA content and isozyme polymorphisms, 17 accessions were reclassified and/or their taxonomic status criticized (Doležalová et al. 2004). Within a set of 95 accessions provided by gene banks in the Czech Republic, Germany, Netherlands, UK and the USA, nominally representing 12 species (*L. aculeata*, *L. altaica*, *L. dentata*, *L. dregeana*, *L. indica*, *L. livida*, *L. perennis*, *L. quercina*, *L. saligna*, *L. serriola*, *L. tatarica* and *L. virosa*), a morphological assessment confirmed the taxonomic identities of only 50 accessions; 31 accessions were re-determined (Lebeda et al. 2007d). Examples are given in Fig. 5. The remaining 14 accessions represented mixtures of *L. serriola* forms, mixtures of different *Lactuca* species, and interspecific hybrids (Doležalová et al. 2007a) (Fig. 6).

An understanding of accession redundancy/duplication within and among genebanks is another important aspect of efficient plant genetic resource management (Spooner et al. 2005). Comparison of passport data from four large *Lactuca* collections

Fig. 4 Wild *Lactuca* species involved in lettuce improvement: **a** cultivated *L. sativa*; wild species, **b** *L. serriola* f. *serriola*, **c** *L. serriola* f. *integrifolia*, **d** *L. saligna*, **e** *L. aculeata*, **f** *L. virosa*

(CGN, WRPIS, IPK and HRI) showed that 60% of 95 accessions are duplicated at least once among these collections (van Hintum and Boukema 1999). A morphological assessment of the abovementioned set of 95 *Lactuca* species accessions identified 34 duplicate groups on the basis of passport data, and showed that 69 accessions can be considered as morphological duplicates (Doležalová et al. 2007a; Lebeda et al. 2007d).

Field studies and collection activities

An increasing interest in determining the geographic distribution of wild *Lactuca* populations and sampling those populations in natural habitats resulted in the initiation of collection expeditions coordinated by the Department of Botany, Palacký University in Olomouc (Czech Republic) beginning in the early 1990s. From 1995 to 2008, expeditions were conducted in 14 European countries (Austria, Croatia, the Czech Republic, France, Hungary, Germany, Greece, Italy, Lithuania, The Netherlands, Slovakia, Slovenia, Spain, Sweden, Switzerland, the United Kingdom), 15 states of the USA (Arizona, California, Colorado, Idaho, Iowa, Nevada, North Carolina, Minnesota, Montana, Oregon, South Dakota, Utah, Washington, Wisconsin, Wyoming), and Canada. Field studies and germplasm collections were also made in Turkey, Israel, Jordan, Kazakhstan, South Korea, New Zealand and South Africa (Fig. 7). Collectively, these efforts have resulted in the collection of nearly 1,300 seed samples of 12 wild *Lactuca* species (Křístková and Lebeda 1999; Doležalová et al. 2001; Křístková et al. 2001; Lebeda et al. 2001b, c, 2007e; Beharav et al. 2008b; Doležalová et al. 2008).

Expeditions to collect *L. serriola* germplasm in four European countries were conducted within the

Fig. 5 Redetermination of accessions received from main world gene banks (RICP, IPK, GNG, HRI, WG, LET), on the genus level **a** *L. dentata* (acc. PI 234204 LET) re-determined as *Sonchus oleraceus*; and on species level, **b** *L. livida* (acc. RICP09H5801127) re-determined as *L. dregeana*

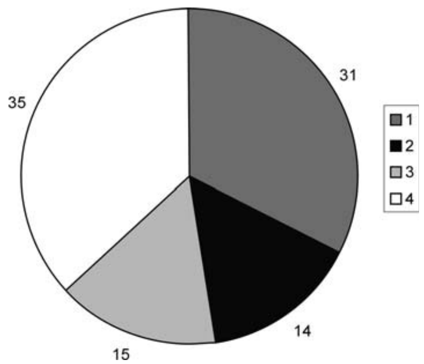


Fig. 6 Taxonomic status of a set of 95 *Lactuca* species accessions representing 12 species received from main world gene banks (RICP, IPK, GNG, HRI, WG, LET). 1) plants of 31 morphologically uniform accessions, their taxonomic status re-determined; 2) 14 accessions represented by mixtures of *L. serriola* forms, different *Lactuca* species or interspecific hybrids; 3) taxonomic status of 15 accessions of *L. serriola* completed by determination of a lower taxonomic unit (f. *serriola*, f. *integrifolia*); 4) plants of 35 morphologically uniform accessions, their declared taxonomic status confirmed

framework of the EU-funded project "GENE-MINE" in 2001 (Lebeda et al. 2007a). The seed material (800 accessions from 50 locations) was used for regeneration, inclusion in national genebanks in the respective countries, and research purposes in follow-up studies (e.g., Lebeda and Petrželová 2004a; Lebeda et al. 2008a).

In cooperation with the Institute of Evolution (University of Haifa, Israel), expeditions focusing on the wild species, *L. saligna*, were conducted in 2004–2007 in Israel (Beharav et al. 2008a, b), following international standards for germplasm acquisition (Guarino et al. 1995) designed in a manner to avoid the collection of duplicates (van Hintum and Boukema 1999; Lebeda et al. 2004a).

Descriptor development

Precise descriptions of genetic resources serve as tool for their correct taxonomic determination and help define both interspecific and intraspecific variation (Lebeda et al. 2007b). A basic international descriptor list has been described for the genetic resources of *L. sativa* and of *L. serriola* and related species from the primary gene pool by a representatives of European genebanks within the activities of the European Cooperative Programme (ECP/GR), Working Group of Leafy Vegetables (Lebeda and Boukema 2005; Maggioni et al. 2008). In addition, an international list of the most important morphological characters of wild *Lactuca* species was created through the EU-funded project "GENE-MINE" (Doležalová et al. 2003a).

There have also been national descriptor lists published for the characterization of major *Lactuca* collections, including those from the Centre for Genetic Resources (CGN, Wageningen, The Netherlands) (Boukema et al. 1990), the Western Regional Plant Introduction Station (Pullman, Washington, USA) (McGuire et al. 1993), and the National Programme of Conservation and Utilization of Plant Genetic Resources of the Czech Republic for both cultivated lettuce (*Lactuca sativa* L.) (Křístková et al. 2008) and wild species (Doležalová et al. 2002a).

As descriptor lists for cultivated lettuce are developed or revised, serious consideration should be given to the inclusion of phenotypic traits of the wild *Lactuca* species being used to breed new lettuce

Fig. 7 Field studies and collecting activities coordinated by the Department of Botany, PU Olomouc, Czech Republic

cultivars. Because of these breeding efforts, during last decade new lettuce cultivars have been released with characteristics that do not conform to earlier groups of morphotypes.

Characterization and evaluation of wild *Lactuca* germplasm

Morphology

Morphological assessment of accessions can be performed during their regeneration by genebanks (Doležalová et al. 2002a, 2003a; Křístková et al. 2008), but this can have serious limitations, as the expression of morphological traits under controlled, regeneration conditions may differ significantly from expression under typical field conditions. Detailed studies of morphological variation have been performed for collections of *L. serriola* and *L. saligna*. Fifty *L. serriola* populations collected in four European countries (Czech Republic, Germany, The Netherlands, United Kingdom) (Lebeda et al. 2007a) were cultivated in a greenhouse under controlled conditions. Assessment included 26 quantitative and qualitative characters of stems (e.g., stem length), rosette and cauline leaves (e.g., depth of incisions) (Fig. 8), inflorescences and flowers (e.g., anthocyanin coloration on bracts) (summarized in Lebeda et al. 2007b), and fruits (e.g., length and width of achene body, length of achene beak and number of ribs) (Doležalová et al. 2007b) (Fig. 9). A similar morphological assessment was performed for about 70 populations of *L. saligna* from Czech Republic, France, Italy, Portugal, Israel, Jordan and Turkey (Křístková et al. 2007a; Beharav et al. 2008a, b). These studies revealed considerable (and previously unremarked) phenotypic variation, which must be seriously considered in future research and characterization activities with wild *Lactuca* germplasm, especially in relation to genotyping.

Phenology

The genus *Lactuca* is extremely variable in terms of phenology and plant development. Among developmental characteristics, substantial differences in time of anthesis were recorded among a geographically diverse set of accessions of *L. serriola* (Doležalová et al. 2005; Lebeda et al. 2007b, c). Substantial

