

Rootless aquatic plant *Aldrovanda vesiculosa*: physiological polarity, mineral nutrition, and importance of carnivory

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Abstract

Various ecophysiological investigations are presented in *Aldrovanda vesiculosa*, a rootless aquatic carnivorous plant. A distinct polarity of N, P, and Ca tissue content per dry mass (DM) unit was found along *Aldrovanda* shoots. Due to effective re-utilization, relatively small proportions of N (10 - 13 %) and P (33 - 43 %) are probably lost with senescent leaf whorls, while there is complete loss of all Ca, K, and Mg. The total content of starch and free sugars was 26 - 47 % DM along adult shoots, with the maximum in the 7th - 10th whorls. About 30 % of the total maximum sugar content was probably lost with dead whorls. The plant was found to take up 5 - 7 times more NH_4^+ to NO_3^- from a mineral medium. Under nearly-natural conditions in an outdoor cultivation container, catching of prey led to significantly more rapid growth than in unfed plants. DM of the fed controls was 48 % higher than in the unfed plants. The controls produced 0.69 branches per plant, while the unfed plants did not produce any. However, the N and P content per DM unit increased by 6 - 25 % in the apices and the first 6 whorls in the unfed variant, as compared to the fed controls. It may be suggested that carnivory is very important for *Aldrovanda*.

Additional key words: apical shoot growth, basal shoot senescence, growth effect of carnivory, mineral and sugar content, NH_4^+ , NO_3^- , HPO_4^{2-} uptake.

Introduction

Aldrovanda vesiculosa L. (*Droseraceae*) is a critically endangered and rare aquatic carnivorous plant of the Old World (Adamec 1995a, Kamiński *et al.* 1996). It is rootless, free-floating, and grows just below the surface in shallow standing dystrophic waters (Lloyd 1942, Adamec 1995a). Its snapping traps (3 - 6 mm long) have always excited curiosity among physiologists. Its shoots have a highly regular and modular structure composed of whorls of 6 - 8 leaves and internodes (Fig. 1). *Aldrovanda* has the same life form, and a similar growth strategy as aquatic *Utricularia* species. The principal feature is its rapid apical shoot growth (1 - 2 new whorls a day; Lloyd 1942, Mazrimas 1978), while the basal part is continuously senescing and decomposing. Adult *Aldrovanda* plants are usually only 8 - 15 cm long, with

12 - 20 leaf whorls (Kamiński 1987a,b, Adamec 1999). That is why the gradient in photosynthetic activity (Adamec 1997a), metabolite allocation (Fabian-Galan and Salageanu 1968), hormonal, and mineral content between the growing shoot apex and decomposing base should be very steep. Rapid apical growth and shoot turnover are necessary to overcome shoot covering with epiphytic algae and contribute to fast vegetative propagation over a relatively short growing season (Adamec 1999). The European plants propagate only vegetatively by apical branching of the shoots (Kamiński 1987a, Adamec 1995a). A high frequency of branching indicates favourable growth conditions. In autumn, apical winter buds (turions; 6 mm long) are formed, while the rest of the shoot decays.

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Abbreviations: FM - fresh mass, DM - dry mass.

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Aldrovanda can take up a substantial proportion of mineral nutrients and also organic carbon (Adamec 1999) from prey. Kamiński (1987b) found that, in a greenhouse growth experiment in a diluted mineral nutrient

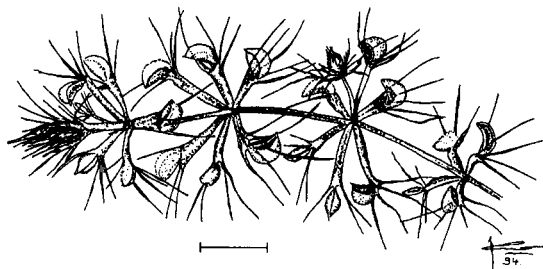


Fig. 1. Illustration of *Aldrovanda vesiculosa* by I. Pencák (with kind author's permission). The bar represents 1 cm.

Materials and methods

Aldrovanda vesiculosa L. was collected from Lake Dlugie in east Poland. Plants were cultivated outdoors in a plastic container (area 1 or 2.5 m²) and *Carex* litter was used as the substrate (Adamec 1997a,b).

