LITTORELLA UNIFLORA (L.) ASCHERSON: A REVIEW

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Littorella uniflora (L.) Ascherson, a member of *Plantaginaceae* family, belongs to a group of isoetids – small, slow-growing, evergreen aquatic plants. They are characterized by strong and stiff basal leaves and a large amount of root biomass. Oligotrophic and mesotrophic freshwaters are typical habitats for this plant. *L. uniflora* is a boreal subatlantic European species. It is spread over whole western and northern Europe including the United Kingdom and Ireland. Austria, Czech Republic, and Poland lie on the southeast border of *L. uniflora* distribution. In the Czech Republic, as well as in the Netherlands or Ireland, the number of suitable habitats is rapidly decreasing. Therefore it is important to understand the needs of this macrophyte in order to propose quality rescue management to restore its population. This paper gives brief information about biology and ecological adaptations of *L. uniflora*. It also focuses on threats, distribution, and management at some of its current localities in the Czech Republic.

denuded fishpond bottom; Plantaginaceae; oligotrophic habitat; isoetid



doi: 10.2478/sab-2014-0101 Received for publication on October 1, 2013 Accepted for publication on June 3, 2014

Plant description

Littorella uniflora is a small, amphibious water plant with a thick rhizome and numerous adventitious roots. It is characterized by a large amount of root biomass (S c u l t h o r p e, 1985). *L. uniflora* is able to grow under submerged emerged conditions. After emergence, the submerged leaves rapidly die and aerial leaves are formed within few days (H o s t r u p, W i e g l e b, 1991). Leaves forming a basal rosette are grass-like, cylindrical, obtuse on the top, and sheath extended at the base. They are thick, bald, with an elliptic cross-section (Fig. 1).

Their size depends on the presence and type of the stress factors (Farmer, Spence, 1986; Robe, Griffits, 1998). Normally, they are 4–12 cm long (Slavík, 2000), but Hejný (2000) mentions the length of up to 20 cm. Terrestrial form creates as much as five times more leaves that can be shorter, pointed with a distinguished top and bottom side (Procházka, Husák, 1999). Both forms differ in the amount of stomata and lacunal space (Nielsen, Sand-Jensen, 1997; Robe, Griffits, 1998).

Epidermis of the submerged leaves lacks stomata and their diameter is about 2–3 times larger than that of aerial leaves as a consequence of larger lacunal space (Hostrup, Wiegleb, 1991).

Male flowers grow up from the base of leaves on slender stalks which are up to 9 cm long (Slavík, 2000). Oval bracts are made under half of the stalk. Each bract ends with a male flower composed of calyx and corolla. Male sepals are oblong-elliptic with thin white margins. A 4-mm long corolla made of a soft pipe terminates with four light edges of-elliptic shape. Stamens with yellow anthers are up to 2 cm long (Slavík, 2000). Usually two female flowers grow up at the base of the stem, sessile and hidden among the bases of the leaves (Hut chin s on, 1975). They are made of triangular lobes and a 3-mm long sepal. A conspicuous pistil can be as much as 12 mm long (Fig. 2).

Development of the sex organs occurs only with the emerged form. The submerged individuals are sterile and reproduce only by runners (West, 1905) as much as 60 cm long (Procházka, Husák, 1999). Flowering occurs from May to September (Slavík, 2000)

^{*} Supported by the Internal Grant Agency of the Faculty of Environmental Sciences (IGA), Project No. 20124277.

as early as three or four weeks after the emergence (R ob e, Griffits, 1998). *L. uniflora* is an anemophilous plant (H u t c h i n s o n, 1975; S c u l t h o r p e, 1985; H e j n ý, 2000).

