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POND CONSERVATION

Competition in microcosm between a clonal plant species (*Bolboschoenus maritimus*) and a rare quillwort (*Isoetes setacea*) from Mediterranean temporary pools of southern France

Mouhssine Rhazi · Patrick Grillas · Laïla Rhazi · Anne Charpentier · Frédéric Médail

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Abstract *Bolboschoenus maritimus*, a clonal species, is locally invasive in Mediterranean temporary pools where it threatens endangered rare plant species such as *Isoetes setacea*. The combination of management modifications (grazing) and of the progressive accumulation of fine sediments in the pools contributed to the establishment of competitive perennial plants such as *B. maritimus*. The competitive advantage of *B. maritimus* on *I. setacea* has been studied in controlled conditions. The goal of this experiment was to assess the role of environmental conditions in the output of the competition between *Bolboschoenus* and *Isoetes*, notably hydrology and soil richness. For this purpose, *Isoetes* was cultivated alone (three individuals/pot) and with *Bolboschoenus* (three individuals of both species). The experiment was run with five replicates on six types of sediment (gradient of richness in sand/silt/clay) combined with three hydrological treatments (flooded, wet. and dry). The competitive advantage of *Bolboschoenus* was measured as the ratio of the production of *Isoetes* in mixture versus monoculture. The results showed that *Isoetes* was always outcompeted by *Bolboschoenus*. However, the competitive advantage of *Bolboschoenus* on *Isoetes*, was more related to hydrology than to soil richness. The competitive advantage of *Bolboschoenus* was very high in wet and flooded conditions and very low in dry conditions. This situation may lead to the extinction, medium-term, of the populations of *I. setacea*. The introduction of ovine grazing or of cut back practices in temporary pools could reduce the *B. maritimus* biomass and help toward the conservation of *I. setacea* populations.

Keywords Competition · *Bolboschoenus maritimus* · *Isoetes setacea* · Temporary pools · Hydrology · Soil

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M. Rhazi
Department of Biology, Faculty of Sciences and Techniques, Moulay Ismail University, BP 509, Boutalamine, Errachidia, Morocco
e-mail: rhazimouhssine@yahoo.fr

P. Grillas (✉)
Tour du Valat, Le Sambuc, 13200 Arles, France
e-mail: grillas@tourduvalat.org

L. Rhazi
Laboratory of Aquatic Ecology and Environment, Hassan II University, BP 5366, Maarif Casablanca, Morocco

A. Charpentier
CEFE, Montpellier II, University, Montpellier, France

F. Médail
Mediterranean Institute of Ecology and Paleoecology (IMEP, UMR CNRS-IRD 6116), Aix-Marseille University (University Paul Cézanne), Europôle Méditerranéen de l'Arbois, BP 80, 13545 Aix-en-Provence Cedex 04, France

Introduction

Competitive exclusion is often advanced as a hypothesis to explain the regression or the disappearance of rare and threatened species (e.g., Gaston, 1994; Vilà & Weiner, 2004). For wetlands, the development of invasive and competitive species can result from many causes such changes in the management (e.g., eutrophication) or in ecological processes (e.g., sedimentation). The success and impacts of the competitive colonizing species depend on the life history traits of the invaders, the environmental characteristics of the colonized ecosystem and the biotic interactions with the other species of the receiving community (e.g., Connel, 1975; Tilma, 1988; Vilà & Weiner, 2004). Competitor plants are characterized by particular life history traits (e.g., Grime, 2001): the clonal vegetative multiplication and the varied modes of dispersal are key factors in the persistence and diffusion of this group. The intensity of the competition, and therefore, the exclusion potential generally increases with the productivity (Keddy, 1989; Wisheu & Keddy, 1992; Twolan-Strutt & Keddy, 1996).

Nevertheless, in spite of the numerous works performed on the conceptual and applied aspects of interspecific competition, few experimental studies have confronted the level of interference between a threatened plant versus a competitor plant (but see Huenneke & Thomson, 1995; Walck et al., 1999). In the Mediterranean region, where water stress levels are often high, the analysis of functional traits of endemic species, which are often rare and threatened plants, indicates that the "competitive" strategy (*sensu* Grime, 2001) is under-represented with 3–7% of the endemic flora of the south-eastern France (Médail & Verlaque, 1997). If we consider the Leaf–Height–Seed (L–H–S) *sensu* Westoby (1998), endemic plants possess generally a weak competitive capacity, but they only differ from their widespread congeners by their smaller stature (Lavergne et al., 2003).