Estimation of mineral nutrient content in plants: Adult non-branched plants, 11 - 13 cm long, were sampled on 15 August 1995. They were cleaned free of periphyton, prey was completely removed from traps, and the shoots rinsed with distilled water. Plant shoots were cut into segments of successive ages: apices (with immature leaves), 1st - 6th adult leaf whorls, 7th - 10th whorls, 11th - 14th whorls, and 15th - 18th whorls. The segments of five plants were pooled together. The last living whorl of yellow-green colour and the first successive dead one of brownish colour were also sampled in 20 plants. Ripe turions were sampled on 5 November 1995. The sampled material was immediately dried (80 °C, 4 h). Dry mass (DM, 1.5 - 2.3 mg) was mineralized with 0.2 cm³ of 65 % HNO₃ (140 °C, 30 min). P content was estimated by adding 0.7 cm³ of 60 % HClO₄ (150 °C, 3 h); N content by adding 0.5 cm³ of a mixture of 5 % potassium persulphate, 3 % H₃BO₃, and 0.38 mM NaOH (120 °C, 30 min). Ca, Mg, K, and Na concentrations in diluted mineralized samples were measured by atomic absorption spectrometer (AAS IN, Zeiss, Jena, Germany). NH₄-N and PO₄-P concentrations were determined colorimetrically by an automatic FIAstar 5010 Analyzer (Tecator, Sweden). Two parallel samples were always analyzed and mean values shown. The parallel values usually did not differ more than 5 % from the mean.

Estimation of sugar and chlorophyll a content in plants: Adult non-branched plants, 9 - 10 cm long, with

solution, feeding plants by zooplankton promoted plant growth by 170 %. The same effect also occurred after addition of *Carex* (sedge) rhizomes to aquaria, probably due to a release of CO₂ and some organic substances. A synergistic growth effect was found when feeding was combined with the addition of rhizomes.

In this paper, various ecophysiological investigations of *Aldrovanda* are presented. They relate to the steep physiological polarity of shoots (gradient of mineral nutrients and sugars along shoots), uptake of mineral ions (NH₄⁺, NO₃⁻, H₂PO₄⁻) by shoots, and influence of catching prey on the growth and nutrient tissue content. In general, the aim was to elucidate the functioning of the steep physiological polarity in *Aldrovanda* and some consequences of rapid shoot turnover concerning the cycling of mineral nutrients and sugars.

18 - 19 adult leaf whorls, were sampled on 25 July 1995. The segments of 12 plants were pooled together to get 30 - 40 mg of DM for one analysis. Soluble sugars were extracted with 80 % ethanol at 70 °C and sucrose, glucose, and fructose concentrations in lyophilised and redissolved samples were estimated using HPLC. In the extracted DM, starch was hydrolysed with 32 % HClO₄ and glucose was estimated by the anthrone method (for all analytical details see Čížková *et al.* 1996).

In parallel shoot segments of the first five types and also in ripe turions (5 November), chlorophyll a content was measured colorimetrically in 90 % acetone:methanol (5:1 by volume) extract at 664 nm (Pechar 1987). Two parallel samples of three plants were always analyzed.

Uptake of mineral ions: Adult plants, sampled on 18 August 1995, were cleaned of periphyton and only large prey were carefully removed from the traps. The brown, dead parts of shoot bases were removed and the plants were washed by tap water and rinsed with distilled water. They were placed in an experimental medium and exposed to day-light in a greenhouse for 3 h as pre-treatment. The medium contained: 30 μM NH₄NO₃, 6 μM K₂HPO₄, 34 μM K₂SO₄, 100 μM CaCl₂, 10 μM MgCl₂, 0.2 mM NaHCO₃, and *ca.* 0.1 - 0.2 mM CO₂. pH ranged from 6.4 to 6.7. Then the plants were blotted dry and each put in 100 cm³ of fresh medium to determine the rate of ion uptake. Simultaneous uptake of NO₃⁻, NH₄⁺, and HPO₄²⁻ was compared in intact 9 - 10 cm plants (15 - 16 leaf whorls), excised 4 - 5 cm apical parts (8 - 9 whorls), and by excised 5-cm basal parts (7 - 8 whorls). Plants were exposed to day-light (PAR between 91 - 240 W m⁻²) at the temperature of 25-27 °C in the greenhouse for 6 h. After 6 h, the media were sampled and analysed by

FIAsstar Analyzer (see above). Ion uptake rate was calculated from the decrease of the initial ion concentration. All variants consisted of 4 replicates.