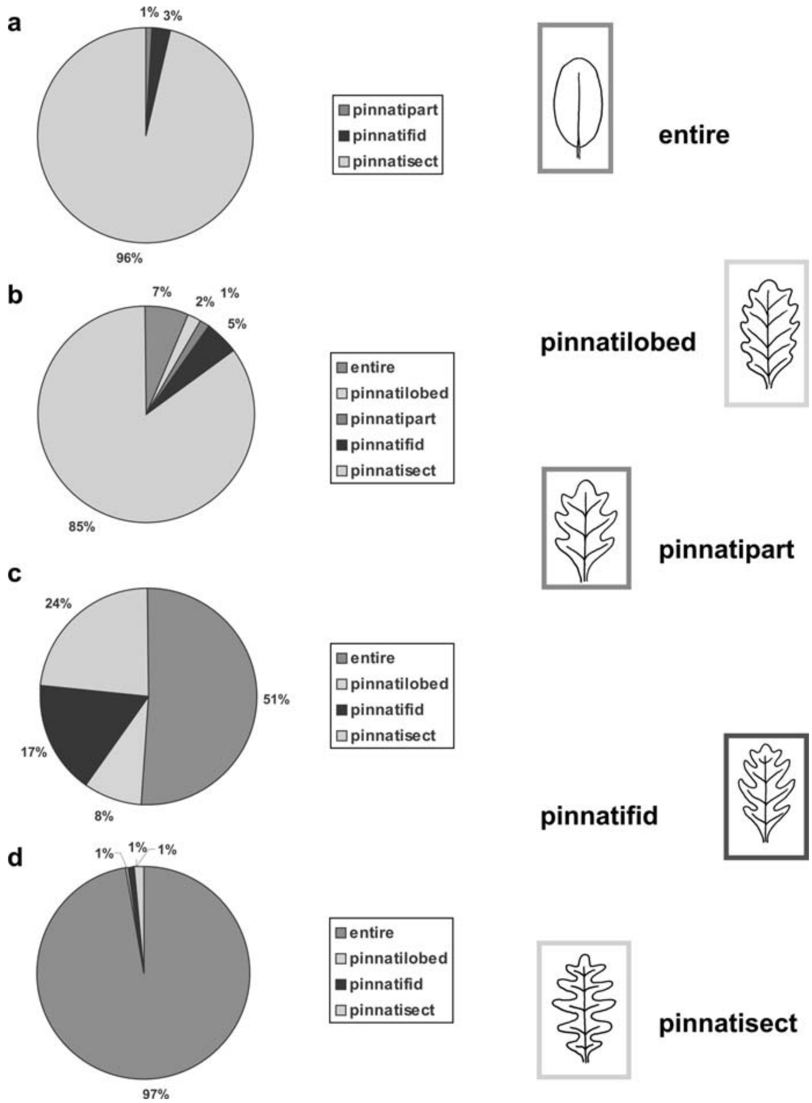


Fig. 8 Example of variability in a qualitative character. Descriptor number 1.3.7.—Divided cauline leaf—depth of incisions, fully developed leaf from the middle part of stem at a stage of full flowering of *Lactuca serriola* accessions from **a** Czech Republic, **b** Germany, **c** The Netherlands, **d** United Kingdom

differences in developmental stages (beginning of bolting and flowering) were recorded among 89 *L. serriola* samples from different ecogeographic regions in Europe when grown under common conditions in a greenhouse. Developmental stages of plants, as influenced through selective processes under the original eco-geographic conditions where they evolved (Lebeda et al. 2001b, c), can persist when plants are cultivated under common environmental conditions and may be fixed genetically (Křístková et al. 2007b).

Karyology and DNA content

Wild *Lactuca* species can be divided into three main groups, according to their base chromosome number (Feráková 1977). The first group is relatively small and contains perennial species of Europe and the Himalayas with haploid chromosome number, $n = 8$. The haploid chromosome number, $n = 9$, characterizes the majority of European and Mediterranean species, as well as species from the Middle East, Africa and India. The third group, containing of

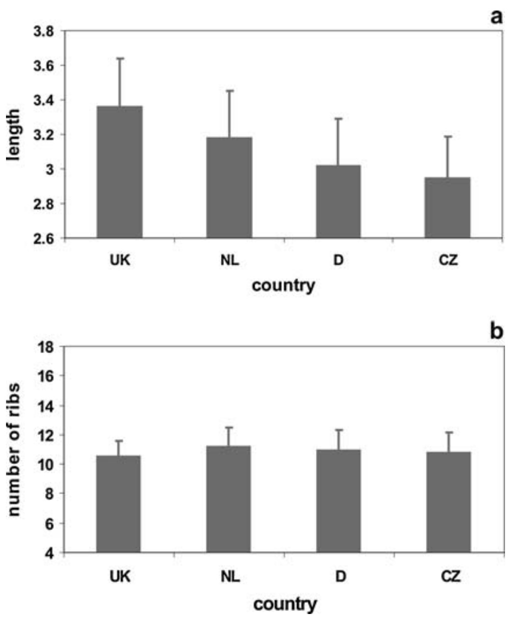


Fig. 9 Example of variability in two quantitative characters. Means of achene length (**a**) and number of ribs (**b**) of *Lactuca serriola* collected in four European countries (*CZ* Czech Republic, *D* Germany, *NL* The Netherlands, *UK* United Kingdom)

North American species distributed from Canada to Florida, is marked by a haploid chromosome number of $n = 17$. It is of amphidiploid origin and is somewhat geographically and genetically isolated. Our understanding of genus remains incomplete, because the chromosome numbers of numerous *Lactuca* species are not known (Lebeda and Astley 1999) or may differ from reported data, as was reported by Doležalová et al. (2002b) for certain North American species.

To date, analyses of variation in nuclear DNA content have been performed on only a limited number of *Lactuca* species (i.e., *L. sativa*, *L. serriola*, *L. saligna*, and *L. virosa*) (Bennett and Leitch 1995; Koopman and De Jong 1996; Koopman 1999, 2000). Flow cytometry was tested for its reliability as a tool to distinguish among *Lactuca* species (Koopman 1999, 2000). Doležalová et al. (2002b) analyzed 50 accessions of 25 *Lactuca* species, along with *Mycelis muralis*, for chromosome number and relative DNA-content variation. Later, Koopman (2002) showed that five *Lactuca* species (*L. viminea*, *L. virosa*, *L. serriola*, *L. sativa* and *L. sibirica*) have significant intraspecific variation in DNA content, but concluded that only the variation within *L. virosa* seemed to have evolutionary significance. More recent studies have focused on intraspecific differences in DNA content in *L. serriola* germplasm originating from 12 European countries (Lebeda et al. 2004c, 2007c).

Karyotype analysis and relative DNA content were used to help characterize *L. sativa*, *L. serriola*, *L. saligna* and *L. virosa* and describe their evolutionary relationships (Koopman and De Jong 1996). Matoba et al. (2007) described detailed karyotype analyses of lettuce and allied species. These analyses revealed a dissimilarity between *L. virosa* and the remaining species. The simultaneous FISH (Fluorescence in situ hybridization) of 5S and 18S rDNAs revealed that both rDNA loci of *L. sativa*, *L. serriola* and *L. saligna* were identical; however, those of *L. virosa* differed from the other species, supporting a closer relationship between *L. sativa*/*L. serriola* and *L. saligna* than with *L. virosa*.

Protein and molecular diversity

The status of characterization of *Lactuca* species germplasm by protein and molecular markers has been recently summarized by Dziechciarková et al. (2004a) and Lebeda et al. (2007c). Various methods and approaches have been applied for this purpose; however, only a relatively limited number of wild *Lactuca* species and accessions have been analysed (Table 2) (e.g., Jansen et al. 2006). More extensive studies covering a broader geographic range and a larger number of populations are needed to describe relationships between ecogeographical conditions and corresponding genetic polymorphisms. Studies of this sort for *L. saligna* and *L. serriola* are now underway (Dziechciarková et al. 2004b; Kitner et al. 2008; Kuang et al. 2006, 2008; Lebeda et al. 2008c).

Biochemical diversity

The body of research on the evaluation of *Lactuca* germplasm also includes work on the detection and characterization of secondary phytochemicals, such as sesquiterpene lactones, phenolics, glucosides, and flavonoids, of pharmacological importance (Rees and Harborne 1984; Kisiel and Barszcz 1998; Kisiel and Zielinska 2000) (Fig. 10). This aspect has probably been underestimated, but we see increasing potential

Table 2 Survey of wild *Lactuca* species characterized by isozyme analysis and molecular markers

Taxon	Method	References
L. serriola	Isozymes	Kesseli and Michelmore (1986), Cole et al. (1991), Lebeda et al. (1999, 2001a), Doležalová et al. (2003b), Mizutani and Tanaka (2003) and Dziechciarková et al. (2004b)
	RFLP	Kesseli et al. (1991) and Vermeulen et al. (1994)
	AFLP	Hill et al. (1996), Koopman et al. (2001) and Kuang et al. (2008)
	TRAP	Hu et al. (2005)
	Microsatellites	Witsenboer et al. (1997) and van de Wiel et al. (1998, 1999)
	ITS-1 DNA seq.	Koopman et al. (1998)
	SSAP	van de Wiel et al. (2004)
	NBS-profiling	van de Wiel et al. (2004) and Sicard et al. (1999)
L. saligna	Isozymes	Kesseli and Michelmore (1986), Cole et al. (1991), Lebeda et al. (1999, 2001a), Doležalová et al. (2003b) and Mizutani and Tanaka (2003)
	RFLP	Kesseli et al. (1991) and Vermeulen et al. (1994)
	AFLP	Hill et al. (1996), Jeuken et al. (2001) and Koopman et al. (2001)
	TRAP	Hu et al. (2005)
	Microsatellites	Witsenboer et al. (1997) and van de Wiel et al. (1998, 1999)
	ITS-1 DNA seq.	Koopman et al. (1998)
	NBS-profiling	Sicard et al. (1999)
L. virosa	Isozymes	Kesseli and Michelmore (1986), Cole et al. (1991), Lebeda et al. (1999, 2001a), Doležalová et al. (2003b) and Mizutani and Tanaka (2003)
	RFLP	Kesseli et al. (1991) and Vermeulen et al. (1994)
	AFLP	Hill et al. (1996) and Koopman et al. (2001)
	Microsatellites	Witsenboer et al. (1997) and van de Wiel et al. (1998, 1999)
	ITS-1 DNA seq.	Koopman et al. (1998)
	NBS-profiling	Sicard et al. (1999)
L. indica	Isozymes	Lebeda et al. (1999, 2001a), Doležalová et al. (2003b) and Mizutani and Tanaka (2003)
	RFLP	Kesseli et al. (1991)
	AFLP	Hill et al. (1996) and Koopman et al. (2001)
	Microsatellites	Witsenboer et al. (1997)
	ITS-1 DNA seq.	Koopman et al. (1998)
	NBS-profiling	Sicard et al. (1999)
L. perennis	Isozymes	Lebeda et al. (1999, 2001a) and Doležalová et al. (2003b)
	RFLP	Kesseli et al. (1991) and Vermeulen et al. (1994)
	AFLP	Hill et al. (1996) and Koopman et al. (2001)
	Microsatellites	Witsenboer et al. (1997)
	ITS-1 DNA seq.	Koopman et al. (1998)
	NBS-profiling	Sicard et al. (1999)
L. canadensis and *L. taraxacifolia*	Isozymes	Lebeda et al. (1999, 2001a) and Doležalová et al. (2003b)
L. quercina and *L. sibirica*	AFLP	Koopman et al. (2001)
	ITS-1 DNA seq.	Koopman et al. (1998)