Several methods have been developed for assessing the importance of interspecific competition (e.g., Mead & Wille, 1980; Connoll, 1986; Akey et al., 1991; Goldberg et al., 1999). These methods generally confront the relative performances of the species (density and/or productivity) in mixed culture and in monoculture. The analysis of the ratio of biomass in mixed versus pure culture (Goldberg et al., 1999) has been frequently used as it provides robust results and is easy to undertake.

In the Nature Reserve of Roque-Haute (43°18′ N; 3°22′ E; Hérault, Southern France), *Bolboschoenus maritimus* recently colonized only a few pools (Trabaud, 1998; Rhazi, 2005) among the 205 pools that it contains. This recent situation probably results from a combination of management modifications (grazing) and of the progressive accumulation of fine sediments in the pools. The colonization of *B. maritimus* could have important consequences in terms of conservation as it could have a negative impact on the Mediterranean Temporary Pools type of vegetation, habitat of European importance in the Habitats Directive 92/43/EEC (Gaudillat et al., 2002), and on the numerous rare and protected species associated to the temporary pools. Among these species, *Isoetes setacea*, an endemic of the Western Mediterranean, is abundant in the pools and finds its main location among the few places where the species exists in France (Rhazi et al., 2004). The on-going replacement of *I. setacea* by *B. maritimus* was suggested by the abundance of the macrospores of *Isoetes setacea* that were found in seed banks within the patches of *B. maritimus*, contrasting with the absence of *Isoetes* in the extant vegetation (Grillas et al., 2004a). The eutrophication and the decrease of the drought stress in summer, both resulting from sediment accumulation in the pools, are two likely mechanisms that could explain the success of *B. maritimus* in the pools of Roque-Haute. Therefore, the extension of *B. maritimus* in more pools is expected, if we consider the ongoing process of global change and increase of dryness in the Mediterranean region. However, at the current pioneer stage of colonization, the dispersal of *B. maritimus* could be limited by a low seed production resulting from a low number of genotypes (clones) which reduces the success of sexual reproduction of this strictly allogamous species (Charpentier et al., 2000).

The objective of this work was to assess the range of environmental conditions in which *I. setacea* would not be displaced by *B. maritimus*. With this perspective, an experiment was conducted to (1) test the impact of hydrological regime and the type of substratum on the output of competition and the sexual reproduction of *Isoetes setacea* and *Bolboschoenus maritimus*; (2) estimate the survival chances of *Isoetes setacea* facing this new competitor.

Materials and methods

Site study

Roque-Haute Nature Reserve (43°18′ N; 3°22′ E; Hérault, Southern France) contains 205 temporary pools on basaltic substratum wherein are found many rare and protected species of plants and amphibians (Molina, 1998; Médail et al., 1998; Jakob et al., 1998). Most of the pools have an artificial origin, as a result of the extraction of the basalt during the nineteenth and beginning of the twentieth century (Crochet, 1998). The Nature Reserve was created in 1975 to protect four rare ferns characteristics of the Mediterranean temporary pools: *Isoetes setacea*, *I. durieui*, *Pilularia minuta,* and *Marsilea strigosa*. The vegetation of the Mediterranean temporary pools is dominated by annual and geophyte species with often short periods of growth within the annual cycle and a weak vegetative development (Braun-Blanquet, 1936; Deil, 2005). These traits are interpreted as adaptations to the high unpredictability and low productivity of the habitat (Médail et al., 1998). Since its creation, the vegetation of the pools of Roque-Haute has shown important modifications, notably the colonization by helophytes such as *Bolboschoenus maritimus* and by shrubs (*Ulmus minor* or *Fraxinus angustifolia*) (Trabaud, 1998; Rhazi et al., 2004). These modifications probably result from management modifications (ending of sheep grazing), and of a primary succession dynamics due to the progressive accumulation of fine sediments in some pools after the ending of basalt extraction.

