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Morphological variation of *Lactuca serriola* L. achenes as a function of their geographic origin

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Abstract – The morphological characteristics of achenes of *Lactuca serriola* represented by 34 local populations from Slovenia and 12 local populations from Sweden were studied in relation to their eco-geographical conditions. In total, eight quantitative morphological characters were evaluated: length and width of achene body; index length/width of achene body; number of ribs on achene body; length of beak; length of pappus bristles; pappus area and discus diameter. Nested ANOVA analysis indicated significant differences in length and width of achene body, length of pappus bristles, and pappus area between Slovenian and Swedish populations. Achenes from Slovenia were longer, wider and possessed longer pappus bristles than achenes from Sweden. Among geographical factors, latitude had the greatest impact on the morphological characters evaluated. Significant differences in seven parameters were also found between populations within countries and between samples within populations. It is probable that this variation has a genetic basis with sufficient variation within populations to permit continued selection.

Keywords: Achen, *Lactuca serriola*, eco-geographical conditions, fruit, morphology, pappus, wind-dispersed diaspore

Introduction

Wind dispersal is a natural mode of spreading achenes common in many plant communities, comprising 10–30% on average, and up to 70%, of the flora in temperate plant communities, with obvious morphological adaptations of achenes (WILLSON et al. 1990). Various morphological attributes such as hairs, wings, achene shape and size facilitate their aerodynamic transport, essentially by lowering wing- and/or plume-loading (the ratio of mass to surface area). Adaptive structural designs on the surface of achene body increase the

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roughness and thereby increase the drag that the air exerts on the achene in flight and prolong its travel time through the air (NATHAN et al. 2001).

Many studies have focused on the morphology of wind-dispersed diaspores of herbaceous members of the Asteraceae or trees of different families in relation to their fall speed (terminal velocity, setting velocity) (GREEN 1980, AUGSPURGER 1986, MATLACK 1987, ANDERSEN 1993a, GRAVUER et al. 2003, CHMIELEWSKI and STRAIN 2007). The morphology of achenes has been studied in numerous plant species. The proportion between size, shape, and weight of achene body, beak length, length of pappus bristles, and the number of ribs play an important role in plant dispersal under different eco-geographical and climatic conditions (ANDERSEN 1992, 1993a, GRAVUER et al. 2003, RIBA et al. 2005, LACROIX et al. 2007, KATINAS and CRISCI 2008, MONTY and MAHY 2010).

Elaborate mathematical models of diaspore dispersal take into account not only the morphological and physical parameters of the diaspores, but also physical environmental parameters (SCHULTZ et al. 1991, BULLOCK and CLARKE 2000), and examine different emission scenarios of dispersal and spread of wind-spread (ANDERSEN 1993b), climate-limited species, including *L. serriola* (BULLOCK et al. 2012). TACKENBERG et al. (2003) applied simulation modeling of wind dispersed plant diaspores to 335 plant species, and revealed considerable variation in the wind dispersal potential of species classified as the same morphological type of diaspores. Thus, the dispersal and survival ability with regard to morphological parameters and mass of diaspores must be assessed for individual species.

The dispersal of achenes is influenced by the height and structure of surrounding plants, the location of plants within the population (ANDERSEN 1993b, LAVOREL et al. 1994, WELHAM and SETTER 1998, BLUMENTHAL and JORDAN 2001, OESTER et al. 2009), and by the position of plant population in the centre of species distribution or on the margin, and degree of isolation of islands vary significantly among species with the same morphological type of diaspore (FRESNILLO and EHLERS 2008). FRESNILLO and EHLERS (2008) stated that for plants producing wind dispersed seeds, the height of mother plant, the spacing of branches and the position of fruits on the plant may directly affect the dispersal potential of released seeds or fruits to be carried away by wind. Differences in dispersal rate may thus occur even if there are no apparent differences in the morphology of the diaspores themselves (DONOHUE 1999). PERONI (1994) described evolutionary change in dispersal ability between old and young populations, where young often show higher dispersal rates than older populations. The chance that achenes will be dispersed over long distances increases with decreased setting velocity (FRESNILLO and EHLERS 2008). The ability to be dispersed long distances is attributed to diaspores' lower achene mass and advantageous proportion of achene mass to pappus mass and/or area (CHMIELEWSKI and STRAIN 2007).

Our scientific interest focuses on different aspects of infraspecific variation on *Lactuca serriola* L. (prickly lettuce, compass lettuce, fam. Asteraceae) (LEBEDA and ASTLEY 1999, LEBEDA et al. 1999, 2009). However, detailed data about variability in achene morphology related to eco-geographical conditions are limited (NOVOTNÁ et al. 2011). Prickly lettuce is considered one of the direct progenitors of cultivated lettuce *Lactuca sativa* L. (DE VRIES 1997). It belongs to the primary gene-pool of lettuce and plays an important role in modern lettuce breeding programs as a source of race-specific resistance genes against lettuce downy mildew (*Bremia lactucae* Regel) (LEBEDA et al. 2007b). Recently, *L. serriola* has spread throughout Europe as an invasive weed (JEHLÍK 1998, LEBEDA et al. 2001, 2004, BRANT and HOLEC 2004, HOOFTMAN et al. 2006, D'ANDREA et al. 2009).

