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## *Oenanthe aquatica* (L.) POIR.: Seed Reproduction, Population Structure, Habitat Conditions and Distribution in Czechoslovakia

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### KEYWORDS

*Oenanthe aquatica*, Ecology, Distribution, Population structure, Seed reproduction, Aquatic weeds

### ABSTRACT

The paper summarizes data concerning the biology and ecology of *Oenanthe aquatica*. The species is commonly distributed all over Czechoslovakia, from lowlands to the submontane belt, especially in fishpond and river basins. *O. aquatica* shows no special relationship to the chemical and physical soil properties, and is well adapted to habitats with a changing water level. The reproduction of *O. aquatica* depends on emerging of the bottom. The most developed populations are formed by biennial plants and arise in the year following summer or autumn drainage.

### INTRODUCTION

*Oenanthe aquatica* grows predominantly in shallow water reservoirs or oxbows with standing water; occasionally in field depressions temporarily filled by water. It occurs relatively frequently and can form crowded stands, but the life span of its communities is limited. The plant shows morphological variation depending on changing habitat conditions. A detailed description of the plant and its taxonomic evaluation and classification (as *Phellandrium aquaticum* L.) are given in the monograph by BERTOŤOVÁ (1973).

Communities with dominant *O. aquatica* occur temporarily (sometimes repeatedly) depending on changes of water level. Under optimal conditions, *O. aquatica* can overgrow the entire surface of small ponds and become an undesirable weed. Knowledge of its biology (namely conditions of reproduction or spreading) can explain the origin of these crowded stands, and, eventually, the way to limit them. In this paper, we compare biological properties of the species (variability, life cycle, reproduction) with properties of its natural habitats and explain their mutual relationships.

## METHODS

The distribution of *O. aquatica* in Czechoslovakia was assessed on the basis of literature data, herbarium specimens and the authors' own data.

Scientific names of plants are given according to ROTHMALER (1982). Phytocoenological relevés were made using a seven grade Braun-Blanquet scale, and the phytocoenological nomenclature according to MORAVEC et al. (1983) was used. Terms of ecophases were used according to HEJNÝ (1960).

Water depth was measured together with recording of phytocoenological relevés at all habitats where *O. aquatica* has been found. Braun-Blanquet scale was transformed to cover values in per cent according to VAN DER MAAREL (1979).

## POPULATION STUDY

Population structure was compared at four habitats in South Moravia (three habitats at the Nesyt fishpond - populations of annual plants, one at the Allah IV fishpond - a population of biennial plants). From each population 100 randomly chosen plants were sampled, divided into length classes of 1 cm and from this range 30 plants were taken for detailed measurements. From this narrower sample, the following data were obtained: number of living and dead leaves and different leaf forms, number of inflorescences and dry biomass of aboveground organs. Biomass production per 1 m<sup>2</sup> was counted from the total dry mass of the sample of 100 plants and plant density per 1 m<sup>2</sup>. Plant biomass was dried at 90 °C (methods according to KVĚT 1966). Sampling was repeated four times during one growing season; only on the eastern shore of the Nesyt fishpond was one sample taken in August, owing to the sparse stand of *O. aquatica*. For statistical evaluation of differences between populations, analysis of variance was used (SNEDECOR and COCHRAN 1971).

## SEED REPRODUCTION

Seed size was investigated in four localities. At each locality seeds were collected from as many plants as possible. From satisfactorily large samples of seeds the lowest necessary sample size (100 seeds) was determined. This size sample of seeds was taken from all localities. Achenes were measured by means of a measuring magnifier (only the achene without remnants of the style). All seed samples were collected in the same growing season, which excluded the influence of different courses of the weather during different growing seasons.

The floating capacity of seeds was investigated immediately after ripening. The seeds were

sampled in a small pond near the town of Třeboň in South Bohemia. (Methods according to LHOTSKÁ 1968).

Seed germination was tested under the following conditions:

1) immediately after ripening (0 to 4 days after sampling, at a temperature of 20 °C and alternating light régime 8 hours light/16 hours darkness).

2) after stratification: during the winter season the seeds were kept under natural conditions; they were divided into two groups, under different conditions:

a) with aeration, similar to an emerged pond bottom; seeds were enclosed in nylon bags and placed below the soil surface in the experimental garden; temperature depended on the weather during winter, the surface soil layer was frozen, temporarily covered by snow;

b) without aeration, under water as in the pond: seeds in polyethylene bottles with water were put into a shallow reservoir (about 30 cm depth), during winter under ice (or frozen in ice).

In the following spring, germination was tested. All seeds germinated at 20 °C in an alternating light régime of 8 hours light/16 hours darkness, kept in a temperature controlled incubator. Variants in air were put in Petri dishes on filter paper continually saturated by water, variants in water were placed in glass beakers with distilled water.

3) Compared germination of seeds from different localities; the most favourable combination of conditions was used: seeds stratified in water and germinating in air, at 20 °C in alternating light régime light-darkness 8/16 hours.

4) in darkness and an alternating light régime 8/16 hours, at a constant temperature of 20 °C; seeds under different conditions of stratification and germination (in water or in air) were tested.

5) at different constant temperatures (within the range 5 °C to 40 °C), and in an alternating light régime (8 hours light, 16 hours darkness).

Each variant for the testing of seed germination contained 300 seeds (3 x 100 was the lowest sample size necessary): for diagrams, the means from those 3 x 100 seeds were used. Results of germination experiments were tested by a three-way table test of independence using the G-statistic (SOKAL and ROHLF 1969).

#### SOIL ANALYSES

For chemical analyses, soil samples were collected from the rhizosphere of *O. aquatica* (upper soil horizon 0 - 0.2 m) from 67 habitats in Bohemia, Moravia and Slovakia. In each soil sample the following analyses were made: pH in H<sub>2</sub>O and in KCl electrometrically, N-NH<sub>4</sub><sup>+</sup> colorimetrically with use of Nessler's reagent, total N by distillation using Kjeldahl's method, P-PO<sub>4</sub><sup>3-</sup> colorimetrically according to Egner (HRAŠKO et al. 1962); exchangable ions K<sup>+</sup>, Na<sup>2+</sup>, Ca<sup>2+</sup> by flame photometer and Mg<sup>2+</sup> by atomic absorption spectrophotometer, N-NO<sub>3</sub> colorimetrically using phenol 2,4 disulphon acid (JACKSON 1958). Organic matter was determined as oxidable carbon (C<sub>ox</sub>) by oxidation with K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub> and H<sub>2</sub>SO<sub>4</sub>, according to method of Springer and Klee (THUN et al. 1955).

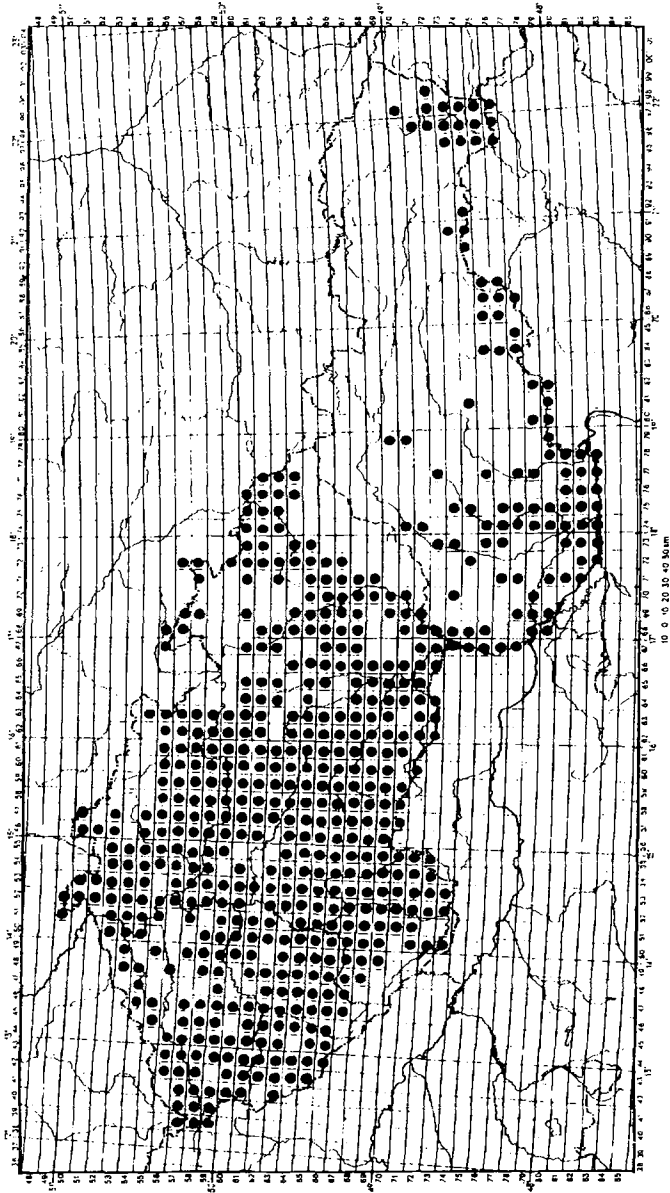


Fig. 1. The distribution of *Oenanthe aquatica* in Czechoslovakia.

## RESULTS

### DISTRIBUTION IN CZECHOSLOVAKIA

*Oenanthe aquatica* is a species with continuous distribution throughout the meridional zone of Europe and W. Asia, extending weakly into boreal and submeridional zones. It is absent in S. Europe on the Pyrenean Peninsula, S. Italy, and S. Greece; northward it reaches Central Sweden, S. Finland, and Karelia in the Russia. The area of distribution in Asia includes W. Siberia to the Altaj Mts.; some isolated localities are found in Turkey and Transcaucasia. A map of the total area of distribution of *O. aquatica* was given by MEUSEL et al. (1978).

In Czechoslovakia, *O. aquatica* is commonly distributed, but its frequency of occurrence varies. The limiting factors seem to be the presence of suitable habitats and altitude. Consequently, centres of distribution of *O. aquatica* lie in different vegetational belts in both the Hercynian and Carpathian-Pannonian regions (Fig. 1).

In the Hercynian region of Bohemia, *O. aquatica* occurs from lowlands to the submontane belt; most frequently in fishpond basins, but rarely in littoral zones along the shores of running waters. In Thermophyticum lowlands (terms of phytogeographic division of Czechoslovakia according to SKALICKÝ 1988), the species is abundant only in some districts with standing waters (environments of towns of Rožďalovice, Kolín, and Pardubice), while it is rare in the area of chalk tables westward of the Vltava river (e.g., district of Slánsko-bělohorská tabule), or in the district of Střední Poohří (with exception of the Ohře river banks). *O. aquatica* is most frequent in S. Bohemian and N. Bohemian fishpond regions, in the supracolline belt of Mesophyticum (S. Bohemian basins, Blatná-area, Horažďovice-area, Českomoravská vysočina upland, Doksy-area). In plain regions with frequent standing waters, *O. aquatica* may exist even in the submontane belt; it occurs in Oreophyticum in Žďárské vrchy hills (near the Dářko fishpond), in Jihlavské vrchy hills (along the Jihlávka river) and in Brdy hills (in the Padrťské rybníky fishponds - 640 m alt.), where it probably reaches its maximum altitude in Czechoslovakia. In other parts of Oreophyticum, only a few marginal localities are found in the southern part of the Šumava, Slavkovský les and Krušné hory mountains; *O. aquatica* is absent from the whole of the Krkonoše and Jeseníky mountains, even at lower altitudes.

In the Carpathian-Pannonian region, the vertical frequency of occurrence of *O. aquatica* is different from that in Bohemia. The species prevails there only in the lowlands of the Pannonian area of Moravia (Dolnomoravský úval, Hornomoravský úval, Dyjsko-Svratecký úval lowlands), and Slovakia (Záhorská nížina, Podunajská nížina, Východoslovenská nížina lowlands); more rarely in the Matricum region (Ipelso-rimavská brázda basin, S. Slovakian karst - wetlands near Turňanské Podhradie village). In the Carpathian region, *O. aquatica* occurs only sporadically along rivers: in the Váh river valley it reaches up to the town of Trenčín in the Nitra valley to Prievidza, in the Hron valley to Nová Baňa. In Central Carpathian basins, the species has been found only rarely: in the Turčianská kotlina basin (not found at present), and near Vígláš village under Polana Mt. (360 m alt.). The last locality of *O. aquatica* is probably the highest in altitude in Slovakia. In these rare localities, *O. aquatica* could occur only temporarily, brought randomly by water birds.