Effect of catching prey on plant growth: Apical shoot segments of adult plants, with 5 or 5.5 adult leaf whorls, 2.6 - 3.4 cm long, were used for a 17-d growth experiment (18 June - 5 July 1997). To estimate the growth rate as a production of new leaf whorls d^{-1} , the internode between the third and fourth adult whorls was tagged carefully by a short piece of fine thread (*cf.* Friday 1989). Thus, it was possible to measure readily the growth rate during the whole experiment, in spite of the possible decay of the last basal whorls. Twelve tagged control apical segments (mean FM 67.9 mg, SD 8.0 mg; DM 6.27 mg, SD 0.94 mg, $n = 10$; trap size *ca.* 3.5 mm) were put in each of two plastic frames, with a diameter of 0.3 m. The bottom- and topless frames floated on the surface of the 2.5 m² cultivation container and only kept the plants together. Two other groups of 12 apical segments were put in two floating nets (0.3 × 0.3 m), with a bottom mesh size of 44 μm. The position of the nets and frames varied randomly. Water depth in the enclosures was *ca.* 3 cm. Thus, these plants grew under the same conditions as the controls, but were deprived of prey. Every other two days, the mesh in the enclosures was thoroughly cleaned and washed by tap water. Zooplankton (*Scapholeberis* spp., ostracods, size 1 - 2 mm) was added to the container to feed the control plants.

Results and discussion

A. vesiculosa has a very steep physiological polarity along its shoots linked with a very rapid turnover of leaf whorls. Over the warm summer season, the total life-time of a leaf whorl in adult plants, consisting of the shoot apex and 15 - 20 adult leaf whorls (Kamiński 1987a), may be as short as 10 - 20 d. Since the plant length remains constant, an increase of DM can only be allocated to branching.

The N, P, and Ca contents per unit DM, in shoot segments of different age, showed a distinct polarity in adult *Aldrovanda* shoots (Table 1). Content of N per unit DM in apices was about 13 times higher than that in the last living whorls and 4.8 times higher in the case of P. However, N content decreased unequally along the shoots, while P content changed in a more uniform manner. The gradient of Ca content in *Aldrovanda* was the reverse to that of N and P. Ca content in the last living whorls was about 4.4 times higher than that in the apices. K and Mg contents were constant along the shoots. Na content was the highest in the 11th - 14th whorls.

About 30 - 50 % of adult *Aldrovanda* traps within the control plants fed on zooplankton had one prey throughout the experiment, while the plants without prey had preys in *ca.* 5 - 10 % of adult traps only at the start. During the growth experiment, the minimum water temperature was 12.2 °C, while the maximum was 32.0 °C. The irradiance at plant level was 70 - 80 % of that incident in the open area. The medium was rather poor in mineral nutrients (0.3 μM NO₃⁻, 1 - 2 μM NH₄⁺, 0.4 μM H₂PO₄⁻, 50 μM K⁺; Adamec 1997b). pH was 7.1 - 7.3, [O₂] 0.20 - 0.25 mM, and [CO₂] 0.1 - 0.2 mM.

Total shoot length, number of adult whorls, position of the tag, and branching of shoots were estimated in all plants at 2 - 4 d intervals. Young leaf whorls were counted as adult if they bore functional traps and were spatially separated from the apex. If they had an intermediate character, they were counted as 0.5. At the end of the experiment, prey was thoroughly removed from all traps, the plants were cleaned, rinsed with distilled water, blotted dry, weighed for FM, and dried for DM. A fraction of the plants were cut into three segments (apices, 1st - 6th adult leaf whorls, 7th - 10th whorls) and dried for estimation of N and P tissue content (persulphate mineralization, *FIAsstar*). The growth analysis data, for the last two sampling dates, were subjected to a two-way ANOVA (Tukey test) to test the variability between the two parallel blocks of plants. As no significant difference in any parameter was found between the blocks at $P = 0.05$, the data for the two blocks were pooled together.

Relatively high amounts of Ca, Mg, K, and Na were lost with the first dead whorls. N and P contents in turions were 21 - 34 % higher than those in the apices, while Ca, K, and Na were lower.

The contents of N, P, Ca, and Mg in adult whorls in Table 1 are much lower than those published for *Aldrovanda* by Kamiński (1987a) at natural sites. This difference might partly be caused by inclusion of prey in analysed shoots in the paper cited. A similar gradient of N content in leaves (3.6 - 1.7 % DM) was found along the shoots of an aquatic carnivorous species, *Utricularia vulgaris* (Friday and Quarmby 1994). *Aldrovanda* is entirely dependent on prey and free water as a source of mineral nutrients. Owing to its rapid growth, an extensive re-utilization of some mineral nutrients from senescent shoots may be assumed to occur. *Aldrovanda* probably loses only a minor proportion of N (10 - 13 %) and P content (33 - 43 %) with its last living whorls, as compared to the content in adult shoot segments, while it loses all Ca, Mg, and K (Table 1). The tissue content of

Table 1. Mineral content in shoot segments of successive ages of adult *A. vesiculosa* and in turions. Last living whorls were still yellow-green, while the successive first dead ones were brownish. Data given in % of dry mass.