Originally a meridional-temperate, western Euro-Asian species, prickly lettuce is now distributed worldwide (LEBEDA et al. 2004). The northern limit of its distribution in Europe is near 65° N in Finland and 55° N in Great Britain. The northernmost localities in Norway and Sweden are at 60° N (FERÁKOVÁ 1977). The greatest genetic diversity of this species in Europe is around the Mediterranean basin, including the Near East (Asia) and coastal Northern Africa (LEBEDA et al. 2004). *Lactuca serriola* is an annual or winter-annual therophyte; it is a ruderal species, growing preferably on disturbed soil. From an ecological viewpoint, this species is an »r« strategist with a short life cycle (FERÁKOVÁ 1977, D' ANDREA et al. 2009). It expands along roads, highways, railways and embankments (LEBEDA et al. 2001). The spread of this species is very closely related to human activities, mainly by transportation, building constructions, while anthropogenic climate changes are likely to accelerate this process (D' ANDREA et al. 2009).

According to many previous studies (DOLEŽALOVÁ et al. 2001, LEBEDA et al. 2001, HOOFTMAN et al. 2006, LEBEDA et al. 2007b), during the last 20 years prickly lettuce has shown an enormous range expansion with populations increasing in Europe and in some parts of Scandinavia (D' ANDREA et al. 2009). In the Netherlands, the occurrence of *L. serriola* has significantly increased since 1940, indicating that the species currently occurs in a broader range of vegetation types. Except for its original ruderal habitats, *L. serriola* currently occurs in more closed vegetation types, which are less continental and more humid (HOOFTMAN et al. 2006).

Within this highly polymorphic species there are two forms distinguished by the shape of their cauline leaves; f. *serriola* with divided leaves, and f. *integrifolia* with entire leaves (FERÁKOVÁ 1977).The two forms are not equally distributed around the world. In Europe, *L. serriola* f. *serriola* is distributed in the majority of European countries, but the distribution of f. *integrifolia* is restricted to the southern and western parts of Europe (LEBEDA et al. 2007a, b), and is most prevalent in the United Kingdom (PRINCE and CARTER 1977, CARTER and PRINCE 1982). The beginning of the flowering and the period between bolting and flowering are strongly influenced by local eco-geographical conditions (LEBEDA et al. 2007b).

Prickly lettuce can only reproduce sexually, producing plumed achenes (Figs. 1a, 1b). The spread of *L. serriola* is facilitated by the pappus on the top of achene body acting as a parachute (COUSENS et al. 2008). The diaspores of the genus *Lactuca* are monomorphic, in contrast to many other members of the Asteraceae where dimorphism or polymorphism are typical (HARPER et al. 1970, BAKER and DOWD 1982, IMBERT et al. 1996). Achenes of *L. serriola* are relatively small. The length of the achene body is 3 mm and together with the beak is 6–8 mm (DOSTÁL 1989, GRULICH 2004). Achenes are ±1 mm broad, oblong-ovate in shape, moderately flattened, and brown to grayish in color. The achene surface has 5 to 10 ribs with short fine bristles located in the apical part of the ribs and pointing towards the apex of achene. The beak is white, filiform, and as long as, or longer than the achene body. The monomorphic pappus consists of 2 rows of whitish hairs, which exceed the involucral bracts (FERÁKOVÁ 1977). The pappus is 3–4.5 mm long, white, and deciduous (FERÁKOVÁ 1977, DOSTÁL 1989, GRULICH 2004). Pappus bristles of *L. serriola* are smooth, consisting of two or three vertical rows of cells (TUISL 1968).

The first compilation of data on morphological parameters of *L. serriola* achenes was presented by NOVOTNÁ et al. (2011) where achene parameters from 50 populations of prickly lettuce from the Czech Republic, Germany, the Netherlands and the United Kingdom

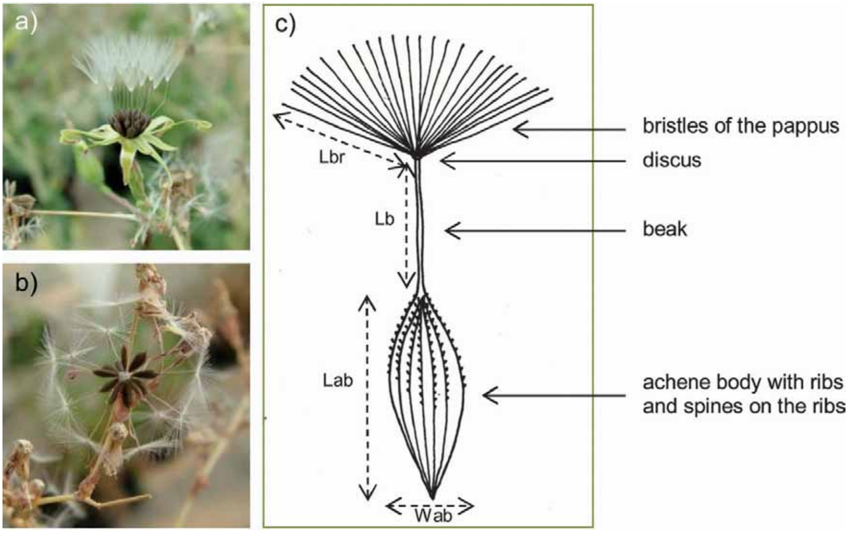

Fig. 1. *Lactuca serriola*: a) position of freshly mature achenes with pappus (in the morning), b) final position of mature achenes (at noon), c) schematic drawing of achene with beak and pappus, and measured morphological parameters: Lbr – length of bristles, Lb – length of beak, Lab – length of achene body, Wab – width of achene body.