The distribution of *O. aquatica* in Slovakia was studied in detail by BERTOVÁ (1973, 1984), and the distribution there is well known. In Bohemia and Moravia, the distribution of *O. aquatica* is not well known; data on its occurrence are lacking for some districts, where the species probably occurs. It is possible that *O. aquatica* was not always recorded and collected

during floristic investigations. Besides, *O. aquatica* probably is really missing in the Moravian part of the Carpathian mountains (districts of Carpathian Mesophyticum). This fact is supported by the detailed investigations performed during a floristic summer school in 1973 in the environment of Valašské Klobouky. Over a wide area involving the Hostýnské vrchy, Vizovické vrchy, Zlínské vrchy and Bílé Karpaty hills, *O. aquatica* was not found (cf. ELSNEROVÁ et al. 1985).

Because *O. aquatica* can spread by seeds and its seeds are able to survive long-lasting unfavourable conditions (see following chapters), we can assume new ephemeral occurrences of *O. aquatica* on additional sites from the lowlands to the submontane belt. Besides, if the species is not found on some localities at present, it does not mean its extinction, namely at habitats under high water level. The reappearance of *O. aquatica* is possible there after the water level falls.

#### OCCURRENCE IN PLANT COMMUNITIES

*Oenanthe aquatica* is a characteristic species of the alliance *Oenanthion aquaticae* HEJNÝ 1948 apud VICHEREK 1962 (order *Oenanthetalia aquaticae* HEJNÝ 1965). The alliance includes plant communities optimally developed in the lower sublittoral of standing water - fishponds, oxbows or other periodically flooded habitats. The communities are very variable; they occur periodically depending on decrease of the water table, often after a very long period of anabiosis of seeds or vegetative reproductive organs under water (KOPECKÝ and HEJNÝ 1965, HEJNÝ 1967, HEJNÝ and HUSÁK 1978).

*O. aquatica* represents a dominant species in the ass. *Glycerio fluitantis-Oenanthetum aquaticae* (EGGLER 1933) HEJNÝ 1948 em. 1978, distributed over all areas of Czechoslovakia from lowlands to uplands. HEJNÝ (1948) and NEUHÄUSL (1959) described it from South Bohemia. HEJNÝ and HUSÁK (1978) described subass. *oenanthesum aquaticae* (EGGLER 1933) HEJNÝ 1978, with only dominant *O. aquatica*. It may be represented by the following relevé:

Korytní, 14.7.1983, rel. size 15 m<sup>2</sup>, height of the stand above water level 1 m, depth of water 0.3 m, cover E<sub>1</sub> = 100 %

*Oenanthe aquatica* 4, *Alisma plantago-aquatica* +, *Sparganium ramosum* +, *Typha latifolia* +, *Lemna minor* 3, *Spirodela polyrhiza* 3.

In warmer lowland regions of Czechoslovakia, the ass. *Rorippo amphibiae-Oenanthetum aquaticae* (Soó 1928) LOHMEYER 1950 occurs in periodical waters (temporary drying depressions), in pools or oxbows in alluvia of larger rivers, and in fishponds. The plant composition of this community is shown by the following relevé:

Mahenovo Jezero, 14.7.1982, rel. size 20 m<sup>2</sup>, height of the stand above water level 1 m, depth of water 0.5 m, cover E<sub>1</sub> = 100 %

*Oenanthe aquatica* 2, *Rorippa amphibia* 3, *Eleocharis palustris* 1, *Glyceria maxima* +, *Spirodela polyrhiza* 2, *Lemna trisulca* 2, *Lemna gibba* 3, *Hydrocharis morsus-ranae* 1, *Potamogeton pusillus* 2.

Very typical, however, are stands with only dominant *O. aquatica*, where the abundance of other plant species is negligible:

Zatín, 3.7.1985, rel. size 15 m<sup>2</sup>, height of the stand above water level 1 m, depth of water 1 m, cover E<sub>1</sub> = 85 %

*Oenanthe aquatica* 5, *Spirodela polyrhiza* 1, *Stratiotes aloides* 1.

*O. aquatica* inhabits similar habitats as other species forming communities of the all. *Oenanthon*; it may be present there mixed with some other equally abundant species or only as a companion to other dominant species (*Alisma plantago-aquatica*, *A. lanceolatum*, *Eleocharis palustris*, *Bolboschoenus maritimus* ssp. *maritimus* etc.).

In standing waters, a synusia of duckweeds (species of the all. *Lemnon minoris* TX. 1955) often accompany stands of *O. aquatica*. After a decrease in the water level, many submerged or floating species forming stable water communities in deep water can also survive in the shallow water layer - for example species of the ass. *Lemno-Hydrocharitetum morsus-ranae* (OBERDORFER 1957) PASSARGE 1978, *Stratiotetum aloidis* (NOWIŃSKI 1930) MILJAN 1933, *Potameto natantis-Nymphaeetum candidae* HEJNÝ in DYKJOVÁ and KVĚT 1978, *Nupharo lutei-Nymphaeetum albae* NOWIŃSKI 1930. These communities shift to deeper water and remain in contact with *O. aquatica* stands. Mixtures of *O. aquatica* plants with those submerged species occur frequently in shallow water along the shoreline (see the following relevé):

Kameničná 28.6.1985, rel. size 10 m<sup>2</sup>, height of the stand above water level 0.3 m, depth of water 0.8 m, cover E<sub>1</sub> = 80 %

*Oenanthe aquatica* +, *Rorippa amphibia* +, *Alisma lanceolatum* +, *Sagittaria sagittifolia* 1, *Sparganium ramosum* +, *Rumex hydrolapathum* r, *Lemna minor* +, *Spirodela polyrhiza* 1, *Lemna trisulca* +, *Lemna gibba* +, *Salvinia natans* +, *Riccia fluitans* +, *Hydrocharis morsus-ranae* 2, *Nuphar luteum* 2, *Nymphoides peltata* +, *Myriophyllum spicatum* 2, *Batrachium circinatum* 1, *Mentha aquatica* +.

The occurrence of *O. aquatica* in reed and tall sedge communities is rare. In those communities, *O. aquatica* occurs more frequently only in *Glycerietum maximae* HUECK 1931. This may be due to the same ecological optimum of both *O. aquatica* and *Glyceria maxima* (deep muddy sediments, prolonged limosal ecophase). Other reedswamp species are stronger competitors than *O. aquatica* and suppress it mainly by shading (HROUDOVÁ 1980); *O. aquatica* populations can establish themselves only in open water sites (lagoons in reed stands).

A decrease in the water level and drying of the bottom surface enable germination of the seeds of *O. aquatica*. The seedlings are often found forming a dense cover in emerged pond bottoms (see Plate 1, 2), mainly on sites with permanently moist soil (areas above fishpond dams, near springs in the bottom or central parts of fishponds, along permanently flowing streams). From these seedlings, very abundant crowded stands of *O. aquatica* can arise, formed by tall, richly branched and fertile plants (Plate 2). These communities are very similar to those growing in shallow water; they differ floristically by the presence of species characteristic for emerged bottoms:

Stříbrný, 25.8.1982, rel. size 25 m<sup>2</sup>, height of the stand 0.7 m, cover E<sub>1</sub> = 100 %

*Oenanthe aquatica* 5, *Glyceria maxima* +, *Carex bohemica* 1, *Rorippa palustris* +, *Polygonum lapathifolium* 1, *Polygonum hydropiper* +, *Bidens radiata* +.

On permanently moist bottoms, *O. aquatica* occurs frequently in communities with other species of the all. *Oenanthon*, mainly with *Alisma* species:

Polány, 3.7.1985, rel. size 18 m<sup>2</sup>, height of the stand 1.7 m, cover E<sub>1</sub> = 100 %

*Oenanthe aquatica* 3, *Alisma lanceolatum* 2, *Rorippa amphibia* +, *Callitriche palustris* +, *Peplis portula* 1, *Elatine alsinastrum* 1, *Ranunculus flammula* +, *Juncus bufonius* 2, *Gnaphalium uliginosum* +, *Polygonum hydropiper* 1, *Bidens tripartita* +, *Alopecurus aequalis* +, *Matricaria maritima* +, *Bidens frondosa* r, *Echinochloa crus-galli* +, *Agropyrum repens* +, *Lythrum hyssopifolium* +.

The range of other communities of emerged pond bottoms where *O. aquatica* can grow is very wide. In the limosal ecophase, *O. aquatica* can occur in communities of the all. *Littorellion*, together with *Callitriche palustris*, *Eleocharis acicularis* or *Elatine* sp. div.; AMBROŽ (1939) has found it in the ass. *Eleocharidetum acicularis* W. KOCH 1926. In the terrestrial ecophase, *O. aquatica* is often present in communities of the all. *Elatini-Eleocharition ovatae* PIETSCH 1937 or the all. *Bidention tripartiti* NORDHAGEN 1940: in ass. *Eleocharito-Caricetum bohemicae* (KLIKA 1935) PIETSCH in PIETSCH and MÜLLER-STOLL 1965, recorded e.g. by KLIKA (1935), AMBROŽ (1939) and JÍLEK (1956), in ass. *Bidentetum tripartiti* W. KOCH 1926 or in ass. *Rumicetum maritimi* SISSINGH ex TÜXEN 1950. KLIKA (1935) and AMBROŽ (1939) recorded it in the ass. *Polygono lapathifolii-Bidentetum tripartiti* W. KOCH 1926. In some cases, *O. aquatica* can be present as a companion in reed and tall sedge communities, inhabiting free spaces on the emerged bottom between tufts or plants of reeds or sedges.

In general, the range of communities in which *O. aquatica* occurs is very wide and, in some cases, no distinct difference between littoral and terrestrial communities can be observed.

#### SUBSTRATUM

Literature data on the relation of *O. aquatica* to soil chemistry are very rare. In comparison with some other species belonging to the all. *Oenanthon* inhabiting similar habitats in shallow littoral (*Sagittaria sagittifolia*, *Butomus umbellatus*, *Bolboschoenus maritimus*), *O. aquatica* is probably adapted to the widest range of nutrient contents in the substratum (HROUDOVÁ 1980). *O. aquatica* shows a wide range of occurrence in relation to physical soil properties; it grows on deep, fine-grained sediments as well as on sandy erosion belts of fishponds. Its optimally developed stands arise in habitats with deep muddy upper horizons (NOVÁČEK 1937, NEUHÄUSL 1959, HEJNÝ 1980), mostly in sedimentary zones of shallow standing waters. It can, however, grow also on coarse-grained substrata (JÍLEK 1956, KOPECKÝ 1962).

Table 1. Correlation coefficients for soil chemistry and *Oenanthe aquatica* cover in 67 habitats.

	pH <sub>H2O</sub>	pH <sub>KCl</sub>	Na <sup>+</sup>	K <sup>+</sup>	Mg <sup>2+</sup>	Ca <sup>2+</sup>	P-PO <sub>4</sub>	N-NH <sub>4</sub>	N-NO <sub>3</sub>	N <sub>tox</sub>	C <sub>ox</sub>
cover	-0.03	-0.09	0.07	0.05	0.08	0.03	0.14	0.16	-0.17	-0.01	-0.01

no correlation coefficient is significant at the P = 0.05 level



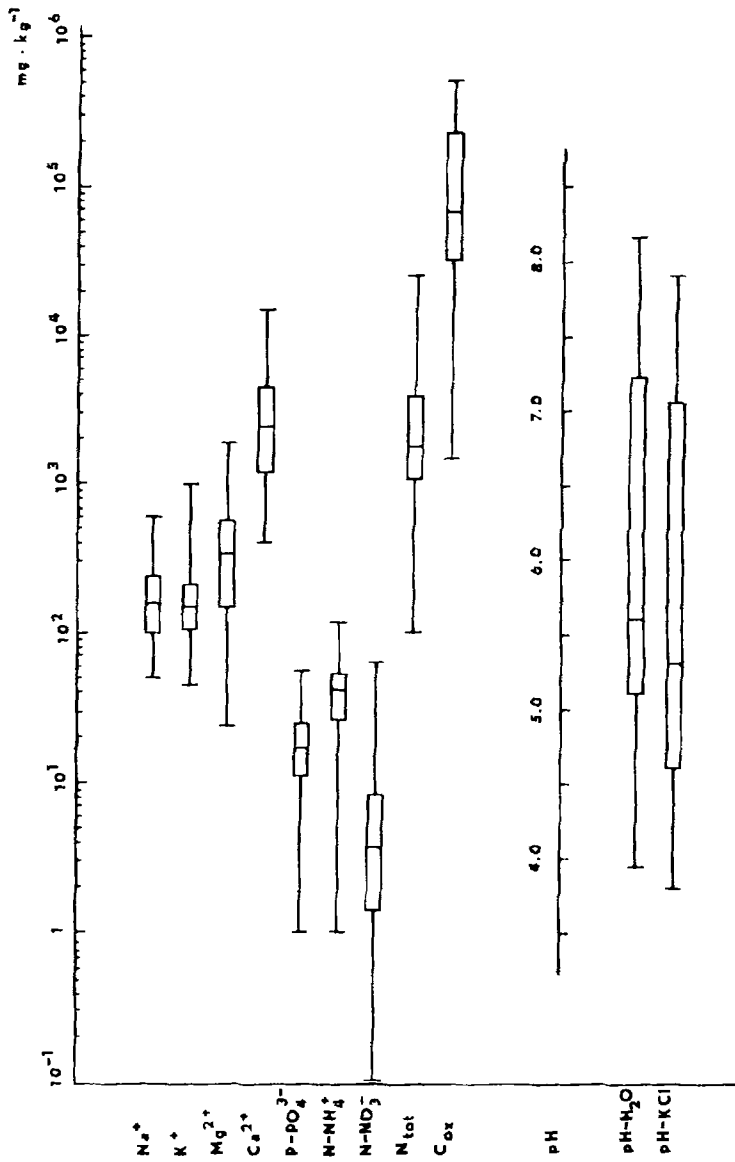


Fig. 2. Variation in soil reaction and mineral nutrient content in soils from 67 habitats of *Oenanthe aquatica* in Czechoslovakia (lines indicate amplitude of occurrence, blocks indicate median and quartiles).