Table 2 continued

Taxon	Method	References
L. aculeata, *L. altaica*, *L. dregeana*, *L. tatarica*, *L. tenerrima* and *L. viminea*	Isozymes	Lebeda et al. (1999, 2001a) and Doležalová et al. (2003b)
	AFLP	Koopman et al. (2001)
	ITS-1 DNA seq.	Koopman et al. (1998)

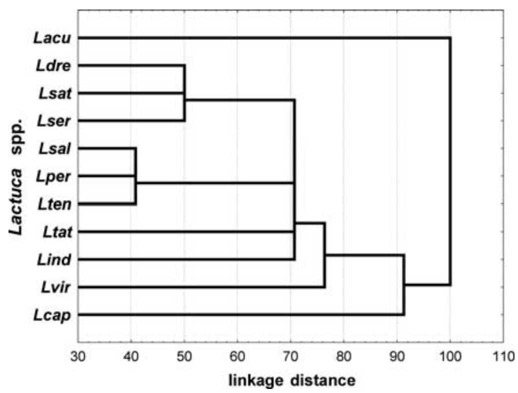


Fig. 10 A dendrogram showing clustering (Tree clustering method) of *Lactuca* species in relationship to the content of different sesquiterpene lactones in leaves [elaborated by authors on the basis of data in Michalska et al. (2008)]

for the exploitation of at least some wild *Lactuca* germplasm in medicinal and pharmacological applications (Chen et al. 2007; Kim et al. 2007). Recently, phytochemical analyses have also been applied to the clarification of taxonomical relationships among various Asteraceae (Bohm and Stuessy 2001) including *Lactuca* species (Michalska et al. 2008).

Resistance to diseases and pests

Recent advancement in research and breeding of lettuce for resistance to diseases and pests has been summarized elsewhere (Lebeda et al. 2007c; Mou 2008). Many sources of resistance to pathogens and pests have been found and described in wild *Lactuca* species (Table 3). Traditionally, *Bremia lactucae* has been considered the most important pathogen causing disease in cultivated lettuce. Limited availability of durable sources of resistance to *Bremia* has stimulated interest among breeders in new sources from wild *Lactuca* species (Lebeda et al. 2002, 2007c). Numerous reports (Lebeda and Zinkernagel 2003b; Beharav et al. 2006; Petrželová et al. 2007; Lebeda et al. 2008a) have demonstrated that wild *Lactuca* germplasm, especially of *L. saligna* and *L. serriola*, has enormous potential. More intensive exploitation of these new sources of resistance is primarily based on the increasing number of wild, characterized *Lactuca* accessions from various ecogeographical areas (Lebeda et al. 2004a, b, 2007c, 2008a, b, c). *Lactuca saligna* is currently considered to be the most important source of highly efficient resistance, which is expected to be nonhost specific (Lebeda et al. 2002; Lebeda and Zinkernagel 2003b; Petrželová et al. 2007). However, our understanding of both the mechanism (Lebeda and Reinink 1994; Lebeda and Pink 1998; Lebeda et al. 2001b, c, 2002, 2006, 2008b; Sedlářová et al. 2007a) and genetics (Jeuken and Lindhout 2002, 2004; Jeuken et al. 2001, 2008; Zhang 2008) of this resistance is still incomplete.

Conclusions and future prospects

Despite enormous progress in research on wild *Lactuca* germplasm, this review has demonstrated many important gaps in our understanding. The following list of topics can be considered as key challenges for future research and exploitation in lettuce breeding:

1. Complex taxonomic and phylogenetic relationships within the genus;
2. Detailed floristic, biogeographic and ecologic delimitation of the distributions of known *Lactuca* spp.;
3. Clarification of the structure of *Lactuca* gene pools;
4. Reconsideration of germplasm collection structure from the viewpoint of diversity, quality, and quantity;

Table 3 Survey of wild *Lactuca* species described as a sources of resistance to the most important pathogens and pests of lettuce

Taxon	Pathogens and pests	References
L. serriola	*Lettuce Mosaic Virus* (LMV)	Maisonneuve et al. (1999)
	Corky Root	Mou and Bull (2004)
	Bremia lactucae	Welch et al. (1965), Norwood et al. (1981), Lebeda (1986, 1989, 1990, 2002), Gustafsson (1989), Lebeda and Jendrůlek (1989), Crute (1990, 1992a, b, c), Lebeda and Boukema (1991), Reuveni et al. (1991), Bonnier et al. (1992), Lebeda and Pink (1998), Doležalová et al. (2001), Lebeda and Petrželová (2001, 2004a, b, 2005, 2007), Lebeda et al. (2001a, b, c, 2002, 2004b, 2007a, b, c, 2008a, b), Jeuken and Lindhout (2002), Michelmore (2002), Lebeda and Zinkernagel (2003b), Maisonneuve (2003), Petrželová and Lebeda (2003, 2004a, b, c), Michelmore and Ochoa (2005), Beharav et al. (2006), Hooftman et al. (2007), Kuang et al. (2006), Mieslerová et al. (2007) and Sedlářová et al. (2007a, b)
	Golovinomyces cichoracearum	Lebeda (1985a, b, 1994, 1999) and Lebeda and Buczkowski (1986)
		Lebeda and Mieslerová (2003)
	(Lettuce Powdery Mildew)	
	Verticillium Wilt	Grube et al. (2005a, b)
L. saligna	*Lettuce Mosaic Virus* (LMV)	Maisonneuve et al. (1999)
	Other Yellowing Virus Diseases	McCreight (1987)
	Tomato Spotted Wilt Virus (TSWV)	Wang et al. (1992)
	Cucumber Mosaic Virus (CMV)	Provvidenti et al. (1980)
	Bremia lactucae	Netzer et al. (1976), Provvidenti et al. (1980), Lebeda (1986, 1990), Gustafsson (1989), Lebeda and Pink (1998), Bonnier et al. (1992), Lebeda and Reinink (1994), Lebeda et al. (2001b, c, 2002, 2006, 2007c), Sedlářová and Lebeda (2001), Sedlářová et al. (2001, 2007a, b), Jeuken and Lindhout (2002), Michelmore (2002), Lebeda and Zinkernagel (2003a, b), Maisonneuve (2003), Michelmore and Ochoa (2005), Beharav et al. (2006), Petrželová et al. (2007), Kitner et al. (2008) and Zhang (2008)
	Golovinomyces cichoracearum	Lebeda (1985a, b, 1994, 1999), Lebeda and Buczkowski (1986) and Lebeda and Mieslerová (2003)
	Stemphylium Leaf Spot	Netzer et al. (1985)
L. virosa	*Lettuce Mosaic Virus* (LMV)	Maisonneuve et al. (1999) and Ryder (2002)
	Mirafiori Lettuce Big-Vein Virus (MLBVV)	Bos and Huijberts (1990), Hayes et al. (2004, 2008) and Hayes and Ryder (2007)
	Beet Western Yellows Virus (BWYV)	Maisonneuve et al. (1991)
	Corky Root	Mou and Bull (2004)
	Bremia lactucae	Norwood et al. (1981), Bonnier et al. (1992), Lebeda and Reinink (1994), Lebeda and Pink (1998), Maisonneuve et al. (1999), Sedlářová et al. (2001, 2007a), Lebeda et al. (2002, 2006, 2007c), Michelmore (2002), Lebeda and Zinkernagel (2003b), Maisonneuve (2003), Michelmore and Ochoa (2005) and Beharav et al. (2006)
	Golovinomyces cichoracearum	Lebeda (1985a, b, 1994, 1999) and Michelmore and Ochoa (2005)
	Verticillium Wilt	Grube et al. (2005a, b)
L. indica	*Bremia lactucae*	Lebeda (1990) and Lebeda and Petrželová (2001)

Table 3 continued

Taxon	Pathogens and pests	References
L. perennis	*Lettuce Mosaic Virus* (LMV)	Maisonneuve et al. (1995)
	Beet Western Yellows Virus (BWYV)	Walkey and Pink (1990)
	Golovinomyces cichoracearum	Lebeda (1985a, b, 1994, 1999) and Lebeda and Buczkowski (1986)
L. quercina	*Bremia lactucae*	Lebeda and Petrželová (2001)
	Golovinomyces cichoracearum	Lebeda (1985a, 1999)
L. sibirica	*Golovinomyces cichoracearum*	Lebeda (1985a, 1999)
L. aculeata	*Bremia lactucae*	Lebeda (1990)
	Golovinomyces cichoracearum	Lebeda (1985b, 1994) and Lebeda and Buczkowski (1986)
L. biennis	*Bremia lactucae*	Lebeda and Petrželová (2001)
L. tatarica	*Bremia lactucae*	Lebeda and Petrželová (2001)
	Golovinomyces cichoracearum	Lebeda (1985b, 1994) and Lebeda and Buczkowski (1986)
L. tenerrima	*Golovinomyces cichoracearum*	Lebeda (1985b, 1994)
L. viminea	*Bremia lactucae*	Lebeda and Petrželová (2001)
	Golovinomyces cichoracearum	Lebeda (1985a, b, 1994, 1999)
L. viminea subsp. *chondrilliflora*	*Golovinomyces cichoracearum*	Lebeda et al. (2002)

5. Collecting and exploration missions, especially to areas of high species richness and diversity (e.g., South Africa and Asia);
6. Enlargement of activities focused on complex characterization and evaluation with importance for the management of wild *Lactuca* genebank collections and their efficient utilization in lettuce breeding;
7. Broad international cooperation among diverse institutions, including Bioversity International.