were analyzed. NOVOTNÁ et al. (2011) showed that the two leafy forms of *L. serriola*, f. *serriola*, and f. *integrifolia,* differ in achene morphology. Achenes of f. *serriola* are shorter, thinner, with a shorter beak, lower length/width index, and have a higher number of ribs than those of the f. *integrifolia*. NOVOTNÁ et al. (2011) concluded that achene morphology was significantly correlated with longitude, latitude, and soil texture of original habitats of samples from the four countries mentioned above. Achene length and width increased along an east-west transect. Mean beak length had a similar trend with the exception of achenes from German populations. The number of ribs increased from east to west in continental Europe, whereas the lowest number of ribs was recorded in achenes collected in the Czech Republic and the United Kingdom. NOVOTNÁ et al. (2011) also showed that with increasing latitude, i.e. from south to north, *L. serriola* achenes were longer, narrower, with fewer ribs, and longer beaks.

To support the general conclusions based on the principles of morphological variation of achenes mentioned above, results need to be complemented by data on achene morphology from plants originating from additional regions with contrasting eco-geographical conditions. To do this, we analysed *L. serriola* achenes from Slovenia and Sweden. These countries differ not only in their geographical position, but also in environmental conditions. The Mediterranean region including Slovenia is characterized by the highest diversity of European *Lactuca* spp. and is considered the probable area of lettuce domestication (DE VRIES 1997, LEBEDA et al. 2004, 2007b). Slovenian populations of prickly lettuce are older than Scandinavian populations. The northernmost European localities of *L. serriola* in Norway and Sweden are located at 60° N (FERÁKOVÁ 1977) and intense spread of prickly lettuce in some parts of Scandinavia was observed during past 20 years only (D'ANDREA et al. 2009).

The main objective of the current study was to provide answers to the following questions: 1) Are there differences in the morphological parameters of *L. serriola* achenes between populations in the northern European limits of the species' distribution (Sweden) and populations in southern Europe (Slovenia)? 2) Which morphological parameters of achenes are significantly influenced by the original eco-geographical conditions?

Material and methods

Plant material

Initial experimental material was collected during explorations to Slovenia and Sweden in 2000 (DOLEŽALOVÁ et al. 2001). The set of *Lactuca serriola* samples used in the study consisted of 72 achene samples from 34 local populations in Slovenia (SVN) (Fig. 2a) and

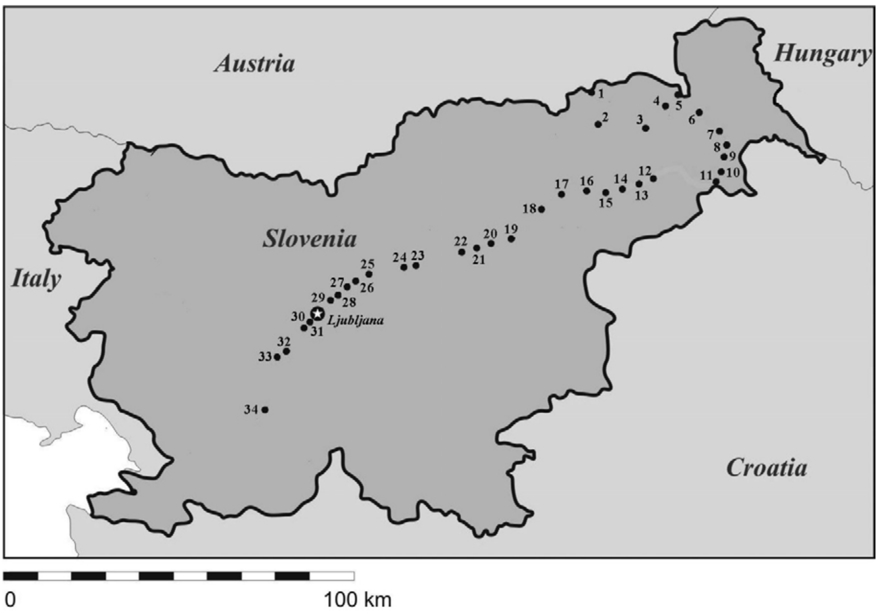

Fig. 2a. Geographic locations of *Lactuca serriola* local populations sampled in Slovenia.

47 achene samples from 12 local populations in Sweden (SWE) (Fig. 2b). Description of the *L. serriola* local populations in their original habitats and collection sites in Slovenia and Sweden was given by DOLEŽALOVÁ et al. (2001). One to six samples per collection site were collected, depending on the number of plants in the local population. Samples from Slovenia were collected from latitude 45°46'31'' N to 46°40'50'' N, and from longitude 14°12'51'' E to 16°11'35'' E (Fig. 2a). Collection locations were situated at an altitude of 187 to 594 m a.s.l. The mean annual temperature in Ljubljana, the capital of Slovenia, for the period of 1991–2000 was 10.9 °C (STATISTICAL OFFICE OF THE REPUBLIC OF SLOVENIA 2011). Collection sites in Sweden were located at latitude of 55°36'11'' N to 59°58'16'' N, and between longitude of 12°49'48'' E, and 18°03'52'' E (Fig. 2b). Achenes were collected

Fig. 2b. Geographic locations of *Lactuca serriola* local populations sampled in Sweden.

at an elevation of 3 to 158 m a.s.l. The mean annual temperature in Stockholm is 6.6 °C (ANONYMOUS, 2011). Detail passport data related to the achene samples are available from the authors.

