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The Introduction of the Aquatic Carnivorous Plant *Aldrovanda vesiculosa* to New Potential Sites in the Czech Republic: A Five-Year Investigation

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Abstract: Five microsites in shallow dystrophic waters were selected for the introduction of a critically endangered aquatic carnivorous plant *Aldrovanda vesiculosa* in the Třeboň region in S Bohemia, the Czech Republic. The selected sites were fen pools close to two hypertrophic fishponds, Ptačí blato (four microsites) and Domanínský (one microsite). In June 1995, 30 plants from an allochthonous population in E Poland were introduced in each of the microsites. Water chemistry and plant growth dynamics were investigated at the microsites throughout the 1995–1996 seasons, and the maximum size of the subpopulations were estimated during the 1997–1999 seasons. The selected waters may be characterized as oligo-mesotrophic.

The warm and dry 1995 season resulted in a low water level (ca. 10 cm below average) and plant propagation was poor at all but one microsite. However, the rainy and colder 1996 season resulted in a high water level, and thus rapid plant propagation occurred at all four microsites at the Ptačí blato fishpond and between 841 and 2669 turions were formed. Here, the doubling time of the apices was between 13.5–19.3 days in the summer. At the Domanínský fishpond, however, the growth was relatively poor in 1996. The overwintering rate of turions (19–100%) was found as being high enough to keep the introduced plant populations stable. At each of the four microsites at Ptačí blato, the maximum numbers of shoot apices were estimated to be between 1,000–20,000 in the 1997–1999 seasons. Depth of free water appears to be the crucial factor for the rapid growth of *Aldrovanda* at some selected sites; water depth below 5 cm is unfavourable. Overall, *Aldrovanda* was successfully established in an intensively agricultural landscape in the Třeboň region.

Introduction

Aldrovanda vesiculosa L. is a critically endangered aquatic carnivorous plant, rapidly vanishing from Europe. The origin of its recent population in Europe is still unclear (Berta 1961, Adamec & Tichý 1997). Moreover, its historical postglacial spread in Europe was highly irregular, variable in time and area, and probably dependent on the migratory routes of water birds (Berta 1961, Huber 1961). In Europe, it has been recorded at about 150 sites in the last two centuries. However, it has declined markedly in the last century, especially in the last 30 years, with only a few dozen sites remaining (Adamec 1995a, Kamiński et al. 1996).

In Europe, *Aldrovanda* propagates only by the apical branching of shoots (Kamiński 1987a, Adamec & Tichý 1997). Apical winter buds (turions) are formed in the autumn. Recently,

Table 1. The characteristics of the selected microsites.

Microsite	Pool No.	Mean/min. water depth (cm)	Total coverage (%)	Plant dominants (1995)
Ptačí blato fishpond				
PB1C	1	15–50/5	80–100	*Carex rostrata*
PB1T	1	15–50/3	80–100	*Typha angustifolia*
PB2	2	10–40/0	80–100	*Carex rostrata, Drepanocladus aduncus*
PB9	9	10–40/0	80	*Phragmites australis, Calliergon cordifolium*
Domanínský fishpond				
D	-	20–35/5	80	*Carex rostrata*

ADAMEC (1999) selected several shallow dystrophic wetlands in S and N Bohemia (the Czech Republic) in order to investigate the plant growth dynamics of *Aldrovanda* at these sites within nylon enclosures. The study suggested that considerable turion losses in natural *Aldrovanda* stands could be compensated for by rapid seasonal shoot growth and branching, which thus maintains an abundant plant population.

The aims of the present study were to introduce *Aldrovanda* plants in five suitable microsites in two selected shallow dystrophic sites in the Třeboňsko Biosphere Reserve and Protected Landscape Area, S Bohemia, the Czech Republic, to investigate the growth dynamics of the introduced plants together with habitat factors over two seasons, and to estimate the maximum size of the subpopulations over the next three seasons. The selection of these sites and microsites was based on assessments of suitable water depth (0.15–0.5 m), water level fluctuations, dominant aquatic and emergent vegetation, the degree of shading by emergent vegetation, the character of bottom sediment, water transparency, and the CO_2 concentration in the water. The selection of the sites and microsites was optimized after considering the results of the above-mentioned *Aldrovanda* growth study in nylon enclosures (ADAMEC 1999).

