

1. University of Aix-Marseille III, Faculty of Sciences and Techniques, Saint Jérôme, 13397 Marseille Cedex 20, France

2. Tour du Valat, A research center for the conservation of Mediterranean wetlands, Le Sambuc, 13200 Arles, France

3. University Hassan II Ain Chock, Faculty of Science, Aquatic Ecology and Environment Laboratory, BP 5366 Maarif Casablanca, Morocco

4. University of Montpellier II, CEFE, Montpellier, France

Introduction

In Mediterranean temporary pools, helophytes such as *Bolboschoenus maritimus* are locally invasive. In the natural reserve of Roque-Haute (Southern France), *B. maritimus* encroached into several temporary pools (Rhazi 2005) where it threatens the characteristic rare species. Based on an analysis of the spore bank Grillas and Tan Ham (1998) suggested that *Isoetes setacea*, a rare and protected quillwort in France, may have been extirpated by competition with *B. maritimus* from different sites in the reserve. The competitive advantage of *Bolboschoenus* on *Isoetes* has been studied in a range of hydromorphic and soil conditions. The general hypothesis was that in low production conditions *I. setacea* could have a competitive advantage on *B. maritimus*. The objectives of this work were to:

1. study the effect of the hydrology and of the soil richness on the production and the reproduction of *I. setacea* and of *B. maritimus*.
2. measure the competitive advantage of *Bolboschoenus* on *Isoetes* in different hydrologic and richness soil situations
3. evaluate the probability of survival of *I. setacea* in the pools of the Nature reserve

Materials and methods

The bulbs of *I. setacea* and tubers of *B. maritimus* were taken of two different pools from the reserve of Roque-Haute. *Isoetes* has been cultivated alone (3 bulbs/pot) and in mixture with *Bolboschoenus* (3 individuals per species). The experiment was run with 5 replicates, on 6 types of sediment (degree of enrichment in sand (S)/ silt (L)/ clay (C)) combined with 3 hydrologic treatments (floods, watered and dry). The 6 types of soil were: (0%C, 75%L, 25%S); (25%C, 25%L, 50%S); (50%C, 25%L, 25%S); (75%C, 25%L, 0%S); (90%C, 0%L, 10%S) and (100%C, 0%L, 0%S). The percentages of humidity used were: Flooded: 100%; Wet: 47% and Dry: 18%. The duration lasted 76 days (15 April-30 June). The variables measured were: the length of the individuals, the underground biomass produced the weight of seeds and spores produced.

The relative competitive strength of the two species has been measured as the Ratio of performance of *Isoetes* in mixture (Pmix) on its performance in pure stands (Ppure), (Pmix/Ppure) (Goldberg et al. 1999).

The comparisons between treatments have been made by analysis of variance and differences between pairs by the test of Tukey-Kramer for the length of the individuals, the produced underground biomass and weight of spores of *Isoetes*. The difference between weight of seeds of *Bolboschoenus* was tested with the non parametric test of Kruskal-Wallis (but only between the flooded and wet treatments for *Bolboschoenus*, seen the absence of production of seeds in the dry treatment).

Results and discussion

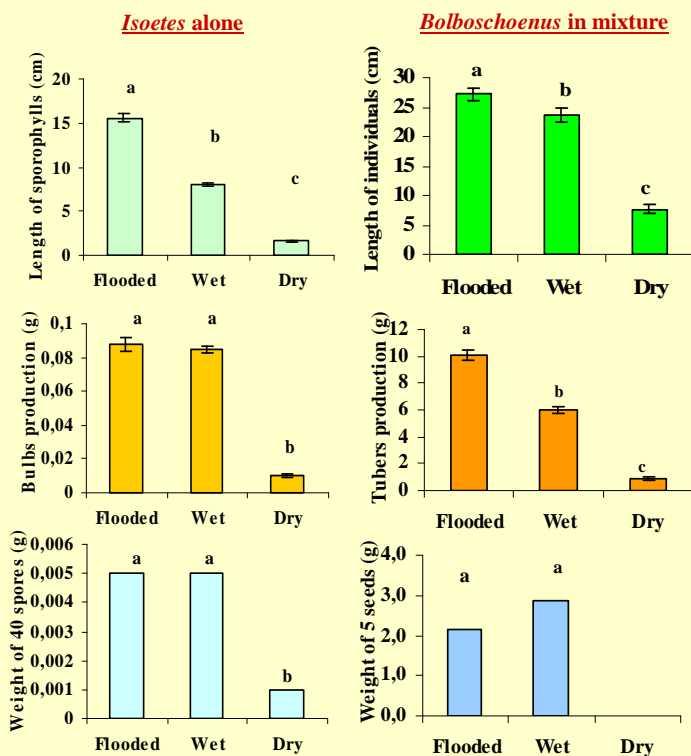


Figure 1: Results of the variance analysis on the comparison between hydrologic treatments of the length of the individuals, the produced underground biomass and the weight of seeds at *Isoetes* in monoculture and *Bolboschoenus* in mixture. Different letters on the diagram indicates that the difference between treatments is significant ($P < 0.05$).