The achene samples were regenerated in the greenhouse in 2006 at the Department of Botany (Faculty of Science, Palacký University in Olomouc, Czech Republic) located at the 49°34'29,61'' N, 17°16'54,29'' E, and 208 m a.s.l. Each sample was represented by 16 plants. Plants were cultivated in plastic pots with garden soil under a standard protocol for regeneration of plant genetic resources of *Lactuca* spp. (BOUKEMA et al. 1990, LEBEDA et al. 2007b). During vegetative growth, the taxonomic status of samples was verified and the infraspecific classification was determined.

Five plants per sample were used for morphological assessment of achenes. Around 60 mature achenes were collected from 3 to 4 heads from single plants at the beginning of fruit maturity. Achenes from each single plant were kept separate and measured. The samples are maintained at the Department of Botany (Faculty of Science, 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 and width of the achene body (Lab and Wab respectively); length/width index of achene body (Lab/Wab index); length of beak (Lb); number of ribs (Nr); length of pappus bristles (Lbr); pappus area (Paparea); and diameter of discus (Discus). Achene morphological features evaluated are schematically illustrated in Fig. 1c. Achenes were measured using the ImageJ computer program (ImageJ 1.32j, Wayne Rasband. National Institutes of Health, USA) after being scanned as JPGs at a resolution of 400 dpi. Calibration was determined by the program on a scanned ruler. Measurements of distance were converted into mm with an accuracy of 0.01 mm. Length and width of achene were measured at the longest and widest point of the achene body. The shape of the achene body was determined from the Lab/Wab index. The length of the beak (Lb) was the distance from the apical point of the achene body to the discus. Length of the pappus bristles (Lbr) was measured from the point of attachment of the bristle on the discus to the apex of the bristle. The area of the pappus (Paparea) was calculated as the surface of the circle, where the radius is given by the length of the bristle. For this purpose five bristles per achene were measured.

Ten achenes of each plant were randomly chosen to determine the number of ribs (Nr). A magnifying glass was used to count the number of ribs on each side of the achene and the numbers totaled.

Statistical analysis

Statistical analysis of morphological characters of *Lactuca serriola* achenes were performed using NCSS software, version 2007 (HINTZE 2001). Morphological differences between achenes were evaluated using the nested ANOVA General Linear Models (GLM) in NCSS.

Three geographical parameters, latitude, longitude, and altitude were analyzed. Associations between morphological characters of the achenes and geographical parameters of the plant populations/collection sites were determined using CANOCO for Windows 4.5 and CanoDraw for Windows 4.5 (TER BRAAK and ŠMILAUER 2002). 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 geographical factors was determined using the method 'forward selection'. Monte-Carlo permutation test with 999 permutations was used to test the significance of the environmental factors used in RDA.

Results

Character of *Lactuca serriola* populations

According to the shape of cauline leaves, all plants from Slovenia were determined to be *L. serriola* f. *serriola*. Within samples from Sweden, *L. serriola* f. *serriola* was the dominant form, while the occurrence of *L. serriola* f. *integrifolia* was determined in only three plants within one sample from population 45 (Fig. 2b, Tab. 1).

Tab. 1. *Lactuca serriola* form *serriola* and *integrifolia* for populations collected in Slovenia and Sweden.

L. serriola	Number of entities analysed		
	Slovenia	Sweden	Total
Populations	34	12	46
Achene samples	72	47	119
Plants f. *integrifolia* (frequency)	0 (0%)	3 (1.61%)	3 (0.61%)
Plants f. *serriola* (frequency)	304 (100%)	183 (98.39%)	487 (99.39%)

Data for the morphological characters of *L. serriola* achenes from Slovenia were obtained from 304 plants, representing 72 achene samples from 34 collection sites. Corresponding data for achenes from Sweden were obtained by measuring achenes from 186 plants, representing 47 achene samples from 12 collection sites. Sample 192/00-3 (local population 41) was not analyzed for four achene body parameters, Lab, Wab, Lb, and Lab/Wab index because achenes were damaged during measurements.

Comparison of morphological characters of achenes from Slovenia and Sweden

Achenes from Slovenia were longer and wider than those from Sweden (Tab. 2, Figs. 3a, 3b). There were significant differences in mean *L. serriola* achene length and width from Slovenia and Sweden (Tab. 3). Significant differences in the length and width of achenes were observed among local populations and within samples in both countries. No significant differences in the length/width index or the length of the beak were observed for

Tab. 2. Descriptive statistics of morphological characteristics of *L. serriola* achenes from Slovenia and Sweden.

Morphological Character[a]	Parameters of *L. serriola* achenes											
	Slovenia						Sweden					
	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
Lab/Wab index	15178	304	2.99	0.39	1.72	5.77	9236	185	3.04	0.39	0.97	5.19
Lb	15178	304	4.20	0.53	1.73	6.52	9236	185	4.35	0.51	1.89	5.99
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

[a]Lab – length of achene body (mm). Wab – width of achene body (mm). Lab/Wab index – index length/width of achene body. Lb – length of beak (mm). 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, maximum values.