MATERIALS AND METHODS

Plants of *A. vesiculosa* were collected from Lake Długie in the Łęszna-Włodawa Lake District in E Poland (51°26'N, 23°06'E) in June 1993. The plants were cultivated outdoors in a plastic container (ADAMEC 1997a,b).

The selected sites, the Ptačí blato and the Domanínský fishponds, are described in detail by ADAMEC (1999). Important characteristics of the microsites are shown in Tab. 1. Microsites PB2, PB9, and D were selected at about the same places as in the above-mentioned growth study. Each microsite was labelled by a wooden rod. In mid-July 1995, the total coverage of macrophytes, plant dominants (≥ 40% of total coverage) and subdominants (10–40% of total coverage) were estimated in a 2 × 2 m area.

Field observations

On 12–13 June 1995, 30 adult *Aldrovanda* plants, with a total of 32–48 shoot apices, were introduced in a 0.3 × 0.3 m area in the centre of each of the microsites. The groups of introduced plants differed appreciably in their length and branching from each other (see Tab. 2). The growth characteristics of the introduced plants, water level, and basic water chemistry were measured according to ADAMEC (1999) several times throughout the 1995–1996 seasons.

Table 2. The development of introduced subpopulations *A. vesiculosa* in 1995-1999. The plants were counted in 1995–1996, while the total numbers of apices were estimated in 1997–1999. PL – number of plants (density.m^{-2} in parentheses); AP – total number of apices; LE – mean shoot length (cm); 1) – sum of the values for PB1C and PB1T; 2) – see PB1C.

		1995				1996					1997	1998	1999
Micro-site	Param.	12–13 Jun	13–14 Jul	16 Aug	18 Sep	20–21 Apr	6 May	29–30 May	16–17 Jul	9–10 Sep	7 Sep	16 Aug	22 Aug
PB1C	PL	30	66	135	338	55	105	119	1540	2618	-	-	-
	AP	48	-	258	480	79	175	176	2058	2669	4000	20000[1)]	15000[1)]
	LE	9.4	9.0	7.0	4.3	-	3.7	8.3	8.8	9.8	-	-	-
PB1T	PL	30	(19)	30	35	27	42	101	742	832	-	-	-
	AP	42	-	-	52	39	58	142	936	841	2000	2)	2)
	LE	8.8	8.1	9.5	3.7	-	4.1	10.4	5.7	8.9	-	-	-
PB2	PL	30	48	(6)	31	21	48	47	466	888	-	-	-
	AP	42	-	-	36	35	72	65	617	908	1000	12000	10000
	LE	7.4	8.9	6.8	3.7	-	2.5	6.1	7.1	7.7	-	-	-
PB9	PL	30	27	20	32	4	10	18	82	734	-	-	-
	AP	39	-	-	52	6	15	27	152	984	4000	4000	2000
	LE	7.2	9.6	9.3	5.2	-	2.1	7.7	8.8	8.5	-	-	-
D	PL	30	(6)	32	52	7	54	68	113	137	-	-	-
	AP	32	-	-	67	11	94	79	145	142	300	30	50
	LE	4.4	6.2	8.5	5.8	-	2.7	3.4	5.3	5.4	-	-	-

At each observation, except in July and August 1995, all plants at a microsite and the number of first and second order branches on each plant were counted. Twenty plants were randomly selected from an area in a dense stand of *Aldrovanda* and the total length of the main shoot and the number of leaf whorls with mature traps were estimated. In September, the number of turions were counted. Only those overwintered turions and/or germinating plants which floated close to the water surface were counted in the spring. In all cases, the measured and counted plants were returned to the centre of the introduction area and scattered in a 1–4 m^2 area. The central parts of the microsites (2 × 2 m) were not disturbed. In the 1997–1999 seasons, the total numbers of apices were estimated at microsites between mid-August and early September. The estimates were based on plant density and area of the plant stands.