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References

Beharav A, Lewinsohn D, Lebeda A, Nevo E (2006) New wild *Lactuca* genetic resources with resistance against *Bremia lactucae*. Genet Resour Crop Evol 53:467–474. doi:10.1007/s10722-004-1932-7

Beharav A, Ben-David R, Doležalová I, Lebeda A (2008a) Eco-geographical distribution of *Lactuca saligna* natural populations in Israel. Isr J Plant Sci 56: (in press)

Beharav A, Lebeda A, Doležalová I, Ben-David R (2008b) Collecting of genetic diversity in natural populations of wild plant species: case study on *Lactuca saligna* and *L. aculeata* in Israel. In: Prohens J, Badenes ML (eds) Modern variety breeding for present and future needs. Editorial Universidad Politécnica de Valencia, Valencia, Spain, pp 75–76 (Abstract)

Bennett MD, Leitch IJ (1995) Nuclear DNA amounts in angiosperms. Ann Bot (Lond) 76:113–176. doi:10.1006/anbo.1995.1085

Bohm BA, Stuessy TF (2001) Flavonoids of the sunflower family (Asteraceae). Springer, Wien and New York

Bonnier FJM, Reinink K, Groenwold R (1992) New sources of major gene resistance in *Lactuca* to *Bremia lactucae*. Euphytica 61:203–211. doi:10.1007/BF00039659

Bos L, Huijberts N (1990) Screening for resistance to big-vein disease of lettuce (*Lactuca sativa*). Crop Prot 9:446–452. doi:10.1016/0261-2194(90)90135-T

Boukema IW, Hazekamp T, van Hintum TJL (1990) The CGN collections reviews, the CGN lettuce collection. Centre for Genetic Resources, Wageningen

Chen YH, Chen HY, Hsu CL, Yen GC (2007) Induction of apoptosis by the *Lactuca indica* L. in human leukemia cell line and its active components. J Agric Food Chem 55:1743–1749. doi:10.1021/jf063118t

Cole RA, Sutherland RA, Riggall WE (1991) The use of polyacrylamide gradient gel electrophoresis to identify variation in isozymes as markers for *Lactuca* species and resistance to the lettuce root aphid *Pemphigus bursarius*. Euphytica 56:237–242. doi:10.1007/BF00042370

Crute IR (1990) Resistance to *Bremia lactucae* (downy mildew) in British populations of *Lactuca serriola* (prickly lettuce). In: Burdon JJ, Leather SR (eds) Pests, pathogens and plant communities. Blackwell Scientific Publications, Oxford, pp 203–217

Crute IR (1992a) Downy mildew of lettuce. In: Chaube HS, Kumar J, Mukhopadhyay AN, Singh US (eds) Plant diseases of international importance, vol II. Diseases of vegetable and oil seed crops. Prentice Hall, Englewood Cliffs, pp 165–185

Crute IR (1992b) From breeding to cloning (and back again?): a case study with lettuce downy mildew. Annu Rev Phytopathol 30:485–506. doi:10.1146/annurev.py.30.090192.002413

Crute IR (1992c) The role of resistance breeding in the integrated control of downy mildew (*Bremia lactucae*) in protected lettuce. Euphytica 63:95–102. doi:10.1007/BF00023915

Doležalová I, Lebeda A, Křístková E (2001) Prickly lettuce (*Lactuca serriola* L.) germplasm collecting and distribution study in Slovenia and Sweden. Plant Genet Resour Newsl 128:41–44

Doležalová I, Křístková E, Lebeda A, Vinter V (2002a) Description of morphological characters of wild *Lactuca* L. spp. genetic resources (English-Czech version). Hortic Sci Prague 29:56–83

Doležalová I, Lebeda A, Janeček J, Čihalíková J, Křístková E, Vránová O (2002b) Variation in chromosome numbers and nuclear DNA contents in genetic resources of *Lactuca* L. species (Asteraceae). Genet Resour Crop Evol 49:383–395

Doležalová I, Křístková E, Lebeda A, Vinter V, Astley D, Boukema IW (2003a) Basic morphological descriptors for genetic resources of wild *Lactuca* spp. Plant Genet Resour Newsl 134:1–9

Doležalová I, Lebeda A, Dziechciarková M, Křístková E, Astley D, van de Wiel CCM (2003b) Relationships among morphological characters, isozymes polymorphism and DNA variability—the impact on *Lactuca* germplasm taxonomy. Czech J Genet Plant Breed 39:59–67

Doležalová I, Lebeda A, Tiefenbachová I, Křístková E (2004) Taxonomic reconsideration of some *Lactuca* spp. germplasm maintained in world genebank collections. Acta Hortic 634:193–201

Doležalová I, Lebeda A, Křístková E, Novotná A (2005) Morphological variation of *Lactuca serriola* populations from some European countries. In: Abstracts, XVII International Botanical Congress, Vienna, 17–23 July 2005, p 548

Doležalová I, Lebeda A, Křístková E, Novotná A (2007a) Relevance of morphologic assessment of wild *Lactuca* spp. germplasm for their taxonomic determination. Bulletin of Botanical Gardens, Museums & Collections, Polish Botanical Society. Botanical Garden—Center for Biological Diversity Conservation of the Polish Academy of Science, Warsaw, 16A: 22

Doležalová I, Lebeda A, Novotná A, Kršková M (2007b) Variation in fruit morphology of *Lactuca serriola* populations from Czech Republic, Germany, Netherlands and United Kingdom. In: Eucarpia Leafy Vegetables 2007 Conference Abstracts, Warwick HRI, Wellesbourne, 18–20 April 2007, p 8

Doležalová I, Lebeda A, Vondráková D (2008) Current status of the *Lactuca* working collection of Palacký University in Olomouc, Czech Republic. In: Maggioni L, Lebeda A, Boukema I, Lipman E (eds) Report of a working group on leafy vegetables. First meeting, 13–14 October 2005, Olomouc, Czech Republic. Bioversity International, Rome, pp 27–33

Dziechciarková M, Lebeda A, Doležalová I, Astley D (2004a) Characterization of *Lactuca* spp. germplasm by protein and molecular markers—a review. Plant Soil Environ 50:47–58

Dziechciarková M, Lebeda A, Doležalová I, Křístková E (2004b) Isozyme variation in European *Lactuca serriola* germplasm. In: Vollmann J, Grausgruber H, Ruckenbauer P (eds) Genetic variation for plant breeding. Proceedings of the 17th Eucarpia general congress, 8–11 September 2004, Tulln, Austria. BOKU-University of Natural Resources and Applied Life Sciences, Vienna, pp 103–107

Feráková V (1977) The genus *Lactuca* L. in Europe. Univerzita Komenského, Bratislava

Funk VA, Bayer RJ, Keeley S, Chan R, Watson L, Gemeinholzer B, Schilling E, Panero JL, Baldwin BG, Garcia-Jacas N, Susanna A, Jansen RK (2005) Everywhere but Antarctica: using a supertree to understand the diversity and distribution of the Compositae. Biol Skr 55:343–374

Gass T, Frese L (eds) (1999) Implementation of the global plan of action in Europe—conservation and sustainable utilization of plant genetic resources for food and agriculture. Proc of the European Symp, 1998, Braunschweig (Germany). Int Plant Gen Res Ins (IPGRI), Rome, Italy

Grube RC, Hayes R, Mou B, McCreight JD (2005a) Lettuce breeding. California lettuce research board annual report, 2004–2005. California Lettuce Research Board, Salinas

Grube RC, Wintermantel WM, Hand P, Aburomia R, Pink DAC, Ryder EJ (2005b) Genetic analysis and mapping of resistance to lettuce dieback: a soilborne disease caused by tombusviruses. Theor Appl Genet 110:259–268. doi:10.1007/s00122-004-1825-3

Guarino L, Rao RV, Reid R (eds) (1995) Collecting plant genetic diversity. Technical guidelines. CAB International, Wallingford

Gustafsson I (1989) Potential sources of resistance to lettuce downy mildew (*Bremia lactucae*) in different *Lactuca* species. Euphytica 40:227–232

Hayes RJ, Ryder EJ (2007) Introgression of novel alleles for partial resistance to big vein disease from *Lactuca virosa* into cultivated lettuce. HortScience 42:35–39

Hayes RJ, Ryder E, Robinson B (2004) Introgression of big vein tolerance from *Lactuca virosa* L. into cultivated lettuce (*Lactuca sativa* L.). HortScience 39:881

Hayes RJ, Ryder EJ, Wintermantel WM (2008) Genetic variation for big-vein symptom expression and resistance to

Mirafiori lettuce big-vein virus in *Lactuca virosa* L., a wild relative of cultivated lettuce. Euphytica 164:493–500. doi:10.1007/s10681-008-9738-x

Hill M, Witsenboer H, Zabeau M, Vos P, Kesseli R, Michelmore R (1996) PCR-based fingerprinting using AFLPs as a tool for studying genetic relationships in *Lactuca* spp. Theor Appl Genet 93:1202–1210. doi:10.1007/BF00223451

Hooftman DAP, Nieuwenhuis BPS, Posthuma KI, Oostermeijer JGB, den Nijs HJCM (2007) Introgression potential of downy mildew resistance from lettuce to *Lactuca serriola* and its relevance for plant fitness. Basic Appl Ecol 8:135–146. doi:10.1016/j.baae.2006.03.008