Concerning soil chemistry, the amplitude of occurrence of *O. aquatica* is wide as well (Fig. 2). Compared, for example, with *Sagittaria sagittifolia* (HROUDOVÁ et al. 1988), *O. aquatica* is more tolerant as to  $K^+$  content and particularly as to  $Mg^{2+}$  content. Similarly, in pH and total nitrogen content, *O. aquatica* also shows a wider range. In comparison with *S. sagittifolia*, *O. aquatica* can also inhabit habitats with minimum content of  $P-PO_4^{3-}$ ,  $N-NH_4^+$  and  $N-NO_3^-$ ; on the other hand, it tolerates well (or even prefers) a high  $N-NH_4^+$  content in soil sediments; this is connected with the frequent occurrence of *O. aquatica* on deep layers of sapropel sediments.

Optimal development of stands of *O. aquatica* is not due any special chemical composition of the soil. It is expressed by the relationship between abundance of *O. aquatica* and chemical soil properties (Tab. 1). No significant dependence of plant cover on nutrient contents and reaction was found.

#### DEPENDENCE ON WATER DEPTH

Fluctuations of water level are characteristic for *Oenanthe aquatica* habitats; the most important is the temporary emergence of bottom preceding strong development of stands of *O. aquatica* (NOVÁČEK 1937, JÍLEK 1956, NEUHÄUSL 1959, HEJNÝ 1960, ZAHLHEIMER 1979). Extensive stands occur most frequently in shallow water, in open water areas, or in the belt on the inner side of the reedbelt (NEUHÄUSL 1959, NEDELICU 1967). Well developed and fertile plants, however, are often found even in terrestrial ecophase (in communities on an emerged bottom). According to HEJNÝ (1960), dominance of *O. aquatica* on the emerged bottom indicates a long-lasting limosal ecophase. In the limosal or terrestrial ecophase, the species can also occur in the bottom layer of reeds, following a falling water level (FIALA and KVĚT 1971).

Frequency of occurrence of *O. aquatica* fluctuates considerably in time, from year to year; in some cases, a stand exists only during one growing season and then disappears or it may appear again some years later (EKZERCEV 1966, BELAVSKAJA and KUTOVA 1966). Its occurrence is particularly dependent on the water régime of the habitat.

*O. aquatica* was found in the following depth ranges:

0 - 0.2 m (ANDREI 1971), 0.2 - 0.4 m (KÁRPÁTI 1963), to the depth of 0.3 - 0.5 m (NEUHÄUSL 1959), 0.25 - 1 m (NEDELICU 1967), in communities of the all. *Potamion* in the depth 0.8 - 1 m (HILBIG 1971). GLÜCK (1911) has given the water depth for submerged plants 0.2 - 0.5 m, rarely to 1 m; very tall plants (*f. eximia*) were found at depths of 2 - 2.5 m (GLÜCK 1936).

Frequency of occurrence of *O. aquatica* changes with increasing depth of the water (Fig. 3). The total range of occurrence is 0 to 1 m, which agrees with the literature data. The proportion of plants found on emerged bottoms is considerable (over half of all habitats). This may be explained by the fact that plants can successfully develop from germinating seeds to vegetative stage only on emerged bottoms. Establishment of *O. aquatica* plants on emerged bottoms does not always lead to immediate formation of a community with dominant *O. aquatica*, but it is necessary for its formation in the subsequent year under a shallow water layer. From the total number of terrestrial stands of seedlings, only a small proportion develops in littoral stands during the next growing season. This is evident from the habitats/cover ratio at different depths in the littoral ecophase (water depth 0.2 - 0.8 m) where the high cover rates occur. The high cover rate at depths of 0.9 - 1 m is caused by the small number of habitats at both depths; *O. aquatica* was found only in one case, but with maximum cover rate. This relationship is probably due to a simultaneous effect of habitat

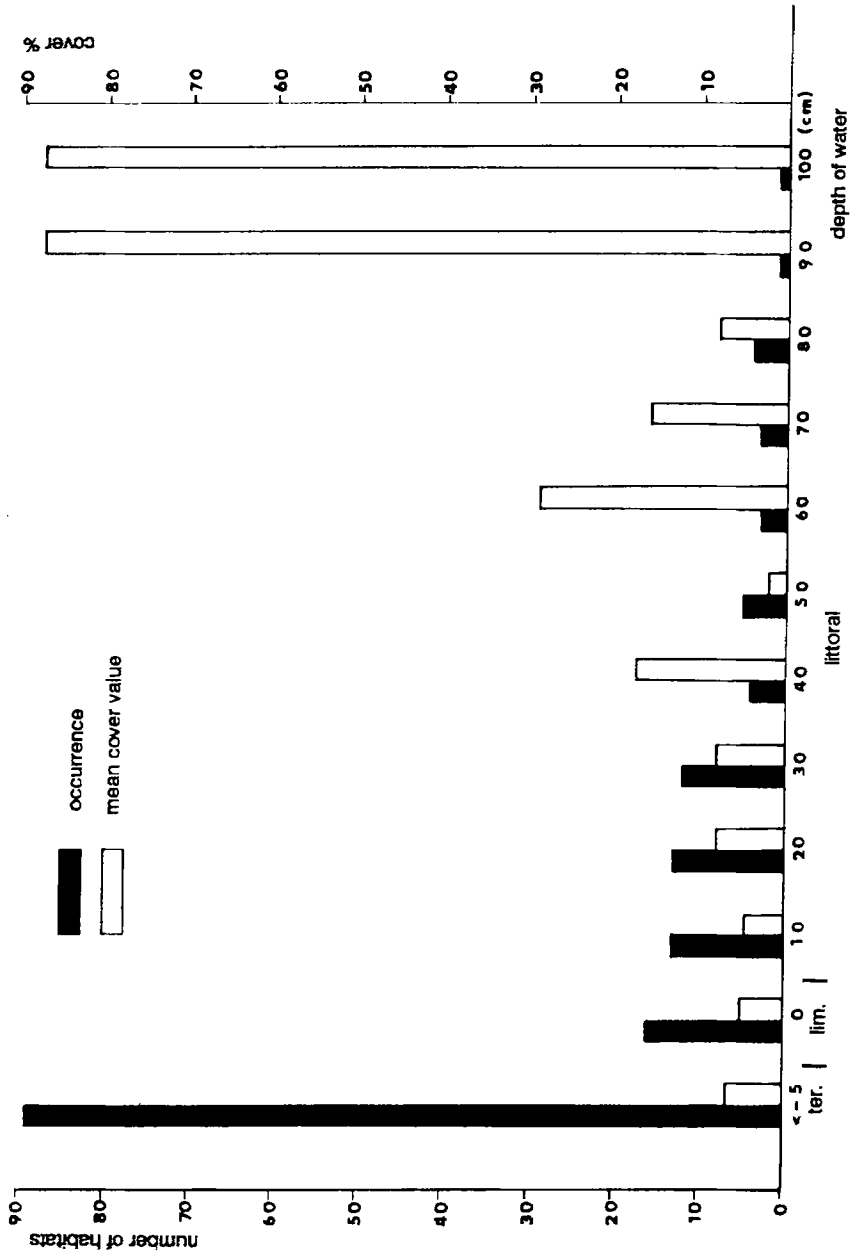


Fig. 3. Frequency of habitats and cover degree of *Oenanthe aquatica* in different depths of water (data from 164 recent habitats of *Oenanthe aquatica* in Czechoslovakia).

conditions and plant competition. Out of the high number of seedlings arising on emerged bottoms, only the best developed strong individuals are able to survive under competition with all seedlings of other species and, under favourable water level dynamics, are able to adapt themselves to subsequent rising water levels. The density of plants thus decreases with the increase of water depth. Only plants which have survived the winter season can give rise to optimally developed stands in the littoral ecophase in the following growing season - a further factor of natural selection. *O. aquatica* can thus serve as an example of a plant species in which conditions of maximum frequency of occurrence are not identical with conditions of maximum cover rate and biomass production.

#### ADAPTATIONS TO CHANGES OF WATER LEVEL

In submerged plants, the leaf blade is highly dissected into very fine, capillary segments (f. *submersa* GLÜCK). In this form, the plant can survive the winter season, or it may remain in this stage during the whole growing season (GLÜCK 1911).

Terrestrial form (f. *terrestris* GLÜCK) may have some first leaves similar to submerged leaves (with fine capillary segments), especially in early spring in limosal ecophases. These first leaves are smaller, firmer and not so dissected in comparison with submerged leaves. They have shorter petioles and somewhat shorter blade segments. Typical terrestrial leaves have blades with broader flat segments. The stem is branched, firm, with grooves on the surface. Terrestrial plants flower and are usually richly fertile (Plate 1). Leaf rosettes that arise in the terrestrial ecophase can survive the winter and give rise to biennial plants (GLÜCK 1911, HROUDOVÁ 1981) as in Plate 2.

The most typical and well developed plants are those growing in shallow littoral zones, such as f. *semimersa* GLÜCK (Plate 3). In the first stage, the plants are submerged; after reaching the surface, they produce aerial leaves with broader, flat segments of blade, identical with the leaves of terrestrial plants. The submerged leaves decay gradually and adventitious roots start to grow in the stem nodes under water level (HEJNÝ 1960). This lower part of the stem can be very thick and, according to BERTO VÁ (1973), can reach 8 cm in diameter. The upper aerial part of the plant is usually richly branched with many inflorescences and, in a well developed stand, the plants can reach over 2 m in length (HROUDOVÁ 1980).

All leaf forms are temporary and can even represent developmental stages of ontogenesis (see "primärblätter" of GLÜCK 1911), or growth forms adapted to habitat conditions.

In its anatomy, *O. aquatica* is remarkable for aerenchymatous tissue in the central part of the stem. Plants growing on an emerged bottom, in the limosal-terrestrial ecophase, have the central part of the stem formed by aerenchyma which passes gradually to parenchymatous tissue surrounding vascular bundles (Fig. 4). Between the circle of vascular bundles and the epidermis, there is a parenchymatous tissue with large straggling lacunae (transition to aerenchyma) passing to a parenchymatous layer under the epidermis. Plants growing in the littoral usually have a great central cavity in the thickened part of the stem and nearly all of the remaining tissues in the stem are aerenchymatous (Fig. 5, Plate 4). No parenchyma is formed here and vascular bundles are surrounded and interconnected by sclerenchymatous tissue, hardening the stem around its periphery.