Between 10:00–17:00 local summer time the dissolved O_2 concentration, pH, and water temperature were measured in dense *Aldrovanda* stands ca. 2 cm below the water surface. Total alkalinity (TA; TA=$[HCO_3^-]+2.[CO_3^{2-}]+[OH^-]-[H^+]$) was estimated by Gran titration and $[CO_2]$ was calculated from the TA and pH values. In June and July 1995, filtrated water samples were analyzed for macro-nutrients (for all details see ADAMEC 1999). The concentration of humic acids in the filtrated water samples was estimated using a modification of a standard colorimetric method (PEKÁRKOVÁ & LISCHKE 1974). The modification is based on direct colorimetry at 420 nm of alkalized water sample (20 ml water + 0.5 ml 0.5 $mol.l^{-1}$ NaOH) in a 5 cm wide cuvette. Purified humic acids were used as calibration standards. It was found that the method was also very sensitive to tannin and thus, it records a sum of humic acids and tannins.

Table 3. Concentration of macronutrients and the sum of humic acids and tannins (HAT) in water in the stands of introduced *A. vesiculosa* in the Třeboň region, Czech Republic. Mean of two values from June and July 1995 is always shown.

Microsite	NO_3-N	NH_4-N	PO_4-P	K	Ca	Mg	Na	HAT
	$\mu g.l^{-1}$			$mg.l^{-1}$				
PB1C	11	14	11	3.2	24.0	5.7	9.0	8.0
PB1T	0	3	9	3.0	19.6	5.5	9.0	7.7
PB2	14	13	15	1.3	27.7	4.8	8.3	21.3
PB9	11	9	10	0.3	14.0	3.2	6.2	13.7
D	25	13	13	6.1	18.0	5.0	5.7	9.5

RESULTS AND DISCUSSION

Summer growth and overwintering

In the 1995 season rapid growth of the introduced *Aldrovanda* plants occurred only at site PB1C where the total number of apices increased ten times (Tab. 2). The relatively short shoots and low branching found at site D in July 1995 reflect the introduction of much shorter and less-branched plants in site D but this could not limit the plant growth dynamics in August and later on. In the 1996 summer season, plant growth was vigorous at all microsites at Ptačí blato, but was rather poor at site D. In addition, about 250–300 other turions were found near microsite PB1T and 200–250 near PB9 in late September 1996. These plants had drifted out of the microsite area due to wind, and evidently were not counted. Assuming an exponential character of its propagation (Adamec 1999), doubling time of apices between 29–30 May to 16–17 July 1996 was 13.5 d at PB1C, 17.6 d PB1T, 14.8 d PB2, and 19.3 d at PB9. The same values (14.3–21.4 d) were found for *Aldrovanda* propagation in nylon enclosures at sites PB2 and PB9 in the very warm summer of 1994 (Adamec 1999). Since each introduced subpopulation consisted of both very short, freshly-separated branches (2–4 cm) and long adults plants, the standard deviation of the data has not been calculated.