Fruit is a yellow-brown to auburn, minute (1.5–2.5 mm) one seeded nut. Fruits are produced in small quantities, with a maximum of about twenty per plant per year (Arts, van der Heijden, 1990). L. uniflora is an anemochorous plant (Hejný, 2000). John, Richert (2011) excluded the possibility of the hydrochory by their experiment. There are different opinions on seed bank longevity. Although Thompson et al. (1997) called it transtendent, the other authors indicated it is persistent (W y n h o f f, 1988; B e k k e r et al., 1999). Bekker et al. (1999) also found seeds in 80-year old sediment, but they did not mention the germinative capacity. Wynhoff (1988) mentioned that seeds keep the germination viability for more than 30 years. According to the sediment age, seeds can be found at the depth of 5-15 cm (Thopson et al., 1997; Bekker et al., 1999). In the case of sediment accretion of fishpond reservoirs it is necessary to take into consideration the depth of up to 50 cm (Šumberová, 2013, pers. comm.).

Under optimal conditions, germination takes place early in the spring. Arts, van der Heijden (1990) regarded light, moisture, and temperature as the most important parameters. These conditions can be accomplished, for example, by summer drainage (Hejný, 1978; Šumberová, 2011). tion on environmental growth conditions). Unlike most water plants, L. uniflora has high radial oxygen loss (ROL) (Schmolders, Roelofs, 1996). The highest ROL was measured at the base of the root, the lowest at the top of the root (Smith et al., 1990). Due to the high ROL values, the zone around the roots is strongly oxygenated which has a high impact on the nutrient uptake (Smith et al., 1990; Schmolders, Roelofs, 1996). Farmer (1985) and Wigand et al. (1998) mentioned the presence of mycorrhiza on the roots of L. uniflora. It helps to take up phosphorus which is inaccessible for the other plants. Therefore the amount of phosphorus in the sediment is more important than that in the water layer. High ROL is responsible for oxidation of Fe(II) to Fe(III) which co-precipitates phosphate to form highly insoluble iron (III)-phosphates. This phenomenon gives L.uniflora an advantage over the other rooted plants in competition for phosphorus (Christensen et al., 1997).

The other way how *L. uniflora* influences its environment is the reduction of sulphate to sulphide. Sulphides reduce iron(III)-phosphates and cause mobilization of phosphorus in sediment (S m o l d e r s et al., 2001). However, highly aerobic conditions in the sediment can slow down this process (C h r i s t e n s e n et al., 1997).

L. uniflora grows in the waterbodies with a low nutrient availability in the sediment. The main source of nitrogen are nitrates (S c h u u r k e s et al., 1986). S a n d - J e n s e n et al. (1982) and R i s g a a r d -

Biology

The same as the other isoetids, *L. uniflora* grows at non-productive oligotrophic habitats. (see the sec-



Fig.1. Littorella uniflora - flower detail (Procházka, Husák, 1999)



Fig.2. *Littorella uniflora* - leaf cross section (Procházka, Husák, 1999)

P e t e r s e n , Jensen (1997) found out that the high ROL values promote nitrification of ammonium to nitrates. That gives *L. uniflora* an advantage in comparison with other water plants which use ammonium as a main source of nitrogen. Also, it has been evidenced that *L. uniflora* cannot cope with high nitrogen concentrations in the sediment. It appears that phosphorus (C h r i s t i a n s e n et al., 1985) and carbon (R o e l o f s et al., 1994) are the growth limiting elements.

L. uniflora can be found in water with low carbon dioxide and bicarbonate levels in the water layer. In these carbon poor environments, carbon dioxide levels in the sediments are usually up to hundred-fold higher than in the water layer (Smolders et al., 2002). In contrast to most other aquatic macrophytes, L. uniflora assimilates carbon dioxide very efficiently from the sediment (Pedersen, Sand-Jensen, 1992). Nielsen, Sand-Jensen (1997) and Smolders et al. (2002) reported that carbon dioxide from the sediment accounts for 70-100% of the carbon uptake of L. uniflora. On the other hand L. uniflora is unable to use bicarbonate as a carbon source (M a d s e n, 2002). Furthermore, the specific adaptation of the plants to the carbon dioxide uptake from the sediments does not permit an efficient uptake of bicarbonate or carbon dioxide from the water layer. These adaptations include a thick leaf, cuticle without stomata, a well developed root system, and presence of a continuous system of gas-filled interconnected lacunae (Boston, 1986; Madsen, 2002).