The soil conditions had no significant effect on the different measured parameters. The lengths of the plants of both species were significantly higher in the flooded conditions than in the two other treatments (*Isoetes*: $F=457.3$; $dF=2$; $P < 0.001$), (*Bolboschoenus*: $F=83.8$; $dF=2$; $P < 0.001$). The underground biomass was significantly higher in the Flooded and Wet treatments than in the Dry conditions (*Isoetes*: $F=238.8$; $dF=2$; $P < 0.001$), (*Bolboschoenus*: $F=290.2$; $dF=2$; $P < 0.001$) (Fig.1).

The weight of spores (sporanges) produced by *Isoetes* were significantly higher in the Flooded and Wet treatments than in the Dry treatment ($F=156.5$; $dF=2$; $P < 0.001$) (Fig. 1). *B. maritimus* produced seeds only in the Flooded and Wet treatments ($\chi^2=3.4$; $dF=1$; $P > 0.05$) (Fig.1).

Competitive advantage of *Bolboschoenus* on *Isoetes*

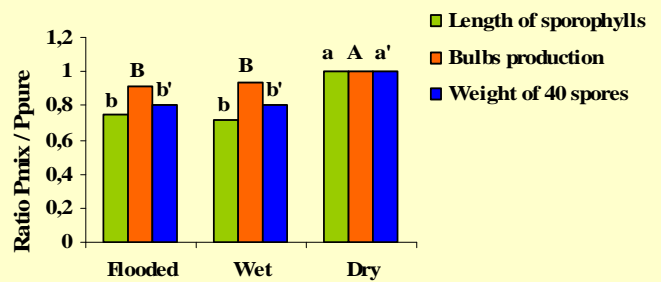


Figure 2: Results of the variance analysis on the comparison between hydrologic treatments of the ratio (Pmix/Ppure) established for the length of the individuals, the produced underground biomass and the weight of seeds at *Isoetes*. Different letters on the diagram indicates that the difference between treatments is significant ($P < 0.05$).

In the Flooded and Wet treatments (Ratios: Length of sporophylls: $F=408$; $dF=2$; $P < 0.001$. Bulbs production: $F=182.5$; $dF=2$; $P < 0.001$. Weight of 40 spores: $\chi^2=53.3$; $dF=2$; $P < 0.001$) (Fig. 2), *B. maritimus* presents an important competitive advantage on *I. setacea* (Ratio < 1) (Vilà and Weiner, 2004). In these 2 hydrologic conditions, *B. maritimus* reproduce successfully (Fig.1). The size of the individuals of *B. maritimus* was twice as large as that of *Isoetes*. The underground production of *B. maritimus* was 100 times larger than the bulbs production of *Isoetes* (Fig.1). The reduction of the performance of *Isoetes* in mixed culture is due to the strong competition imposed by *B. maritimus* under these two hydrologic conditions. The relationship between competition intensity and production has already been shown (e.g. Dutoit et al., 2001; Weigelt et al., 2002). The very large competitive advantage of *B. maritimus* threatens the populations of *I. setacea* in the field. It supports the hypothesis of the replacement of *Isoetes setacea* by *B. maritimus* in several pools of the Nature reserve of Roque-Haute (Grillas and Tan Ham, 1998).

In Dry condition (Fig. 2), the competitive advantage of *B. maritimus* over *Isoetes* becomes weak but do not reverse (Ratio ≈ 1). Indeed, the drought decreases significantly the production of *B. maritimus* which in addition did not produce seeds (Fig.1). However, in spite of the weak production of *Bolboschoenus*, *Isoetes* did not show any competitive advantage on *Bolboschoenus* (Fig. 2).

Probability of survival of *I. setacea* in Roque-Haute pools

The competitive performance of *I. setacea* was weak. In contrast with previous studies on submersed macrophytes (Chambers and Prepas, 1990; Bonis 1993), the survival of the populations of *Isoetes setacea* in the field is not therefore dependent of its competitive strength. The large plasticity of that species (flexibility of its development cycle) and resistance to extreme drought are probably the most important traits that explain the success of the species in temporary pools. *I. setacea* is characterized by a precocious development and could finish its cycle of development quickly while adopting an ephemerophyte strategy of life (Barbero et al., 1982)

An intense drought stress did not allow *Isoetes* to have a competitive advantage on *Bolboschoenus maritimus* in the short-term. The bulbs of *Isoetes* are able to survive to severe and lasting drought that bulbs of *B. maritimus* cannot overcome (Rhazi unpublished data). The recent encroachment of *B. maritimus* in the temporary pools of Roque-Haute was probably made possible by the ecological succession that took place in these ecosystems through accumulation of sediment and organic matter. The results of this work show that in all situations *B. maritimus* will probably out-compete *Isoetes setacea*. Only in very dry soil conditions where *B. maritimus* cannot survive; *Isoetes setacea* will be able to maintain its populations. *Isoetes* cannot have an advantage of competition on *Bolboschoenus* that in case of strong and prolonged drought. Such a drought led to the absence of sexual reproduction for *B. maritimus* and probably to the disappearance of its populations especially as its tubers are very sensitive to these conditions. The introduction of grazing in the pools could help *Isoetes* to maintain in the pools through the reduction of the biomass of *B. maritimus*.