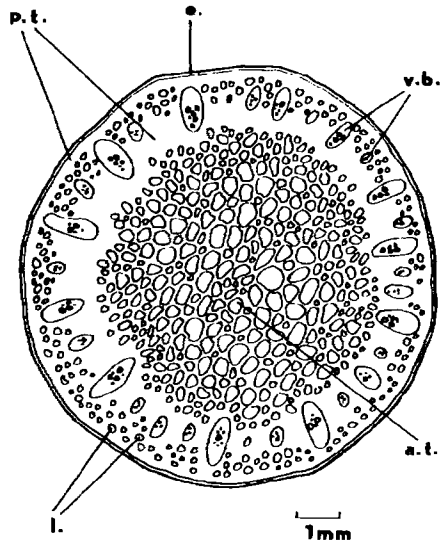


Fig. 4. Transverse section of the lower part of a stem of *Oenanthe aquatica* growing on an emerged pond bottom; e - epidermis, a.t. - aerenchymatous tissue, v.b. - vascular bundles, l. - lacunae

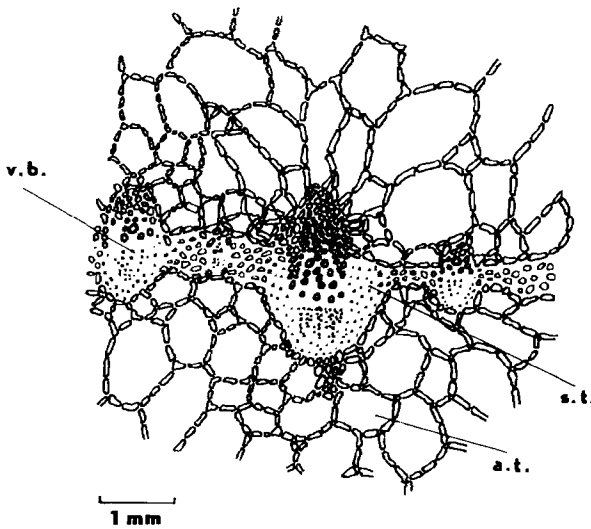


Fig. 5. Detail transverse section of *Oenanthe aquatica* stem (plant growing in littoral ecophase); a.t. - aerenchymatous tissue, s.t. - sclerenchymatous tissue, v.b. - vascular bundles.

## LIFE CYCLE AND POPULATION STRUCTURE

*Oenanthe aquatica* can be an annual or a biennial plant. Seedlings usually establish themselves on emerged pond bottoms and terrestrial stands of annual plants arise during summer draining. *O. aquatica* is frequently present as a crowded population of small plants forming continuous cover with their leaf rosettes (Plate 1, 2). Littoral stands usually arise in the year following summer drainage of the pond, in the shallow water layer. They consist of biennial plants (Plate 3) originating from autumn seedlings that have survived the winter season in the stage of leaf rosettes. Terrestrial stands on emerged bottoms can be formed by autumn and spring seedlings (Plate 1, 2) and their development depends on the moisture and nutrient conditions of the habitat.

In previous investigations (HROUDOVÁ 1980), the following differences were found between annual and biennial populations of *O. aquatica*:

## 1) stand density and plant size (Tab. 2, Fig. 6)

In early summer, a dense cover of seedlings is typical for limosal-terrestrial ecophases on muddy bottoms; on open sandy shores, sparser stands of seedlings can frequently arise, limited by the water supply in the soil. In the underwater layer, the stand density is influenced by water environment and by the competition of other submerged plant species. The population structure of biennial plants is different: the population of biennial plants at the Allah fishpond was formed by very tall well developed plants, representing strong

Table 2. Plant density and biomass production of *Oenanthe aquatica* per 1 m<sup>2</sup> in populations of annual and biennial plants (according to HROUDOVÁ 1980).

	Number of plants per 1 m <sup>2</sup>	Total dry biomass per 1 m <sup>2</sup> (g)			
		23.5.	6.6.-9.6.	29.6.-1.7.	11.8.-13.8.
Nesyt - Sedlecká bay annual terrestrial plants in reed stand	500	21.89	26.71	208.66	351.38
Nesyt - Sedlecká bay annual submerged plants	about 200	2.78	7.53	10.34	-
Nesyt - E shore annual terrestrial plants on the open shore	20	-	-	-	36.54
Allah IV biennial littoral plants	about 70	-	46.85	288.16	1368.58

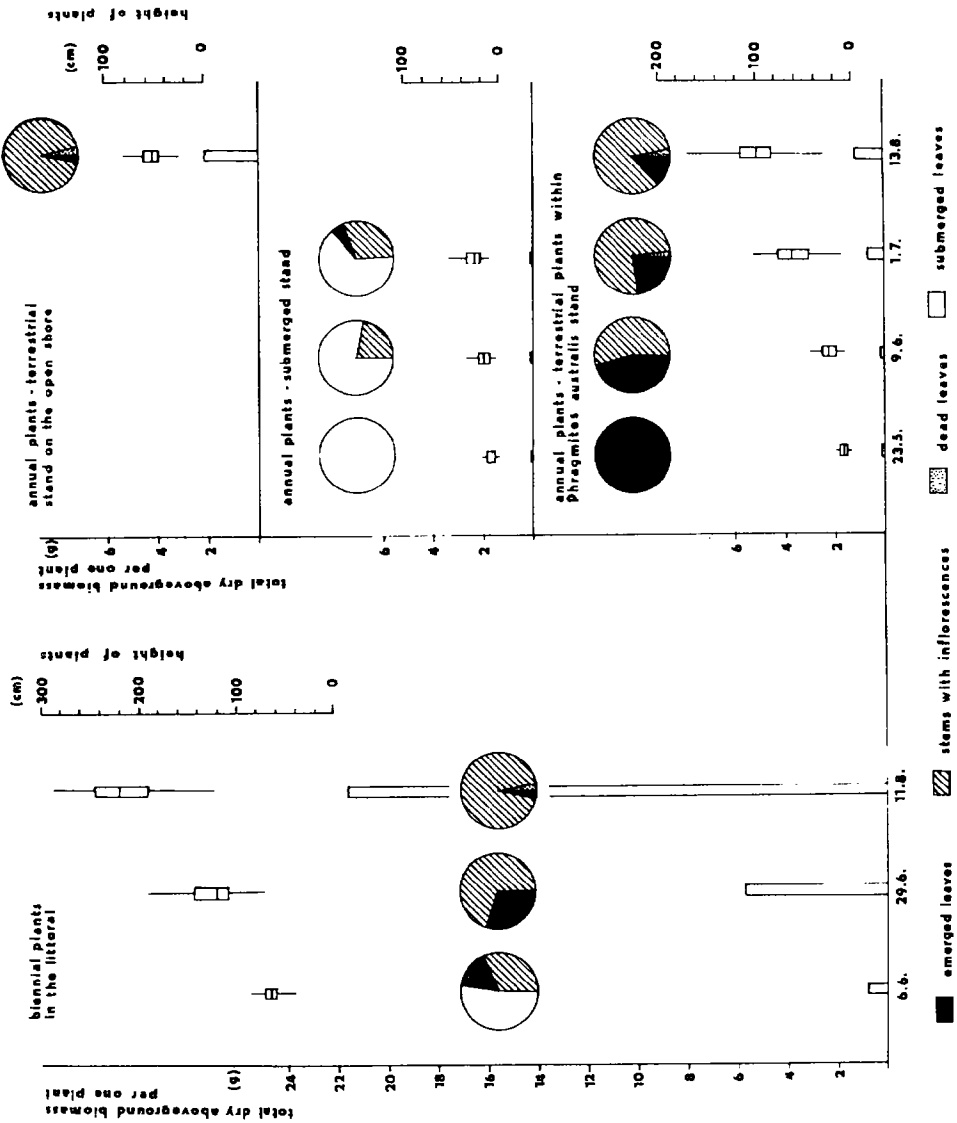


Fig. 6. Biomass production per plant, proportions of plant organs and changes in plant height in different populations of *Oenanthe aquatica* during one growing season. The circles show the proportion of biomass in individual plant organs (in per cent). Variation in height: lines indicate total range of values, blocks indicate median and quartiles.

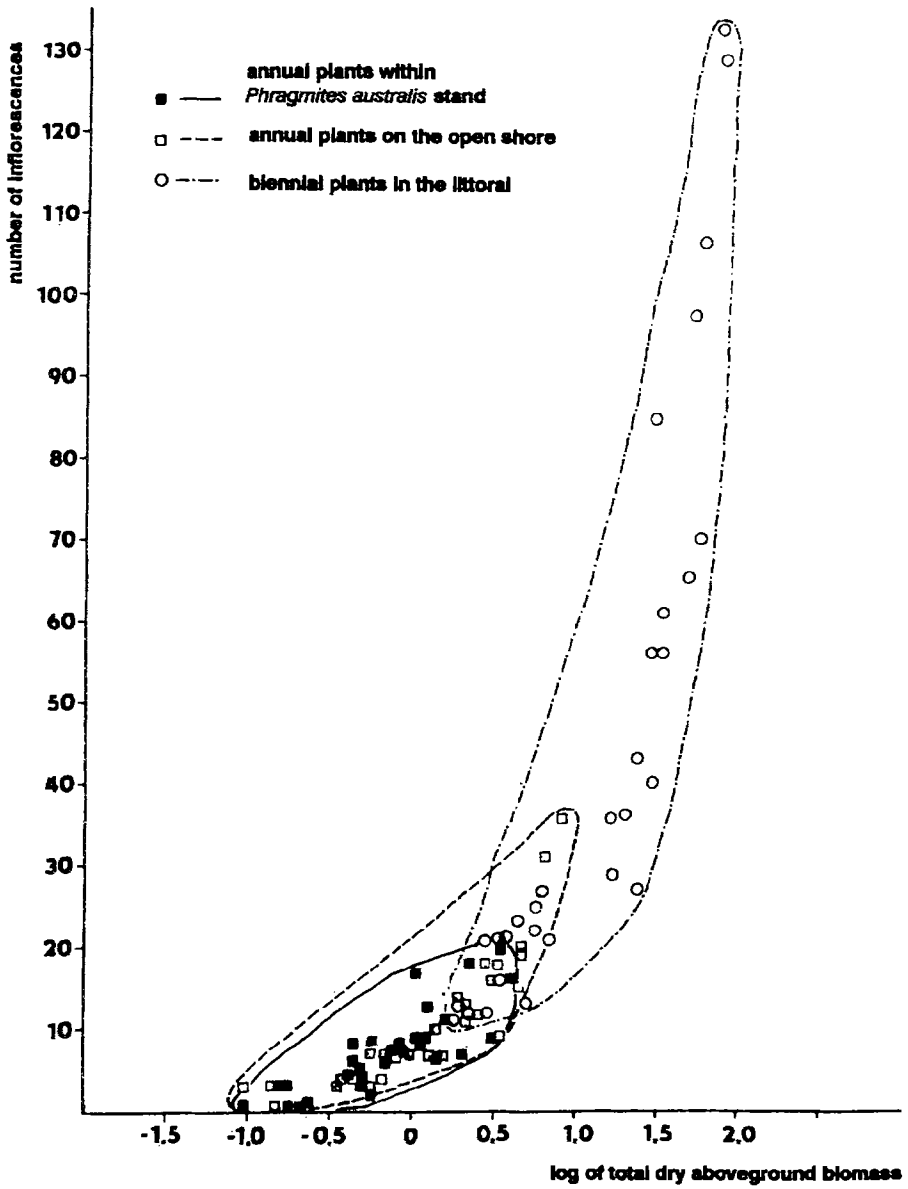


Fig. 7. Plant size and fertility of *Oenanthe aquatica* in populations of annual and biennial plants.



competitors. The optimal density/size ratio there resulted from the competitive process during previous development from autumn seedlings. The biennial plants were considerably taller than the annual ones and this difference increased during the growing season.

#### 2) proportion of different leaf forms and its changes during the growing season

The proportion of submerged and emerged leaves depends on the height of the water level and the duration of flooding. In the submerged stand at the Nesyt fishpond, the water level gradually increased from 0.3 to 0.5 m. The plants only exceptionally reached to the water level and rarely formed emerged leaves above the water surface (Fig. 6). During July, all plants died; this may have been caused by competition (shading) by the dense cover of other submerged plant species (*Potamogeton pectinatus*, *Ranunculus rionii*, *Zannichellia palustris* ssp. *pedicellata*), or by anaerobic conditions near the bottom. On the other hand, biennial plants originating from autumn seedlings were able to grow successfully through the water layer about 0.7 m and to form emerged leaves. The water level gradually decreased there to 0.3 m; during June, all submerged leaves died and disappeared. The leaves/stems ratio became similar to that in terrestrial annual plants (Fig. 6).

