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Oral presentation:

Ecological relationships of *Isoëtes lacustris* L. with its environment: results of field studies in Europe.

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Introduction

Two *Isoëtes* species occur in northern and central Europe, the aquatics *Isoëtes echinospora* Dur. and, even in earlier times, much more frequently, I. lacustris L. The evergreen perennial I. lacustris inhabits lakes in subalpine/alpine steppe to lowland regions in subarctic as well as in temperate climate, occurring occasionally to depths of 10 m. For some decades, however, this quillwort has been negatively affected in northern Europe and even has been threatened with extinction in western and central Europe. (By the way, it is the same for I. echinospora). These population declines are reported to be largely due to:

1.) Habitat destruction from changes in water levels by the establishment of reservoirs and hydroelectric power plants;
2.) Habitat degradation through the nutrification of lakes by run-off and drainage from bog and fertilized farmland, excessive recreational use of lakes causing both pollution and physical damage, and by urban and industrial air pollution.

These impacts result in lakes becoming increasingly eutrophicated, acidified, or dystrophic. As reported by many authors, increasing nutrient availability encourages fast-growing competitive species as well as the development of plankton and epiphytic algae. Such growth causes a decrease in light availability for quillworts. Filamentous algae and competitive *Sphagnum* species provide similar competition in acidified lakes. The spectral composition of daylight is changed in dystrophic sites (Mäkirinta 1978a,b).

Szmeja (1994) estimates the life-span of *Isoëtes lacustris* to be 8 to 10 years in optimum conditions, less in disturbed lakes; in their third year, nearly all plants became fertile, in the Polish lake Krasne. During summer new leaves develop within the rosette and the peripheral leaves of mature plants decay, releasing their spores. Even in winter, however, mature sporophylls may be found on the plants. The net result is that individual *Isoëtes lacustris* stands appear to be essentially the same throughout the course of a year. The number of leaves/ plant also appears to be about the same for the 5 to 7 year fertile period of each mature plant.

Although much investigation has been conducted on *Isoëtes lacustris* physiology (e.g., biomass production, leaf-renewal rates), little has been documented on its population biology. The aim of the investigation, therefore, was to examine *Isoëtes* plant growth dependent on habitat characteristics. The continuation of the studies reported here focus in particular on the proportion of different age-states within particular populations in relation to lake ecological conditions.

Methods

The present study is based on the examination of quillwort populations in a multitude of lakes throughout Europe between 1995 and the present. All site investigations of these deep-water species employed the use of SCUBA diving equipment. This permitted some data collection without the removal of plants and also allowed relatively unlimited investigation time on-site. Other than ecological studies presently underway in New Zealand, these investigations apparently constitute the only comprehensive in situ examinations undertaken of deep-water *Isoëtes* populations.

Six biometrical attributes were measured on thirty sporogenous plants per lake (Fig. 1). These include:
Number of leaves per rosette;
numbers of megaspores per sporangium;
number of spores per plant;
mean cormus diameter;
mean total root length per plant;
rosette surface area.

The sampled plants were collected from the centre of each population at a depth, on average, of two meters. Mean values were calculated for the data gathered from each lake.

Statistical evaluations by use of SPSS were also conducted on samples of other *Isoëtes* taxa to test the relationships determined in the present study. Those taxa include I. prototypus Britton, I. macrospora Dur., I. x dodgei A.A. Eaton, I. x hickeyi W.C. Taylor & N. Luebke, I. echinospora Dur., I. riparia Engelmann ex A. Braun, I. tuckermanii A. Braun ex Engelmann in A. Gray, I. X harveyi A.A. Eaton, I. melanopoda Gay & Durieu, I. histrix Bory & Durieu.

Isoëtes growth may be affected by climate, air pollution and contamination of the catchment area of the inhabited lake (Fig. 2). Accordingly, the following environmental factors were also determined for sampled populations:
growing season length, including consideration of latitudinal and altitudinal influences;
water pH , as an indication of possible trends towards eutrophication or acidification;
Secchi depth, describing water transparency as an indication of plankton algae in eutrophic sites;
water colour (given by Hazen number) for characterizing dystrophic lakes.