The turion overwintering rate was sufficiently high at all microsites to maintain abundant stocks of *Aldrovanda* (Tab. 2). By 6 May 1996, 81–100% of the turions successfully survived at PB1T, PB2, and D, while only 19–22% at PB1C and PB9 survived (cf. Adamec 1995b). The data in Tab. 2 provide reliable information on the overwintering rate of turions. On 6 May 1996, the total number of plants corresponded to the total number of germinating turions, but this did not hold true later. The first turions released from the bottom in mid-April 1996. Between 40–64% of the total overwintering turions floated up at Ptačí blato as early as 20–21 April, but only about 13% at D. This delay at D could be caused by the deeper and colder water. Throughout the winter of 1995–1996, there was at least a 10 cm free water column at all microsites at Ptačí blato. Overall, turions overwintered much better under water at Ptačí blato in the present study (mean ca. 56%) than they did in the wet bottom throughout the winter of 1994–1995 (27%), when a portion of the turions was grazed by small rodents (Adamec 1999). The rapid seasonal growth of *Aldrovanda* at the microsites did not generally correspond with the turion overwintering rate (Tab. 2), as found also by Adamec (1999). The seasonal growth dynamics of *Aldrovanda* is markedly oscillatory and thus, even considerable turion losses at natural sites can be compensated for by rapid seasonal propagation. Furthermore, the high variability in turion overwintering rates, together with the dependence

Tab. 4. Water chemistry in stands of *A. vesiculosa* at the microsites over the 1995–1996 seasons. Mean and range of 8 measurements are shown; TA – total alkalinity.

Parameter		Microsites				
		PB1C	PB1T	PB2	PB9	D
$[O_2]$	Mean	6.6	7.6	7.7	7.8	4.5
$(mg.l^{-1})$	Range	5.1–9.3	4.4–13.6	3.8–12.8	4.1–20.4	1.6–10.8
pH	Mean	7.07	7.11	6.35	6.64	5.85
	Range	6.76–7.69	6.65–7.96	5.77–7.43	6.25–7.92	5.00–7.42
TA	Mean	1.46	1.06	0.66	0.88	1.15
$(meq.l^{-1})$	Range	0.75–2.17	0.54–1.90	0.17–1.10	0.30–1.45	0.11–2.60
$[CO_2]$	Mean	0.27	0.17	0.45	0.44	0.64
$(mmol.l^{-1})$	Range	0.08–0.37	0.04–0.41	0.06–0.87	0.04–1.17	0.15–2.76

of the seasonal plant propagation rate on water level, could explain why the distribution of *Aldrovanda* at a site is irregular in time (ADAMEC 1995a).

Habitat conditions

The selected microsites may be characterized as oligo-mesotrophic and dystrophic (Tab. 3). The oxygen concentration at the sites always exceeded 1.6 $mg.l^{-1}$ (Tab. 4) and could not limit plant growth CO_2 concentrations usually exceeded 0.08 $mmol.l^{-1}$. At all sites throughout the two seasons, the most common pH and $[CO_2]$ values were within a narrow range (pH: median 6.99; quartiles 6.53, 7.20; $[CO_2]$: median 0.32 mM; quartiles 0.16, 0.41 mM). The water depth in all of the *Aldrovanda* stands decreased during the 1995 summer season, so that by mid-August, the actual depth of the free water column at the surface level was only 0–3 cm at PB1T, PB2, PB9, and D, while ca. 5 cm at PB1C (data not shown). In contrast, the water level was very high at all sites throughout the 1996 season and the free water column was at least 10–20 cm deep. Generally, all of the water chemistry characteristics (Tabs. 3, 4) were similar to those found in the nylon enclosures at these sites in the summer of 1994 (ADAMEC 1999). Furthermore, the main hydrochemical as well as phytosociological characteristics at suitable microsites at Ptačí blato are comparable with those found at suitable natural sites in Poland or Slovakia (cf. KAMIŃSKI 1987a,b, ADAMEC 1995a).

As follows from the data (Tab. 4) high $[CO_2]$ (> 0.1 $mmol.l^{-1}$) is obviously not the crucial ecological factor for the rapid growth of *Aldrovanda* in the field, as stressed by ADAMEC (1995a, 1997a, 1999). Shading by emergent vegetation could not be the limiting factor for *Aldrovanda* growth at the sites either (ADAMEC 1997a, 1999). Thus, providing that other ecological factors were favourable, the depth of the free water column was probably important for its rapid growth and propagation. In accordance with ADAMEC (1999), a free-water depth of 5 cm is suggested as a summer minimum for its rapid growth, and below 3 cm as unfavourable.