#### 3) plant fertility

The development of inflorescences and seed production are in proportion to total plant size, and are conditioned by sunshine supply. Submerged plants did not reach the generative stage; in the terrestrial populations of annual plants, plant fertility in the population shaded by a stand of *Phragmites australis* was somewhat lower. The fertility of biennial plants markedly surpassed that of the annual plants (Fig. 7).

#### 4) biomass production

There are great differences between annual and biennial plants. The highest biomass production was in biennial plants in the littoral ecophase (Fig. 6, 7). *Oenanthe aquatica* represented a strong competitor there, able to overgrow a large fishpond area. The final proportion of biomass of living leaves, stems and dead leaves was nearly the same as in the terrestrial annual plants growing on the open shore without any competitive limitation. In the population of annual plants in the stand of *Phragmites australis*, the high plant density decreased biomass production per single plant, but the total biomass production per 1 m<sup>2</sup> area was higher than in the sparse stand on the open shore (Tab. 2.). In submerged plants, the total biomass production was negligible.

In general, the biennial plants considerably surpass the annual ones in plant size, biomass production and fertility both per plant, and per unit of area (Tabs. 2, 3, Fig. 7). A longer period (to the second growing season) is necessary to reach the optimum density/size ratio in populations of *O. aquatica*. In the second growing season, the plants grow under relatively stable habitat conditions. *O. aquatica* dominates there and the size of its plants and their spatial relationships indicate full utilization of habitat resources. *O. aquatica* in such populations may be considered as a C-strategist (sensu GRIME 1978, 1979). In this stage, it becomes an undesirable weed in fishpond management.

In the annual plants, the seedling development depends considerably on habitat conditions: height of water level, water and nutrient supply in the soil, competition of other plant species. They influence the growth of plants and cause significant differences between populations (Tab. 3). In annual plant populations there are the following common characters: lower biomass production per plant, high plant density at the starting point of population development, fast development from seeds to fertile plants, dependence on changes of habitat conditions. This makes it possible to consider *O. aquatica* in these

Table 3. A test of variation in plant size and biomass production per one plant in populations of annual and biennial plants of *Oenanthe aquatica*. Analysis of variance used for testing (SNEDECOR and COCHRAN 1971); \*\*means highly significant differences ( $P < 0.01$ ) between populations.

sampling date	F - values			
	23.5.	6.6.-9.6.	29.6.-1.7.	11.8.-13.8.
height of plants	2.02	166.40**	132.74**	188.09**
number of living leaves	26.34**	130.42**	27.08**	24.71**
number of inflorescences	-	-	2.55	28.25**
Biomass - living leaves	18.13**	77.44**	35.14**	22.24**
- stems	-	45.25**	29.25**	24.94**
- total	18.38**	66.58**	31.03**	25.06**

populations as R-strategist. The two kinds of populations are, however, closely connected: the plants need to pass through the developmental phase of ruderal character to become strong competitors.

#### REPRODUCTION

*Oenanthe aquatica* reproduces only by seeds. The term seed is used here in the sense of a generative reproduction unit; in the morphological sense, it is a one-seed fruit (achene).

Seed production fluctuates depending on habitat conditions and life cycle (annual and biennial plants). The highest seed production is in biennial plants originating from autumn seedlings and growing in the following year in a littoral ecophase; for example, in the Allah fishpond or the Oborský fishpond (Tab. 4). In the latter locality, some very tall plants produced up to 40,000 seeds. Seed production is lower in annual plants, in accordance with their smaller size and lower biomass production. Besides, seed production can be limited by insects: achenes are sometimes eaten out by insects of the family *Chalcidoidea - Eurytomidae*; for example, in 1983 achenes of *O. aquatica* from the Jordánek fishpond were heavily invaded and damaged.

Seeds from different populations can differ in size. Seed size varies in the range of each single population; in some populations, however, seeds are generally minute compared with larger seeds in other populations. This may be caused either genetically or by the influence of habitat conditions. Seeds of *O. aquatica* from several localities were measured and compared (Tab. 5). In both littoral populations, the seed size was nearly the same, and in populations of emerged bottoms, the seed size differed according to the degree of drying of the soil. The following relationships of seed size may be assumed:

- a) to habitat conditions, especially to the water régime in the soil. Satisfactory water supply seems to support the growth of seeds;
- b) to the life cycle of plants. Littoral stands are thought to be formed by biennial plants. These more robust tall plants can form larger seeds than annual plants on the emerged bottom;
- c) to seed germination. No direct dependence of seed germination on seed size, however, was found (see p. 322).

Table 4. Seed production of *Oenanthe aquatica* in different habitats; data from localities marked + according to HROUDOVÁ 1980. s. d. - standard deviation, n - number of studied plants.

Site Date	mean number of umbels per plant	number of seeds per plant		n
		mean	s.d.	
Allah IV <sup>+</sup> (littoral) 11.8.1972	44.2	5 087.7	4 003.5	30
Nesyt-Sedlecká bay <sup>+</sup> (emerged bottom) 13.8.1972	8.3	814.2	493.0	30
Nesyt- E shore <sup>+</sup> (emerged bottom) 13.8.1972	11.3	1 599.6	1 145.7	30
Kačležský (emerged bottom) 26.8.1983	-	856.9	706.9	20
Oborský (emerged bottom) 22.8.1983	-	16 991.4	14 873.7	10
Rožboud (emerged bottom) 23.8.1983	-	7 829.8	7 258.9	10

Table 5. Means, standard deviations, and homogeneity test (LSD, 99 %) of achene length of *Oenanthe aquatica* from different habitats.

Locality	Population, habitat	achene length mm			homogeneous groups
		n	x	s.d.	
Přední Svinětický	annual, emerged bottom	100	3.24	0.36	a
Kačležský	annual, emerged bottom	100	3.79	0.44	b
Jordánek	biennial, littoral ecophase	100	4.01	0.37	c
Blažejov	biennial, littoral ecophase	100	4.03	0.43	c

Different letters indicate non-homogeneous groups

In general, the size ranges of seeds from all populations investigated overlap; in terms of taxonomy, the size of achenes evidently varies in the range of the same taxonomic unit; it cannot be considered as var. *microcarpum* (BECK) BERTOŤOVÁ with 2 - 2.5 mm long achenes, recorded by BERTOŤOVÁ (1973) from South Slovakia.

Achenes fall around the plants. They can spread by water if the maternal plant grows through the water layer. The floating ability of seeds has been described by some authors: ULBRICH (1928) included *O. aquatica* in the group of plants having seeds able to float from 2 to 10 days, and spread by wind and animals. The floating capacity of seeds is conditioned by the presence of air tissue in the pericarp, as in some other water species of the carrot family. According to RYČIN (1948) achenes of *O. aquatica* can float and are distributed by water, and, besides, they may be spread on the feathers of water birds. In our investigations, seeds of *O. aquatica* sank under water level relatively quickly (Fig. 8). At first they floated for some hours; most of them sank to the bottom within two days (in accordance with the literature data). In some cases, achenes sunk to the bottom started to germinate and then rose again to the surface, which can explain the gentle repeated increase of the floating curve. Under natural conditions, it can be observed in late summer when germinating young seedlings are found floating on the water surface. Seedlings of *O. aquatica* in the stage of two leaves were also found floating on the cover of filamentous algae. The floating seedling is shown in Fig. 9. Both seeds and seedlings of *O. aquatica* can spread by water; the proportion of seeds germinating immediately after ripening, however, is not large (see below).

Penty of *O. aquatica* seeds germinate in natural habitats. The seedlings can be found at almost any time during the growing season and are very recognizable (Fig. 9). According to GLUCK (1911) seeds germinate fast and easily; in most cases ripe seeds need a short period of rest before germination, and thus seedlings can arise in the same autumn after ripening. The development of seedlings in autumn up to the beginning of October was observed by NOVÁČEK (1937) and KORELJAKOVA (1977). Numerous seedlings can be observed on emerged bottoms after a fall in the water level (AMBROŽ 1939, JILFK 1956, KORELJAKOVA 1977), or in drifts along shores, brought by waves. According to HEJNÝ (1960) seeds of *O. aquatica* germinate well in the limosal ecophase. According to these authors, seeds of *O. aquatica* germinate best on the emerged bottom with the soil fully saturated by water. It is evident that for germination seeds need not only a simple increase in temperature but the simultaneous action of other factors: satisfactory water and air supply. Possible combinations of germination conditions in the field are quite diverse (Tab. 6).

The following factors influence seed germination of *O. aquatica*:

#### a) Seed dormancy

Freshly ripened seeds rarely germinate: germination in air reached 10 % and in water only nearly 1 %. Compared with results previously obtained (HROUDOVÁ 1980), these values are considerably lower: in the course of 7 days freshly ripened seeds collected 14.9.1971 near the town of Třeboň reached 60 % of germination in air, and 80 % in 30 days. Seeds were kept fresh (without drying) within about two weeks after sampling and then tested for germination. In the case of possible after-ripening of *O. aquatica* seeds, the time of two weeks after spontaneous detachment of seeds from the plant seems to be sufficient for germination to start. The second possible explanation of different results in seed germination rates seems to be the dependence of germination on the time of seed ripening. In the first case, the seeds were ripe and germinated in September, 1971; in the second case, in August, nearly one month earlier. In both cases, the aeration resulted in faster germination and a higher total number of germinating seeds.

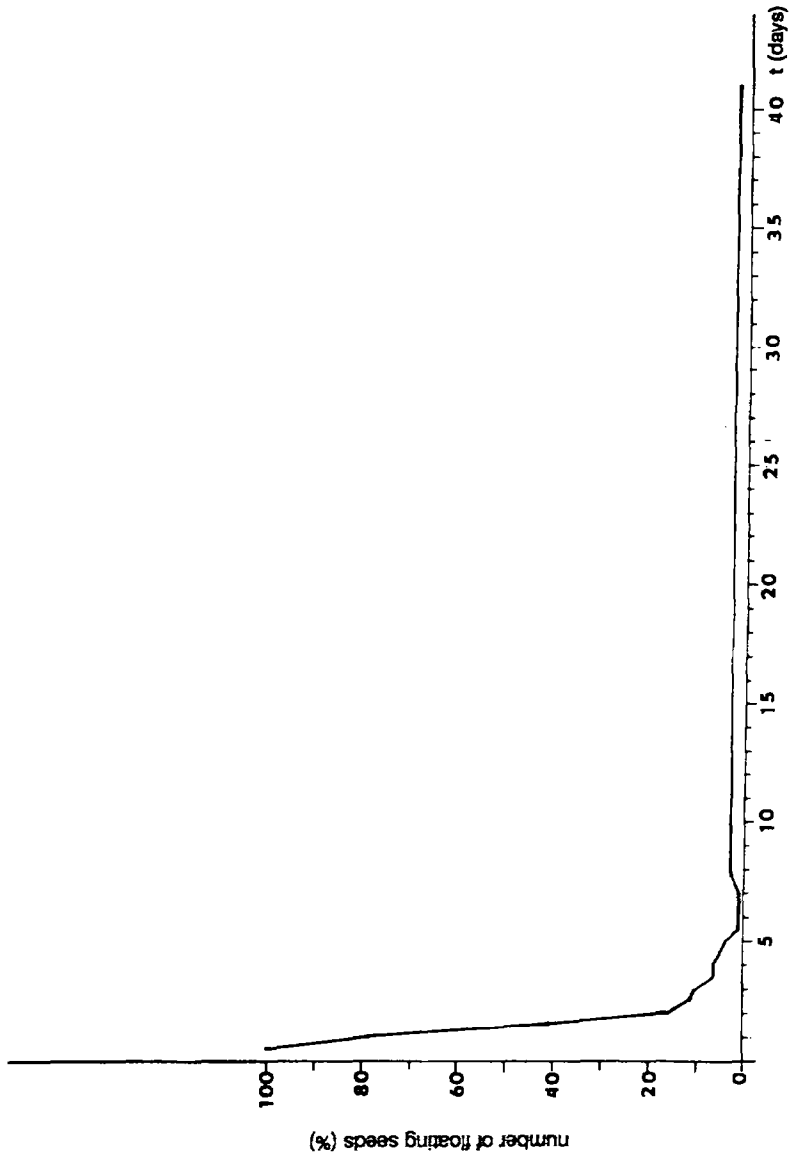


Fig. 8. Floating capacity of seeds of *Oenanthe aquatica* (fresh seeds immediately after ripening).