The species

Isoetes setacea

Isoetes setacea (Isoetaceae) is a heterosporous Lycopodiophyta whose height varies between 3 and 40 cm. It is a perennial amphibious (bulbous geophyte) species, characteristic of temporary pools (Braun-Blanquet, 1936). It presents cylindrical sporophylls, disposed in rosettes, with megasporangia (external sporophylls) or microsporangia (internal sporophylls) at the base. It has a haploid–diploid digenetic life cycle with a very short gametophytic stage (Prelli, 2002). *Isoetes setacea* is a western Mediterranean species, occurring in Portugal, Spain, France, and Morocco (Quézel, 1998; Titolet & Rhazi, 1999). In France, it has a national protection status (Olivier et al., 1995), currently occurring in only four locations: in the Hérault (Roque–Haute plateau and Béziers plain) and in the Pyrénées–Orientales (around the Saint-Estève pool and on the Rodès plateau) (Grillas et al., 2004b).

Bolboschoenus maritimus

Bolboschoenus maritimus is a perennial Cyperaceae with an average height of 1.20 m. It is often found in shallow, freshwater, or brackish swamps (Kantru, 1996) and considered a widespread species in France. *B. maritimus* has a modular development, with an aerial stem developing a tuber at its base and a system of rhizomes (1–3) that produce new aerial stems (Charpentier et al., 1998). Therefore, during an annual cycle, a seedling can be at the origin of several tens of stems, interconnected by the rhizomes. At the end of the summer, when the aerial parts of the plant die, the tubers and rhizomes remain dormant in the soil. In the spring, only some stems form the aerial apical inflorescences with several spikelets to hermaphrodite flowers. The seeds are produced after anemophilous pollination and remain dormant for some years in the soil (Clevering, 1995). Their germination is dependent on the amount of light and seedlings have a higher chance of surviving when the water depth is low (Clevering, 1995).

Competition experiments between *Bolboschoenus maritimus* and *Isoetes setacea*

Two experiments were carried out during this study. The first compared the development and production of *Isoetes setacea* monocultures in different substrata and in three distinct hydrological situations. The second experiment was to assess the competition between *Bolboschoenus maritimus* and *Isoetes setacea* in the same conditions of substratum and hydrology that were analyzed in the first experiment.

Bulbs of *Isoetes setacea* were harvested in the summer of 2001, in a pool (pool 51) in the Roque–Haute Nature Reserve (43°18′ N; 3° 22′ E). In the laboratory, the bulbs were sorted and kept in paper bags at room temperature before being used for the two experiments. Tubers of *Bolboschoenus maritimus* were also harvested in the summer of 2001, in a pool (pool 66) in the Reserve. In the laboratory, the tubers were covered with slightly humid sand and kept in a refrigerator at 5°C, until the beginning of the experiment in the following spring.

Effect of the hydrology and the granulometry of the substratum on Isoetes setacea in pure culture

For the experiment, 90 pots, with 16 cm in height and 20 cm in diameter, were used. Each one was filled with one of the following six types of substratum made up of sand (S), silt (I), and clay (C): (IS: 0% C, 75% I, 25% S); (SIC: 25% C, 25% I, 50% S); (CIS: 50% C, 25% I, 25% S); (CI: 75% C, 25% I, 0% S); (CS: 90% C, 0% I, 10% S) and (C: 100% C, 0% I, 0% S). These substrata were sterilized at 100°C.

Three randomly chosen bulbs of *Isoetes setacea* were weighed (min./max.: 1.63/2.2 g) and placed in each pot. The effect of hydrology was tested on each of the six types of substrata (five replicates/substratum) according to three hydrological treatments:

- "*Flooded*": each pot was completely flooded (top layer of soil was under 6 cm of water) (the percentage of water saturation was of 100%).
- "*Wet*": the pots were watered with a frequency of 5 min/h (percentage of water saturation after watering was of 47%; SD: 2.9%)
- "*Dry*": the pots were manually and weakly watered two times a week (percentage of water saturation after watering was of 18%; SD: 7.5%).

The experiment, carried out in a greenhouse, started on April 15, 2002 and finished on June 30, 2002 (76 days). The number and length of the sporophylls of *I. setacea* were measured every 2 weeks. At the end of the experiment, the bulbs were harvested and their weight measured. The number of microsporangia, megasporangia, and macrospores per macrosporangia were counted; the weight of 40 macrospores and that of a microsporangia was measured for each plant.