Results

It is evident that plants differing in the number of their leaves provide consistently different sets of other biometrical data too (Tab. 1). Few-leaved plants are characterized by a disproportionately low rosette surface area, a smaller number of spores per plant, and a shorter total root length (Vöge 1997a,b). These three parameters appear to be particularly important for the continued existence of the I. lacustris plants. We interpret these findings as suggesting that small rosette surface area indicates decreased photosynthetic potential, that the low production of megaspores negatively affects reproductive potential, and that fewer and/ or shorter roots limit the uptake of indispensable carbon dioxide.

This study indicates that if the mean number of leaves per rosette is known, an estimation of the other five biometric attributes investigated here (Fig. 1) can be calculated with considerable confidence, viz., highly significant regressions ($P < 0.001$). All the regressions are valid for both European *Isoëtes* species. Tests of a further eight *Isoëtes* taxa from Canada, the United States of America and Italy - even the species supporting ephemeral leaves in which a new leaf rosette is developed every year (I. melanopoda, I. histrix) proved to support the regressions (Vöge 1999). Thus, we conclude that monitoring the number of leaves/ plant provides a reliable indicator of the growth and reproductive status of particular quillwort populations.

The nutrient (N and P) concentrations of particular *Isoëtes* populations were characterized by a macrophyte species inventory. It was determined (with significant regressions) that with a shorter growing season, populations experiencing a higher Hazen number or a lower Secchi depth (in meter), a smaller number of leaves per rosette were recorded. Table 2 relates leaves/ plant with the various environmental factors tested. According to Farmer & Spence (1986), *Isoëtes lacustris* is relatively stress tolerant with respect to low light. However, Gacia & Ballesteros (1994) observed low water temperatures and highly reduced light levels to prevent leaf production. These findings confirm the hypothesis that optimum light availability and the length of the growing season are highly important to aquatic quillwort species. Accordingly, microclimate would also have to be taken into account in a site with extreme environmental conditions.

The graphic expression of the relationship between water pH and the number of spores per macrosporangium is a parable.The maximum number of spores (122) was found in water of pH 6.6. In acidic water (pH 4.8) or alkaline water (pH 8.4) most plants were without megaspores. An average of about 30 spores are to be expected in water of pH 5 or 8.1, and 80 megaspores in water of pH 5.3 or 7.9. Szmeja et al. (1997) found the quillwort to be adapted to various habitat conditions in Polish lakes, tolerating the pH range 4.5 - 8.8.

The number of leaves / plant was used in defining age-states. Table 3 indicates that the height of *Isoëtes* individuals does not accurately characterize age-states. The plantlets in the Early-juvenile age-state, possessing about 3 leaves on average, differ in their mean leaf length. The plants in the Late-juvenile and Fertile age-states are also of somewhat different rosette length in different sites. The number of leaves, however, was always found to be less than ten in the infertile Late-juvenile age-state, and at least ten in the Fertile age-state.

Old (senile) plants are highly variable in the mean height of their rosettes since the leaves differ in number and break off very easily. In contrast to juvenile and fertile plants, young light-green leaves are not observed in senile individuals since leaf-renewal has ceased. In old plants the corm also often is asymmetric and the roots are relatively long and numerous.

In clear water lakes in temperate climate regions of Europe, the number of fertile plants is much higher than that of plants in Late-juvenile age state. Differing proportions of age-state representation, however, appears to indicate divergent ecological conditions. In the German lake Wollingster See in a temperate climate region which contained rather brown water, the proportion of plants in Early-juvenile, Late-juvenile and Fertile age-states was determined to be 2 : 3 : 5. The relatively small share of fertile plants may indicate a shorter (fertile) life-span and is believed to result from lower-than-optimum light availability: Secchi depth is only one meter now. Average leaf number of fertile plants had decreased from 17 to 11 within twelve years in this lake, corresponding with an increased water colour.

The proportion of Early-juvenile, Late-juvenile and Fertile age-states in a subarctic lake population in northern Norway was found to be 1 : 4 : 1. The large proportion of plants in the Late-juvenile age-state may be explained by the short growing season and the fact that the plants need a longer time to become fertile here than in a temperate climate region. The senile individuals are not factored into the description of proportional representation as they usually decay very quickly. In acidified sites, however, senile plants are found more frequently due to a decreased rate of decomposition as a result of the lack of bacteria (Lazarek 1985).

It appears that not all potentially fertile plants (viz., those with more than ten leaves) develop spores when growing in suboptimal conditions. Even though their mean number of leaves was respectively 14.8 and 23.6, for example, plants in an eutrophicated lake in Ireland and an acidified lake in Norway, did not contain any megaspores. These plants cannot be assigned to the Juvenile age-state.