**b) Origin of seeds from different localities and drying of seeds to different degrees**

In some localities, there were two kinds of seeds at the same time: freshly ripened seeds yellow-green in colour, starting to detach from the plant, and dry gray-black seeds ripened earlier but still remaining on the plant. Because we supposed physiological differences between the two kinds of seeds, they were collected separately and in germination experiments were called "fresh" and "dry" seeds. It is apparent from Fig. 10 that dry seeds germinated slowly at the beginning of germination, but during the experiment their germination caught up with the rate of the fresh seeds, and the final total germination rate of dry seeds was somewhat higher than that of fresh seeds; the only exception was found in seeds from the locality Jordánek - both kinds of seeds germinated well and fresh seeds germinated better than dry seeds. In comparison with previous germination experiments (HROUDOVÁ 1980), the results were different: very few seeds stratified under natural conditions in soil germinated in air, about 4 % of seeds from two different localities.

Differences in germination between seeds originating from different localities were remarkable: the total germination rate varied in the range of 40 - 90 %. All seeds were collected in the same growing season, approximately at the same time, and ripened to the same degree (when seeds started to detach from the plant). Differences in germination do not correspond to the size of seeds as in the case of another plant species (HENDRIX 1984); the biggest seeds from the locality of Blažejov germinated least of all, and, on the contrary, seeds of nearly the same size from the Jordánek fishpond germinated best. Seed size, however, was not measured in dependence on the gradual increase in number of inflorescences or the position of seeds in the inflorescence, but seeds were randomly chosen and measured from a mixture representing the whole population (Tab. 5). Seed size seems to be related to habitat conditions while seed germination depends rather on the different physiological stages of seeds at the time of sampling, not apparent on the outside.

**c) Light and darkness**

Light strongly influences seed germination (Tab. 7, 8). In all cases, seeds in continuous darkness germinated only slightly compared with those under an alternating light-darkness régime. Only the best germinating seeds from the Jordánek fishpond, under the most favourable combination of stratification and germination conditions, reached 18.7 % of total germination rate in darkness; this rate is, however, remarkably lower as compared with 93.7 % in light. Limited germination in darkness is probably useful under water level to prevent seed germination until the water level falls.

**d) Temperature optimum and range of germination**

Optimum germination temperature is about 20 - 25 °C (Fig. 11), and individual variants differ depending on stratification and germination conditions. Under the most favourable conditions (seeds stratified in water, germinating in air), seeds germinated optimally between 20 - 25 °C and germination decreased regularly towards both temperature limits. Seeds stratified and germinating under aerated conditions germinated optimally at a somewhat higher temperature (25 °C) and, on the contrary, seeds stratified and germinating in water germinated better at lower temperatures (about 10 °C). Seeds stratified in air and germinating in water showed generally low germination with optimum at 25 °C. The whole temperature range of germination lies between 5 °C and 40 °C and no seeds germinated at these temperature limits. In some cases, temperature does not only influence total germination rate, but also germination energy, i.e. the time needed to reach total germination rate (DYKYJ-SAJFERTO VÁ and DYKYJ 1943). In the case of *O. aquatica*, less

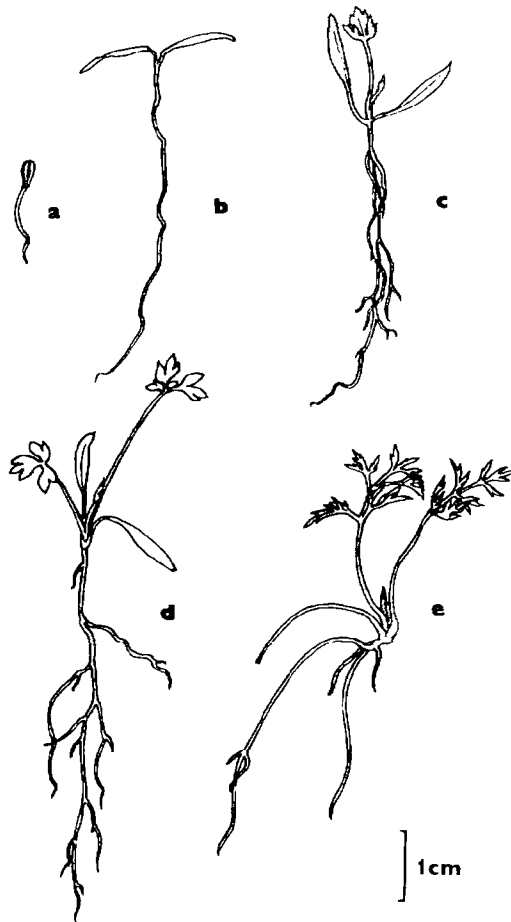


Fig. 9. Development of *Oenanthe aquatica* seedlings: a - germinating seed, b - d - seedlings, e - floating seedling.

favourable temperature conditions acted on germination first by delaying the start of germination (lag phase - the time between the start of incubation and the start of germination - was prolonged mainly at low temperature), and then by a slow increase to the final rate (Fig. 12). It is in accordance with the known facts that limiting rates of temperature range can be reached during long-term observation, while the temperature optimum of germination may be observed in a shorter time (BEWLEY and BLACK 1982). The delayed start of germination is more distinct under the influence of other less favourable factors (Fig. 12B); the combination of stratification and germination in water delayed the start of germination at nearly all temperatures, with the exception of 25 °C.

Table 6. Possible conditions of stratification and germination of *Oenanthe aquatica* seeds in natural habitats. These combinations served as a basis for laboratory experiments.

conditions of germination	no stratification		stratification in	
			air	water
air	ripe seeds germinate immediately after fall on emerged bottom	ripe seeds fall on emerged bottom where they survive winter and germinate in spring, also on emerged bottom	ripe seeds fall into water where they survive winter and germinate on emerged bottom after drawdown	
water	ripe seeds germinate immediately after fall into water	ripe seeds fall on emerged bottom where they survive winter and germinate under water when the water level has risen	ripe seeds fall into water where they survive winter and also germinate in spring	

#### e) Aerobic and anaerobic conditions

Seeds of *O. aquatica* germinate better under aerobic conditions (Tab. 7, Fig. 11). In all experiments, germination was higher in air than in water. On the other hand, winter stratification in water influenced germination more favourably than stratification under aerobic conditions. Thus, the most favourable combination was stratification in water and germination in air, the worst combination stratification during winter in air and then germination in water.

When comparing natural conditions of seed hibernation and germination with laboratory investigations, the most favourable combination of these conditions found in the laboratory corresponds to the most frequent case of crowded germination of *O. aquatica* seeds: germination on emerged bottoms after the fall of water level following a dormant stage in the water layer (perhaps even a long hydrophase) - a sequence of hydrophase to limosal (terrestrial) ecophase. Seeds are also able to germinate relatively well if air is available during wintering (in the case of seeds falling on emerged soil) and when seeds germinate also in air (during continuous emerging of the bottom). However, a continuous satisfactory supply of water is necessary in this case (long limosal ecophase to terrestrial ecophase). In the sequence hydrophase - littoral ecophase (germination in water) and, especially, terrestrial ecophase - littoral ecophase, the germination rates are considerably lower and, in addition, germination is conditioned by light. Lack of light limits germination in deep water and in the shade of plants. This limitation is highly functional, because the viability of seedlings is strongly reduced under water level by habitat conditions (lack of light and oxygen), and by the competition of submerged plants (HROUDOVÁ 1980). The decrease in optimum temperature for germination under water probably represents adaptation to the generally lower temperatures of water environment in comparison with the temperature of soil surface on emerged bottoms.



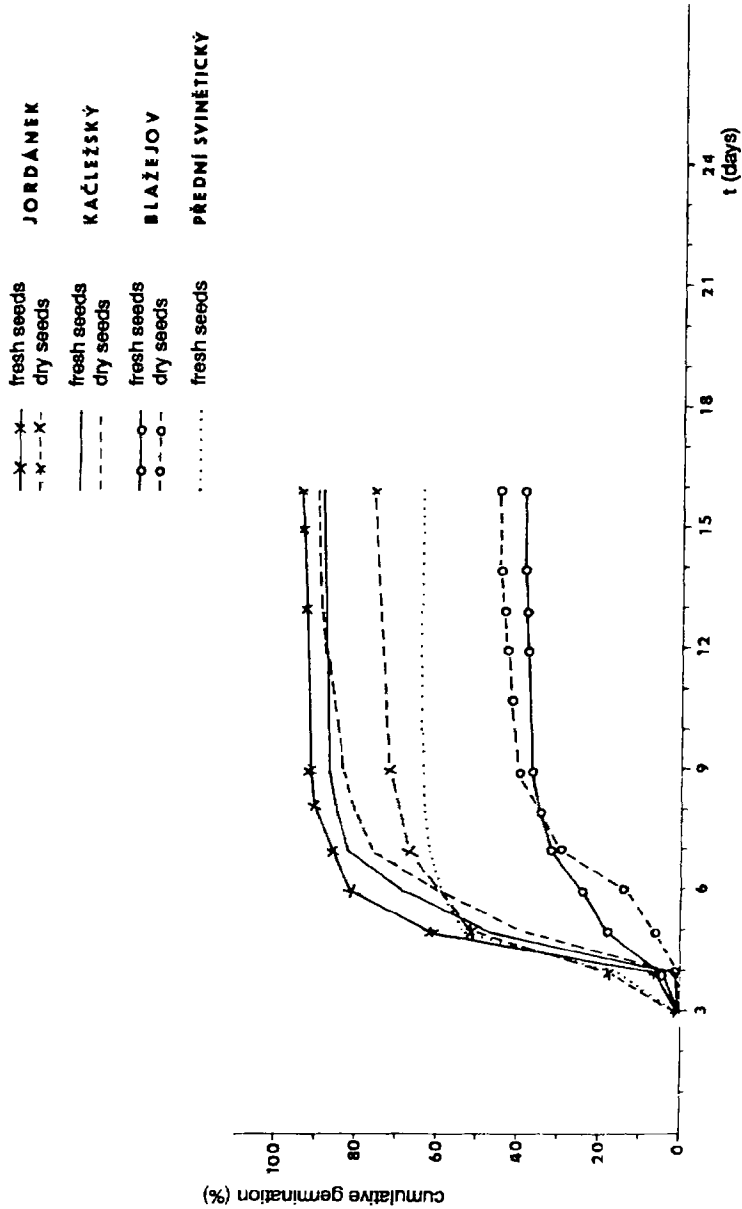


Fig. 10. Cumulative germination of seeds of *Oenanthe aquatica* from different localities, fresh sampled or dried before stratification. Stratification medium: water; germination medium: air; germination light régime: 8 hours light/16 hours darkness; germination temperature: 20 °C.

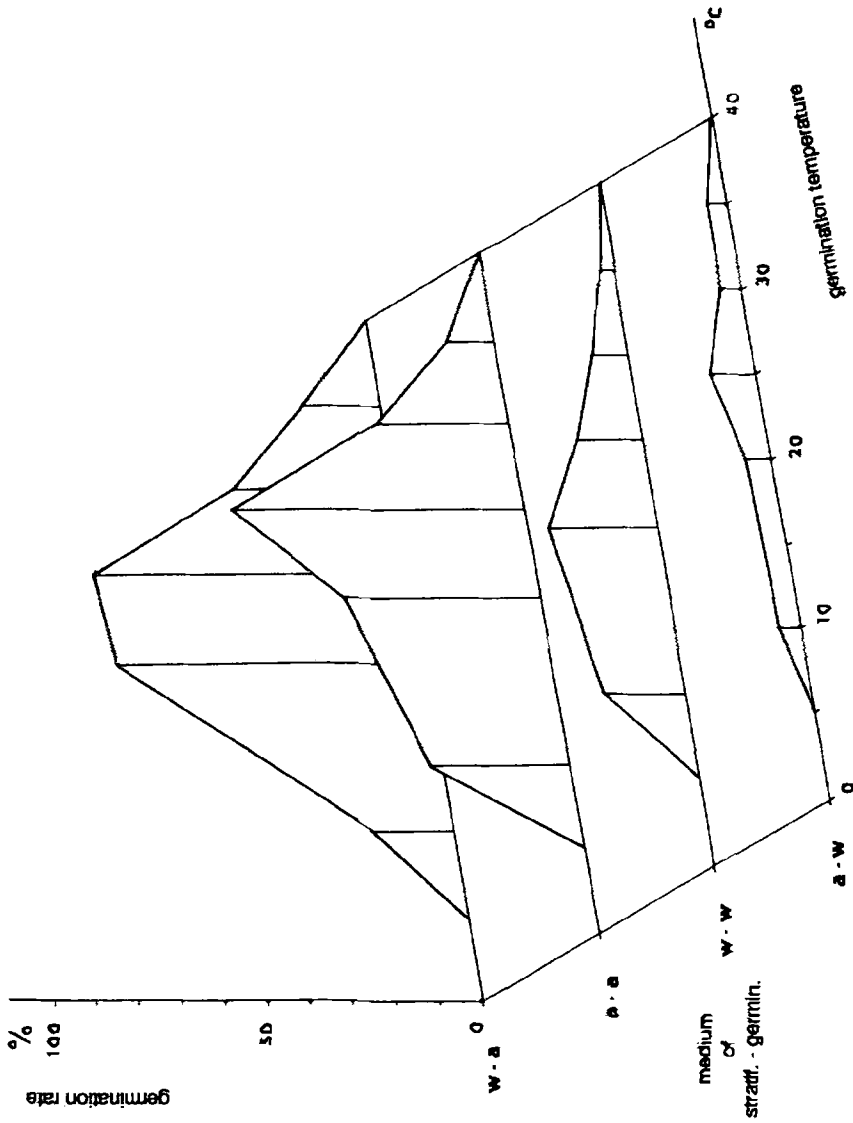


Fig. 11. Dependence of seed germination rate on temperature and different conditions of stratification and germination. The germination rates are means from four localities: Jordánek, Kačlebský, Blažejov, Přední Svinětický; the light régime the same as in Fig. 10; w - a - stratification under water, germination in air, a - a - stratification and germination in air, w - w - stratification and germination under water, a - w - stratification in air, germination under water.