Competition between Bolboschoenus maritimus and Isoetes setacea

A series of 90 pots with the same type of treatments ("hydrology" and "substratum") and the same number of replicates were prepared. In each pot, three bulbs of *Isoetes setacea* and three tubers of *Bolboschoenus maritimus*, randomly chosen and previously weighed (min./max.: 1.732/2.36 g and min./max.: 1.613/18.42 g, respectively) were placed according to a constant alternate disposition to facilitate their location. The pots used in these experimentations have the same characteristics and offer a sufficient space for the growth of the plants of both species.

The experiment, carried out in a greenhouse, started on April 12, 2002 and finished on June 30, 2002 (79 days). During this experiment, the plants of both *Isoetes* and *Bolboschoenus* were measured every 2 weeks:

- For *Isoetes setacea*, the same measurements were taken as those carried out in the first experiment.
- For *Bolboschoenus maritimus*, the following measurements were taken for each pot: number of vegetative and reproductive stems, mean stem length, mean number of leafs per stem and number of ears and spikelets of each reproductive stem. At the end of the experiment, the number of tubers produced per individual was counted and weighed. The spikelets were harvested and the number of seeds produced counted. The length of the seeds, as well as the weight of 5 seeds per individual, was recorded.

Retained model of competition

Several models have been created to study the competition between species. Among these models, the "Absolute competition intensity" (ACI), the "Relative competition intensity" (RCI) (Grace, 1995), as well as the "log Response Ratio" (logRR) (Goldberg et al., 1999), are often used. The use of the ACI or the RCI models can lead to contradictory conclusions, creating the problem of choosing the more suitable model (Grace, 1995). No qualitative difference has been found between the RCI and the "logRR" models (Weigelt et al., 2002). Hedges et al. (1999) and Weigelt et al. (2002) encourage the use, mainly for statistical reasons, of "logRR". Moreover, this model enables the linearization of the measurements and the normalization of the data distribution. Besides, Goldberg et al. (1999) believe that the "logRR" model can provide more appropriate results for the analysis of competition interactions than the RCI model. Finally, the "logRR" model is symmetrical for the competition interactions between species and does not impose a limit on the possible maximum of competition intensity. The model used in this study, therefore, draws inspiration from the one established by Goldberg et al. (1999).

Data analysis

The morphological variables measured, for both species, were strongly correlated. In order to reduce the number of redundant variables, a Correspondence analysis (CA) per species was carried out, using all the variables, and a limited number of them were retained. The variables retained were, for *I. setacea*, the number and length of the sporophylls, the weight gained by the bulbs, the number of megasporangia and microsporangia, and the weight of the 40 spores. The stem length, the weight gained by the tubers, and the number and weight of the seeds were the variables retained for *B. maritimus*.

The two-factors analyses of variance (ANOVA-2) on the variables measured for both *Isoetes setacea* and *Bolboschoenus maritimus*, identified a significant effect due to the "hydrological" treatment but not the "substratum" treatment or the interaction between these two factors. The "substratum" variable has therefore been suppressed. After the verification of the data distribution, analyses of variance (ANOVA-1), followed by mean comparisons (Tukey–Kramer test), were used to test the effect of the "hydrological" treatment on the different variables of both species. These tests were also used to analyze the initial biomass and weight gain ratios of "*Bolboschoenus* tubers/*Isoetes* bulbs". When the distribution of the data was not normal (number of seeds per ear and weight of five seeds, both *B. maritimus* measurements), the non-parametric test of Kruskall–Wallis was used.

The effect of *B. maritimus*, in the three "hydrological" treatments, on the different variables of vegetative production and sexual reproduction of *I. setacea*, was measured as the ratio: P_{mix}/P_{pure}, where P_{pure} represents the performance of *Isoetes* in monoculture and P_{mix} its performance in mixture. This model is similar to that of Goldberg et al. (1999) (log Response Ratio $= \log(P_{mix}/P_{pure})$. The presence of the logarithm in the model of Goldberg et al. (1999) enables the normalization of the data distribution (Hedges et al., 1999). In the model used, the distribution of the vegetative production data was normal (Shapiro–Wilk test W, $P > 0.05$) but the sexual reproduction data was not, even after transformation. The differences in the ratios (P_{mix}/P_{pure}) between the three "hydrological" treatments was tested by an analysis of variance, followed by a means comparison per pairs (Tukey–Kramer test).