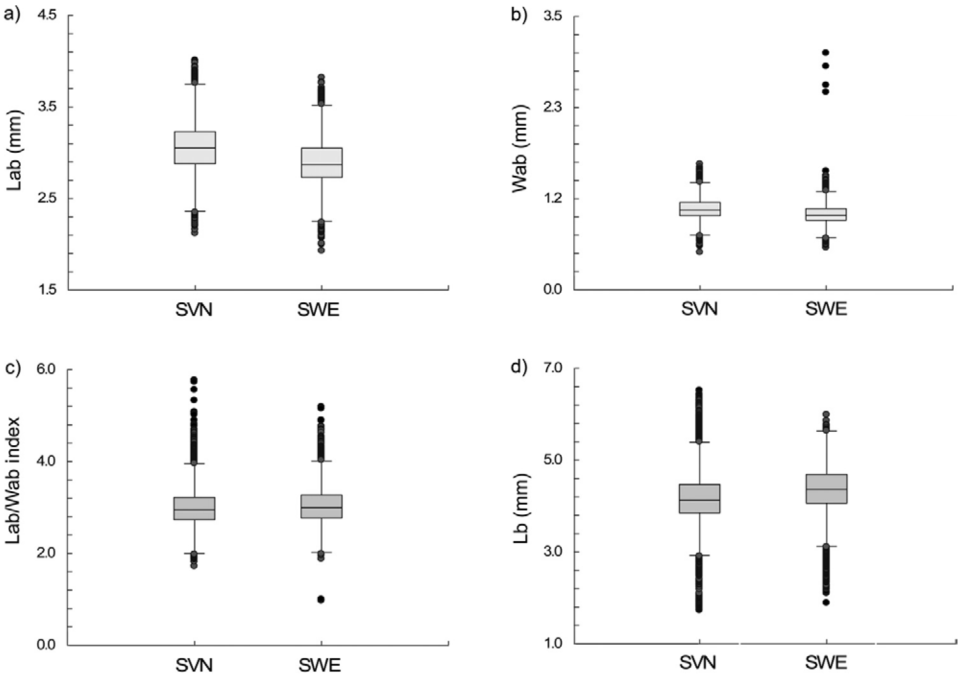

Fig. 3. Morphology characteristics of achene bodies of *Lactuca serriola* from Slovenia (SVN) and Sweden (SWE): a) Length of achene body (Lab), b) Width of achene body (Wab), c) Index of length/width of achene body (Lab/Wab index), d) Length of beak (Lb).

Tab. 3. Morphological characteristics of *L. serriola* achenes from119 samples and 46 local populations from Slovenia and Sweden analysed by Nested ANOVA.

Morphological characteristics[a]	Source of variation	df	SS	F-ratio
Lab	Country	1	167.34	28.97***
	Local populations within countries	44	254.14	2.27***
	Samples within countries	73	185.83	56.04***
Wab	Country	1	31.15	29.42***
	Local populations within countries	44	46.59	3.8***
	Samples within countries	73	20.36	21.28***
Lab/Wab index	Country	1	13.73	1.3 ns
	Local populations within countries	44	463.52	5.43***
	Samples within countries	73	141.64	15.41***
Lb	Country	1	138.75	2.56 ns
	Local populations within countries	44	2388.87	5.04***
	Samples within countries	73	786.58	75.61***

[a]Lab – length of achene body. Wab – width of achene body. Lab/Wab index – index length of achene body/width of achene body. Lb – length of beak. df – Degree of freedom. SS – Sum of Squares. ***$p < 0.05$. ns – not significant.

Slovenia and Swedish samples. Means are shown in table 2 and in figures 3c and 3d. However, significant differencesin Lb and the Lab/Wab index were detected among local populations and within samples in both countries ($p < 0.05$) (Tab. 3).

Comparison of mean length of pappus bristles (Lbr) and pappus area (Paparea) showed significant differences between countries, local populations within countries, and achene samples within countries ($p < 0.05$) (Tab. 4). Slovenia local populations had higher values for these morphological characters than the Swedish local populations (Tab. 2, Figs. 4a, 4b).

No significant differences in the diameter of discus (Discus) and the number of ribs (Nr) were found between countries (Tab. 4). Values of means are shown in table 2 and Figures 4c and 4d. On the other hand, comparison of local populations and achene samples within countries showed significant differences ($p < 0.05$) (Tab. 4).