The growth experiment has confirmed the suitable character of *Aldrovanda* habitats: shallow dystrophic wetlands dominated by loose stands of *Carex rostrata*, *Phragmites australis*, or *Typha angustifolia* (cf. KAMIŃSKI 1987a, ADAMEC 1995a). However, as a result of extremely high water levels (ca. 0.7 m) the character of all of the microsites at Ptačí blato has changed markedly since late May 1996. The water has become considerably darker and this state has persisted over the 1996–1997 seasons. At the high water level state, nutrient-rich and hard fishpond water inflowed to a certain extent into the pools, resulting in their accelerated eutrophication. At PB1C and PB2, the density of former *Carex rostrata*-dominant stands was reduced to ca. 20–40% in the summer of 1996, in favour of invasive *Typha latifolia*, *Carex gracilis*, *Utricularia australis*, *Potamogeton natans*, *Chara fragilis*, and algal mats (*Mougeotia* sp., *Spirogyra* sp.). Simultaneously, the layer of old litter and detritus increased to about 10–20 cm. Since *Aldrovanda* is a very weak competitive species which relies on its carnivory for survival, low available nutrient concentrations in water and sediment are necessary to overcome its potential competitors (ADAMEC 1995a). In deep water throughout the 1996–1999 seasons, a good deal of *Aldrovanda* plants (ca. 20–50%) were repeatedly driven by wind to unsuitable areas. The action of wind on the topography of populations within sites has greatly been underestimated as an important ecological factor (ADAMEC 1995a).

Development of subpopulations

In the 1997 and 1998 seasons, at high water levels, *Aldrovanda* subpopulations expanded even though all microsites at Ptačí blato exhibited symptoms of eutrophication (Tab. 2). A slight decline in all subpopulations was observed at Ptačí blato in 1999 as a result of very low water levels.

The subpopulations extended over 100–400 m^2 in 1998 and 1999. It appears that the carrying capacity for *Aldrovanda* was reached at all microsites at Ptačí blato in 1998. The relative suitability of these microsites for *Aldrovanda* can be shown by plant flowering. Ca. 25 plants flowered at PB2 and four at PB9 in late August 1997. None of the plants set seeds. However, hundreds of plants flowered at PB1C and PB2 in mid-August 1998 and over 60 capsules with ripe seeds were found at PB1C in early October. Such an abundant seed set has never been described in Europe (ADAMEC & TICHÝ 1997). Therefore, it is possible to hypothesise that *Aldrovanda* is spread by water birds also in the form of seeds.

CONCLUSION

According to the prepared Red book of plants of the Czech Republic (1999), *Aldrovanda* has been declared an extinct species of the Czech flora. In other European countries, it is a critically endangered species (ADAMEC 1995a). As a result of this study, several new sites of its allochthonous population from E Poland have been established in the Třeboň region, the Czech Republic, where it had never been documented. The possible reasons for its previous natural absence here may be based on the relatively long distance of formerly existing sites from this region (ca. 270 km, Silesia, Poland) and on the regular emptying of the fishponds. Similar introductions of *Aldrovanda* succeeded in Switzerland as early as 1908 and a stable subpopulation has been growing there since then (BERTA 1961, HUBER 1961). Recently, introduction to new sites is probably the only effective way to keep and propagate the vanishing European population. In support of such an activity, it may be added that (a) *Aldrovanda* is spread by water birds and its European spread has been variable in time and area (ADAMEC 1995a); (b) populations from central Italy, Switzerland, and E Poland are probably genetically homogeneous (ADAMEC & TICHÝ 1997); (c) *Aldrovanda* cannot behave as an invasive species at new sites (sensu ADAMEC 1995a).

This study has revealed that *Aldrovanda* can also grow in an intensively agricultural landscape, close to hypertrophic fishponds. However, low-cost management will have to be done at new sites in the future, i.e. removal of excessive wetland vegetation within its dense stands.

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