Results

Effect of hydrology on *Isoetes setacea* in monoculture

The hydrological factor had a significant effect on all the variables measured, with significantly lower values for the dry treatment (Table 1). The length of the sporophylls and the number of microsporangia per plant were significantly higher in the flooded treatment than in the wet one. Conversely, the number of sporophylls and the number of megasporangia per plant were significantly higher in the wet treatment (Table 1). The biomass gain per bulb and the weight of the macrospores did not differ between the wet and flooded treatments.

Effect of hydrology on *Bolboschoenus maritimus* and *Isoetes setacea* in competition

Bolboschoenus maritimus

The hydrological treatment had a significant effect on the stem length and biomass gain of the tubers of *B. maritimus*. The averages for both these variables were significantly different between the three treatments, with maximal values recorded in the flooded treatment and minimal values in the dry treatment (Table 1). No sexual reproduction was observed in the dry treatment. The number of seeds per spikelet and the mean seed weight did not differ significantly between the flooded and wet treatments (Table 1).

Isoetes setacea

When *Isoetes setacea* was grown with *B. maritimus*, its response to the different hydrological treatments was similar to the response when grown in monoculture. The results of the comparison of the variables of vegetative production between the three treatments were analogous to those found when this species was grown on its own.

The number of megasporangia produced per plant was significantly higher in the flooded treatment than in the wet and dry treatments (Table 1). The number of microsporangia produced per plant and the weight of the

Table 1 The results of the analysis of variances between the three hydrological treatments of the pure culture and the mixture of *Isoetes setacea* (for the number and the length of the sporophylls, bulbs production, number of microsporangia and macrosporangia, and the weight of 40 spores) as well as the means comparison (*F* flooded treatment, *W* wet treatment, and *D* dry treatment. *Different letters* indicate a significant difference between treatments $P < 0.05$) and the results of the analysis of variances between the three hydrological treatments (flooded, wet, and dry) of *Bolboschoenus maritimus* for the length of the individuals, the tubers' production, and the results of the Kruskal–Wallis test between the flooded and wet treatments for the number of seeds by ears and the weight of five seeds/ears, as well as the medians

	ANOVA			Means ± standard errors			Means comparison
	d*F*	*F*	*P*	Flooded	Wet	Dry	
Isoetes in pure culture							
Sporophylls number	2	426.51	***	9.91 ± 0.32	14.47 ± 0.30	2.92 ± 0.19	$W^1F^2D^3$
Sporophylls length (cm)	2	457.33	***	15.58 ± 0.52	7.97 ± 0.19	1.60 ± 0.13	$F^1W^2D^3$
Bulbs production (g)	2	233.85	***	0.09 ± 0.01	0.09 ± 0.00	0.01 ± 0.00	$F^1W^1D^2$
Microsporangia number	2	373.00	***	5.92 ± 0.18	5.36 ± 0.10	0.73 ± 0.15	$F^1W^2D^3$
Macrosporangia number	2	257.51	***	11.32 ± 0.57	13.08 ± 0.38	0.93 ± 0.18	$W^1F^2D^3$
Weight of 40 spores (g)	2	156.56	***	0.005 ± 0.00	0.005 ± 0.00	0.001 ± 0.00	$F^1W^1D^2$
Isoetes in mixture							
Sporophylls number	2	369.37	***	6.98 ± 0.21	12.37 ± 0.31	2.93 ± 0.19	$W^1F^2D^3$
Sporophylls length (cm)	2	258.22	***	11.58 ± 0.48	5.72 ± 0.20	1.60 ± 0.12	$F^1W^2D^3$
Bulbs production (g)	2	220.09	***	0.08 ± 0.00	0.08 ± 0.00	0.01 ± 0.00	$F^1W^1D^2$
Microsporangia number	2	112.85	***	3.32 ± 0.17	3.33 ± 0.08	0.73 ± 0.14	$F^1W^1D^2$
Macrosporangia number	2	177.41	***	7.20 ± 0.52	11.00 ± 0.35	0.93 ± 0.18	$W^1F^2D^3$
Weight of 40 spores (g)	2	147.28	***	0.004 ± 0.00	0.004 ± 0.00	0.001 ± 0.00	$F^1W^1D^2$
B. maritimus in mixture							
Individuals length (cm)	2	83.81	***	27.13 ± 1.16	23.65 ± 1.14	7.72 ± 0.71	$F^1W^2D^3$
Tubers production (g)	2	290.22	***	10.05 ± 0.37	5.97 ± 0.23	0.91 ± 0.16	$F^1W^2D^3$

	d*F*	χ^2	*P*	Flooded	Wet	Means comparison
B. maritimus in mixture						
Seeds number	1	0.75	ns	10.16	10.00	F^1W^1
Weight of seeds (g)	1	3.36	ns	2.16	2.88	F^1W^1

ns non-significant

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

40 spores were significantly higher in both the flooded and wet treatments than in the dry one (Table 1).