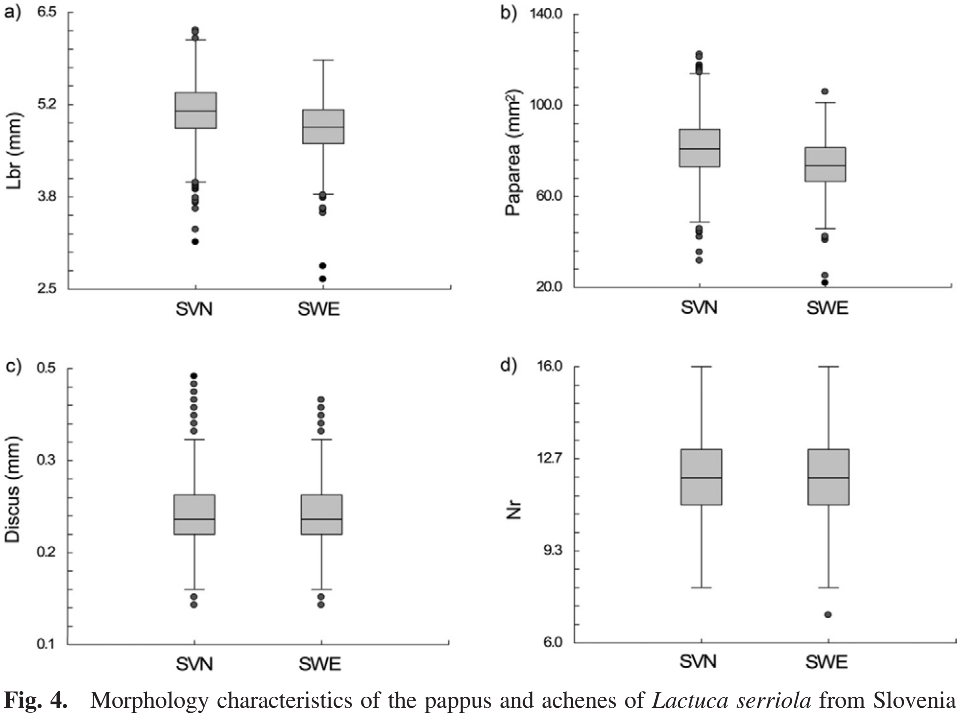

Fig. 4. Morphology characteristics of the pappus and achenes of *Lactuca serriola* from Slovenia (SVN) and Sweden (SWE): a) Length of bristles (Lbr), b) Pappus area (Paparea), c) Diameter of discus (Discus), d) Number of ribs (Nr).

Associations of achene morphology with geographical factors

Associations between morphological parameters of *L. serriola* achenes and geographical factors of collection sites were evaluated by RDA (Figs. 5, 6). Latitude had a significant influence on the morphological characters of *L. serriola* achene body ($F = 665.66$, $p < 0.001$), and also on morphological characters of achene ribs and pappus ($F = 240.47$, $p = 0.002$) (Tab. 5). As the latitude increases, the length/width index of the achene body (Lab/Wab index) and length of beak (Lb) increased, conversely the length (Lab) and width (Wab) of the

Tab. 4. Morphological characteristics of achene ribs and pappus of *L. serriola* from 119 samples and 46 local populations from Slovenia and Sweden analysed by Nested ANOVA.

Morphological characteristics	Source of variation	df	SS	F-ratio
Lbr	Country	1	64.32	18.31***
	Local populations within countries	44	154.57	2.85***
	Samples within countries	73	89.92	13.25***
Paparea	Country	1	62664.8	18.11***
	Local populations within countries	44	152252	3.00***
	Samples within countries	73	84141.5	13.08***
Discus	Country	1	0	0 ns
	Local populations within countries	44	0.45	2.15***
	Samples within countries	73	0.35	3.87***
Nr	Country	1	0.34	0.01 ns
	Local populations within countries	44	1302.32	3.22***
	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 – Degree of freedom. SS – Sum of Squares. ***$p < 0.05$. ns – not significant.

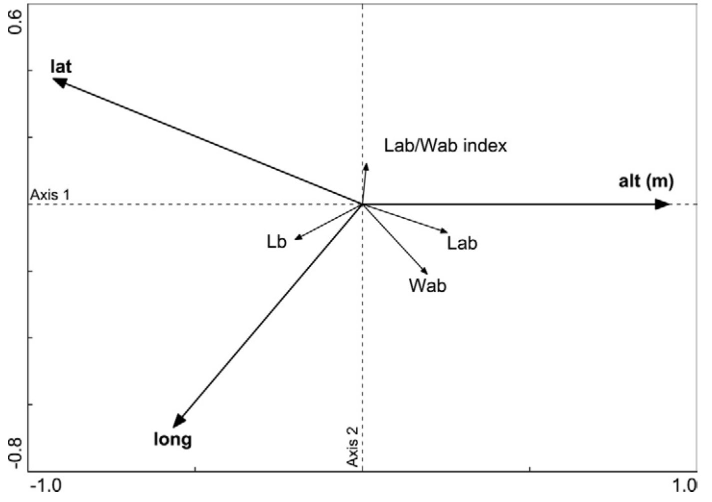

Fig. 5. Correlation of morphological characteristics of achene body of *Lactuca serriola* from Slovenia and Sweden with geographical factors selected by forward selection using Redundancy Analysis. Axis 1 and Axis 2 account for 4.5% of the variability in species data. Lab – length of achene body, Wab – width of achene body, Lb – length of beak, Lab/Wab index – index length/width of achene body, lat – latitude, long – longitude, alt (m) – altitude.

achene body were decreased (Fig. 5). Length of the pappus bristles (Lbr) and pappus area (Paparea) had lower values at higher latitudes. For discus diameter (Discus) and number of ribs (Nr), no relationship with geographical location of collection sites was found (Fig. 6).