Hu J, Ochoa OE, Truco MJ, Vick BA (2005) Application of the TRAP technique to lettuce (*Lactuca sativa* L.) genotyping. Euphytica 144:225–235. doi:10.1007/s10681-005-6431-1

Jansen J, Verbakel H, Peleman J, van Hintum TJL (2006) A note on the measurement of genetic diversity within genebank accessions of lettuce (*Lactuca sativa* L.) using AFLP markers. Theor Appl Genet 112:554–561. doi:10.1007/s00122-005-0162-5

Jeuken M, Lindhout P (2002) *Lactuca saligna*, a non-host for lettuce downy mildew (*Bremia lactucae*), harbors a new race-specific *Dm* gene and three QTLs for resistance. Theor Appl Genet 105:384–391. doi:10.1007/s00122-002-0943-z

Jeuken MJW, Lindhout P (2004) The development of lettuce backcross inbred lines (BILs) for exploitation of the *Lactuca saligna* (wild lettuce) germplasm. Theor Appl Genet 109:394–401. doi:10.1007/s00122-004-1643-7

Jeuken M, van Wijk R, Peleman J, Lindhout P (2001) An integrated interspecific AFLP map of lettuce (*Lactuca*) based on two *L. sativa* × *L. saligna* F-2 populations. Theor Appl Genet 103:638–647. doi:10.1007/s001220100657

Jeuken MJW, Pelgrom K, Stam P, Lindhout P (2008) Efficient QTL detection for nonhost resistence in wild lettuce: backcross inbred lines versus F_2 population. Theor Appl Genet 116:845–857. doi:10.1007/s00122-008-0718-2

Kesseli RV, Michelmore RW (1986) Genetic variation and phylogenies detected from isozyme markers in species of *Lactuca*. J Hered 77:324–331

Kesseli RV, Ochoa O, Michelmore RW (1991) Variation at RFLP loci in *Lactuca* spp. and origin of cultivated lettuce (*L. sativa*). Genome 34:430–436

Kim KH, Kim YH, Lee KR (2007) Isolation of quinic acid derivatives and flavonoids from the aerial parts of *Lactuca indica* L. and their hepatoprotective activity in vitro. Bioorg Med Chem Lett 17:6739–6743. doi:10.1016/j.bmcl.2007.10.046

Kisiel W, Barszcz B (1998) A germacrolide glucoside from *Lactuca tatarica*. Phytochemistry 48:205–206. doi:10.1016/S0031-9422(97)01106-0

Kisiel W, Zielinska K (2000) Sesquiterpenoids and phenolics from *Lactuca perennis*. Fitoterapia 71:86–87. doi:10.1016/S0367-326X(99)00112-4

Kitner M, Lebeda A, Doležalová I, Maras M, Křístková E, Nevo E, Pavlíček T, Meglic V, Beharav A (2008) AFLP analysis of *Lactuca saligna* germplasm collections from four European and three Middle Eastern countries. Isr J Plant Sci 56: (in press)

Koopman WJM (1999) Plant systematics as useful tool for plant breeders, examples from lettuce. In: Lebeda A, Křístková E (eds) Eucarpia leafy vegetables ′99. Proceedings of the Eucarpia meeting on leafy vegetables genetics and breeding, Palacký University in Olomouc, Olomouc, pp 95–105

Koopman WJM (2000) Identifying lettuce species (*Lactuca* subs. *Lactuca*, Asteraceae). A practical application of flow cytometry. Euphytica 116:151–159. doi:10.1023/A:1004086503349

Koopman WJM (2002) Zooming in on the lettuce genome: species relationships in *Lactuca* s.l. inferred from chromosomal and molecular characters. Ph.D. dissertation, Wageningen University, Wageningen

Koopman WJM, De Jong HJ (1996) A numerical analysis of karyotypes and DNA amounts in lettuce cultivars and species (*Lactuca* subsp. *Lactuca*, Compositae). Acta Bot Neerl 45:211–222

Koopman WJM, Guetta E, Van de Wiel CCM, Vosman B, Van den Berg RG (1998) Phylogenetic relationships among *Lactuca* (Asteraceae) species and related genera based on ITS-1 DNA sequences. Am J Bot 85:1517–1530. doi:10.2307/2446479

Koopman WJM, Zevenbergen MJ, van den Berg RG (2001) Species relationships in *Lactuca* s.l. (Lactuceae, Asteraceae) inferred from AFLP fingerprints. Am J Bot 88:1881–1887. doi:10.2307/3558364

Křístková E, Lebeda A (1999) Collection of *Lactuca* spp. genetic resources in the Czech Republic. In: Lebeda A, Křístková E (eds) Eucarpia leafy vegetables ′99. Proceedings of the Eucarpia meeting on leafy vegetables genetics and breeding, Palacký University in Olomouc, Olomouc, pp 109–116

Křístková E, Lebeda A, Doležalová I (2001) Collecting and evaluating of *Lactuca serriola* germplasm in Europe. In: Swiecicki W, Naganowska B, Wolko B (eds) Broad variation and precise characterization—limitation for the future. Eucarpia, Section Genetic Resources, Poznań, pp 49–52

Křístková E, Lebeda A, Doležalová I (2007a) Phenotypic variability of *Lactuca saligna* germplasm collected in Italy and France. In: Eucarpia leafy vegetables 2007, Conference Abstracts, University of Warwick, Warwick HRI, UK, Poster Presentations, 18–20 April 2007, p 15

Křístková E, Lebeda A, Doležalová I, Vinter V, Křístková A (2007b) Variation in developmental stages of *Lactuca serriola* L. (prickly lettuce) germplasm from different European countries. In: Eucarpia leafy vegetables 2007, Conference Abstracts, University of Warwick, Warwick HRI, UK, Poster Presentations, 18–20 April 2007, p. 16

Křístková E, Doležalová I, Lebeda A, Vinter V, Novotná A (2008) Description of morphological characters of lettuce (*Lactuca sativa* L.) genetic resources. Hortic Sci Prague 38:113–129

Kuang H, Ochoa OE, Nevo E, Michelmore RW (2006) The disease resistance gene *Dm*3 is infrequent in natural populations of *Lactuca serriola* due to deletions and frequent gene conversions at the *RGC2*locus. Plant J 47:38–48. doi:10.1111/j.1365-313X.2006.02755.x

Kuang H, van Eck HJ, Sicard D, Michelmore R, Nevo E (2008) Evolution and genetic population structure of prickly lettuce (*Lactuca serriola*) and its *RGC2* resistance gene cluster. Genetics 178:1547–1558. doi:10.1534/genetics.107.080796

Lebeda A (1985a) Occurrence of natural infection of powdery mildew (*Erysiphe cichoracearum*) by the genus *Lactuca* in Czechoslovakia. Acta Phytopath Acad Sci Hung 20: 149–162

Lebeda A (1985b) Differences in resistance of wild *Lactuca* species to natural infection of lettuce powdery mildew (*Erysiphe cichoracearum*). Euphytica 34:521–523. doi:10.1007/BF00022949

Lebeda A (1986) Specificity of interactions between wild *Lactuca* spp. and *Bremia lactucae* isolates from *Lactuca serriola*. J Phytopathol 117:54–64. doi:10.1111/j.1439-0434.1986.tb04360.x

Lebeda A (1989) Response of lettuce cultivars carrying the resistance gene *Dm*11 to isolates of *Bremia lactucae* from *Lactuca serriola*. Plant Breed 102:311–316. doi:10.1111/j.1439-0523.1989.tb01261.x

Lebeda A (1990) The location of sources of field resistance to *Bremia lactucae* in wild *Lactuca* species. Plant Breed 105:75–77. doi:10.1111/j.1439-0523.1990.tb00455.x

Lebeda A (1994) Evaluation of wild *Lactuca* species for resistance of natural infection of powdery mildew (*Erysiphe cichoracearum*). Genet Resour Crop Evol 41: 55–57. doi:10.1007/BF00051424

Lebeda A (1999) Powdery mildew on lettuce and wild *Lactuca* species. The First International Powdery Mildew Conference, August 29–September 2, 1999, Avignon (France); Abstracts, pp 16–17

Lebeda A (2002) Occurrence and variation in virulance of *Bremia lactucae* in natural populations of *Lactuca serriola*. In: Spencer-Phillips PTN, Gisi U, Lebeda A (eds) Advances in downy mildew research. Kluwer, Dordrecht, pp 179–183

Lebeda A, Astley D (1999) World genetic resources of *Lactuca* spp., their taxonomy and biodiversity. In: Lebeda A, Křístková E (eds) Eucarpia leafy vegetables ′99. Proceedings of the Eucarpia meeting on leafy vegetables genetics and breeding. Palacký University in Olomouc, Olomouc, pp 81–94

Lebeda A, Boukema IW (1991) Further investigation of the specificity of interactions between wild *Lactuca* spp. and *Bremia lactucae* isolates from *Lactuca serriola*. J Phytopathol 133:57–64. doi:10.1111/j.1439-0434.1991.tb00137.x

Lebeda A, Boukema IW (2001) Leafy vegetables genetic resources. In: Maggioni L, Spellman O (eds) Report of a network coordinating group on vegetables; ad hoc meeting, 26–27 May 2000, Vila Real, Portugal. International Plant Genetic Resources Institute, Rome, pp 48–57

Lebeda A, Boukema IW (2005) Ad hoc meeting on leafy vegetables. In: Thomas G, Astley D, Boukema IW, Daunay MC, Del Greco A, Diez MJ, van Dooijweert W, Keller J, Kotlińska T, Lebeda A, Lipman E, Maggioni L, Rosa E (eds) Report of a vegetable network. Joint Meeting with an ad hoc group of leafy vegetables, 22–24 May 2003, Skierniewice, Poland. International Plant Genetic Resources Institute, Rome, pp 82–94