Environmental growth conditions

L. uniflora is a tenagophyte (H e j n ý, 2000). It occurs in shallow shores of lentic water, i.e. under the conditions of the Czech Republic in fishponds and drinking water reservoirs, in north and west Europe softwater lakes come into consideration.

Most authors reported a 2-metre depth as limiting for *L.uniflora* occurrence (S a n d - J e n s e n, 1978; S z m e j a, 1994; H e j n ý, 2000), however, T h u n m a r k (1931) found *L.uniflora* vegetation at the depth of 4.5 m in the Swedish lake Fiolen. S z m e j a (1994) and S z a n k o w s k i, K l o s o w s k i (2006) mentioned a depth range of 20–70 cm as a centre of *L. uniflora* distribution.

H e j n ý (2000) considered *L. uniflora* as S-strategist able to tolerate stress conditions such as nutrient deficiency and cleansing in shoreline (F a r m e r, S p e n c e, 1986; S z m e j a, 1994). *L. uniflora* is the best competitor of all the species of the isoetid group (F a r m e r, S p e n c e, 1986). In the case of optimal environmental condition it is able to create a dense vegetation bed, impervious for another submerged water plants (J í l e k, 1956; S a n d - J e n s e n, 1978).

Although H e j n ý (2000) considered *L. uniflora* a strictly oligotrophic species, F a r m e r, S p e n c e (1986) and M u r p h y (2002) showed its considerable

tolerance to dystrophic and mesotrophic waters. This finding has been confirmed by $H u s \dot{a} k$, A d a m e c (1998) who reported *L. uniflora* individuals in the mesotrophic fishpond Králek near Kardašova Řečice (South Bohemia, Czech Republic).

The pH range of water bodies in which *L. uni-flora* has been reported is quite wide (4.4 to nearly 9) (Iversen, 1929; Jensen, 1979; Arts, van der Heijden, 1990; Palmer et al., 1992; Szankowski, Klosowski, 2006). Roelofs (1984) mentioned a high tolerance to low pH. Only one pH report has come from the Czech Republic so far; Husák, Adamec (1998) measured a pH value of 7.5 in Králek fishpond.

Alkalinity range of waters with the occurrence of L. uniflora varies from 0.1 to 2.2 mmol/l (Vestergaar, S an d - Jensen, 2000; Palmer et al., 1992). In the laboratory experiment, Bellemakers et al. (1996) proved that the growth of L. uniflora was not influenced by sediment alkalinity increase, but water alkalinity increase might have greatly impacted it (McElarney et al., 2010).

In general, we can say that *L. uniflora* prefers water environment with high water transparency, low alkalinity, pH, chlorophyll content and low concentration of total phosphorus and nitrogen. *L. uniflora* prefers sandy, clayey or peaty sediments with occasional occurrence of an organic matter layer (H e j n ý, 2000; S z a n k o w s k i, K l o s o w s k i, 2006). F a r m e r, S p e n c e (1986) found out that *L. uniflora* was able to grow at the bare peat.

Vegetation pattern

L. uniflora belongs to the Eleocharito-Littorelletum uniflorae Chouard 1924 association. This association, especially when submerged, exhibits a very low species diversity (C h y t r ý , 2011). In many cases, only two species share the same habitat, L. uniflora and Eleocharis acicularis. After emersion, small, annual plants like Gypsophila muralis, Radiola linoides or other low nutrient species may occur. If the level of nutrient in the sediment is high, species like Carex bohemica or Persicaria lapathifolia crop up. In acidified lakes, where Juncus bulbosus may become dominant, L. uniflora can be dislodged from their habitats (R o e l o f s et al., 1994) (see the chapter on the threats to L. uniflora).