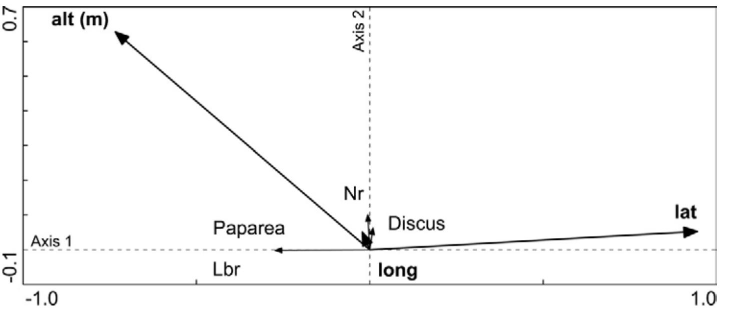

Fig. 6. Correlation of morphological characteristics of achene ribs and pappus of *Lactuca serriola* achenes from Slovenia and Sweden with geographical factors selected by forward selection using Redundancy Analysis. Axis 1 and Axis 2 acount for 6.6% of the variability in species data. Lbr – length of bristles, Paparea – area of pappus, Discus – diameter of discus, Nr – number of ribs. lat – latitude, long – longitude, alt (m) – altitude.

Tab. 5. Impact of geographical factors affecting morphological characteristics of *L. serriola* achenes using the forward selection method of Redundancy Analysis.

Variables	Achene body[a]		Achene ribs and Pappus[b]	
	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

[a]Lab – length of achene body. Wab – width of achene body. Lab/Wab index – index length of achene body/width of achene body. Lb – length of beak.
[b]Lbr – length of bristles. Paparea – area of pappus. Discus – diameter of discus. Nr – number of ribs.

Longitude and altitude had a lower impact on morphological parameters of *L. serriola* achenes (Tab. 5). With decreasing longitude, achenes were characterized by shorter, but wider bodies, longer beaks and lower length/width index (Fig. 5). With increasing longitude, all pappus characters became longer (Fig. 6). In places of higher elevation, longer and wider *L. serriola* achenes with shorter beaks, longer pappus, wider discus and higher number of ribs occurred (Figs. 5, 6).

Discussion

Length and width of achenes

Samples of *Lactuca serriola* from Slovenia differed significantly from those from Sweden in length and width of achene body. Generally, achenes of prickly lettuce were longer and wider in Slovenia than in Sweden. This is supported by RDA analysis showing shorter length and width of achene body as one goes north. Mean values for *L. serriola* f. *serriola* achenes from the Czech Republic which is geographically located between Slovenia and Sweden reported by NOVOTNÁ et al. (2011) are: Lab 2.95 mm, Wab 0.93 mm, Lab/Wab 3.21.

While the width of Czech achenes reach the lowest value, the length of achene body for Czech populations confirmed the trend of a decreasing value from the south to the north. The differences in the length/width index of the achene body between the Slovenian and Swedish populations of prickly lettuce are not statistically significant; however the Lab/Wab achene index from these two countries increased toward the north. Toward the north, achenes are shorter and narrower. This parameter must be considered with regard to the beak length and pappus area.

Achene ribs

The number of ribs between populations from Slovenia and Sweden was not significantly different. In both countries, the mean value was 11.7 ribs, more than the 5–10 ribs described for this species by FERÁKOVÁ (1977), and more than reported by NOVOTNÁ et al. (2011) for achenes from the Czech Republic, Germany, the Netherlands, and United Kingdom. However, NOVOTNÁ et al. (2011) stressed that the achenes from central European populations (from the Czech Republic and Germany) created a distinct group, significantly different based on the number of ribs from the group of Dutch and English populations. NATHAN et al. (2011) paid particular attention to various morphological features of diaspores, including those which increase the roughness of the seed surface, thereby increasing the drag force on the seed in flight, both of which increase travel time through the air. Our study shows that there is a variation in number of ribs. We did not measure the bristles on achene ribs, however we noticed differences in their quantity and quality among samples. The architecture of bristles and ribs with regard to species dispersion and evolution needs to be studied in more detail.

Beak

The difference in the length of the beak between Slovenian and Swedish populations was not statistically significant. However, the beak of achenes from Slovenia was shorter than the beak of achenes from Sweden. Similar phenomenon was observed by NOVOTNÁ et al. (2011) on *Lactuca serriola* populations from Czech Republic, Germany, the Netherlands and Great Britain, where toward the west and the north the beak became longer.

ANDERSEN (1993a) studied the morphology and settling velocity of some wind-dispersed species of the Asteraceae, including *L. serriola*. He found that diaspores with beaked achenes have significantly lower setting velocities than diaspores with unbeaked achenes, even though beaked and unbeaked achenes do not differ in plume loading, i.e. the ratio of diaspore weight/plume area (MATLACK 1987). Lower setting velocity is one of the prerequisites of better dispersal ability which is attributed to younger populations (CHMIELEWSKI and STRAIN 2007). So, toward the north, achenes of younger populations of prickly lettuces are favored by longer beaks that reach lower setting velocity compared to older southern populations.

Discus and pappus

No significant difference was found for discus diameter between Slovenia and Swedish populations. The mean value of that trait from both countries was 0.27 mm. According to correlation analysis, a weak correlation was found with latitude and longitude.

Our recent study showed significant differences in the length of pappus bristles and the area of pappus of *L. serriola* from Slovenia and Sweden. When we compared achene size to pappus area, Slovenian achenes, with a significantly larger achene body, also possessed significantly longer pappus bristles and a larger pappus area than the smaller-sized Swedish achenes. Dispersal ability is positively related not only to lower mass of achene, but also by advantageous proportion between achene mass and pappus. This scenario was demonstrated empirically on several wind dispersed plant species from the Asteraceae by CODY and OVERTON (1996).