Lebeda A, Buczkowski J (1986) Occurrence of *Erysiphe cichoracearum* perithecia on wild *Lactuca* species. J Phytopathol 115:21–28. doi:10.1111/j.1439-0434.1986.tb00857.x

Lebeda A, Jendrůlek T (1989) Application of multivariate analysis for characterizing the relationships between wild *Lactuca* spp. and *Bremia lactucae*. Acta Phytopathol Entomol Hung 24:317–331

Lebeda A, Mieslerová B (2003) Lettuce powdery mildew—an unknown disease of lettuce. In: van Hintum ThJL, Lebeda A, Pink DA, Schut JW (eds) Eucarpia leafy vegetables 2003. Proceedings of the Eucarpia meeting on leafy vegetables genetics and breeding, Noordwijkerhout, Centre for Genetics Resources, Wageningen, p 164

Lebeda A, Petrželová I (2001) Occurrence and characterization of race-specific resistance to *Bremia lactucae* in wild *Lactuca* spp. In: Swiecicki W, Naganowska B, Wolko B (eds) Broad variation and precise characterization—limitation for the future. Eucarpia, Section Genetic Resources, Prodruk, Poznan, pp 232–233

Lebeda A, Petrželová I (2004a) Occurrence of race-specific resistance to *Bremia lactucae* in *Lactuca serriola* germplasm originating from four European countries. In: Vollmann J, Grausgruber H, Ruckenbauer P (eds) Genetic variation for plant breeding. Proceedings of the 17th EUCARPIA General Congress, 8–11 September 2004, Tulln, Austria. BOKU-University of Natural Resources and Applied Life Sciences, Vienna, pp 113–116

Lebeda A, Petrželová I (2004b) Variation and distribution of virulence phenotypes of *Bremia lactucae* in natural populations of *Lactuca serriola*. Plant Pathol 53:316–324. doi:10.1111/j.0032-0862.2004.01003.x

Lebeda A, Petrželová I (2005) Comparison of resistance to *Bremia lactucae* in populations of *Lactuca serriola* occurring in Central Europe (Czech Republic) and the British Isles (England, UK). In: Bullitta S (ed) Plant genetic resources of geographical and "other" islands (Conservation, evaluation and use for plant breeding). Book of Abstracts. XVII Eucarpia Genetic Resources Section Meeting, 30 March–2 April 2005, CNR-ISPAAM, sezione Sassari Publisher, Sassari, p 14

Lebeda A, Petrželová I (2007) Race-specific resistance to *Bremia lactucae* in European populations of *Lactuca serriola*. In: Eucarpia leafy vegetables 2007. Conference Abstracts, University of Warwick, Warwick HRI, UK, Oral Presentations, 18–20 April 2007, p 11

Lebeda A, Pink DAC (1998) Histological aspects of the response of wild *Lactuca* spp. and their hybrids, with *L. sativa* to lettuce downy mildew (*Bremia lactucae*). Plant Pathol 47:723–736

Lebeda A, Reinink K (1994) Histological characterization of resistance in *Lactuca saligna* to lettuce downy mildew (*Bremia lactucae*). Physiol Mol Plant Pathol 44:125–139. doi:10.1016/S0885-5765(05)80106-7

Lebeda A, Zinkernagel V (2003a) Evolution and distribution of virulence in the German population of *Bremia lactucae*. Plant Pathol 52:41–51. doi:10.1046/j.1365-3059.2003.00802.x

Lebeda A, Zinkernagel V (2003b) Characterization of new highly virulent German isolates of *Bremia lactucae* and efficiency of resistance in wild *Lactuca* spp. germplasm. J Phytopathol 151:274–282

Lebeda A, Doležalová I, Křístková E, Janeček J, Vinter V, Vránová O, Doležal K, Tarkowski P, Petrželová P, Trávníček B, Novotný R, Janeček J (1999) Complex research of taxonomy and ecobiology of wild *Lactuca* spp. genetic resources. In: Lebeda A, Křístková E (eds) Eucarpia leafy vegetables ′99. Proceedings of the Eucarpia meeting on leafy vegetables genetics and breeding, Palacký University in Olomouc, Olomouc, pp 117–131

Lebeda A, Doležalová I, Křístková E, Janeček J, Vinter V, Vránová O, Doležal K, Tarkowski P, Petrželová P, Trávníček B, Novotný R (2001a) Biodiversity of genetic resources of wild *Lactuca* spp. In: Święcicki W, Naganowska B, Wolko B (eds) Broad variation and precise characterization—limitation for the future. Prodruk, Poznań, pp 53–56

Lebeda A, Doležalová I, Křístková E, Mieslerová B (2001b) Biodiversity and ecogeography of wild *Lactuca* spp. in some European countries. Genet Resour Crop Evol 48:153–164. doi:10.1023/A:1011265614395

Lebeda A, Pink DAC, Mieslerová B (2001c) Host-parasite specificity and defense variability in the *Lactuca* spp.—*Bremia lactucae* pathosystem. J Plant Pathol 83:25–35

Lebeda A, Pink DAC, Astley D (2002) Aspects of the interactions between wild *Lactuca* spp. and related genera and lettuce downy mildew (*Bremia lactucae*). In: Spencer-Phillips PTN, Gisi U, Lebeda A (eds) Advances in downy mildew research. Kluwer, Dordrecht, pp 85–117

Lebeda A, Doležalová I, Astley D (2004a) Representation of wild *Lactuca* spp. (Asteraceae, Lactuceae) in world genebank collections. Genet Resour Crop Evol 51:167–174. doi:10.1023/B:GRES.0000020860.66075.f7

Lebeda A, Doležalová I, Feráková V, Astley D (2004b) Geographical distribution of wild *Lactuca* spp. (Asteraceae, Lactuceae). Bot Rev 70:328–356. doi:10.1663/0006-8101(2004)070[0328:GDOWLS]2.0.CO;2

Lebeda A, Doležalová I, Janeček J, Gasmanová N (2004c) Differences in relative DNA content of *Lactuca serriola* germplasm collected in Europe. In: Summaries and Program, 17th International lettuce and leafy vegetable conference, 28–31 August 2004, Sandman Hotel, Montreal-Longueuil. Agriculture and Agri-Food Canada, Montreal, pp 29–30

Lebeda A, Sedlářová M, Lynn J, Pink DAC (2006) Phenotypic and histological expression of different genetic backgrounds in interactions between lettuce, wild *Lactuca* spp., *L. sativa* × *L. serriola* hybrids and *Bremia lactucae*. Eur J Plant Pathol 115:431–441. doi:10.1007/s10658-006-9034-3

Lebeda A, Doležalová I, Křístková E, Dehmer KJ, Astley D, Van de Wiel CCM, Van Treuren R (2007a) Acquisition and ecological characterization of *Lactuca serriola* L. germplasm collected in the Czech Republic, Germany, the Netherlands and United Kingdom. Genet Resour Crop Evol 54:555–562. doi:10.1007/s10722-006-0012-6

Lebeda A, Doležalová I, Křístková E, Novotná A (2007b) Comparative study of variation of some morphological characteristics of *Lactuca serriola* germplasm collected in Central Europe (Czech Republic) and the British Isles (England, UK). (Abstract). In: Bullitta S (ed) Plant genetic resources of geographical and "other" islands (conservation, evaluation and use for plant breeding). Proceedings of the XVII Eucarpia genetic resources section meeting; 30 March–2 April 2005, Castelsardo, Italy. CNR-IS-PAAM, sezione Sassari Publisher, Sassari, pp 95–96

Lebeda A, Ryder EJ, Grube R, Doležalová I, Křístková E (2007c) Lettuce (Asteraceae; *Lactuca* spp.), Chapter 9. In: Singh R (ed) Genetic resources, chromosome engineering, and crop improvement series, vol 3—vegetable crops. CRC Press, Boca Raton, pp 377–472

Lebeda A, Doležalová I, Křístková E, Novotná A (2007d) Taxonomic determination of plant genetic resources—impact and consequences: case study of *Lactuca* spp. In: Hauptvogel P, Benediková D, Hauptvogel R (eds) Plant genetic resources and their exploitation in the plant breeding for food and agriculture. Book of Abstracts. 18th EUCARPIA genetic resources section meeting, May 23–26, 2007, Piešťany, Slovak Republic. PNprint, s.r.o., Piešťany, Slovak Republic, pp 39–40

Lebeda A, Doležalová I, Křístková E, Mieslerová B, Kitner M, Navrátilová B, Duchoslav M, Havránek P, Vondráková D (2007e) Germplasm collections of crop wild relatives—research, study and use on the Department of Botany, Palacký University in Olomouc (Czech Republic). In: Hauptvogel P, Benediková D, Hauptvogel R (eds) Plant genetic resources and their exploitation in the plant breeding for food and agriculture. Book of Abstracts. 18th EUCARPIA genetic resources section meeting, May 23–26, 2007, Piešťany, Slovak Republic. PNprint, s.r.o., Piešťany, Slovak Republic, pp 94–95

Lebeda A, Petrželová I, Maryška Z (2008a) Structure and variation in the wild-plant pathosystem: *Lactuca serriola*–*Bremia lactucae*. Eur J Plant Pathol 122:127–146. doi:10.1007/s10658-008-9291-4

Lebeda A, Sedlářová M, Petřivalský M, Prokopová J (2008b) Diversity of defence mechanisms in plant-oomycete interactions: a case study of *Lactuca* spp. and *Bremia lactucae*. Eur J Plant Pathol 122:71–89. doi:10.1007/s10658-008-9292-3

Lebeda A, Doležalová I, Dziechciarková M, Kitner M, Křístková E, Lindhout P (2008c) Genetic polymorphism of European populations of *Lactuca serriola.* Genet Resour Crop Evol (submitted)