Distribution

L. uniflora is a boreal subatlantic European species (Procházka, Husák, 1999; Arts, 2002). In West Europe it can be found in Ireland, Great Britain, the Netherlands or France (Schoof-van Pelt, 1973; Palmer et al., 1992). In North Europe it can be found in Scandinavia up to 66° 26'N (Procházka, Husák, 1999; Lawesson, 2004). The southern border of distribution stretches from the Azores to Spain, Portugal, northern Italy, across Austria, the Czech Republic to Poland and Belarus (Procházka, Husák, 1999; Mucina et al., 2003; Szankowski, Klosowski, 2006).

The Czech Republic lies on the southeast border of the *L. uniflora* distribution. Historically, *L. uniflora* was reported from many water bodies in the Czech Republic. Sporadic reports came from the ponds of the Doksy, Brdy hills, Šumava Mts. or Nové Hrady regions (K l i k a , 1935). Mostly it was detected in the ponds of the České Budějovice Basin (J í l e k , 1956; H e j n ý , 1967), but the centre of its distribution was the Třeboň Basin and Jidřichův Hradec area, both located in South Bohemia (P o k o r n ý et al., 1990; H u s á k , A d a m e c , 1998; P r o c h á z k a , H u s á k , 1999).

Recent population of *L. uniflora* can be found only at eight localities in the Czech Republic (Š u m b e r o v á, 2011), namely: Staňkovský fishpond (R e k t o r i s, 2013, pers. comm.), Hejtman fishpond (P r o c h á z k a, H u s á k, 1999), Králek, Nový, and Osika fishponds (D v o ř á k o v á, B o u blík, 2002; H e s o u n et al., 2008), water reservoir Karhov and Horní Mrzatec fishpond (E k r t o v á, Č e c h, 2008) in South Bohemia, and water reservoir Láz in the military area of Brdy hills, Central Bohemia (Š k r l a n t, 2010) (Fig. 3).

Threats to Littorella uniflora

As Arts (2002) suggested, a high decrease of isoetid biotopes during the 20th century was noticed. Roelofs et al. (1984) reported a dramatic decrease of the *L. uniflora* habitats on the area of the Netherlands since the 1950s. The decline was caused by two main reasons – acidification and eutrophication. Mc Elarney et al. (2010) pointed out that the decline of *L. uniflora* in north and west Ireland during the last twenty years was caused by fertilizing of the forest and field soil and following nutrient runoff. The same habitat decline is known from the Czech Republic (Š u m b er o v á, 2011).

Eutrophication and acidification are two main reasons for occurrence decrease of isoetid species (Smolders et al., 2002). In the case of the Czech



Fig.3. Littorella distribution in the Czech Republic (Š u m b e r o v á, 2011)

Republic, the fishpond management is another threat for *L. uniflora* habitats (H e j n ý , 1967).

Eutrophication

With the increasing organic matter content in water bodies the intensity of decomposition process is rising. High amounts of nutrients are released to water during the decomposition process. It causes a rapid development of submerged and free floating water plants (A r t s et al., 1990). S z m e j a (1994) described an indirect effect of high emerged marophytes such as *Phragmites australis* on the habitats otherwise suitable for *L*. *uniflora*. R o e l o f s et al. (1994) found out that *L*. *uniflora* can thrive even in lakes with a high organic matter content. These lakes are strictly oligotrophic with high carbon to nitrogen ratio and low conductivity. Microbiological reduction in such lakes is very low, it takes place only at the oxygenated rhizosphere.

The rising nutrient content in water changes the shoot to root ratio (R o e l o f s et al., 1994; S p i e r e n b u r g et al., 2012) and the higher shoot to root ratio in the nutrient-richer sediment probably increases the chance for the plant to be uprooted during a windstorm or other similar disturbance (S m o l d e r s et al., 2002; S p i e r e n b u r g et al., 2012).