Very detailed studies of the pappus characters, especially of the pappus bristles of weedy and non-weedy aster species were made by CHMIELEWSKI and STRAIN (2007). They concluded that the achenes of weedier aster species have the potential to remain in the air longer and thus can be dispersed further on average than achenes of non-weedy aster species. The greater dispersal ability of weedy species is due to comparatively lower values of terminal velocity resulting from the lower achene mass.

SHELDOM and BURROWS (1973) found a negative curvilinear relationship between terminal velocity and the ratio of pappus diameter/achene diameter for 17 species. In our study we did not measure the diameter of achenes, and we substituted achene width for this parameter. The ratio of pappus diameter/achene width is for the Slovenian achenes 10.01, and 10.34 for Swedish achenes. From the curve constructed by SHELDOM and BURROWS (1973), the extrapolated terminal velocity for Slovenian achenes is 0.8 m/s, and 0.6 to 0.4 m/s for Swedish achenes.

These data are in agreement with scenarios on wind dispersibility of achenes in old and young populations proposed by FRESNILLO and EHLERS (2008). They stated that the terminal velocity of achenes in old populations is higher, so a subsequent reduction in dispersal ability as the population ages is expected due to the risk of long dispersal seeds landing in unsuitable habitats. In old populations, this would favor genotypes with a lower dispersal rate. Populations in newly colonized areas are expected to have high dispersal potential, because they were established from seed with parameters enabling long-distance flight. However, diaspores with high dispersal ability may be blown off newly reached areas, and this should select for a reduction in dispersal ability in future generations originating from individuals that produce diaspores with low dispersal ability (CODY and OVERTON 1996).

FRESNILLO and EHLERS (2008) compared the dispersal ability of three wind dispersed plant species (*Cirsium arvense*, *Epilobium angustifolium* and *E. hirsutum*) from populations on a mainland and three islands. They found that the achenes of *C. arvense* (Asteraceae) from the mainland had a significantly longer pappus than the achenes from the island populations. The conclusion of HARPER et al. (1970) that the achenes from islands have shorter pappi and lower dispersal ability than achenes from mainland was in agreement with our results (Table 2). Prickly lettuce is not yet completely settled throughout the territory of southern Sweden, local populations are partly isolated, so from this regard we can consider them as »islands«, conversely to the situation in Slovenia where this species is distributed throughout whole country. This phenomenon was described by DOLEŽALOVÁ et al. (2001) and confirmed during recent field observations in 2009 and 2010. STRYKSTRA et al. (1998) showed that pappus size of *Arnica montana* was significantly, but weakly positively correlated with achene mass. Heavier achenes with high germination and seedling quality, therefore, stay closer to the point of release than lighter ones. Long distance dispersal as a prerequisite of the establishment of new populations of *A. montana* depends on the transport by human activity.

A lower proportion of pappused achenes were found in older populations of *Lactuca muralis* (synonym. *Mycelis muralis*) than in newer colonies (CODY and OVERTON 1996). They stated that it is unclear whether the observations were due to genetic differences or phenotypic plasticity; however, the existence of variation between populations had been established.

According to SHELDON and BURROWS (1973), the efficiency of dispersal is determined more by the fine details of pappus geometry, which directly affects its aerodynamic properties, than by the size ratio of pappus to achene. The pappus is generally thought of primarily as a long-distance seed dispersal mechanism. SHELDON and BURROWS (1973) cited the suggestion of GOEBEL (1905) that the primary function of the pappus could be to be a transpiration apparatus for the fruit. STEVENS at al. (1983) suggested that the pappus of *Chrysothamnus nauseosus* plays an important role in orientation of achene on the soil surface and adhesion, both of which increase survival when achenes surface-germinate. This theory is at least partly supported by MEYER (1997) who did not observe a significant correlation between absolute achene mass and relative pappus mass of *Chrysothamnus nauseosus*.

Associations of evaluated morphological characters of achenes with geographical factors

Among geographical factors, latitude had the greatest influence on length and width of achene body. Despite this, at higher altitudes, longer and wider achenes were found. 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 diaspore mass was one of the strongest predictors of dispersal ability. At higher altitudes, wider achenes are preferred because their dispersal ability increases.

Variation within local populations and within samples

In our current study significant differences in the length and width of achene body, index of both parameters, length of pappus bristles, pappus area, diameter of discus, and number of ribs were found between populations within countries and between samples within populations. ANDERSEN (1992) hypothesizes that the high intraspecific variability in seed settling velocities of eight wind–dispersed Asteraceae is connected with risk-spreading strategy of species. The highly significant between-plant differences in achene mass found in populations of *Chrysothamnus nauseosus* (Asteraceae) are genetically fixed, as reported by MEYER (1997). Significant variability within the populations observed in the current study probably has a genetic basis indicating sufficient variation within populations to permit continuous selection.

Future research

Experiments with only a few species may lead to tentative conclusions, but can hardly be generalized for a larger group of species. In our study we did not examine physical parameters of achenes of *L. serriola* regarding their setting velocity, but we did document the significant differences in crucial traits of *L. serriola* achenes from two eco-geographically distinct areas in Europe. We discussed each parameter separately, however, their integration and interpretation need a more comprehensive treatment. Data from the current study will be combined with those obtained by NOVOTNÁ et al. (2011), helping to contribute to the elucidation of evolutionary and taxonomical concepts for *L. serriola*.

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