Lebeda A, Doležalová I, Křístková E, Kitner M, Petrželová I, Mieslerová B, Novotná A (2008d) Wild *Lactuca* germplasm for lettuce breeding: recent status, gaps and challenges. In: Prohens J, Badenes MJ (eds) Modern variety breeding for present and future needs. Proceedings of the 18th EUCARPIA General Congress, September 9–12, 2008, Editorial Universidad Politécnica de Valencia, Valencia, pp 49–60

Maggioni L, Lebeda A, Boukema I, Lipman E (eds) (2008) Report of a working group on leafy vegetables. First meeting, 13–14 October 2005, Olomouc, Czech Republic. Bioversity International, Rome

Maisonneuve B (2003) *Lactuca virosa*, a source of disease resistance genes for lettuce breeding: results and difficulties for gene introgression. In: van Hintum TJL, Lebeda A, Pink DAC, Schut JW (eds) Eucarpia leafy vegetables '03. CGN Wageningen, The Netherlands, pp 31–35

Maisonneuve B, Chovelon V, Lot H (1991) Inheritance of resistance to beet western yellows virus in *Lactuca virosa* L. HortScience 26:1543–1545

Maisonneuve B, Chupeau MC, Bellec Y, Chupeau Y (1995) Sexual and somatic hybridization in the genus *Lactuca*. Euphytica 85:281–285. doi:10.1007/BF00023957

Maisonneuve B, Bellec Y, Souche S, Lot H (1999) New resistance against downy mildew and lettuce mosaic potyvirus in wild *Lactuca* spp. In: Lebeda A, Křístková E (eds) Eucarpia leafy vegetables ′99. Proceedings of the Eucarpia meeting of leafy vegetables genetics and breeding, Palacký University in Olomouc, Olomouc, pp 191–197

Matoba H, Mizutani T, Nagano K, Hoshi Y, Uchiyama H (2007) Chromosomal study of lettuce and its allied species (*Lactuca* spp., Asteraceae) by means of karyotype analysis and fluorescence in situ hybridization. Hereditas 144:235–243. doi:10.1111/j.2007.0018-0661.02012x

McCreight JD (1987) Resistance in wild lettuce to lettuce infectious yellows. HortScience 22:640–642

McGregor RL, Barkley TM, Brooks RE, Schofield EK (eds) (1986) Flora of the Great Plains. University Press of Kansas, Lawrence

McGuire PE, Ryder EJ, Michelmore RW, Clark RL, Antle R, Emery G, Hannan RW, Kesseli RV, Kurtz EA, Ochoa O, Rubatzky VE, Waycott W (1993) Genetic resources of lettuce and *Lactuca* species in California. An assessment of the USDA and UC collections and recommendations for long-term security. Report no. 12. University of California, Genetic Resources Conservation Program, Davis

Michalska K, Stojakowska A, Malarz J, Doležalová I, Lebeda A, Kisiel W (2008) Systematic implications of sesquiterpene lactones in *Lactuca* species. Biochem Syst Ecol (in press)

Michelmore RW (2002) Genetic variation in lettuce. In: Kurtz E (ed) Annual Report 2001–2002. California Lettuce Research Board, Salinas, pp 77–86

Michelmore RW, Ochoa OE (2005) Breeding crisphead lettuce. California Lettuce Research Board, Annual Report, April 1, 2004 through March 31, 2005. California Research Board, Salinas, pp 68–78

Mieslerová B, Petrželová I, Lebeda A, Česneková E (2007) Occurrence of lettuce downy mildew and powdery mildew in natural populations of prickly lettuce. In: Lebeda A, Spencer-Phillips PTN (eds) Advances in downy mildew research, vol 3. Proceedings of the 2nd international downy mildews symposium, Palacký University in Olomouc and JOLA, v.o.s., Kostelec na Hané, Czech Republic, pp 59–64

Mikel MA (2007) Genealogy of contemporary North American lettuce. HortScience 42:489–493

Mizutani T, Tanaka T (2003) Genetic analyses of isozyme in lettuce, *Lactuca sativa*, and its relatives. J Jap Soc Hortic Sci 72:122–127

Mou B (2008) Lettuce. In: Prohens J, Nuez F (eds) Handbook of plant breeding. Vegetables I. Asteraceae, Brassicaceae, Chenopodiaceae, and Cucurbitaceae. Springer Science, New York, pp 75–116

Mou BQ, Bull C (2004) Screening lettuce germplasm for new sources of resistance to corky root. J Am Soc Hortic Sci 129:712–716

Netzer D, Globerson D, Sacks J (1976) *Lactuca saligna* L. a new sources of resistance to downy mildew (*Bremia lactucae* Reg). Hortic Sci 11:612–613

Netzer D, Globerson D, Weintal C, Elyassi R (1985) Sources and inheritance of resistance to Stemphylium leaf spot of lettuce. Euphytica 34:393–396. doi:10.1007/BF00022934

Norwood JM, Crute IR, Lebeda A (1981) The location and characteristics of novel sources of resistance to *Bremia lactucae* Regel (downy mildew) in wild *Lactuca* L. species. Euphytica 30:659–668. doi:10.1007/BF00038794

Pandey A, Tomer AK, Bhandari DC, Pareek SK (2008) Towards collection of wild relatives of crop plants in India. Genet Resour Crop Evol 55:187–202. doi:10.1007/s10722-007-9227-4

Petrželová I, Lebeda A (2003) Distribution of compatibility types and occurrence of sexual reproduction in natural populations of *Bremia lactucae* on wild *Lactuca serriola* plants. Acta Phytopathol Entomol Hung 38:43–52. doi:10.1556/APhyt.38.2003.1-2.6

Petrželová I, Lebeda A (2004a) Comparison of virulence of *Bremia lactucae* isolates originating from *Lactuca sativa* and *Lactuca serriola*. Acta fytotech zootech 7:248–250

Petrželová I, Lebeda A (2004b) Occurrence of *Bremia lactucae* in natural populations of *Lactuca serriola*. J Phytopathol 152:391–398. doi:10.1111/j.1439-0434.2004.00859.x

Petrželová I, Lebeda A (2004c) Temporal and spatial variation in virulence of natural populations of *Bremia lactucae* occurring on *Lactuca serriola*. In: Spencer-Phillips PTN, Jeger M (eds) Advances in downy mildew research, vol 2. Kluwer, Dordrecht, pp 141–163

Petrželová I, Lebeda A, Nevo E, Beharav A (2007) Variation of response against *Bremia lactucae* in natural populations of *Lactuca saligna*. In: Lebeda A, Spencer-Phillips PTN (eds) Advances in downy mildew research, vol 3. Proceedings of the 2nd international downy mildews symposium, Palacký University in Olomouc and JOLA, v.o.s., Kostelec na Hané, Czech Republic, pp 169–173

Provvidenti R, Robinson RW, Shail W (1980) A source of resistance to a strain of cucumber mosaic virus in *Lactuca saligna* L. HortScience 15:528–529

Rajicic TS, Dehmer KJ (2008) Analysis of wild *Lactuca* gene bank accessions and implications for wild species conservation. In: Maxted N, Ford-Lloyds BV, Kell SP, Iriondo JM, Dulloo ME, Turok J (eds) Crop wild relative conservation and use. CABI International, Wallingford, pp 429–436

Rees S, Harborne J (1984) Flavonoids and other phenolics of *Cichorium* and related members of the Lactuceae (Compositae). Bot J Linn Soc 89:313–319. doi:10.1111/j.1095-8339.1984.tb02563.x

Reuveni R, Shimoni M, Crute IR (1991) An association between high peroxidase activity in lettuce (*Lactuca sativa*) and field resistance to downy mildew (*Bremia lactucae*). J Phytopathol 132:312–318. doi:10.1111/j.1439-0434.1991.tb00126.x

Ryder EJ (2002) A mild systemic reaction to lettuce mosaic virus in lettuce (*Lactuca sativa*), inheritance and interaction with an allele for resistance. J Am Soc Hortic Sci 127:814–818

Sedlářová M, Lebeda A (2001) Histochemical detection and role of phenolic compounds in defence response of *Lactuca* spp. to lettuce downy mildew (*Bremia lactucae*). J Phytopathol 149:1–5. doi:10.1046/j.1439-0434.2001.00698.x

Sedlářová M, Lebeda A, Pink DAC (2001) The early stages of interaction between effective and non-effective race-specific genes in *Lactuca sativa*, wild *Lactuca* spp. and *Bremia lactucae* (race NL16). J Plant Dis Prot 108:477–489

Sedlářová M, Luhová L, Petřivalský M, Lebeda A (2007a) Localisation and metabolism of reactive oxygen species during *Bremia lactucae* pathogenesis in *Lactuca sativa* and wild *Lactuca* spp. Plant Physiol Biochem 45:607–616. doi:10.1016/j.plaphy.2007.05.010

Sedlářová M, Výtisková M, Doležal K, Lebeda A (2007b) Pre-incubation with cytokinins delays chlorophyll degradation in *Lactuca* spp. tissues and reduces *Bremia lactucae* sporulation. In: Lebeda A, Spencer-Phillips PTN (eds) Advances in downy mildew research, vol 3. Proceedings of the 2nd international downy mildews symposium, Palacký University in Olomouc and JOLA, v.o.s., Kostelec na Hané, Czech Republic, pp 185–194

Sicard D, Woo SS, Arroyo-Garcia R, Ochoa O, Nguyen D, Korol A, Nevo E, Michelmore RW (1999) Molecular diversity at the major cluster of disease resistance genes in cultivated and wild *Lactuca* spp. Theor Appl Genet 99:405–418. doi:10.1007/s001220051251