Conclusions

Optimum growth conditions and survival strategies for *Isoëtes lacustris*

The *Isoëtes lacustris* plants examined during these investigations found their optimal growth conditions beneath more than one meter in highly transparent, oligotrophic water on undisturbed substrates. Plants were found in shallower water if light availability was low corresponding to less than 2 m Secchi depth. Living in shallow water, however, results in a shorter life-span and a lower spore production due to ice-scouring and wave impact (Szmeja, 1994). Producing less megaspores these shallow water plants possess statistically significantly fewer leaves and shorter roots (Tab. 1), they easily become uprooted and die.

Another successful strategy may be to develop unusually long leaves. This was observed in an acidified lake in southern Norway, where *Isoëtes* plants were gradually overgrown by *Sphagnum* mosses; only their leaf tips contained chlorophyll. A few years later no *Isoëtes* were found at this site.

It seems clear that the mean number of leaves gradually declines with increasing pollution. The most critical problem is the lowering of light levels and thus photosynthetic potential. A lower light level also results in a smaller photosynthetically active rosette surface thus further reducing photosynthetic output.

Protection and conservation of *Isoëtes lacustris*

There is an urgent need for measures that reduce or stop cultural environmental impacts which negatively affect *Isoëtes* growth conditions. A valuable short-term measure at a local level could be the liming of acidified lakes. The lowering of carbon dioxide content by a long-term program of such treatments, however, might encourage the isoëtids to be replaced by elodëids. Important long-term measures include the continued and enhanced application of air and water pollution emission controls in concert with the monitoring of ecological conditions of quillwort lakes, maintenance and enhancement of ecological integrity protection legislation, and the control and treatment of nutrified and polluted run-off from bogs and farmland. Implicating the regressions established a monitoring project has been proposed (Vöge, submitted). Whatever must be done, the protection and conservation of *Isoëtes lacustris* is worth all such efforts !

Abstract

Statistically significant relationships were established 1) between plant morphology and fertility characteristics, and 2) between plant morphology and lake ecological characteristics, particularly growing season and light availability, from extensive field studies on *Isoëtes lacustris* in lakes throughout Europe. The mean number of leaves/ plant was found to be the most useful characteristic for describing the ecological status and the relative proportion of different age-states of a particular *Isoëtes* population. The structure of *Isoëtes* populations appears to provide an indicator of the ecological integrity of their aquatic environment. Existing I. lacustris populations are severely and increasingly threatened by industrial, urban and agricultural degradation of their aquatic habitats.

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Table 1: *Isoëtes lacustris* leaf numbers in relation to selected morphological attributes

Mean number of leaves per rosette	***Rosette surface area (cm²)***	***Number of spores per plant***	***Number of spores per macrosporangium***	***Cormus diameter (mm)***	***Total root length (m)***
35	213	443	100	25	9.0
10	25	65	38	10	1.5

Table 2: *Isoëtes lacustris* leaf numbers in relation to site ecological conditions

Mean number of leaves per rosette	***Duration of seasonal growth (Months U10 °)***	***Water colour (Hazen)***	***Secchi depth (m)***
<10	2.2	60	1.0
<15	2.7	44	2.0
<20	3.3	31	3.5
<25	3.9	18	6.0
<30	4.5	5	7.5
<40	5.3	T5	10.0

Number of leaves = 8,77 * Number of months U 10°C –11,59 P<0.001

Number of leaves = -0,37 * Hazen + 28,9 P<0.001

Number of leaves = 1,95 * m Secchi depth + 10,80 P<0.01

Table 3: *Isoëtes lacustris* leaf numbers and length in relation to proportional age-state representation
population in different lakes

Age - state	***Mean number of leaves per rosette lakes a, b, c***	***Mean leaf length per rosette (cm)***		
		lake a	***lake b***	***lake c***
Early - juvenile	3	3.2	1.8	3.2
Late - juvenile	T9	9.9	3.3	5.4
Fertile state	U10	11.3	4.6	8.7

a: Mjåvatni, southern Norway
b: Wollingster See, northeastern Germany
c: Rundvann, northern Norway

Fig. 1: Relationships between morphological and fertility characteristics in *Isoëtes lacustris*