Shoot segments	N	P	Ca	Mg	K	Na
Apices	1.31	0.48	0.17	0.16	1.86	0.35
1 st - 6 th whorls	0.98	0.30	0.32	0.21	2.11	0.59
7 th - 10 th whorls	0.66	0.23	0.38	0.16	2.36	0.84
11 th - 14 th whorls	0.76	0.21	0.50	0.16	2.56	1.03
15 th - 18 th whorls	0.77	0.16	0.49	0.16	1.93	0.86
Last living whorls	0.10	0.10	0.75	0.16	2.30	0.56
1 st dead whorls	0.09	0.04	1.10	0.15	0.65	0.19
Turions	1.76	0.58	0.13	0.15	0.87	0.05

P, K, and Na dropped markedly in the first dead whorls. Since the last living and first dead whorls were adjacent, with an age difference of about one day, it may be assumed that almost all mineral nutrients occurring in the former whorls cannot be re-utilized and are lost. However, the data obtained do not prove that the difference in nutrient content between the adult and last living whorls was caused by a complete re-utilization of nutrients towards the apex (*cf.* Friday and Quarmby 1994). A rather effective N and P re-utilization was confirmed in rapidly growing *U. vulgaris* (Friday and Quarmby 1994), while re-utilization was ineffective in the slow-growing *U. purpurea* (Moeller 1980).

Aldrovanda turions are not only storage organs for starch and sugars (Adamec 1995b), but also for N and P (Table 1). Their DM is only 45 - 55 % of that of adult plants. They can contain up to 100 % of the total N and P amount in adult plants, while only about 44 % of Mg, 20 % K, and 19 % of Ca. These results suggest a very effective N and P re-utilization from senescent shoots to the forming of turions in autumn, and generally, a very strong influence of the growing shoot apex to attract mineral nutrients. In *Aldrovanda*, the shoot apex is also a powerful sink for organic nutrients, both of photosynthetic and carnivorous origin. As shown by Fabian-Galan and Salageanu (1968), organic nutrients absorbed from ¹⁴C-labelled prey were transported almost totally from older traps to shoot apices, but they were not transported at all from young ones.

Starch content along adult shoots ranged between 22 - 35 % of DM, with a maximum in the 7th-10th whorls, and sharply declining to 10 % in the last living whorls (Table 2). However, relatively high starch, sucrose and glucose contents (*ca.* 9, 6, and 4 % DM, respectively) were found in the first dead whorls. Sucrose, glucose, and fructose content gradients were similar along the shoots, with a maximum usually in young parts of the shoots and a sharp decline in the old (15th - 18th) whorls. The total content of starch and the free sugars was rather high (26 - 47 % DM; Table 2) along adult *Aldrovanda* shoots and even exceeded that found in turions (24 - 36 % DM;

Adamec 1995b). In adult *U. vulgaris* shoots, a high starch content of 16 % DM was estimated (Winston and Gorham 1979). In growing *Aldrovanda* shoots, starch and free sugars are re-utilized extensively from senescent whorls. However, considerable proportions of starch (about 28 % of the maximum tissue content), sucrose (22 %), glucose (33 %), and fructose (7 %) were estimated in the last living whorls. Almost 30 % of total sugars are probably lost for the plant. The increase of free sugar content in the first dead whorls could be caused by microbial activity during their decomposition. Thus, the rapid growth of *Aldrovanda* is accompanied by considerable sugar losses with dead whorls. This, together with the above mentioned loss of mineral nutrients from senescent whorls, may explain why the senescent shoot bases are often covered by epiphytic algae. However, *Aldrovanda* usually grows under natural conditions which allow high photosynthetic rates (Adamec 1997a). The author has deduced that an adult plant is able to take up a sufficient amount of CO₂ for a daily production of 1 - 2 new leaf whorls, even if no sugar re-utilization occurs. However, at low CO₂ concentration or in shade, sugar re-utilization may become crucial. After a transfer of *Aldrovanda* shoots to a medium with 0.01 - 0.03 mM CO₂, old leaf whorls senesced at a weekly rate of 3.3 whorls, as opposed to only 1.2 whorls in shoots in a medium with 0.2 - 0.5 mM CO₂ (Adamec, unpublished). Chlorophyll *a* content ranged from 1.5 - 3.4 mg kg⁻¹(DM) along the shoots, with a maximum in the 7th - 10th whorls (Table 2), and was comparable with that in turions [2.0 mg kg⁻¹(DM)]. The uptake rate of NH₄⁺ by intact plants did not differ significantly (*P* = 0.05) from that by excised apical and basal parts (Table 3). The ratio between NH₄⁺ and NO₃⁻ uptake rates was 5 - 7 in all types of material. NO₃⁻ uptake was highest in basal parts. The NH₄⁺ preference is typical in aquatic plants inhabiting soft and dystrophic waters (Schuurkes *et al.* 1986). The uptake rate of H₂PO₄⁻ by intact shoots was about 2 - 3 times higher than that by excised apical and basal parts. This might be caused by efflux of phosphate from vascular tissues. Preliminary data show that K⁺ was only taken up by basal parts