In relation to the previous experiment, a reduction in the number and length of the sporophylls, bulb weight gain, number of megasporangia and microsporangia, as well as in the macrospore weight, was found in the flooded and wet treatments but not in the dry treatment (Table 1).

Results of the competition between *Bolboschoenus maritimus* and *Isoetes setacea*

The ratios of the initial biomasses (initial weight of the *Bolboschoenus* tubers/initial weight of the *Isoetes* bulbs) were generally low, ranging between 2.32 and 3.16. By chance, this ratio differed weakly, but significantly, between the treatments in the beginning of the experiment ($F = 9.61$, d$F = 2$, $P = 0.0002$). It was weaker for the flooded treatment than for the wet and dry treatments (Fig. 1). At the end of the experiment, the ratio of the final biomasses (weight gained by the *Bolboschoenus* tubers/weight gained by the *Isoetes* bulbs) was higher than the initial biomasses and significantly different between treatments ($F = 4.79$, d$F = 2$, $P = 0.01$). The final biomass ratio was significantly different between the flooded and wet treatments, but not between these two treatments and the dry one, that presented an intermediate value (Fig. 1).

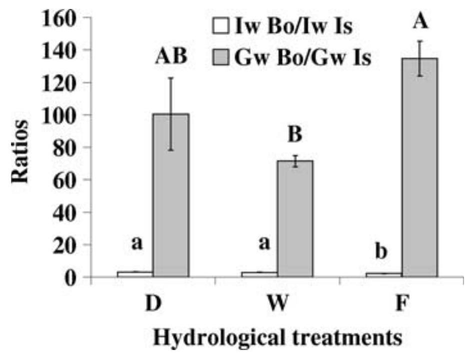

Fig. 1 Results of the analysis of variances on the comparison between the three hydrological treatments: dry (D), wet (W), and flooded (F), the ratios of the initial underground biomasses (Initial weight of tubers of *Bolboschoenus* "Iw Bo"/Initial weight of bulbs of *Isoetes* "Iw Is") and of the produced underground biomasses (Gw Bo/Gw Is). The comparison of ratios between pairs of hydrological treatments has been achieved by the Tukey–Kramer test. *Different letters* (a, b) and (A, B) on the diagram indicate a significant difference of the ratios, respectively, (Iw Bo/Iw Is) and (Gw Bo/Gw Is) between the three hydrological treatments ($P < 0.05$)

The ratio (P_{mix}/P_{pure}) for the number of sporophylls per plant was significantly different between the treatments ($F = 564.63$, d$F = 2$, $P < 0.0001$), with the highest ratio occurring in the dry treatment and the lowest in the flooded treatment (Fig. 2α). Regarding the length of the sporophylls, this ratio was significantly higher in the dry treatment ($F = 408.06$, d$F = 2$, $P < 0.0001$) than in the other two, which did not differ for this variable (Fig. 2α). The ratio for the weight gained by the bulbs was significantly lower in the flooded treatment than in the other two ($F = 182.59$, d$F = 2$, $P < 0.0001$) (Fig. 2α).

The ratios (P_{mix}/P_{pure}) calculated for the number of megasporangia and microsporangia varied significantly between the flooded, wet, and dry treatments (respectively, $X^2 = 65.47$, d$F = 2$, $P < 0.0001$; $X^2 = 47.52$, d$F = 2$, $P < 0.0001$). The highest ratios occurred in the dry treatment and the lowest in the flooded one (Fig. 2β). The ratio calculated for the weight of the macrospores was significantly lower in the flooded treatment than in the other two ($X^2 = 53.32$, d$F = 2$, $P < 0.0001$) (Fig. 2β).