Table 7. Influence of light and medium of stratification and germination on seed germination of *Oenanthe aquatica*, at constant temperature régime 20 °C. Germination rates are percentages from 300 seeds tested.

stratification conditions		water				air			
germination conditions		water		air		water		air	
light régime	8 hours 16 hours	darkness darkness	light darkness	darkness darkness	light darkness	darkness darkness	light darkness	darkness darkness	light darkness
Site (state of seeds)									
Blažejov (fresh)		0.33	13.34	3.00	39.33	0.33	0.33	0.00	0.33
Přední Svinětický (fresh)		1.00	33.66	8.33	64.33	0.00	20.67	8.67	40.00
Jordánek (fresh)		0.00	40.33	18.68	93.67	0.00	3.22	0.33	73.33
Kačležský (fresh)		0.00	12.33	3.00	89.32	0.00	0.00	0.33	45.99
Kačležský (dry)		0.00	11.00	2.33	90.32	0.00	0.33	0.66	3.99

Table 8. Stratification and germination factors (light, air/water) and seed germination tested by a three-way table test of independence (using the G-statistic). Test in parameters indicates a criterion for selection of a subset of the total set.

Factors tested	df	G-value
1. germination in water vs germination in air (stratif. in water)	1	729.22***
2. germination in water vs germination in air (stratif. in air)	1	424.97***
3. stratification in water vs stratification in air	1	560.70***
4. stratification and germination cond. x germination independence	3	1714.89***
5. germination x light cond. independence	1	2263.57***
6. stratif. and germ. cond. x germination x light cond. interaction	3	568.74***
7. stratif. and germin. cond. x germination x light cond. independence	10	4547.21***
8. stratification and germination cond. x light cond. independence	3	0.008 ns

\*\*\* =  $P < 0.001$ ; ns =  $P > 0.05$

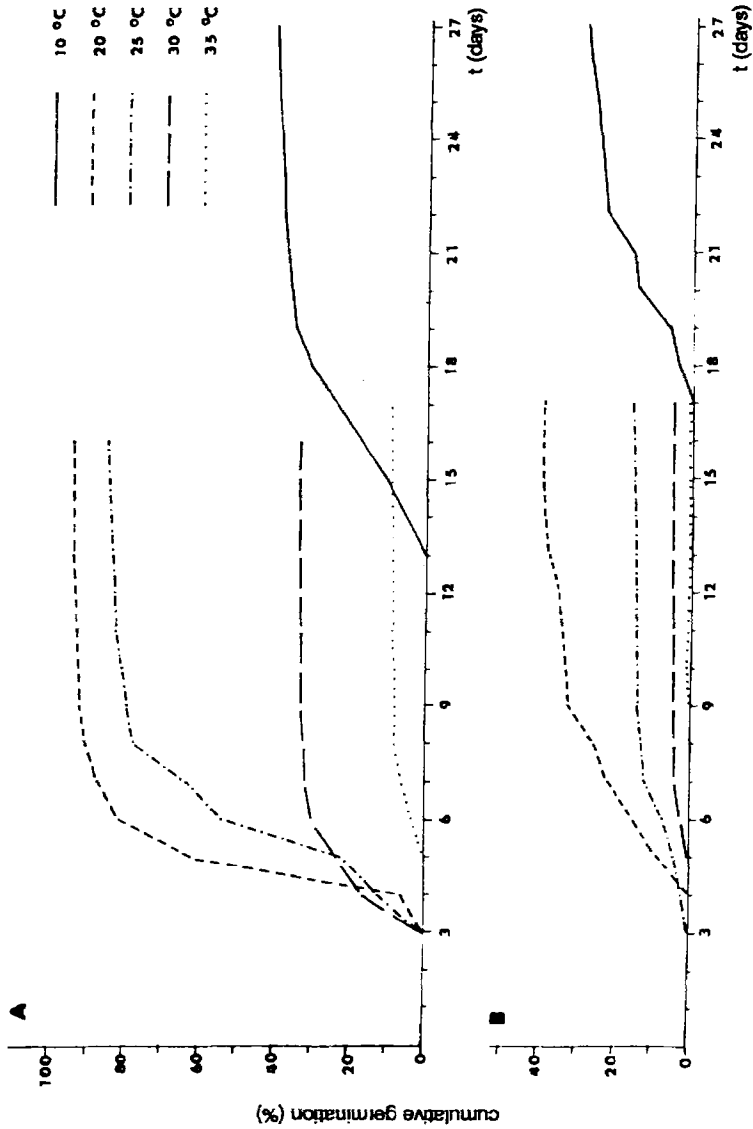


Fig. 12. Cumulative germination of *Oenanthe aquatica* seeds in dependence on temperature. Fresh sampled seeds from the Jordánek fishpond, light régime 8 hours light/16 hours darkness. A - seeds stratified in water and germinating in air, B - seeds stratified and germinating in water.

Temperature controls seed germination in natural conditions. The temperature range of germination is in accordance with the most favourable season for germination in the climatic zone in which a given species occurs (VILLIERS 1978). In the case of *O. aquatica*, the low temperature limit prevents the sprouting of seedlings in late autumn, since germination is retarded by decreasing temperature. In spring, on the contrary, germination is accelerated by gradually increased temperatures up to the optimum of 20 - 25 °C on the soil surface. A further increase in temperature reduces germination and prevents seed germination on overheated soil surfaces of fast drying bottoms where the seedlings would die.

When ripe seeds fall from the plant into water or on the soil surface, seeds remain saturated by moisture from the environment. Under such conditions, a relatively short time of rest seems to be satisfactory for the start of germination (about 14 days). The drying-up of the seeds that remain hanging on the plant probably induces secondary dormancy by hardening the seed coats, this was also observed in other plant species (POPCOV 1976, BEWLEY and BLACK 1982). These dormant seeds usually germinate less under favourable conditions and, in some observations, they need a stronger stimulus for germination (repeated wetting and drying) (HROUDOVÁ 1980).

## CONCLUSIONS

*Oenanthe aquatica* is a species well adapted to habitats with changing water level. It is widely distributed over Czechoslovakia, in suitable habitats.

*O. aquatica* is an example of a plant species in which conditions enabling its occurrence are not the same as conditions for the development of highly fertile stands, producing the maximum biomass. This means that the best developed productive stands are not the most frequent. Concerning soil conditions and water régime of the habitats, *O. aquatica* was found to be present at habitats within a wide range of soil reaction and nutrient content, on fine grained muddy to coarse sandy or gravel substrata, on emerged bottoms to a water depth of 1 m. Stands with dominant *O. aquatica*, highly productive and fertile, can however arise under specific conditions: deep muddy sediments with high C and N content and satisfactory water supply (limosal or littoral ecophase). Besides, the appearance of these stands is preceded by the emergence of the bottom and by stage of crowded seedling stands. This seedling stage is very frequent in natural habitats but does not necessarily lead to the creation of highly productive and fertile stands. These highly productive dominant stands are formed predominantly by biennial plants in the second growing season (Fig. 13). The populations of seedlings giving rise to annual plants have a character of R-strategists, and are able to occupy quickly newly open areas (emerged bottoms). On the contrary, biennial plants, during their longer development, become strong competitors. *O. aquatica* can thus be considered as R-C-strategist.

The invasion ability of *O. aquatica* is made possible by its seed reproduction. High seed production provides a seed bank in the bottom. Seed germination is induced by light, air supply and temperatures about 20 - 25 °C, and the sequence wintering under water layer → germination in aerobic conditions is the most favourable. These conditions are found on emerged pond bottoms where good conditions for further seedling development are found as well. In some cases, seeds can germinate in the autumn after ripening, because they need a relatively short time for resting. Seeds can also germinate in water, but the water environment strongly limits the further survival of seedlings.

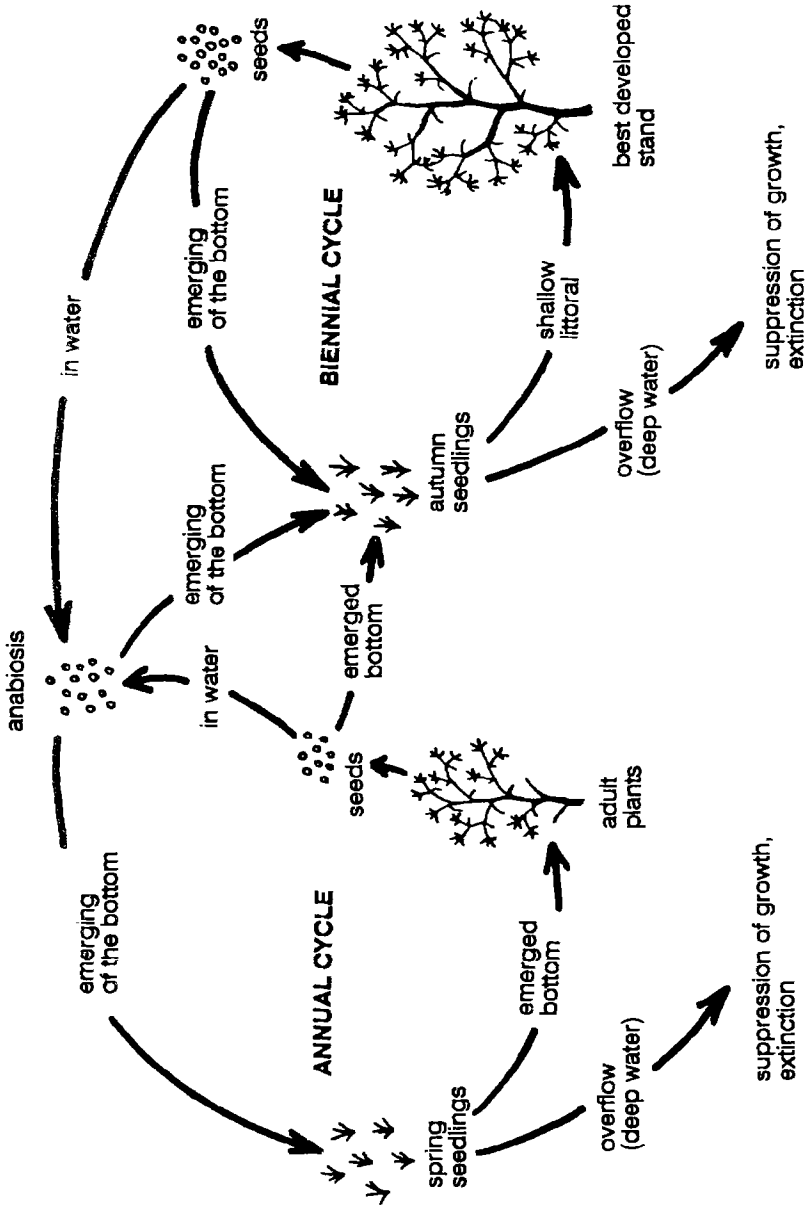


Fig. 13. Life cycle and conditions of different development of *Oenanthe aquatica* populations.