Table 2. Sugar and chlorophyll *a* content in shoot segments of successive ages of adult *Aldrovanda*. DM of segments is given in % of FM, sugar content in % of DM, chlorophyll (Chl) *a* content in mg kg⁻¹(DM).

Shoot segments	DM	Starch	Sucrose	Glucose	Fructose	Total	Chl <i>a</i>
Apices	12.9	24.9	1.8	7.8	4.3	38.8	2.56
1 st - 6 th whorls	11.3	28.0	3.0	8.1	1.8	40.9	3.02
7 th - 10 th whorls	11.4	35.1	2.6	7.1	1.7	46.5	3.36
11 th - 14 th whorls	10.2	29.7	3.2	6.5	1.8	41.2	1.94
15 th - 18 th whorls	9.5	22.4	0.4	2.5	0.9	26.2	1.49
Last living whorls	-	10.0	0.7	2.7	0.3	13.7	-
1 st dead whorls	-	8.8	5.9	3.9	0.4	19.0	-

(326 nmol kg⁻¹ s⁻¹) and its uptake rate by intact plants was about half of that by the basal parts (Adamec, unpublished).

In the 17-day growth experiment, catching of prey led to more vigorous growth of the controls than the unfed variant (Fig. 2). At the end, the shoots without prey were, on average, 3.1 cm shorter and with 3.7 leaf whorls fewer than the fed controls.

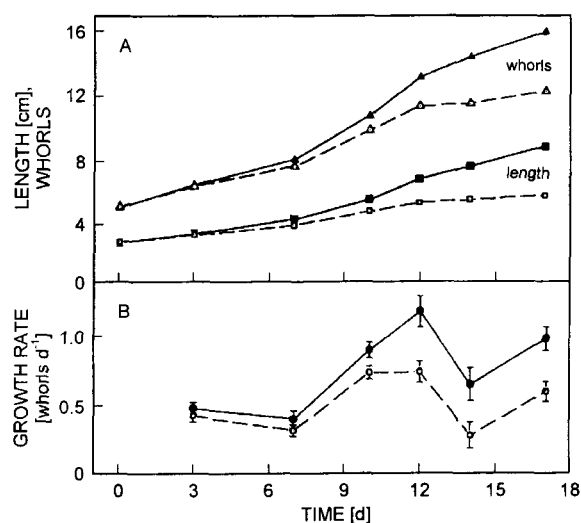
These differences were not statistically significant after three days (*t*-test, $P > 0.05$), while they became highly significant ($P = 0.01$) after 7 d and later. The growth rate of the shoots was greatly dependent on water temperature (data not shown). The growth rate ranged from 0.40 - 1.18 new whorls a day in the fed controls, as compared to only 0.32 - 0.74 in the unfed plants. Beginning from day 10, the difference was statistically

 Table 3. Uptake of NH₄⁺, NO₃⁻, and H₂PO₄⁻ [nmol kg⁻¹(FM) s⁻¹] by *A. vesiculosa* shoots from a solution containing 34 μM NH₄NO₃ and 6 μM KH₂PO₄. Ion uptake by 9 - 10 cm intact plants, 4 - 5 cm apical parts, and 5 cm basal parts occurred during day-light. Mean ± SE ($n = 4$); different letters in each column denote significant differences at $P = 0.05$.