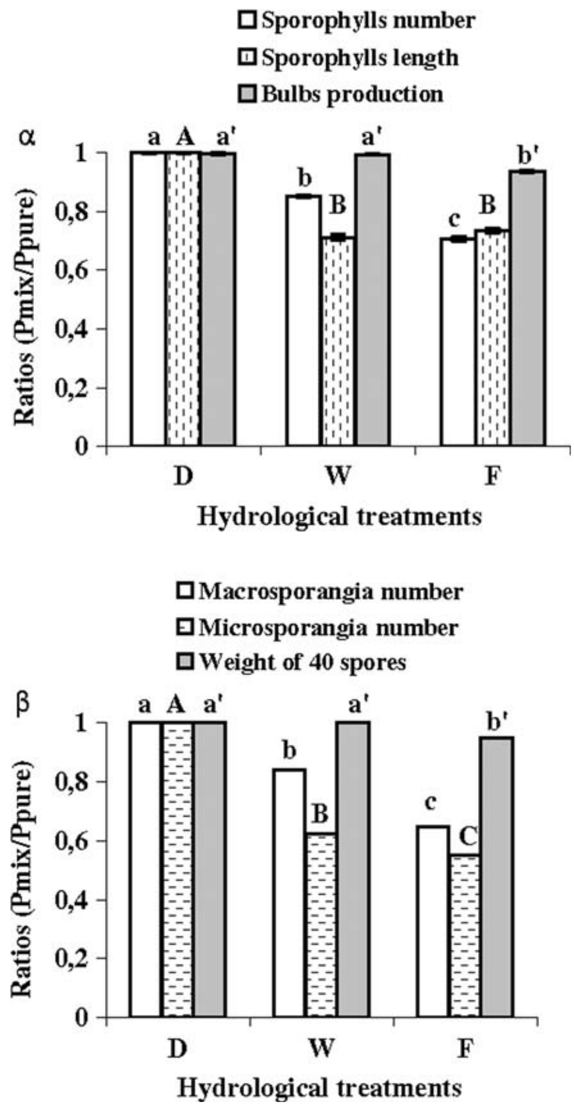

Fig. 2 Results of the parametric analysis of variance (**α**) and of the non-parametric Kruskal–Wallis test (***β***) on the comparison of the ratios (P_{mix}/P_{pure}), established between the number of sporophylls, their length, the bulbs production, the number of macrosporangia and microsporangia, and the weight of 40 spores of *Isoetes setacea* in mixture with *Bolboschoenus maritimus* and their corresponding control, between the three hydrological treatments: dry (D), wet (W), and flooded (F). The comparison between pairs of treatments has been achieved by the Tukey–Kramer test for the vegetative production and by a simple comparison between flooded and wet treatments by the Kruskal–Wallis test for the sexual reproduction. *Different letters* (a, b, c); (A, B, C), and (a′, b′, c′) on the diagram indicate a significant difference between the three hydrological treatments ($P < 0.05$) of the ratios established, respectively, for the number of sporophylls, their length, and the bulbs production (**α**), and, respectively, for the number of macrosporangia and microsporangia and the weight of 40 spores (***β***)

Discussion

In these experiments, several species traits of *Bolboschoenus maritimus* and *Isoetes setacea*, were found to be much affected by the hydrological regime, but they were not modified by the nature of the substratum. Their vegetative development, sexual reproduction, and competitive capacity varied according to the hydrological situations. The two species developed weakly in the dry conditions but were highly productive in the other two treatments, in particular, the flooded one. Clevering & Hundscheid (1998) recorded maximal elongation in *B. maritimus* in a flooded situation, and the same result was obtained by Rhazi (2001) for another amphibious species of the Moroccan temporary pools. For Jackson (1985) and Ridge (1987), the increase of the water levels leads the young shoots of macrophytes to elongate and emerge from the water according to the depth accommodation process. This adaptive strategy seems to have been adopted by the two species studied in this experiment. The aerial vegetative biomass produced by the plants in the flooded situation, distinctly influences the produced underground biomass that seems to be very important in the same hydrological situation.

In the dry condition *B. maritimus*, in contrast to *I. setacea*, was unable to perform a sexual reproduction. However, in flooded and wet conditions, the performance of *B. maritimus* was better than that of *I. setacea*, revealing a high capacity to increase its vegetative productivity. The productivity of biomass has often been used as an indicator of competitive strength and invasive potential (e.g., Claridge & Franklin, 2002).