Stands of *O. aquatica* are undesirable in fishpond management and their restriction can be achieved by preventing seed reproduction:

- 1) by the maintenance of a high stable water level, which prevents seed germination and the survival of seedlings;
- 2) if frequent emergence of the bottom (after fishing) is necessary, it is possible either to prevent seed formation by cutting the stand before seed ripening, or to make survival of seedlings impossible by a rapid rise of the water level after the fishpond drainage.

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#### SUMMARY

In Czechoslovakia, *Oenanthe aquatica* is commonly distributed. Its occurrence is limited by suitable habitats and altitude. It often occurs in various plant communities in habitats with fluctuating water level (all. *Oenanthion aquaticae* HEJNÝ apud VICHEREK 1962, order *Oenanthetalia aquaticae* HEJNÝ 1965). *O. aquatica* is a dominant species in the ass. *Glycerio fluitantis-Oenanthetum aquaticae* (EGLER 1933) HEJNÝ 1948 cm. 1978, and *Rorippo amphibiae-Oenanthetum aquaticae* (SOÓ 1928) LOHMEYER 1950. At the stage of seedlings or leaf rosettes, this species is often abundant in communities of emerged pond bottoms, especially on permanently moist deep muddy sediments.

The most favourable habitat conditions for the growth of *O. aquatica* are as follows: shallow water layer (0 to 1 m) with a temporarily emerging bottom; deep muddy sediments with increased nitrogen and carbon contents. In general, *O. aquatica* is tolerant of physical and chemical soil properties. It shows the following adaptations to changing water level: changes in the morphology of submerged and aerial leaves (different shapes of laminae); different ratio of aerenchyma, parenchyma and sclerenchyma in stems of submerged, littoral and terrestrial plants.

*O. aquatica* plants can be either annual or biennial. Seedlings established in spring on emerged pond bottom can develop to adult fertile plants within one growing season. Late seedlings do not attain the generative stage; they form leaf rosettes which can survive the winter and then give rise to biennial plants. The biennial plants in the littoral ecophase can form abundant stands of very tall, fertile plants. In this stage, *O. aquatica* becomes a strong competitor and strongly influences water environment. *O. aquatica* may be considered as R-C-strategist; the competitive phase is, however, conditioned by a preceding ruderal phase in population development.

This species reproduces only by seeds. High seed production, hydrochory and crowded seed germination under suitable conditions enable the establishment of abundant dense stands of *O. aquatica* on emerged bottoms or detritus drifted ashore. The highest number of seeds is produced by biennial plants originating from autumn seedlings and growing in the littoral ecophase. Seeds germinate successfully after stratification in water and then placed in aerobic conditions, at 20 to 25 °C and an alternating light-darkness régime (8 - 16 h). This corresponds to habitat conditions in summer-drained fishponds with a long limosal ecophase.

*O. aquatica* may become an undesirable weed in fishponds. Its occurrence is restricted by a high and stable water level. In the case of fluctuating water level, other measures may be used to prevent seed formation and germination: high water level in spring, rapid rise of water level after summer drainage, or cutting of the stand prior to seed ripening.

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Plate 6-9

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**APPENDIX**

List of localities of *Oenanthe aquatica* given in tables, figures and phytococnological relevés

**Central Bohemia****Praha:**

Jordánek: the Jordánek fishpond near the road between the villages of Šeberov and Hrnčfě, at the SE end of the village of Šeberov, Praha 4

**South Bohemia****Strakonice district:**

Korytní: the Korytní fishpond about 500 m NE from the village of Albrechtice, about 2 km E from the village of Drahonice

Přední Svinětický: the Přední Svinětický fishpond about 1 km N from the village of Svinětice, about 5 km W from the town of Vodňany

**Písek district:**

Oborský: the Oborský fishpond at the S end of the Obora forest at the W end of the town of Protivín

**Jindřichův Hradec district:**

Blažejov: a small fishpond at the NE end of the village of Blažejov, about 5 km E from the town of Jindřichův Hradec

Kačležský: the Kačležský fishpond about 1 km W from the village of Člunek, about 7 km ESE from the town of Jindřichův Hradec

Stříbrný: the Stříbrný fishpond about 3 km W from the village of Nová Olešná

**South Moravia****Břeclav district:**

Allah IV: the Allah IV<sup>th</sup> fishpond about 2 km NE from the town of Valtice

Mahenovo Jezero: E part of the oxbow about 1.5 km E from the village of Bulhary, NW from the town of Lednice

**South Slovakia****Komárno district:**

Kameničná: an oxbow of the Váh river at the S end of the village of Kameničná (mouth of the Lúčnošovský canal)

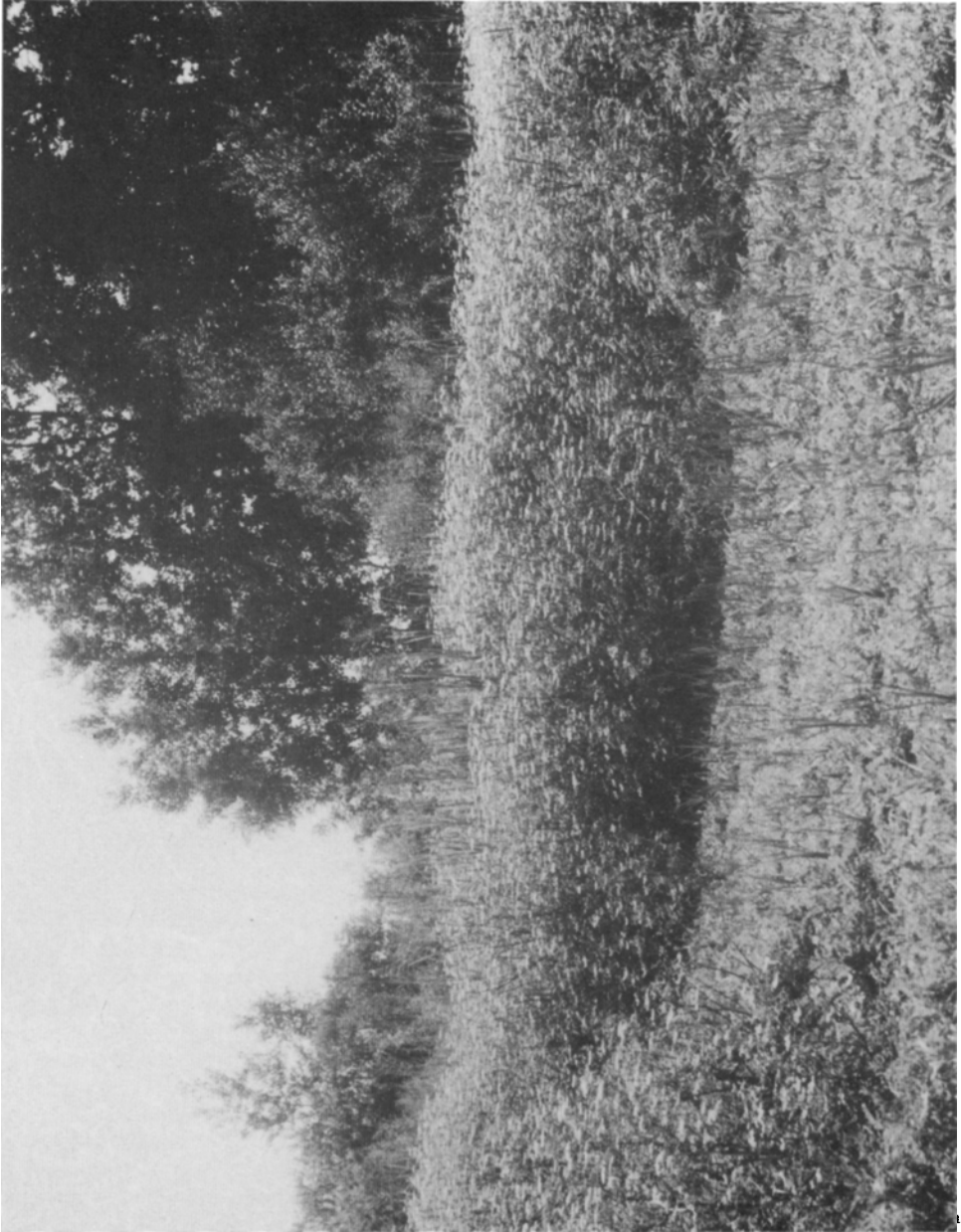
**East Slovakia****Trebišov district:**

Poľany: a field depression near the road between the villages of Poľany and Solníčka

Zatín: an oxbow of the Tice river about 1 km E from the village of Zatín



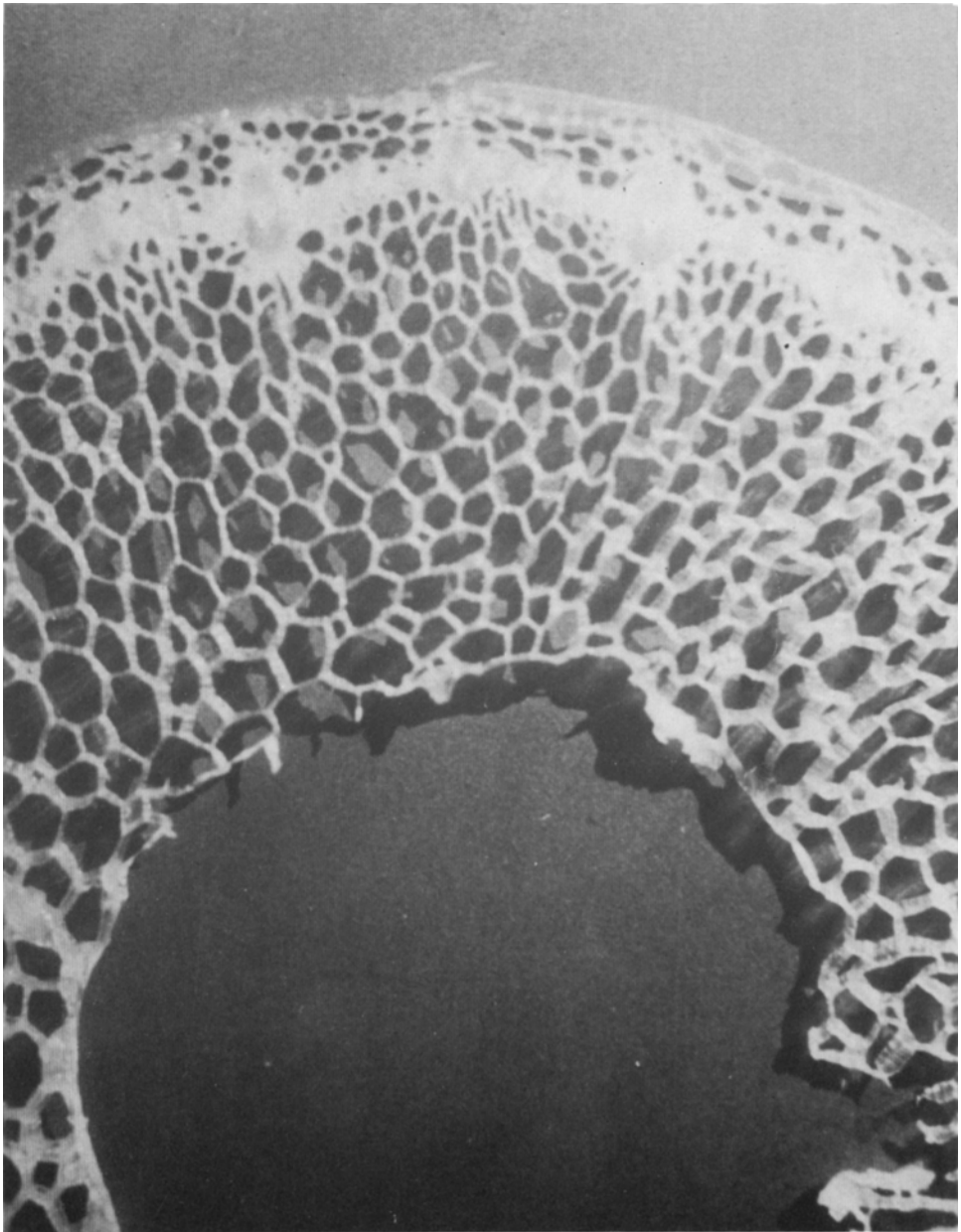
with undergrowth of later seedlings with leaf rosettes.



belt along the shore in the background; the open area is overgrown by seedlings germinating during early summer.



Emerged plant of *Oenanthe aquatica* in a littoral stand.



Transverse section of the basal part of a stem of *Oenanthe aquatica* growing in shallow water.