	NH ₄ ⁺	NO ₃ ⁻	H ₂ PO ₄ ⁻
Intact plants	370 ± 31.0 a	49 ± 13.0 ab	24.0 ± 4.2 a
Apical parts	317 ± 6.9 a	54 ± 7.6 b	12.0 ± 1.3 b
Basal parts	364 ± 38.0 a	73 ± 0.4 a	7.5 ± 2.9 b

significant at $P = 0.05$. After 17 d, mean shoot FM was 170.5 mg and DM 15.7 mg in the fed controls, while only 98.6 and 8.2 mg in the unfed variant (Table 5). The controls and variant differed greatly from each other in the calculated doubling time of biomass (T_2). In the controls, FM and DM doubled in 12.8 d, whereas T_2 in the unfed variant were 31.6 and 44.5 d for FM and DM, respectively. The maximum size of newly formed traps was 3.5 - 4.0 mm in the controls, but only 2.0 - 2.5 mm in the unfed variant. The absence of prey eliminated shoot branching, while the controls produced 0.69 branches per

plant (Table 4). The absence of prey caused the N content per DM in the two apical shoot segments in the unfed variant to increase 6 - 8 % over the controls (Table 5). P content in the two apical segments in the variant increased 23 - 25 % over the controls, but it was the same in the basal segments.

 Fig. 2. Time-course of the *Aldrovanda* shoots growth with or


without prey: A - the total length of the shoots and number of adult leaf whorls (SE are within the symbols), B - the growth rate (mean ± SE). Closed symbols - fed controls, open symbols - unfed variant.

The growth experiment with short apical shoot segments of *Aldrovanda*, performed under nearly-natural conditions, has shown a great importance of carnivory for the growth and propagation of the plant (Fig. 2, Table 4). A similar feeding effect on *Aldrovanda* growth was also proved by Kamiński (1987b). At the start of the experiment, all apical shoot segments had ca. 5 - 10 % of all traps with a caught prey which was digested over the next few days. The great difference found in the doubling times of FM and DM reflects substantial differences in shoot growth rates (Table 4). However, the crucial

difference between the fed and unfed plants was found in the branching rate. Branching is the essential and the only way of *Aldrovanda* propagation (Kamiński 1987a, Adamec 1995a). As follows from other findings (Adamec 1999), branching depends much more on sufficient carbon uptake (either high photosynthetic rate or organic

carbon uptake from prey) than on mineral nutrient uptake from prey. This suggestion may further be supported by the finding of higher N and P tissue content in the apices and the youngest adult shoot segments in the unfed plants, as compared to the fed ones (Table 5). This finding

Table 4. The growth of *Aldrovanda*, with or without prey: FM and DM after 17 d, FM- and DM-based doubling time (T_2), maximum size of younger traps and number of branches.

	FM [mg plant ⁻¹]	DM	DM [% FM]	T_2 (FM) [d]	T_2 (DM) [d]	Trap size [mm]	Branches [plant ⁻¹]
Control	170.5 ± 5.8	15.7	9.14	12.8	12.8	3.5 - 4.0	0.69
Unfed	98.6 ± 3.3	8.2	8.29	31.6	44.5	2.0 - 2.5	0.00

also suggests that prey may be a relatively important source of organic carbon. Besides the organic carbon uptake, the lower N and P tissue content in the apical parts of fed plants may be explained as a result of rapid growth, i.e., "relatively slow" N and P translocation into rapidly growing apical tissues. The same has also been reported for other carnivorous plants (Adamec 1997c). The polarity of mineral nutrient tissue content in *Aldrovanda* is very steep, but it can be somewhat steeper in plants without prey, in which N and P re-utilization is probably more efficient.

The more rapidly *Aldrovanda* grows, the higher is the senescence rate of basal whorls, with greater losses of mineral and organic nutrients. To ensure its fast apical growth, loss of nutrients in senescent organs must be compensated for by a permanent nutrient uptake from water or prey. The present data show that *Aldrovanda* can

grow theoretically without any prey in a nutrient-poor medium. Ecologically, however, the catching of prey is indispensable, as the plants could not propagate at all or very slowly without it (cf. Adamec 1997c).

Table 5. Nitrogen and phosphorus content [% DM] in shoot segments of successive ages of *Aldrovanda* after 17 d. Mean of two parallel determinations is always shown.

	Fed N	P	Unfed N	P
Apices	1.18	0.35	1.28	0.43
1 st - 6 th whorls	0.79	0.20	0.85	0.25
7 th - 10 th whorls	0.69	0.16	0.65	0.16

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