Another problem in the reduced sediments is the inability of plants to oxidize the whole root surface. In non-reduced sediments plaque is created from oxidized iron and this plaque may limit phosphorus uptake because phosphorus precipitates within the plaque (C h r i s t e n s e n, W i g a n d, 1998). In reduced sediments plaque cannot be created and phosphorus is accessible to other macrophytes. Reduction of sulphate to sulphide is quite disadvantageous, too. Sulphide causes mobilization of phosphorus and moreover it is phytotoxic (S m o l d e r s et al., 2002).

A common phenomenon is the increase of the nutrient content by agricultural activities in the catchment area. Thanks to slow growth rate and its form, isoetids are badly adapted to nutrient intake from the water layer. They are overgrown by fast-growing, emerged water plants which increase the organic matter content of the sediments after senescence or directly shade the *Littorella* stands (A r t s, L e u v e n, 1988; S z m e j a, 1994).

Shading by epiphytic algae is the final threat connected with eutrophication. Epiphytic algae respond to high nutrient input faster than phytoplankton or macrophytes. S an d - J e n s e n, S o n d e r g a a r d (1981) found out that light attenuation caused by shading can reach 80%, which decreases maximum colonization depth of *L. uniflora*.

Acidification

In West Europe, many lakes with natural community of isoetids are overgrown by *Juncus bulbosus* and

Sphagnum sp. Acidification due to increased atmospheric deposition of sulphur and nitrogen compounds was found to be the main reason for the observed changes (Roelofs et al., 1984, 1994; Arts, 2002). High deposition of ammonium sulphate has been detrimental to the isoetid systems. Nitrification of ammonium in the water layer leads to its acidification. Once the water layer is acidified to pH 4.5, nitrification is inhibited and nitrogen accumulates as ammonium, hence the storage of the nitrate used by L. uniflora is decreasing (Bellemakers et al., 1996, Smolders et al., 2002). Also, acidification causes reduction of carbon storage in the sediments and promotes the increase of carbon dioxide concentration in the water layer (Roelofs et al., 1994, Bellemakers et al., 1996). These factors (ammonia as nitrogen source, increased availability of carbon dioxide in water) promote the growth of J. bulbosus and Sphagnum sp., which overgrow L. uniflora and displace it from the water body (Roelofs el al., 1984; Arts, van der Heijden, 1990).

Fish management

At none of the western or northern European localities with a natural occurrence of *L. uniflora* a direct influence of the fish management was found. In the Czech Republic, known for its freshwater fishery, the fishponds are very common. The most important problems of the fishponds are overstocking with highweight common carp (*Cyprinus carpio*) and artificial increase of the fishpond trophy by fertilizers (H e j n ý, 1967; P o k or n ý et al., 1990; P r o c h á z k a, H u s á k, 1999). Old-aged carp feeds on macrozoobenthos by digging in the pond bottom. This can directly disrupt the plant root system or decrease water transparency (Č í t e k et al., 1992).

The increase of the trophy status of fishponds with manure promotes a rapid development of phytoplankton and raises turbidity. A high trophic status also promotes growth of emerged water plants which can overgrow the *L. uniflora* population (S z m e j a, 1994; H e j n \acute{y} et al., 1996).

Conservation and management

Directive 97/62/EC orders to protect oligotrophic waters containing very few minerals of sandy plains (*Littorelletalia uniflorae* Koch 1926) or oligotrophic to mesotrophic standing waters with the vegetation of *Littorelletalia uniflorae* Koch 1926 and/or *Isöeto-Nanojuncetea* Br.-Bl. et Tüxen ex Br.-Bl. et al. 1952 types.