Spooner D, van Treuren R, de Vicente MC (2005) Molecular markers for genebank management. IPGRI Technical Bulletin 10, International Plant Genetic Resources Institute, Rome

van de Wiel CCM, Arens P, Vosman B (1998) Microsatellite fingerprinting in lettuce (*Lactuca sativa* L.) and wild relatives. Plant Cell Rep 17:837–842. doi:10.1007/s002990050494

van de Wiel CCM, Arens P, Vosman B (1999) Microsatellite retrieval in lettuce (*Lactuca sativa* L.). Genome 42:139–149. doi:10.1139/gen-42-1-139

van de Wiel CCM, Flavell A, Syed N, Antonise R, van der Voort JR, van der Linden G (2004) Analysis of gene flow in the lettuce crop-weed complex. In: den Nijs HCM, Bartsch D, Sweet J (eds) Introgression from genetically modified plants into wild relatives. CABI Publishing, Wallingford, pp 163–171

van Hintum TJL, Boukema IW (1999) Genetic resources of leafy vegetables. In: Lebeda A, Křístková E (eds) Eucarpia leafy vegetables ′99. Proceedings of the Eucarpia meeting on leafy vegetables genetics and breeding, Palacký University in Olomouc, Olomouc, pp 59–72

Vermeulen A, Desprez B, Lancelin D, Bannerot H (1994) Relationship among *Cichorium* species and related genera as determined by analysis of mitochondrial RFLPs. Theor Appl Genet 88:159–166. doi:10.1007/BF00225892

Walkey DGA, Pink DCA (1990) Studies on resistance to beet western yellows virus in lettuce (*Lactuca sativa*) and the occurrence of field sources of the virus. Plant Pathol 39:141–155. doi:10.1111/j.1365-3059.1990.tb02485.x

Wang M, Cho JJ, Provvidenti R, Hu JS (1992) Identification of resistance to tomato spotted wilt virus in lettuce. Plant Dis 76:642

Welch JE, Zink FW, Grogan RG (1965) Calmar. Calif Agric 19:3–4

Witsenboer H, Vogel J, Michelmore RW (1997) Identification, genetic localization, and allelic diversity of selectively amplified microsatellite polymorphic loci in lettuce and wild relatives (*Lactuca* spp.). Genome 40:923–936. doi:10.1139/g97-119

Zhang N (2008) Genetic dissection of nonhost resistence of wild lettuce, *Lactuca saligna*, to downy mildew. PhD Thesis, Wageningen University, Wageningen

5. CONCLUSIONS

The first part of this Ph.D. thesis is focused on development of *Lactuca sativa* (lettuce) descriptor. It contains 55 descriptors of choosen morphological features which are very needful for detailed description of many *L. sativa* cultivars and varieties. Totally 15 descriptors are appended by figures.

The next topic was to study morphological variability of *Lactuca serriola* (prickly lettuce, compass plant) achenes. On the basis of search of *L. serriola* populations from the Czech Republic, Germany, the Netherlands and United Kingdom, the singificance difference in achene morphology of two *L. serriola* forms was found. Achenes of *L. serriola* f. *serriola* are shorter, thinner, shorter beaked, with lower length/width index and higher number of ribs than achenes of *L. serriola* f. *integrifolia*. We evaluated also influence of eco-geographic features such as longitude, latitude, altitude, soil texture of the habitats, population size on the studied morphological characters. Significant correlations were found between three of them (longitude, latitude, soil texture) and the studied characters.

We evaluated also morphological variability of *L. serriola* plants from Slovenia and Sweden. Achenes originating from Slovenia were singificantly longer, wider and with longer pappus compared to those from Sweden. Of all evaluated geographical factors, latitude influenced the most the studied morphological characters of *L. serriola* achenes.

The third chapter deals with morphological variability of *L. serriola* rosette and cauline leaves. According to this study, in the Czech Republic only *L. serriola* f. *serriola* with pinnatipart/pinnatisect leaves was found, while in the United Kingdom *L. serriola* f. *integrifolia* having entire leaves was dominant.

The next chapter is focused on study of distribution, ecogeography and ecobiology of germplasm accessions of wild *Lactuca* spp. in USA and Canada. During collecting and observation missions undertaken in North American subcontinent in the first decade of this century, more than 340 seed samples of 7 wild *Lactuca* spp., one interspecific hybrid (*L. canadensis* x *L. ludoviciana*) and one undetermined *Lactuca* sp. were collected. Totally 200 locations in 16 states of USA and 2 provinces in Canada were visited. Mostly *L. serriola* was noted growing typically in road-sides, road ditches, parking sites and petrol stations, grassy slopes and ruderal places. Except of ecogeographical identification presence/absence of downy mildew (*Bremia lactucae*) and/or powdery mildew (*Golovinomyces cichoracearum*) was noted on all germplasm accessions.

In the fifth part the results of intesive research of the genus *Lactuca* L., which have been achieved during last 25 years are summarized. During that time a lot of new knowledge in taxonomy, genetic diversity, morphology, molecular and biochemical diversity as well as in resistance to different pathongens was found. Challenges and plans of the future research in this scientific field are discussed. Future studies should be focused on e.g. enriching *Lactuca* L. world germplasm collection; findings of other possible hot spots in southern Africa, central Asia and North America; improving knowledge in taxonomical description and determination; using wild *Lactuca* spp. such as *L. saligna* and *L. serriola* as durable sources of resistance. Recent molecular studies were very helpful to confirm the broader generic concept of the genus *Lactuca* L. More detailed research about detection and characterization of various chemical compounds in plants of *Lactuca* spp., and about protein and molecular molymorphism of *Lactuca* spp. are needed as well.

6. SOUHRN (SUMMARY, in Czech)

Fenotypov§ variabilita genovĨch zdrojŢ rodu *Lactuca* L., jejich ekobiologie a vyuģit²

První část předkládané disertační práce pojednává o vypracování souboru popisných znaků kulturního salátu (*L. sativa*). Soubor obsahuje 55 vybraných morfologických znaků, přičemž 15 z nich je doplněno obrázky. Z praktického hlediska je tento deskriptor velmi důležitý pro detailní morfologický popis značné vnitrodruhové variability *L. sativa*. Uplatnění nachází zejména u pracovníků genových bank a šlechtitelů kulturního salátu.

Dalším tématem bylo studium morfologické variability nažek lociky kompasové (*L. serriola*). Na základě studia nažek populací tohoto druhu pocházející z České republiky, Německa, Holandska a Velké Británie byl zjištěn signifikantní rozdíl mezi nažkami *L. serriola* f. *serriola* a *L. serriola* f. *integrifolia*. Nažky formy *serriola* jsou kratší, užší, s kratším zobánkem, nižším indexem tvaru a vyšším počtem žeber než nažky formy *integrifolia*. V rámci této práce byl hodnocen i vliv vybraných ekogeografických faktorů (zeměpisné délky, šířky a nadmořské výšky, půdního typu stanoviště a velikosti populace) na studované morfologické znaky. Signifikantní korelační závislosti byly zjištěny pouze mezi zeměpisnou délkou, šířkou, půdním typem a studovanými morfologickými znaky nažek.

Zabývali jsme se také hodnocením morfologické variability nažek populací lociky kompasové (*L. serriola*) ze Slovinska a Švédska. Nažky původem ze Slovinska byly signifikantně delší, širší, s delším chmýrem než nažky ze Švédska. Ze studovaných ekogeografických faktorů nejvíce ovlivňovala morfologii nažek zeměpisná šířka.

Třetí částí disertační práce bylo hodnocení morfologické variability rosetových a stonkových listů lociky kompasové (*L. serriola*). Na základě tohoto výzkumu bylo zjištěno, že na území České republiky byly zaznamenány převážně rostliny *L. serriola* f. *serriola* s peřenodílnými až peřenosečnými listy. Ve Velké Británii byla dominantní forma *integrifolia* s celistvými listy.

V další kapitole jsou uvedeny výsledky několikaletého výzkumu o rozšíření, ekogeografii a ekobiologii genových zdrojů rodu *Lactuca* L. v USA a Kanadě. V letech 2002 až 2008 bylo na 200 lokalitách 16 států USA a dvou Kanadských provincií získáno více než 340 semenných vzorků 7 planých druhů rodu *Lactuca* L., jednoho mezidruhového hybrida (*L. canadensis* x *L. ludoviciana*) a jednoho blíže neurčeného druhu. Nejčastěji byly pozorovány populace *L. serriola* rostoucí hojně na okrajích silnic, v příkopech, u parkovišť, u čerpacích stanic, v blízkosti zatravněných svahů a na

rumištích. Kromě běžných pasportních údajů byla u získaných semenných vrzotů rovněž zaznamenána přítomnost/nepřítomnost plísně salátové ((*Bremia lactucae*) a padlí (*Golovinomyces cichoracearum*).

V poslední kapitole jsou shrnuty dosavadní poznatky intenzivního výzkumu rodu *Lactuca* L., kterých bylo dosaženo během posledních 25 let. Za tuto dobu bylo zjištěno mnoho nových informací v oblasti taxonomie, genetické diversity, morfologie, molekulární biologie, biochemie a resistence. Jsou zde uvedeny také směry budoucího výzkumu. Mělo by se dbát o obohacování světové genofondové kolekce rodu *Lactuca* L. Více prozkoumána by měla být nová ohniska diversity tohoto rodu v jižní Africe, střední Asii a Severní Americe. Mimo jiné by měl být kladen větší důraz na možné využítí lociky vrbové (*L. saligna*) a lociky kompasové (*L. serriola*) jako zdrojů trvalé resistence. Potřebné jsou rovněž detailní studie zabývající se detekcí chemických sloučenin v pletivech rostlin rodu *Lactuca* L., které by našly uplatnění v např. v lékařství a farmakologii.