The results obtained from the soil enrichment experiment were not statistically significant. The abandonment of the exploitation of the basalt in the Roque–Haute was followed by an on-going process of accumulation of fine sediment in the pools originated from the catchments (Grillas et al., 2004a). This accumulation of sediment increases the water retention capacity of the soil, thus decreasing the intensity of drought stress during the summer and hence facilitating the survival of perennial competitors such as *Bolboschoenus maritimus*.

Competitive advantage of *Bolboschoenus maritimus* on *Isoetes setacea*

The competitive advantage of *B. maritimus* over *I. setacea* was very important in flooded and wet situations. A ratio (P_{mix}/P_{pure}) lower than 1 represents a strong interspecific competition between the plants species (Vilà & Weiner, 2004). This competition process involved not only the vegetative growth parameters but also, in the case of *I. setacea*, those linked to sexual reproduction. Under these two hydrological conditions (flooded and wet), the production of the *B. maritimus* distinctly surpassed that of *I. setacea*. The maximal size recorded for *B.* maritimus (height = 65 cm) was four times the maximal size recorded for the quillwort (height = 17.25 cm). Similarly, the maximal underground biomass of *B. maritimus* (biomass = 13.9 g) was 87 times higher than that of the quillwort (biomass = 0.16 g). The reduction of the *I. setacea* performance in the mixture, in comparison to its performance in monoculture, is explained by the strong competition imposed by *B. maritimus* under these two hydrological conditions. Several authors place emphasis on the narrow relationship between the intensity of competition and the productivity (Dutoit et al., 2001; Weigelt et al., 2002). Therefore, the distinctive competitive advantage of *B. maritimus* over the quillwort may lead to the displacement of the populations of *I. setacea*; our results thus support the replacement hypothesis of the *I. setacea* populations by those of *B. maritimus* (Grillas & Tan Ham, 1998).

Under dry conditions, the competitive advantage of *B. maritimus* strongly decreased, with ratios of approximately 1. Indeed, under drought, the productivity of the *B. maritimus* was very low and sexual reproduction was not recorded. However, in spite of the low productivity of *B. maritumus*, *I. setacea* did not reveal any competitive advantage over its competitor. The biological attributes of *I. setacea* (Table 1) under dry conditions reveals that it is unlikely that this species can maintain itself throughout an extended period of dry climate. The absence of competitive advantage of *Isoetes* over *Bolboschoenus* is tied to the low productivity of this fern in the presence of *Bolboschoenus* that still exhibits, under these adverse conditions, an advantage in terms of size and underground biomass production (Table 1).

Chances of survival of *Isoetes setacea*

The results of this study emphasized the weak competitive performance of *I. setacea* in temporary pools recently colonized by a clonal competitive plant. The current survival of this rare and threatened Lycopodiophyta present in isolated and fragmented populations could be related to its strong phenotypic plasticity which is mainly reflected by the high flexibility of its development cycle (Rhazi et al., 2004) and its high tolerance to desiccation. Indeed, *I. setacea* has an early (vernal) development and quickly completes its cycle, often adopting an ephemerophyte life strategy (Barbero et al., 1982). The intense but short drought to which *I. setacea* was exposed did not seem to affect the survival of its populations, but in the short term, these extreme conditions were not sufficient for this species to gain competitive advantage over *B. maritimus*. Nevertheless, the hypothesis that *Isoetes* could win a competitive advantage on *B. maritimus* under more intense and prolonged drought conditions cannot be excluded. Severe droughts strongly limit the biomass of plants (Grillas et al., 1993) and consequently limit the processes of competitive exclusion (Keddy, 1989; Vilà and Weiner, 2004). Indeed, such a drought would lead to the absence of sexual reproduction of *B. maritimus* and probably to the regression of its populations in the long term despite the local persistence of clones. Moreover, after keeping for 6 months, 90 *Bolboschoenus* tubers and 90 *Isoetes* bulbs in paper sachets, in a closed cardboard box at room temperature, none of the *Bolboschoenus* tubers germinated whereas all of the *Isoetes* bulbs did (Rhazi, unpublished data).

From a conservation perspective, the introduction of sheep grazing or of cut back practices in temporary pools could also help toward the maintenance of *I. setacea* populations in these habitats (Rhazi et al., 2004) through the reduction of the *Bolboschoenus maritimus* biomass (Grillas et al., 2004a).

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