Although in the European Red List of vascular plants L. uniflora is categorized as LC (= least concern) (B i l z et al., 2011), in the Czech Red List it is categorized as C1 (= critically endangered) (G r u l i c h, 2012). It corresponds with the Decree No. 395/92 where L. uniflora is categorized as a critically endangered species. Besides the Czech Republic, *L. uniflora* is protected by law in France and Poland (A c t, 1982; A c t, 2004).

Bellemakes et al. (1996) consider liming a suitable acidified lakes management in the Netherlands. Also, they recommend to avoid liming without the removal of the organic sediment layer. Without doing this, mineralization and eutrophication would predominate. By the sediment removal the seed bank of *L. uniflora* becomes thinner, which is not a problem thanks to its persistence. Arts, van der Heijden (1990) consider the sediment removal as a suitable management for *L. uniflora*, too.

Fish management can help sustaining the *L. uni-flora* population – e.g. by periodical summer drainage (H e j n ý, 1978), shoveling of the pond banks (H e j n ý, 1967; H e j n ý, H u s á k, 1978) or by littoral vegetation removal (H e s o u n et al., 2008).

Š u m b e r o v á (2011) suggested water level lowering in several-year intervals with simultaneous removal of nutrient-rich sediments, disturbance of strong amphibious macrophyte competitors such as *Juncus bulbosus* and *Eleocharis acicularis* or removal of stands of tall reeds and sedges.

The only measure to L. uniflora protection in the Czech Republic was the sediment and littoral vegetation removal at the Králek fishpond (Hesoun et al., 2008). From this locality several plants were transferred to the Botanical Institute of the Academy of Sciences of the Czech Republic in Třeboň for cultivation and then they were planted at the original locality of their occurrence, the Svět fishpond (K v ět, 1999). Some experiments with the cultivation of L. uniflora were carried out during the period 2002-2005. L. uniflora was sowed at several Třeboň sand-pits, but the whole population did not survive (Sosnová et al., 2012). L. uniflora is one of the plants proposed for the conservation programme of the Agency of Nature Conservation and Landscape Protection of the Czech Republic (Gabrielová et al., 2012).

CONCLUSION

Littorella uniflora is a small amphibious plant colonizing shallow shores of oligotrophic water bodies. The plant is well adapted to the unproductive environment by strong and stiff basal leaves without stomata and a large amount of root biomass. Except the morphological adaptation, physiological adaptations (high ROL, presence of mycorrhiza, nitrates as a nitrogen source or CAM cycle) can be found making L. uniflora a great competitor in the environment of oligotrophic water bodies.

Growths of *L. uniflora* can be found at two-metre depths, the distribution centre being at 50 cm. Under the optimal conditions (high water transparency, lack of nutrients limiting the occurrence of other water

plant species), *L. uniflora* can form a very compact growth. Besides the acid sandy sediment, *L. uniflora* is able to grow on the bare peat.

The area of *L. uniflora* distribution includes whole western, northern and partly central Europe. The east border of its distribution is delimited by Poland, the Czech Republic, Austria, and Italy. However, the number of sites where this plant occurs is rapidly decreasing. It is mostly due to acidification (most frequent problem in the Netherlands) and eutrophication. Population of *L. uniflora* is unable to react to increased nutrient concentrations in water and in the sediment layer and it is overgrown by fast-growing emergent water plants.

Recent population of L. uniflora can be found only at eight localities in the Czech Republic. At most of them, problems connected with the enhanced eutrophication and fish stock pressure are observed. L. uniflora is found in shallow waters at very low densities as a consequence of low water transparency. If the management regime will not change, the species extinction is very likely. Only in three water reservoirs of the Czech Republic the population proliferates. This is being achieved through the cooperation with the water bodies owners based on the low water level and extensive fish management. These activities are supported by the governmental agency of the nature protection in the Czech Republic. Currently, a scientific research based conservation program is under preparation. In 2015, Czech localities suitable for L. uniflora will be selected and in the next years experimental planting should be started there.

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